ISSN 0172–780X Vol.23 Suppl 4, 2002
NEUROENDOCRINOLOGY LETTERS

Neuro Endocrinology Letters

SPECIAL ISSUE
Vol. 23 Supplement 4 2002
ISSN 0172–780X

Including Psychoneuroimmunology, Neuropsychopharmacology, Reproductive Medicine, Chronobiology and Human Ethology

Your Journal

Editor-in-Chief: Peter G. Fedor-Freybergh
Founder: Derek Gupta

www.nel.edu

Human Ethology and Evolutionary Psychology



Peter G. ***Fedor-Freybergh***

Jan ***Sokol****, Karel* ***Stulík****, Cyril* ***Höschl***

Irenäus ***Eibl-Eibesfeldt***
Karl ***Grammer****, Bernhard* ***Fink****, LeeAnn* ***Renninger***
David M. ***Buss***
Alfonso ***Troisi*** *& Michael* ***McGuire***
Charles ***Crawford*** *& Catherine* ***Salmon***
Glenn E. ***Weisfeld*** *& Carol C.* ***Weisfeld***
Johan M.G. ***van der Dennen***
Doreen ***Kimura***
Devendra ***Singh***
Helen ***Fisher****, Arthur* ***Aron****, Debra* ***Mashek****,*
Haifang ***Li****, Greg* ***Strong*** *& Lucy L.* ***Brown***
Caspar ***Söling*** *& Eckart* ***Voland***
Jaak ***Panksepp****, Joseph R.* ***Moskal****,*
Jules B. ***Panksepp*** *& Roger A.* ***Kroes***

EDITORS:

Bernhard **Fink** & Karl **Grammer**
Ludwig-Boltzmann-Institute for Urban Ethology, Vienna, Austria

HONORARY EDITOR:
Irenäus **Eibl-Eibesfeldt**

Society of Integrated Sciences
PRAGUE • TOKYO • NEW YORK • ST.PETERSBURG
TALLINN • HEIDELBERG • BRATISLAVA • ROME

Laudatio

Both the Psychiatric Centre, Prague, where Zdenek Klein worked, and the Faculty of Humanities and Faculty of Science, Charles University, where he lectured, welcomed with great pleasure the decision of the world renowned journal Neuroendocrinology Letters and its Editor-in-Chief to have established an International Prize in honour of Dr. Zdenek Klein for the best work published within the field of Human Ethology in the Neuroendocrinology Letters. The names of the first laureates confirm the importance and the great value of this award.

Moreover, we strongly and respectfully acknowledge the achievement of Professor Peter G. Fedor-Frebyergh, Editor-in-Chief of Neuroendocrinology Letters and Professor Karl Grammer and Mag. Bernhard Fink, the Editors of this Special Issue, integrating the expertise by selecting the most representative work in this field from distinguished and outstanding authors worldwide in order to honour the memory of Zdenek Klein. We welcome this initiative and are proud that the Charles University of Prague will be the host for bestowing the annual 'Zdenek Klein Award for Human Ethology' on successive Recipients.

We all spend a limited time of life on earth. Life's duration is less important than how we spend it, the deeds which will be remembered by those left behind, and what we bequeath to our successors. In all these respects, although the life of Dr. Zdenek Klein ended prematurely, it was amply filled with exceptional human commitment, creative activity and high moral principles. He clearly belongs to the good old tradition of the Czech cultural and humanistic milieu. As representatives of the institutes mentioned below we wish to render thanks for this acknowledgement of exceptional professional and human qualities of our co-worker and colleague. We remember him with reverence.

Dr. Zdenek Klein (13.6.1944–4.9.2000), a Czech and outstanding human ethologist and anthropologist, studied at the Faculty of Sciences, Charles University, Prague. After graduating, he began his professional life as a scientist at the Psychiatric Research Institute, Prague, but promising career was interrupted by the communist regime of that time. Secret police caught Dr. Klein with 'illegal literature'; he was apprehended, charged and duly imprisoned from 1972 to 1974. Prevented from continuing with his scientific profession after release from prison, he had to work manually but, in his everyday life he kept observing humans and informally carried on his studies into human non-verbal behaviour. As a private person, he also participated in various ethological and anthropological meetings, and maintained contacts with the academic world. With his fine qualifications in human ethology and his skills in observing humans, he became an outstanding authority in the field of non-verbal communication in the former Czechoslovakia and recent Czech Republic.

After the 1990 "Velvet revolution", Dr. Klein could and did return to his research at the Psychiatric Centre, Prague (former Psychiatric Research Institute). In addition to his studies on human ethology, he started research of dermatoglyphes in psychotic patients and those suffering from Alzheimer disease. He developed an original system of markers which enabled dermatoglyphes to be used in the diagnostic process but, unfortunately, this research was unfinished due to his untimely death.

Dr. Klein devoted his time and energy not only to the research but also to teaching and publishing. He is author of several books such as '*Ecce Homo*' (1993), '*Atlas of Semantic Gestures*' (1998), a textbook on ethology (together with Professor Franková) (1997), and a number of scientific papers in local and international journals. He was a member of editorial board of '*Journal of Prenatal and Perinatal Psychology and Medicine*', '*Psychiatrie*' (Psychiatrics), and '*Živa*' (Nature). He initiated and edited the first issue of '*Folia Ethologica*', an irregular journal of Czech and Slovak ethologists. For a long period he edited also '*A Newsletter of the Czech and Slovak Ethological Society*'.

Dr. Klein was a talented and distinguished ethology teacher for students of medicine, natural science and humanistic studies: He lectured at the 3rd Faculty of Medicine, the Faculty of Sciences, and the Faculty of Humanities of the Charles University and at the Czech Postgraduate Institute of Medicine.

Dr. Klein was a long-standing member of several Czech and international societies. In parallel with his scientific activities, he was active in other bodies, such as membership organisation and structure of the 'Society of Capek Brothers'. He founded the '*News*' of this Society and performed the duties of Editor-in-Chief for a long time. He deeply admired Karel Capek, a Czech writer, and internationally-renowned novelist, playwright and essayist; reading Karel Capek's books also helped him to survive the glooms of prison-life. During the last years of his life Dr. Klein took part in the 'Child's Brain Foundation', a non-incremental institution dealing with disabled children.

Dr. Zdenek Klein was highly appreciated and beloved not only by his colleagues, but also by his students and friends for his moral qualities, kind approach, decency, generosity, attitudes to others, and permanent willingness to help. Wherever he appeared, he would soon become a respected member of any professional or special-interest group of people. He had a great talent to express himself with a special kind of gentility, which was appreciated by those who attended his lectures. At the same time this brought him respect, and helped him to solve various problems arising amongst people in a manner which was strifeless and diplomatic.

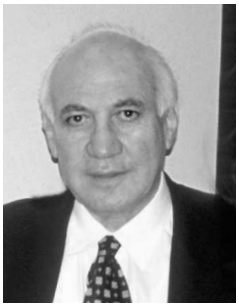
When he unexpectedly passed away after a short and serious disease, we all realised that we lost an unforgettable great person. We will miss him intensely.

Professor **Jan Sokol**, *Ph.D.,*
Dean, the Faculty of Humanities
Charles University Prague
Czech Republic

Professor Ing. **Karel Stulík**, *DrSc.*
Dean, the Faculty of Science
Charles University Prague
Czech Republic

Professor **Cyril Höschl**, *M.D., DrSc*,
Director, Prague Psychiatric Centre
3rd Medical Faculty, Charles University Prague
Czech Republic

Some words from the Editor-in-Chief...



This Special Issue of Neuroendocrinology Letters is dedicated to the memory of the distinguished Anthropologist and Human Ethologist, the Czech Dr. Zdenek Klein, who died on 4 September, 2000, in Prague, at the age of 56.
Under the auspices of Neuroendocrinology Letters, associated with the 'Club of Friends of the Neuroendocrinology Letters' and the 'International Journal of the Prenatal and Perinatal Psychology and Medicine', 'The Zdenek Klein Award for Human Ethology' was founded on August 8, 2001, in order to honour the work and life of the late Zdenek Klein.
The intention is to bestow the award annually for what is judged to be the best work in the fields of Ethology and Human Ethology, with special emphasis on integrated sciences within Human Ethology that has been published in the Neuroendocrinology Letters. The award winning study is to be published annually in the October issue of this Journal.

In 2001, the first recipients of this award were ***Karl Grammer***, ***Bernhard Fink*** and ***Michaela Atzmüller,*** researchers from the Ludwig-Boltzman-Institute of Urban Ethology, Institute of Anthropology at the University in Vienna, together with ***James V. Kohl***, an independent researcher from Las Vegas, Nevada USA, for their work 'Human Pheromones: Integrating Neuroendocrinology and Ethology' (Neuroendocrinology Letters Vol. 22, No.5, October 2001, pp. 309–321).
The Award for the year 2002 was granted to ***Jaak Panksepp***, ***Joseph R. Moskal***, ***Jules B. Panksepp*** and ***Roger A. Kroes***, from the Center for Neuroscience, Mind & Behavior and Department of Psychology and Department of Biological Sciences, Bowling Green State University, Ohio, USA, and from the Falk Center for Molecular Therapeutics and Department of Biomedical Engineering, Northwestern University, USA, respectively, for their Review Article 'Comparative Approaches in Evolutionary Psychology: Molecular Neuroscience Meets the Mind', which is published in this Special Issue (Neuroendocrinol Lett Vol. 23, Special Issue, Supplement 4, December 2002).

The integrative aspect of human ethology has been emphasised and developed also by the late Zdenek Klein, and two of his publications in this Journal are noteworthy: 'An integrative approach to the study of human behaviour' (Neuroendocrinol Lett Vol. 21 No. 5, pp. 422–423) and 'The ethological approach to the study of human behaviour' (Neuroendocrinol Lett Vol. 21, No. 6, pp. 477–481).
Coincidentally with establishment of the Zdenek Klein Award, Human Ethology, the scientific study of human behavior, was added to the Aim and Scope of Neuroendocrinology Letters (NEL), was also displayed on the cover of the Journal with Neuroendocrinology, Psychoneuroimmunology, Neuropsychopharmacology, Reproductive Medicine and Chronobiology, and formed a special Ethology Section on the NEL's website www.nel.edu.

Since the Review article by the first Recipients of the Award was published, several papers, comments and Review Articles on Human Ethology have been published here:

The Scent of Fear by *Kerstin Ackerl, Michaela Atzmueller & Karl Grammer*
(NEL Vol. 23 No. 2, April 2002, pp. 79–84)

Preferred partner characteristics in homosexual men in relation to speculated patterns of brain differentiation by *Frank Muscarella*
(NEL Vol. 23 No. 4, August 2002, pp. 299–302)

Effects of putative male pheromones on female ratings of male attractiveness: Influence of oral contraceptives and the menstrual cycle by *Frances Thorne, Nick Neave, Andrew Scholey,*

Mark Moss & Bernhard Fink (NEL Vol. 23 No. 4, August 2002, pp. 291–297)
Mating types in yeast, vomeronasal organ in rodents, homosexuality in humans: Does a guiding thread exist? by *Daniele Oliva* (NEL Vol. 23 No. 4, August 2002, pp. 287–288)

Human body odour, genetic variability, and sexual orientation: A reply to D. Oliva by *Bernhard Fink & Nick Neave* (NEL Vol. 23 No. 4, August 2002, pp. 289–290)

Homosexual Orientation in Males: Evolutionary and Ethological Aspects by *Frank Muscarella, Bernhard Fink, Karl Grammer & Michael Kirk-Smith* (NEL Vol. 22 No. 6, December 2001, pp. 293–400)

Human Pheromones: "Integrating Neuroendocrinology and Ethology by *James V. Kohl, Michaela Atzmueller, Bernhard Fink & Karl Grammer* (NEL Vol. 22 No. 5, October 2001, pp. 309–321)

Letter to the Editor by *Karl Grammer, Bernhard Fink, Michaela Atzmueller*, (NEL Vol. 22 No. 5, October 2001, p. 401)

Obituary: RNDr. Zdenek Klein, 13.6.1944–4.9.2000 by *Peter G. Fefor-Freybergh* (NEL Vol. 22 No. 5, October 2001, p. 421)

Recipients of Zdenek Klein Award on Human Ethology 2001 (NEL Vol. 22 No. 5, October 2001, p.322)

Remembering Zdenek Klein by *Zbynek Šmahel* (NEL Vol. 22 No. 5, October 2001, pp. 323–324)

The Zdenek Klein Award will be presented at the Charles University and, for the initiating years 2001-2002, a joint ceremony for Recipients will be held in Prague in May 2003 under the auspices of the Faculty of Humanities (Dean, Prof. Jan Sokol, *Ph.D.*) the Faculty of Science, (Dean, Prof. Ing. Karel Stulík, *DrSc.*) and the 3rd Faculty of Medicine (Prof. Cyril Höschl *M.D., DrSc.*, *Director* of the Prague Psychiatric Centre). The Homage written by these distinguished colleagues from the Charles University is published in this issue. I should like to take this opportunity to express my profound gratitude to them as well as to *Doc*. Zbynek Šmahel, *Ph.D.,* and to *Doc.* Ivan Mazura, *Ph.D.,* from the Faculty of Science, for their invaluable initiative and support.

Neuroendocrinology Letters is published in concert with the International Journal of Prenatal and Perinatal Psychology and Medicine by the 'Society of Integrated Sciences', thereby ephasising the interdisciplinary and integrative character of both Journals, working together in mutual 'cross-fertilisation'.

We are very proud that Professor *Dr. Dr. hc.* Eibl-Eibesfeldt, founder of the field of Human Ethology, has graciously accepted my invitation to join the Board of Associated Editors of the Neuroendocrinology Letters. Both Professor Karl Grammer, *Dr. Dip.Biol.* and Mag. Bernhard Fink, *M.Sc*. from the Ludwig-Boltzman-Institute of Urban Ethology in Vienna, Austria are presently members of the Editorial Board of the Neuroendocrinology Letters, and from the very beginning they both exercised utmost support in promoting the affiliation of Human Ethology to this Journal.
It has been my great pleasure and privilege to work with ***Bernhard Fink*** and ***Karl Grammer,*** as Editors of this Special Issue on 'Human Ethology and Evolutionary Psychology'; during the last two years they became my very close and dear friends. Their professional and scientific experience was a *conditio sine qua non* in preparing, editing and publishing this issue. Without their invaluable, consistent and durable engagement, this project of integrating human ethology with the aim and scope of Neuroendocrinology Letters, so developing a continuous effort of creative cooperation between our scientific disciplines and fields would not be viable, neither now nor in the future. Thank you very much!

Last but not least, I should like to express my sincere gratitude, appreciation and admiration to all authors who have submitted their outstanding work within this integrated field of science to this Special Issue, for purposes of both research as well as teaching – thus promoting the basic values of human beings.

Professor Peter G. Fedor-Freybergh, M.D., Ph.D.
Editor-in-Chief: Neuroendocrinology Letters

Neuroendocrinology Letters Special Issue, Suppl 4, Vol.23, 2002
pii: NEL231002E02

Guest Editorial

More than 100 years ago Charles Darwin was one of the first to recognize the value of a comparative approach to the study of human behavior. Since Darwin's most famous books *'On the Origin of Species'* and *'The Expression of Emotions in Man and Animals'*, research has made great progress in understanding the nature of human behavior. This finds its expression in several scientific disciplines but human ethology and (more recently) evolutionary psychology have surely focused most on this topic by maintaining a more holistically and contemporary approach.

This current issue of Neuroendocrinology Letters presents a compilation of review articles from internationally renowned experts within the fields of human ethology and evolutionary psychology. It may initially be surprising that a scientific journal whose primary focus is on neuroendocrinology should pay so much attention to evolutionary approaches to the study of human behavior. However, such a focus is important for two reasons: (1) researchers are beginning more and more to integrate aspects from various scientific disciplines as they recognize that human behavior is too complex to be studied by using a reductionist approach, and (2) Neuroendocrinology Letters has taken up the challenge to open its doors to a more interdisciplinary approach (for example, note that many previous contributions to this journal are from the field of medicine).

It is a great honour that Prof. Fedor-Freybergh has invited us to take on the editorial work for this special issue of Neuroendocrinology Letters. The task was not an easy one as we aimed to maintain a broad spectrum of the widespread field. We were delighted when all of our colleagues whom we had invited to contribute agreed to share their considerable knowledge and expertise to this issue. At this stage we would like to thank all of them for supporting the idea of this special issue. All their contributions are considered not only to be state-of-the art overviews but also a rich resource for students who are interested in the study of human behavior from ethological/evolutionary perspectives.

Investigating human behavior was also the lifework of two colleagues to whom this issue is dedicated: Zdenek Klein and Linda Mealey. Both dedicated their lives and their careers to understand how humans behave the way they do and why, but unfortunately both left us too early. This issue is also regarded in memory of them, and it is

also to keep up their legacy by announcing the 'Zdenek Klein Award' and the 'Linda Mealey Legacy Fund'.

The Zdenek Klein Award for Human Ethology 2002 has been granted to Jaak Panksepp, Joseph R. Moskal, Jules B. Panksepp and Roger A Kroes for their paper '*Comparative Approaches in Evolutionary Psychology: Molecular Neuroscience Meets the Mind*'. The authors present a critical examination of basic principles in evolutionary psychology and suggest once more that only an integrative approach ('*neuroevolutionary psychobiology*') to the study of human behavior provides valuable insight. This article impressively demonstrates that (1) the approaches to, and principles of, the study of human behavior are always a matter of debate (this is the scientific process), and (2) research benefits from inter-disciplinarity. Although the authors within this issue provide their knowledge gained from several years of work, the contents should not only be regarded as facts but also to encourage further discussion and future research.

It is finally to express out thanks to the Editorial Board of Neuroendocrinology Letters, namely Peter Fedor-Freybergh for an excellent collaboration and Lili Maas for spending a lot of time providing her creative ideas to design this issue the way it is. We further acknowledge all the efforts that have been made by the Charles University in Prague with the introduction and organization of the Zdenek Klein Award for Human Ethology. We hope that all this will contribute to further raise the interest of people for the fascinating sciences of human ethology and evolutionary psychology.

Bernhard Fink & Karl Grammer
Ludwig-Boltzmann-Institute for Urban Ethology
Vienna, Austria

Neuroendocrinology Letters Special Issue, Suppl.4, Vol.23, December 2002
Copyright © Neuroendocrinology Letters ISSN 0172–780X **www.nel.edu**

REVIEW ARTICLE

Dynamic Systems and Inferential Information Processing in Human Communication

Karl Grammer, Bernhard Fink & LeeAnn Renninger
Ludwig-Boltzmann-Institute for Urban Ethology, Vienna, AUSTRIA

Correspondence to: Karl Grammer, Ludwig-Boltzmann-Institute for Urban Ethology,
University of Vienna, Althanstrasse 14,
A-1090 Vienna, AUSTRIA
PHONE: +43 1 4277 54766
FAX: +43 1 4277 9547
EMAIL: karl.grammer@univie.ac.at

Submitted: *September 11, 2002*
Accepted: *September 13, 2002*

Key words: **nonverbal communication; automatic movie analysis; motion energy detection; synchronization; inferential communication; dynamic systems; interaction rapport; allomimesis; self-deception; mirror neurons; protean behavior**

*Neuroendocrinology Letters 2002; **23**(Suppl.4):15–22 pii: NEL231002R01* *Copyright © Neuroendocrinology Letters* **www.nel.edu**

Abstract Research in human communication on an ethological basis is almost obsolete. The reasons for this are manifold and lie partially in methodological problems connected to the observation and description of behavior, as well as the nature of human behavior itself. In this chapter, we present a new, non-intrusive, technical approach to the analysis of human non-verbal behavior, which could help to solve the problem of categorization that plagues the traditional approaches. We utilize evolutionary theory to propose a new theory-driven methodological approach to the 'multi-unit multi-channel modulation' problem of human nonverbal communication. Within this concept, communication is seen as context-dependent (the meaning of a signal is adapted to the situation), as a multi-channel and a multi-unit process (a string of many events interrelated in 'communicative' space and time), and as related to the function it serves. Such an approach can be utilized to successfully bridge the gap between evolutionary psychological research, which focuses on social cognition adaptations, and human ethology, which describes every day behavior in an objective, systematic way.

Human communication and information processing

The information processing approach study the nature of human communication uses signal and response, sending and receiving, and encoding and decoding for the structural explanation of interaction between individuals. On the surface, this approach seems quite practical. One organism, the sender, encodes information into a signal. The signal is passed on to another organism, the receiver, who decodes the signal. The receiver is capable of responding appropriately, or not. In this approach a signal is a defined entity, bound within a signal frame. In addition, we can find 'basic trigger signals' which are sent parallel to the actual signal. Trigger signals carry the decoding message. When a 'sender' laughs, for example, his encoded 'signal' of laughter will be decoded by the receiver and interpreted as anything from sexual enticement to ridicule, all depending on the 'trigger signal' of the sender – namely, the sender's body posture [1].

The description of communication from this sequential, information processing level has served as a guideline for communication research for many years, maintaining much of its popularity through the ease of its empirically testable framework. Recent research has shown, however, that this view of communication is most likely too simplified, and that the approach has several flaws. One problematic area is the lack of direct linkage between signals and their causes/effects [2]. A key problem is the assumed 'knowledge' that must accompany signal encoding and decoding. The receiver has to recognize that a signal is present. Then he has to add knowledge in order to be able to decode the meaning of this signal. This means that the receiver has to share knowledge with the sender, and that there have to be signals for the transfer of knowledge. This leads to an infinite regression of definition, a regression that can only be solved when there is a common knowledge that is shared prior to communication [3].

A second problematic area for research based on this approach is the methodology – our attempts to discretely classify a 'signal'. Even if behavior can be categorized in organized single chunks of movement, there is always the feeling that the choice of a particular feature is arbitrary and subjective – a matter of scientific artistry and intuition [4]. This may be one reason, among many, why no catalog of behavioral 'chunks' has yet become a standard across studies. In order for a good catalog to exist (to increase reliability and decrease observer bias), categories would have to be unmistakable, stereotypical, homogeneous and discrete. The result then leads to oversimplification and broad categories. In the typical 'catalog' approach, observers recognize 'movement-Gestalten', put a name on them, and count them – a lexical, language-like process. Finally, categories are not only arbitrary and subjective, but variation in a non-verbal signal (possibly carrying information relevant for communication) might be lost as well as differences in the 'quality' of a behavior [2].

When a continuous behavioral stream is forced into a series of event categories, comparable, but qualitatively distinct, behaviors are subsumed. For example, a 'non-verbal threat signal' can be carried out in many ways – by raising an arm quickly or slowly, with the fist tightly clenched or not, with the movement staying at the maximum flexion for a certain time, or with a slow or quick return to the resting position. Any of these possible movement combinations will produce a different type of 'threat'. Assume the transfer of the movement combination itself to a leg or even a head movement: turning the head quickly towards a target, staring at him, and then slowly looking away. Utilizing various body parts, we can produce 'threat' connotations. The important key for the connotation, however, is the *quality* of the movement itself – an aspect that is typically lost within the categorization.

In total, the main virtue of the information processing approach – that signals can be put into simple, empirically testable frameworks ends up being the main vice. When, if at all, the categorizations of signals become standardized, those classifications tend to be arbitrary, broad and over simplified, and tend to remove the variation and movement quality aspects that may be integral to the signal. After nearly two decades of information processing research, we are left with an unfortunate realization. When categories are used for the assessment of non-verbal behavior the results are rarely reproducible. Further, different signals seem to take various meanings. There are two possible conclusions: (1) either we have the wrong theory, or (2) our methods are not adequate; and in any case, both methodology and theory are intertwined. Flaws in one tend to reflect flaws in the other.

Communication as a dynamic system

In a recent approach, Shanker and King [5] present an alternative view to the traditional information processing theory. In their view, communication is conceptualized not as a system of sequentially transferred signals, but rather as a dynamic system of cross modal attunement. Communication is seen as an interaction that includes attention regulation, engagement, intentional affective signaling, reciprocal affective problem solving, affectively mediated creation of ideas, and affectively mediated thinking [6]. This system can be further conceptualized in terms of engagement and disengagement, synchrony and discord, breakdown and repair. All elements are considered to continuously interact and change with respect to one another by forming a mutual aggregate pattern – the so-called 'co-regulated activity'. The key point is that communication is dynamic.

The classic metaphor for this view is the 'dance' metaphor [7]. The steps and flow of an interaction are moderated through a dance of time-modulated synchrony and dynamic accumulation of signals. Synchronization of body movements (to both our own words and the words and movements of others) is a fundamental part of this process. This synchronization dance is what is commonly perceived by the interactants to be 'rapport'. Research shows that such a process can be perceived. When participants view dyads interacting they are able rate the amount of synchrony that is present and assess 'rapport' accordingly [8].

Consequently, a good empirical test of the dynamic systems theory might begin with a detailed analysis of movement and rapport perception. The results of Grammer, Kruck and Magnusson's [9] analysis of these components underscore the importance of synchronization and dynamic transferring of signals within a specific time structure. Analysis of self-reported 'rapport' ratings from male/female dyads interacting in a waiting room context showed that rhythmical patterning of movements alone – and not their content – was responsible for creating positive feelings in interactions. With the help of a search algorithm called THEME [10], significant results were found for a phenomenon the authors describe as 'hierarchically patterned synchronization'. If a female is interested in a male, highly complex behavioral patterns with a constant time struc-

ture emerge. This means that for behavior 'A' (e.g., she moves her arm), behavior 'B' repeatedly follows in a constant time interval (e.g., he moves his leg). But A and B together form a new unit, 'AB', which might create a pattern with behavior C and so on. With such patterns, communicating partners continuously establish and sustain a feeling of shared rhythm and movement. The patterns are pair-specific and independent of behavioral content. Only a few of the patterns occur twice.

An interesting side note, here, is to mention again our foundation for criticizing the traditional information processing 'catalog' approach to the study of communication. In the study cited above, Grammer, Kruck & Magnusson [9] found that patterns in nonverbal behavior could only be identified by their rhythmical structure and not by their content. In addition to analyzing behaviors for movement quality via THEME, they also maintained traditional catalog methodology quantification. Interestingly enough, all behavioral categories that have been previously found by Moore [11] to be 'courtship signals' were not significantly related to rapport. The conclusion for this research is that there may be at least two levels of communication in courtship: one that operates on an information processing system level, with defined signals, and another that operates on a dynamic, more complex level. While defined signals may have communication value, they are not the key components for the creation of interaction rapport. Rapport operates on a dynamic level.

A study that analyzed human body movements and laughter also pointed toward the existence of an underlying dynamic synchronization pattern [12]. Results showed that when comparing body movements and the power (frequency * amplitude) of laughter, there is a cross lag correlation between female laughter and male movements. Interestingly, the number of significant correlations is connected to female interest. When the female's interest is high, the male synchronizes his body movements with the female's sound production on a micro level. Male's body movements reach their apex of movement exactly at the time where the female laughter has its highest power. This occurs throughout the laughter episode itself; throughout the staccato of laughter the male moves rhythmically in unison. Such findings provide some of the first empirical evidence for the dynamic basis of human communication.

Evolutionary based system constraints for communication in humans

How should research on the dynamic level of communication continue or be structured? One way towards the understanding of the communication process is to look at the evolutionary constraints that may influence the way in which the communication 'dance' will be structured. Although we can identify general principles for communication, we would expect that some domain specific constraints exist. An obvious domain to start with – and one we will elaborate here – is deception and human mate selection. Human mate selection is bound to be closely tied with specific communicative needs, especially that of deception.

General constraints on communication: the advantage of deception

When thinking about human behavior, one must keep in mind that both the natural and the social setting are structural elements of our Environment of Evolutionary Adaptedness (EEA) [13]. Adaptation to the social aspects of the EEA would have been important, as a great deal of an organism's well-being, survival, and reproduction prospects depend on its communication with other members of the group. One perpetual facet of group living is deception. Deception is an important element in generating and maintaining one's adaptive communicational advantage over his/her potential competitors. Presenting one's intentions in a communication may be a costly mistake, since the intentions of one organism may be diametrically opposite from the intentions of another organism. Thus, a conflict situation may arise from the presentation of conflicting goals. This presents the seeds for deception. Organisms would have needed to develop a means of concealing their intentions or any psychophysical features that might negatively affect (a) the achievement of a short-term goal and (b) the chances of reproduction in the long run.

Taken in this evolutionary context, we can say that deception in communication is merely an adaptive response to the demands set upon an individual organism by the environment. Just like various species (e.g. *Hyla arenicolor*, the canyon tree frog [14]) develop highly adaptive cryptic coloration to blend with the environment and escape a predator, humans can use communication signals to conceal their intentions and thus bypass potential goal-inhibiting social-interactive obstacles [2]. In the end, this creates a communication dilemma. The manipulative component of a signal aims to force the receiver into a certain state where he or she willingly accepts the goals of the sender, preferably without recognizing consciously that the sender is being manipulative. The presence of this manipulative side to communicative signals is inevitable due to the strength of its adaptive advantage. Humans are evolved to be deceptive.

What implication does this have for either the information processing or dynamic systems approach to communication? Neither approaches preclude the presence of deception. Organisms are able to falsify a single signal and its meaning, or they might also be able to manipulate the dance-like structure (and mutual influencing) of a dynamic system communication. However, it may be speculated that falsifying a single signal might be more obvious for detection than the more subtle dance like structure. Dynamic communication, then, can be a likely candidate for honest signaling. Coming from a constraints perspective, it seems likely that the study of deception from the dynamic systems approach might be an important addition to our understanding of the communication process.

Domain specific constraints on communication: asymmetric investment

The expectations for signaling and deception in signaling can then be applied to specific domains. Constraints on communication are also likely to stem, for example, from evolutionary differences in the reproductive capabilities of males and females. Since females invest more per offspring, their potential fertility is lower than that of males, and subsequent risk within male-female interactions is higher. Females, as the limiting factor in reproduction, are thus the 'choosers' in courtship, and males have to compete for their accessibility.

The specific consequences of male/female asymmetrical investment can clearly be seen in mate selection preferences [15, 16]. Men's socioeconomic status is the most important choice criterion of women, with social position, prestige, wealth etc. being used as indicators for the available investment. In contrast, women's physical attractiveness is the most important choice criterion for men, as attractiveness, healthiness and youth are all cues linked to reproductive capacity. Further, men are more inclined to multiple short-term mating (e.g., philandering), whereas women are more interested in few, long-term bonds [16]. The differences in evolutionary needs will lead again to a central problem relevant to communication parameters: males and females have different intentions. Whenever conflicting intentions – especially those from a biological, evolved basis – are present, deceptive signaling can be predicted. These interest conflicts between the sexes are central to understanding why efforts to find a mate are fraught with ambivalent signals and deception.

Coming from a constraints perspective, specific predictions about communication parameters can be made. During courtship, especially in its beginning phase, deception is expected to be numerous, e.g. men will exaggerate their status and long-term willingness to invest, and women embellish their physique or feign interest in order to discover men's 'real' attributes. Men, due to their lower reproductive investment, will be expected to be quickly interested in a woman and tend to overtly signal both sexual interest and commitment. The higher investment of women, in contrast, will predispose females to utilize coyness displays and subtle, non-committing and ambivalent signals – an act that serves to lengthen interaction and thereby extend their chance to correctly evaluate a man's real intentions and qualities. As soon as a male gets a clear signal of a female's interest, his tendency to deceive may increase. This is the case because the possible costs of deception are lowered continuously the more she shows her interest – he will not get rejected. Indeed, more than 60% of males report using deception in courtship situations [17]. This constraint (i.e., that females need to avoid showing interest) will have a direct impact on communication: When communicating, women will need to use non-obvious and non-binding channels. Nonverbal communication, in contrast to speech, is said to be just unobtrusive, indirect, subtle and non-committing ([7], see below).

This prediction may also have been derived from folk-psychology and cliché-like knowledge on women's 'natural emotionality'. However, it is also solidly corroborated by data. From earliest childhood onwards, women exhibit more (expressive) nonverbal behavior than men (e.g., facial expressions and touching [7, 18]). To quote DePaulo [19]: *'Differences in ability, motivation, and spontaneous expressiveness all converge to produce what may be one of the most pervasive and important of all individual differences in the use of nonverbal behavior for self-presentational purposes: Sex differences... [women's] body movements are more involved and more expressive'* (p. 222–223).

How does information about such mate selection constraints fit into our approach to communication? We hypothesize that sequential, direct signaling plays a minimal role especially in the opening phase of courtship interaction. When individuals begin verbally communicating, the most important signals are likely to be on the nonverbal dynamic level, since individual signals could be falsified more easily. The dance like structure, on the other hand, is more likely to be an honest signal. We propose that dynamic movement – or, more specifically, movement *quality* – is a likely to be a crucial and important part of the courtship process. Why? Dynamic movement quality allows an observer to make accurate inferences about the internal state of the target. In the next section we will elaborate on the previous research on movement quality affordances, provide a possible methodology for measuring the dynamic movement – inference relationship, and discuss an impetus in the brain-behavior relationship, which might provide for such a system.

The key to dynamic body movement: inferential communication

In Austrian expression psychology, the assessment of movement quality has played an important role as early as the beginning of the 20th century. Fischer [20] introduced an objective movement analysis method based on filmed behavior, where the coordinates of joints in every film picture were measured. Flach [21] postulated, *'A symbol alone, a gesture…is ambiguous. In contrast, the dynamics of a movement are unambiguous and convincing'* (author's translation). Fifty years later, Johansson [22, 23] fixed point-light displays to the joints of participants and filmed their movements in the dark. When the point-light films were shown to observers, they were able to recognize sex, age and movement patterns (e.g., walking) of the filmed participants, but when point-light displays were presented as fixed images, they were rated as randomly distributed [24, 25]. Similar results were also found by Berry and his colleagues [26], whose quantized videos showed that observers are able to detect effort, intention and deception from body movements alone.

Facial and head movements are also rich sources of information. Kempter [27, 28] used short video-clips of politicians that were then rated by observers on 15 personality dimensions. The movements of the politi-

cians were then extracted with the BERN-Coding-System [29] by hand, and transferred to computer avatars. Although all avatars looked alike, they were rated in their personality dimensions exactly like the original politicians that they had imitated. Following these results, Kempter [27, 28] concludes that personality is encoded in body movement. Kempter [27, 28] uses the term 'inferential communication' to describe the fact that movements allow an observer to make inferences about the personality of the moving person.

When it comes to person perception and movement, attractiveness of the communicating agents are expected to play a role. Such a finding would be directly predicted from the evolutionary constraints – spoken about earlier in the paper – of human mate selection. Indeed, facially attractive people (and people with voices rated as nice by others) tend to be more accurate senders of nonverbal emotion information, especially for controlled, posed expressions [30]. This effect is particularly enhanced in females [31].

A major component of the 'what is beautiful is good' stereotype is the belief that attractive people are more socially skillful. However, expressiveness and beauty research then shows that this stereotype has a 'kernel of truth'. Several researchers have suggested that this attractiveness/communication skill link can be readily explained by environmental contingencies, that attractive people (1) receive more favorable expectations from others, (2) enjoy better social exchanges, (3) develop more positive self images, and (4) have more confident interpersonal behavior patterns [32]. As a result of such environmental contingencies, attractive people will logically be better senders than unattractive people.

The movement quality hypothesis, when combined with evolutionary theory, would offer an additional explanation: perhaps attractive people are better communicators because they have a physiognomy (e.g., symmetry) that better supports the encoding of information. A recent study by Grammer *et al*. [33] that analyzed movement quality (dancing) and independent movement attractiveness ratings argues for this view: attractiveness signals good genes and the perception of certain facial qualities as attractive might have evolved as an adaptation to the problem of choosing a high quality mate. It seems likely that also the quality of body movements is directly connected to symmetry and averageness – markers of developmental stability and heterozygosity. When it comes to movement quality, it may be speculated that more or less symmetrical bodies will move differently because of their limb length and mass distribution of muscles. The same argument might also hold for averageness – average bodies, as they represent the population mean, are less likely to have extreme features that might hinder movement ability. This should be detectable in movement quality. Thus, like the inferences that movement quality allows for about demographic information [22], social intentions [26]and personality variables [27, 28], it is possible that movement cues could also provide inferences about a person's internal status, developmental or genetic history.

Several research endeavors have provided evidence that movement quality can also be used as a cue for the inference of internal physiological states. Grammer *et al*. [2] showed that the quality of female body movements (e.g., speed, emphasis and complexity), and not their content, changes with female estrogen levels, and that males react to these changes accordingly with higher excitement, i.e. they start to move more. Studies of menstrual cycle and female reveal similar findings [33]. In a forthcoming paper [33] we will also show that this is the case for movement quality and testosterone in males. This is important research, as the assessment of internal states would be expected to be crucial to interaction. Inference about honest, unfalsifiable signals would be of great advantage. Again, dynamic movement quality seems to be a likely candidate.

Movement quality analysis – an new methodology

A great deal of information might be encoded in movement quality. Actual communication does not only rely on simple signals, however, any 'signal' can do, depending on the way it is performed. In answer to the persuasiveness of the findings mentioned in this paper, we have developed a new analysis technique for the assessment of human movement, which is independent of an observer, dispenses with movement categorization, and circumvents problems with many (different) behaviors cumulating their effects simultaneously and successively. This new approach is based on automatic analysis of body contour changes recorded on digitized films (Automatic Movie Analysis – AMA). AMA subtracts successive video frames from each other and thus determines the total amount of change occurring within a given time span (Motion Energy Detection – MED). Thus, AMA cumulates all movements in the picture into one measure of total picture change. There is no distinction between particular movement patterns. With a thresholding method, it is possible to determine when a movement starts and ends within a series of video frames. This allows for quantitative assessment of movement qualities (e.g., duration, speed, size, etc.; see [2] for a more detailed description) independently of their Gestalt. Besides objectivity, automatic analysis yields high speed and high reliability. AMA procedure is validated by the fact that it is analogous to the organization of human visual perception in two ways: (1) neither color nor depth nor form are necessary to perceptually process movement [34], and (2) movement detection is essentially a processing of contour changes [34]. Thus, if humans assess the qualities of movement, they probably do it in a way that is similar to the way AMA does. With this method we analyzed communication in dyads of the opposite sex in Germany and Japan [35].

In both cultures, when the frequencies 'cataloged' behavior codes were compared to male and female interest, no significant correlations were found. When the

movements were analyzed for quality (AMA) instead of content, however, significant results were found across both samples. Females changed the quality of their behavior when they had high interest in the male. These qualitative changes were not due to mere agitation or excitement – the females actually moved more, but showed smaller and slower movements. These qualitative changes give an impression of slow and determined movements, where the single parts were accentuated. Further, results show that males react to these qualitative modifications positively and rate the situation as more pleasant (although their interest in the partner is not affected). In addition, males who perceive the situation positively talk more.

Interesting connections to these findings comes from other research. Bechinie and Grammer [36] interviewed males and females suffering from the 'broken heart syndrome'. A lover had left all of them within the last three months. A movement quality analysis showed that increasing depression (measured with Beck's depression inventory, BDI) correlated exactly with the same parameters as the courtship study, namely short and slow movements. This means that high depression is manifested behaviorally, creating behaviors that are normally perceived as 'helpless'. If non-depressed females tend to take on the same movement patterns when talking to males in which they are interested, it may be speculated that females are also attempting to communicate a sort of helplessness through their body movements. The function then could be an appeasing one on males, inducing mate bonding or comforting behaviors. We are currently conducting further research to explore the possibility of these connections.

Mirror neurons, allomimesis and the shared manifold

But how can such an inferential communication system work with respect to brain-behavior relationship? The recently discovered 'mirror neurons' could be an answer. Mirror neurons in monkeys [37] appear to form a cortical system that matches observation and execution of goal-related motor action. These also called F5 neurons fire, for instance, when the monkey sees another monkey or human moving his hands to grasp for an object. Fadiga *et al*. [38] was the first to research this system in humans. While testing the excitability of the human motor cortex, they found that motor potentials evoked from the hand muscle area markedly increased when a participant merely watched a person grasping an object. Furthermore, the increase of excitability was present only in those muscles that were used by the subjects when actively performing the observed movements. Similar results were also found by Cochin *et al.'s* [39], EEG analysis of the mirror system. Participants observed movies where human movements were displayed. As a control, objects in movement and still objects were presented. Results showed that the observation of human movements, but not that of objects, desynchronizes the EEG pattern of the precentral motor cortex.

Such findings suggest that humans have a 'mirror matching system'. Whenever we are looking at someone performing an action, there is a concurrent activation of the motor circuits that are recruited when we ourselves perform that action. Although we do not overtly reproduce the observed action, our motor system becomes nevertheless active – as if we were executing that very same action. A mental simulation of a target's actions is of great adaptive benefit. It allows us to build a theory of mind and intention for the observed person. Such a system may provide a necessary bridge from 'doing to 'communicating', as the link between actor and observer becomes a link between the sender and the receiver of a message.

The mirroring itself seems to be movement-related, and the tie between producer and receiver seems to be the goal directedness of the movement. Thus the receiver would not have only a theory of the intentions of what other people will do or enact – we also would have a direct link to the internal states of these people. The fascinating part is that such a system will work in real time without the need for further cognition, and would provide solid basis for empathy, such as that which may be implied from the results of our depression/movement quality findings.

Gallese [40] proposes that motor neurons functionality results in a communicative situation that he calls 'the shared manifold'. The shared manifold would hold information about movement intentions of others, but its presence will also enable an observer to assess a target's emotions, feelings and thus their behavioral tendencies, intentions and goals. In this view the mirror system is crucial to establish an empathic link between different individuals. The shared manifold enables inter-subjective communication. The existence of mirror neurons also sheds new light on a row of previous findings. Mirror neurons could be responsible for a neonates' ability to reflexively imitate facial expressions of adults [41] or the transfer of physiological changes between sender and receiver when seeing a smile [42]. Moreover, the existence of mirror neurons could be a simple explanation for the fact that making voluntarily facial expressions leads to the same physiological changes that one experiences when the emotion is actually felt [42]. Mirror neurons thus might provide the neurophysiological basis of inferential communication.

The dynamic nature of communication

The development of mirror neuron research, when combined with theoretical assumptions about human EEA, and the possible dynamic nature of signals, provides a new approach to communication. Mirror neuron research implies that whenever a stimulus is per-

ceived a hard-wired response is immediately provided. Therefore, honest communication as well as deception may be achieved more successfully by initially bypassing conscious, cortical-cognitive processing and triggering unconscious, limbic-affective processing, and subsequently pairing signals of both direct sequential information transfer and dynamic communication systems. The sequential information transfer could be used when there is shared knowledge about the signals themselves and the situation calls for communication that is direct and unmistakable. But the shared manifold could also contribute to the dynamic decoding process by providing a window to the internal states of the sender and thus reducing the search spaces for the eventual meanings of the signal. Imagine: when I can feel what you mean by observing the quality of your movement, I will be better able to understand the signal meaning itself.

The next step for research in our field is to reintroduce the concept of the adapted mind and the co-evolution of communication. We have demonstrated that the high-risk situation of human mate choice should lead to certain adaptations in communication, which try to avoid deception because of possible loss of investment. The shared manifold itself is a system that seems to protect against deception. The reading of movement quality via the mirror neurons could lead to a reading of a target's internal state – an unfalsifiable signal. Internal states, which change the quality of motions, cannot be produced voluntarily.

When it comes to deception, relatively few countermeasures then remain. Miller [43] identifies three possible counter strategies against deception (a) hiding of intentions ('poker face strategy') (b) tactical deception and misinformation ('KGB-strategy') and (c) adaptive unpredictability ('protean strategy'). The latter concept was developed by Chance [44] and elaborated by Humphries and Driver [45] who called unpredictable behavior 'protean' after the Greek river-god who eluded capture by continually, unpredictably changing form. The adaptive logic of protean behavior lies in the fact that animals generally evolve perceptual and cognitive capacities to entrain, track and predict the movement of other biologically relevant animals such as prey, predators and potential mates. Such predictive abilities mean that unpredictable behavior will often be favored in many natural pursuit-evasion predator-prey situations. Usually, hostile animals or conspecifics capable of correct prediction punish predictability. However, characteristics that cannot be predicted by an opponent can enhance the effectiveness of almost any behavioral tactic. As outlined above – human courtship is one situation where deception and mind reading will play a role [43]. A co-evolutionary arms race in courtship between social prediction and social proteanism can be predicted [43]. In the analysis of a stranger meets stranger situation, Grammer *et al*. [46] were indeed able to show that female interest in the male promotes proteanism and unpredictability in her behavior.

Only such a system could 'fool' the shared manifold by inducing contradicting information in the receiver. But the sender still has a possibility of deception, although it seems costly to falsify internal states. Trivers [47] postulated that self-deception might play a crucial role in communication – somebody who does not know that he/she is deceptive will perform honest signals. On the basis of the shared manifold this makes more than sense.

Such a dynamic system approach in conjunction with the shared manifold offers many advantages over a sequential information processing approach in the explanation and research on human communication. The main advantage is that this system does not need discrete categorical signals. Nevertheless it can explain how the quality of signals can induce different meanings and the communicators also do not need a shared knowledge about signals. Every type of meaning can be inferred by self-inspection at any time in real time. Moreover, such a dynamic system can explain a variety of constraints in human communication.

Yet there are still many problems with this approach. For instance dynamic systems tend to destabilize and become chaotic. This might be solved in two ways. As we have seen in the synchronization between strangers 'signals' are not part of this system. Thus we propose that discrete categorical signals are used in communication in order to stabilize the dynamic system and set it on track. Another possible stabilization factor is the time difference between processes involved in communication. The shared manifold is a fast continuous process. Internal states (e.g., those based on hormones) are slowly running systems. Thus we can hypothesize that the slower running system stabilizes the faster running systems. Besides internal states, attitudes like friendship, dominance, or affects and finally stable and genetically inherited personality traits could serve as stabilizing elements.

Communication research is at the point where human ethology and evolutionary psychology can complete one another. One basic problem connected to this evolutionary psychology approach is that it remains focused on social cognition. The systematic observation of actual behavior, however, might well be used to analyze the impact of social cognition on real life everyday behavior. It is only logical that there had to be a co-evolution of the adapted mind and communication, because under any circumstances the adapted mind must become visible at one point and declare itself communicatively. An approach which combines dynamic and sequential systems, evolutionary social cognition thinking, and methods which allow for the objective quantification of movement quality will bring us one step closer to understanding the complexity of the human communication process.

REFERENCES

1 Grammer K. Strangers meet: laughter and nonverbal signs of interest in opposite-sex encounters. J Nonverb Behav 1991; **14**:209–236.
2 Grammer K, Fieder M & Filova, V. (1997). The communication paradox and possible solutions. In: A Schmitt, K Atzwanger, K Grammer & K Schäfer (Eds.). New Aspects of Human Ethology. New York: Plenum Press; 1997. pp. 91–120.
3 Hofstetter DR. Gödel, Escher, Bach: an eternal golden braid. Harvester: London; 1979.
4 Schleidt WM & Crawley JN. Patterns in the behaviour of organisms. J Soc Biol Struct 1980; **3**:1–15.
5 Shanker S & King BJ. The emergence of a new paradigm in ape language research. Behav Brain Sci. in press.
6 Greenspan S. The Growth of the mind: And the endangered origins of intelligence. Addison-Wesley Publishing Company, Inc; 1997.
7 Argyle M. Bodily communication. London: Methuen; 1988.
8 Bernieri FJ & Rosenthal R. Interpersonal coordination: behaviour matching and interactional synchrony. In: RS Feldman & B Rime (Eds.). Fundamentals of Nonverbal Behavior Part V. Interpersonal Processes. Harvard: Harvard University Press; 1991. pp. 401– 431.
9 Grammer K, Kruck K & Magnusson MS. The Courtship Dance: Patterns of Nonverbal Synchronization in Opposite-Sex Encounters. J Nonverb Behav 1998; **22**(1):3–29.
10 Magnusson MS. Discovering Hidden Time Patterns in Behavior: T-Patterns and their Detection. Behav Res Methods Instrum Comput 2000; **32**(1):93–110.
11 Moore MM. Nonverbal courtship patterns in women: context and consequences. Ethol Sociobiol 1985; **6**:237–47.
12 Grammer K & Weixler P. Laughter as allomimetic behaviour: A microanalysis of sounds and body movements. In: S Sridhara (Ed.). Advances in Ethology 1999 (Suppl. to Ethology); **34**:39.
13 Cosmides L, Tooby J & Barkow JH. Evolutionary psychology and conceptual integration. In: L Cosmides, J Tooby & JH Barkow (Eds.). The adapted mind. Oxford: Oxford University Press; 1992. pp. 3–18.
14 Campbell NA. Biology, 3rd Ed. New York: Benjamin/Cummings; 1993.
15 Buss DM. Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. Behav Brain Sci 1989; **12**:1–49.
16 Buss DM & Schmitt DP. Sexual strategies theory – An evolutionary perspective on human mating. Psychol Rev 1993; **100**:204–232.
17 Tooke W & Camire L. Patterns of deception in intersexual and intrasexual mating strategies. Ethol Sociobiol 1991; **12**:345–364.
18 Henley N & LaFrance M. Gender as culture: Difference and dominance in non-verbal behaviour. In: A Wolfgang (Ed.). Nonverbal behaviour. Perspectives, applications, intercultural insights. Lewiston, NY: Hogrefe; 1984. pp. 351–372.
19 De Paulo BM. Nonverbal Behavior and Self-Presentation. Psych Bull 1992; **111**(2):203–243.
20 Fischer O. Methodik der speziellen Bewegungslehre. In R Tigerstedt (Ed.). Handbuch der physiologischen Methodik. Leipzig: Hirzel; 1911. pp. 120–316.
21 Flach A. Die Psychologie der Ausdrucksbewegung. Archiv für die gesamte Psychologie 1928; **65**:435–534.
22 Johansson G. Visual perception of biological motion and a model of its analysis. Percept Psychophys 1973; **14**:201–211.
23 Johansson G. Spatio-temporal differentiation and integration in visual motion perception. Psychol Res 1976; **38**:379–393.
24 Cutting, JE & Proffitt DE. Gait perception as an example of how we may perceive events. In: RD Walk & DE Proffitt (Eds.). Intersensory perception and sensory integration. New York: Plenum; 1981. pp. 249–273.
25 Runeson S & Frykholm G. Kinematic specification of dynamics as an informational basis for person-and-action perception: Expectation, gender recognition, and deceptive intention. J Exp Psychol 1983; **112**:585–615.
26 Berry DS, Kean KJ, Misovich SJ & Baron RM. Quantized displays of human movement: a methodological alternative to the point light display. J Nonverb Behav 1991; **15**:1–97.
27 Kempter G. Nicht-verbales Verhalten als Auslöser emotionaler Reaktionen. Psychologische Beiträge 1998; **40**(3/4):288–300.
28 Kempter G. Auslösung psychophysiologischer Reaktionen durch Wahrnehmung gestischer Bewegungen. In: E Schröger, A Mecklinger & A Widmann (Hrsg.). Experimentelle Psychologie. Lengerich: Pabst Science; 1999a. pp. 116–117.
29 Frey S & Pool J. A New Approach to the Analysis of Visible Behaviour. Forschungsberichte aus dem Psychologischen Institut der Universität Bern. Bern; 1976.
30 Larrance DT & Zuckerman N. Facial Attractiveness and Vocal Likeability as Determinants of Nonverbal Sending Skills. J Pers 1981; **49**(4):349–362.
31 Poling TH. Sex differences, dominance, and physical attractiveness in the use of non verbal emblems. Psychol Rep 1978; **43**:1087–92.
32 Adams GR. Physical attractiveness research: toward a developmental social psychology of beauty. Hum Dev 1977; **20**:217–239.
33 Grammer K, Keki V, Striebel B, Atzmüller M & Fink B. Bodies in Motion: a window to the soul. In: E Voland & K Grammer (Eds.). Evolutionary Aesthetics. Berlin: Springer; in press.
34 Livingstone MS & Hubel DH. Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. J Neurosci 1987; **7**:3416–68.
35 Grammer K, Honda R, Juette A & Schmitt A. Fuzziness of Nonverbal Courtship Communication: Unblurred by Automatic Movie Analysis. J Pers Soc Psychol 1999; **77**(3):487–508.
36 Bechinie M & Grammer K. The Dark Side of Love: About Breaking up Romantic Relationships (Abstract). In: A Schmitt, K Atzwanger, K Grammer & K Schäfer (Eds.). New Aspects of Human Ethology. New York: Plenum Press; 1997. p. 191.
37 Gallese V, Fadiga L, Fogassi L & Rizzolatti G. Action recognition in the premotor cortex. Brain 1996; **119**:593–609.
38 Fadiga L, Fogassi L, Pavesi G & Rizzolatti G. Motor facilitation during action observation: A magnetic stimulation study. J Neurophysiol 1995; **73**:2608–11.
39 Cochin S, Barthelemy C, Lejeune B, Roux S & Martineau J. Perception of motion and EEG activity in human adults. Electroenc Clin Neurophysiol 1998; **107**:287–295.
40 Gallese V. The 'Shared Manifold' Hypothesis: From Mirror Neurons To Empathy. J Consc Stud 2001; **8**(5–7):33–50.
41 Meltzoff AN & Moore MK. Imitation of facial and manual gestures by human neonates. Science 1977; **198**:75–8.
42 Ekman P, Levenson RW & Friesen WV. Autonomic nervous system activity distinguishes among emotions. Science 1983; **221**:1208–1210
43 Miller GF. (1997). Protean primates: the evolution of adaptive unpredictability in competition and courtship. In: A Whiten & RW Byrne (Eds.). Machiavellian Intelligence II: Extensions and Evaluations. Cambridge: Cambridge University Press; 1997. pp. 312–340.
44 Chance MRA & Russel WMS. Protean displays: a form of all aesthetic behaviour. Proc Zool Soc London, 1959; **132**:65–70.
45 Humphries DA & Driver PM. Protean defense by prey animals. Oecologia 1970; **5**:285–302.
46 Grammer K, Kruck K, Juette A & Fink B. Non-verbal behavior as courtship signals: The role of control and choice in selecting partners. Evol Hum Behav 2000; **21**:371–390.
47 Trivers RL. Deceit and self-deception: The relationship between communication and consciousness. In: H. Robinson & L. Tiger (Eds.). Man and Beast Revisited; 1991. pp. 175–191.

Human Mate Guarding

David M. Buss
University of Texas, Austin, USA.

Correspondence to: David M. Buss,
Department of Psychology,
University of Texas,
Austin, Texas 78712, USA
EMAIL: dbuss@psy.utexas.edu

Submitted: *September 4, 2002*
Accepted: *September 6, 2002*

Key words: **mating; jealousy; conflict; mate guarding**

Neuroendocrinology Letters 2002; ***23****(Suppl.4):23–29 pii: NEL231002R02* *Copyright © Neuroendocrinology Letters* ***www.nel.edu***

Abstract Long-term committed mating is a fundamental strategy in the human repertoire. Successful enactment of this strategy requires solving two related adaptive problems – fending off potential mate poachers and preventing a mates from defecting. Mate guarding adaptations evolved to solve these persistent problems. Those who failed in mate guarding risked suffering substantial reproductive costs ranging from genetic cuckoldry to reputational damage to the entire loss of a mate. Because the precise nature of the adaptive problems confronted differed historically for the sexes, men and women evolved corresponding differences in the underlying psychology of mate guarding. Men's mate guarding, relative to that of women's, is strongly triggered as a consequence of being mated to young and physically attractive women, being confronted by interested rivals who have superior economic resources or prospects, and having a mate who displays signs of sexual involvement with a rival. Women's mate guarding, relative to that of men's, is triggered as a consequence of being mated to men high in income and status striving, rivals who are more physically attractive, and having a partner who shows signs of emotional involvement with another woman. Behavioral output of mate guarding adaptations range from vigilance to violence.

Human Mate Guarding

Reproductive conflicts between individual males and females can occur at every stage of the mating process [1]. Initial clashes take place between individuals when one is interested in mating and the other is not. Among courting pairs, disagreements can emerge over the timing of intercourse, the magnitude of commitment, and the amount of resources that flow between the two. Among already mated pairs, conflict can ensue over the disbursement of reproductively relevant resources to others outside the mateship, including extra-pair mates or genetic relatives. Conflict also emerges over terminating the mateship, when one wants to end it and the other does not. All these conflicts occur because the deployment of a successful reproductive strategy by one individual can interfere at multiple points with the reproductive strategy pursued by the other – a phenomenon called "strategic interference" [2].

This paper focuses on the cluster of conflicts centering on "mate guarding." Mate guarding refers strategies designed to (a) preserve access to a mate while simultaneously (b) preventing the encroachment of intrasexual rivals, and (c) preventing a mate from defecting from the mateship [3]. Adaptations for mate guarding evolved in humans for two fundamental reasons. First, "mate poachers" some-

REVIEW ARTICLE

times attempt to lure an already mated individual for a brief sexual liaison, an affair, or a permanent mateship. Second, mates sometimes become tempted to defect to another partner or leave to prospect for a better partner. Strategies of mate guarding evolved to solve these problems – to curtail, slow, or prevent mate poaching or a mates' defection while maintaining one's own access the reproductively relevant resources of one's mate.

Mate guarding adaptations have been discovered in males of an astonishing variety of species, from insects to mammals. One common strategy is the *concealment of mates from intrasexual competitors* [4]. Concealment is usually accomplished through one of three means – removing the mate from the vicinity of rivals, producing signals that mask the attractant signals of the mate, and muting the conspicuousness of courting and copulation to evade detection by rivals. Among certain butterflies, for example, the male that succeeds in courting a female will fly away with his partner suspended beneath him, taking her away from any other males that are present. Among certain bark beetles, bees, and moths, successful males release a scent that repels other males, makes the mate less attractive to other males, or masks her scent entirely [5]. The third concealment strategy – the reduction of conspicuous displays – occurs among crickets and katydids. The initially noisy courtship calls quickly become muted to "a softer courtship chatter" when a male succeeds in attracting a female [6]. The strong human desire for privacy during sexual intercourse may reflect a strategy that functions to reduce the conspicuousness of mating, and hence to avoid the potential intrusion or disruption by others. All of these concealment strategies reduce the likelihood that a rival will usurp the guarded mate.

A second general strategy of mate guarding found in the animal and insect world is the *physical prevention of takeovers* [7]. Certain male beetles and grasshoppers, for example, maintain close contact with the female prior to copulating, positioning themselves to prevent other males from gaining proximity to her. In the veliid water-strider, males ride on the backs of their mates for hours or days, even while not engaged in copulation, to prevent the encroachment of other males. In other species, males physically fight with rival males to prevent a takeover. In some species of locusts, a male seeking to mate poach sometimes picks up the trail of an about-to-mate pair that has recently departed the vicinity. When he comes upon the couple, the mated male turns and literally wrestles with the newly-arrived male. Although the attempt to physically repel the poacher is sometimes successful, the physical engagement sometimes leaves the female vulnerable to a third male who poaches while the resident male is busy fending off the initial rival. Some males build a "fence" around the female to physically prevent other males from gaining sexual access.

Humans, of course, differ from insects, and indeed, from all other mammals, in countless ways. The value of drawing attention to the various evolved solutions that function as mechanisms of mate guarding is to highlight the fact that many, perhaps all, sexually reproducing species confront the adaptive problem of mate poachers. And there are certain excellent regions in mate guarding "design space," that is structurally similar solutions that have been discovered by a variety of different species, including humans.

The Costs of Mate Guarding Failure

Reproductive costs can be steep for those who fail at mate guarding [8]. For men, a single failure at mate guarding could result in genetic cuckoldry, as happens when man's wife becomes fertilized by a rival man's sperm. In addition to the direct loss of opportunity for reproduction, the husband risks investing years or decades of his own effort in a rival's child in the mistaken believe that the child is his own. To compound these reproductive losses, his wife's maternal efforts now benefit his rival's child rather than his own. Furthermore, if the lapse becomes public, the cuckolded man risks damage to his social reputation, which could bring about a decrement in mate value, a loss of status, and an increased future vulnerability to other mate poachers. Finally, the cuckolded man suffers opportunity costs – matings that he could have pursued as alternatives had he not engaged in this particular mateship. Large are the potential reproductive costs of a single lapse of mate guarding.

Failure at mate guarding can also result in the permanent defection of a man's partner. If a man's partner leaves him, he loses access entirely to her future reproductive value. He loses whatever maternal efforts she would have brought to bear on his future children. He risks losing access to social alliances that she brought to the mateship. And she carries with her personal information about his habits, strengths, weaknesses, and vulnerabilities – information that could be exploited to advantage by an intrasexual rival to whom she disseminates the information.

Women too suffer reproductive costs from failing to guard their partners. A single lapse may be less costly to women than to men, since women do not risk genetic cuckoldry, as men do. Internal fertilization guarantees the woman that she is the mother of her children, regardless of her partner's sexual infidelities. Nonetheless, it is known that men channel resources to women with whom they have sex, and so women who fail at mate guarding risk the loss of those resources. Like men, women suffer an increased risk of contracting a sexually transmitted disease, passed from her husband's mistress to her. If her partner leaves the relationship, she risks a total loss of his resources, all of which can get redirected away from her and her children and toward his new mate and her children. Although the damage to her reputation is likely not to be as heavy as the corresponding damage to a cuckolded man's reputation, it can be damaged nonetheless, as when others infer that the deserted partner has some hidden defect or is lower in desirability than originally perceived to be.

The Prevalence of Mate Poaching

For mate guarding adaptations to have evolved, the problem of mate poaching must have been common enough to select for them. Although we cannot go back in evolutionary time to detect the frequency of mate poaching in the past, modern studies of mate poaching suggest that it is surprisingly prevalent. In one study, 60% of men and 53% of women admitted to having attempted to lure someone else's mate into a committed relationship [9]. Although more than half of these attempts failed, nearly half reportedly succeeded. Similarity between the sexes in long-term poaching attempts contrast with efforts designed for brief sexual encounters – 60% of the men, but only 38% of the women, report attempting to lure someone else's mate into a casual sexual encounter. Far higher percentages of both sexes say that others had attempted to entice them to leave an existing relationship – 93% of the men and 82% of the women for long-term love, and 87% of the men and 94% of the women for a brief sexual encounter. Somewhat smaller percentages report someone attempting to poach their mate, suggesting that poaching ploys are often initiated away from the prying eyes of the unsuspecting "victim." Roughly a third of the sample – 35% of the men and 30% of the women – report that a partner had been *successfully* taken away from them by a mate poacher. Mate poaching, in short, is clearly a common current mating strategy. Although many attempts fail, a sizable proportion appear to succeed. Although the prevalence of mate poaching varies from culture to culture, a recent cross-cultural study involving more than 30 nations points to substantial prevalence worldwide [10]. Mate poaching has probably been successful often enough to have evolved as a distinct sexual strategy – a strategy that established the ground rules for the evolution of the counter-adaptations of mate guarding.

Sexual and Emotional Triggers of Jealousy

Sexual jealousy has been hypothesized to be one of the central psychological mechanisms underlying mate guarding strategies [11, 12, 13]. Sexual jealousy is hypothesized to become activated whenever there is a perceived threat to a mating relationship. The threats can come from a variety of sources – the presence of poachers, cues to infidelity, or even subtle signals that suggest that a partner might be dissatisfied with the current relationship. Once activated, a variety of psychological processes are hypothesized to be set into motion, such as evaluation of the nature and magnitude of the threat and evaluation of potential courses of action. Eventually, these processes usually lead to behavioral output designed to deal with the threat – actions that can range from vigilance to violence.

Since a sexual infidelity historically jeopardized a man's paternity, men's jealousy and mate guarding should be easily triggered by signals of *sexual* betrayal [14]. Infidelities by men, in contrast, pose an equally dangerous reproductive risk for women – the loss of the man's time, attention, energy, parenting, investment, and commitment. Triggers of women's jealousy and mate guarding, as a consequence, should focus heavily on signals of these kinds of losses, such as a man becoming *emotionally* involved with another woman. Emotional involvement is a signal of the long-term commitment of resources to the partner with whom one is involved [15]. Sexual and emotional infidelity in a partner, of course, are correlated in nature [16]. People tend to become emotionally involved with those with whom they have sex. And people often become sexually involved with those they are emotionally close to. But not always. Sex can occur without emotional involvement, as in a one-night stand or a spring break fling. People can get emotionally involved without any sex, as occurs in at least some opposite-sex friendships. Both forms of infidelity, of course, are extremely upsetting to both sexes, and both can signal the dramatic loss of reproductively valuable resources.

When forced to choose which form of infidelity is more upsetting, however, large sex differences emerge consistently. Men are more likely than women to become distressed by sexual infidelity; women are more likely than men to become distressed by emotional infidelity. These fundamental sex differences have now been replicated by many different scientists in many diverse cultures – China (David Geary), Sweden (Michael Wiederman), the Netherlands (Bram Buunk and Pieternel Dijkstra), Germany (Alois Angeitner and Victor Oubaid), Japan (Mariko Hasegawa and Toshikazu Hasegawa), and Korea (Jae Choe)[17].

Some have challenged the evolutionary basis for these findings, proposing an alternative hypothesis based on the differing beliefs men and women hold about the conditional probabilities of the two events [18]. Systematic efforts to pit the alternative hypotheses against each other, however, consistently yield support for the evolutionary hypothesis. In one study, for example, 234 participants were asked to imagine that their partner had become both sexually *and* emotionally involved with someone else, and then asked to state *which component* of the betrayal they found more upsetting. This method renders the conditional probabilities of sexual and emotional infidelity irrelevant, since both forms of infidelity have occurred. Sixty-three percent of the men, but only 13 percent of the women, found *the sexual component* of the infidelity to be more upsetting. In contrast, 87 percent of the women found *the emotional component* of the infidelity to be more upsetting. These sex differences have now been found in Korea and Japan [19]. The preponderance of evidence, in short, supports the evolutionary hypothesis that the fundamental psychological design of the jealousy adaptation differs for the sexes.

Sex differences in the design of the jealousy defense also have been revealed in other facets of the mating game using a range of diverse scientific methods. Recently the fundamental sex differences in jealousy evocation have been replicated using four different measures of *physiological* distress [20]. When asked to

imagine an emotional infidelity, for example, women's skin conductance, heart rate, electromyographic activity, and body temperature all shoot up – physiological events that are highly correlated with the subjective reports of actual distress. Men show greater physiological distress when imagining a partner trying out different sexual positions with a rival.

Another recent study posed an additional set of dilemmas pertaining to forgiveness for a relationship violation [21]. One sample dilemma is as follows: "Please think of a serious or committed romantic relationship that you have ad in the past, that you are currently having, or that you would like to have. Imagine that you discover that the person with whom you've been seriously involved *both* becomes deeply emotionally attached to another person *and* has passionate sexual intercourse with that other person. Which aspect of your partner's involvement would be more difficult for you to forgive?

(A) Your partner's sexual intercourse with that other person.
(B) your partner's emotional attachment to that other person."

Significant sex differences emerged for this and half a dozen variants on this theme. More men than women found it more difficult to forgive a sexual than an emotional infidelity. More women than men found it more difficult to forgive an emotional than a sexual infidelity. Similar sex differences were discovered when the question posed was "Which aspect of your partner's involvement would be more likely to lead you to *break up* with your partner?" Actual divorce statistics verify this sex difference across cultures [22]. Men are more likely than women to seek a divorce because of a partner's sexual infidelity.

In summary, the evolutionary hypothesis of sex-linked design differences in the jealousy defense mechanism has withstood a number of empirical tests. It parsimoniously accounts for a constellation of findings that no other theory can. It accounts for sex differences in distress responses to the original infidelity dilemma. It accounts for the aspect of the betrayal that is more upsetting when both have occurred. It explains why these sex differences occur both psychologically and physiologically. It explains why the sex differences are found across a wide variety of cultures, including those that are sexually liberal such as Sweden and the Netherlands, as well as those that are more sexually conservative, such as China and Korea. And it explains why sexual infidelity by a woman is more likely to lead to breakups, violence, and divorce than a sexual infidelity by a man.

Threatening Characteristics of Rivals

Defenses against threats of infidelity, of course, do not end with the emotional response we call jealousy. Many other design features that characterize this critical defense against betrayal have been discovered. One such design feature centers on *which rivals* are perceived to be the most threatening [23]. Dutch, Korean, and American people were asked to rank 11 rival qualities according to which would be most upsetting. The rival characteristics ranged from "having a better sense of humor than you" to "being a more skilled sexual partner than you." Men in all three cultures, more than women, reported that they would experience greater distress when a rival surpassed them on the dimensions of *financial prospects*, *job prospects*, and *physical strength*. Women in all three cultures, more than men, reported greater distress when a rival had *a more attractive face* or *a more desirable body*.

These sex differences in the qualities of rivals people find most threatening reflect fundamental sex differences in the components of mate value. Physical attractiveness is a more important component of women's than of men's mate value; it provides a wealth of cues to a woman's fertility and reproductive value. Economic potential, and the qualities that lead to resource acquisition, are more important determinants of men's than of women's mate value. Evidence for these universal determinants of desirability were initially discovered in a study of mate preferences in 37 cultures located on six continents and five islands, with a total sample size of 10,047 [24]. The fundamental sex differences in mate preferences have subsequently been replicated by several dozen independent researchers [25, 26]. The qualities men and women find most threatening in a rival mirror these sex-linked components of mate value.

Cognitive Biases and Emotional Wisdom

Humans live in an uncertain social world. We must make inferences about others' intentions and emotional states. How attracted is he to her? How committed is she to him? Does that smile signal sexual interest or mere friendliness? Some states, such as smoldering passions for other people, are intentionally concealed, rendering uncertainty greater and inferences more tortuous. We are forced to make inferences about intentions and concealed deeds using a chaos of cues that are only probabilistically related to the deeds' occurrence. An unexplained scent on one's romantic partner, for example, could signal betrayal or an innocuous olfactory acquisition from a casual conversation.

In reading the minds of others, there are two ways to go wrong. One can infer a psychological state that is not there, such as assuming sexual interest when it is absent. Or one can fail to infer a psychological state that is there, such as remaining oblivious to another's true romantic yearnings. According to a new approach called Error Management Theory, it would be exceedingly unlikely that the cost-benefit consequences of the two types of errors would be identical across their many occurrences [27, 28, 29]. We intuitively understand this in the context of smoke alarms, which are typically set to be hyper sensitive to any hint of smoke. The costs of the occasional false alarm are trivial compared with the catastrophic costs of failing to detect a real house fire. Error Management Theory extends this logic to cost-benefit consequences in evolutionary fitness, and

in particular to reading the mating minds of the opposite sex.

According to Error Management Theory, asymmetries in the cost-benefit consequences of inferences, if they recur over evolutionary time, created selection pressures that produced predictable *cognitive biases*. Just as smoke alarms are "biased" to produce more false positives than false negatives, Error Management Theory predicts that evolved mind-reading mechanisms will be biased to produce more of one type of inferential error than another. In the context of jealousy and mate guarding, it is reasonable to hypothesize that it would be more costly for a person to err by failing to detect a partner's infidelity than to erroneously infer an infidelity that has not occurred [30].

A condition that likely facilitated the evolution of a "jealousy bias" that functioned to over-infer infidelity is the great uncertainty that surrounds the detection of infidelity. One study surveyed a large sample of men and women who were involved in long-term romantic relationships [31]. They asked each person privately whether they were certain or uncertain that their partner had always been faithful to them. Of the women polled, 45% reported that they were certain their partner had been faithful; 41% reported that they were certain that their partner had been unfaithful; and 14% reported that they were uncertain whether or not their partner had been unfaithful. The corresponding figures for men were 36%, 28%, and 36%. That is, more than a third of the men in this sample reported uncertainty about whether or not their partner had remained faithful to them. Given that sexual infidelity is typically intentionally concealed, men's uncertainty should perhaps not be surprising. Nonetheless, it sets the stage for the evolution of a "jealousy bias" designed to minimize errors of failing to detect an infidelity when one occurs.

Although research has just begun to explore this hypothesized jealousy bias, a large literature in psychiatry and clinical psychology points to its existence [32]. Indeed, there are many psychiatric terms to describe individuals afflicted with recurrent false suspicions that their partner is unfaithful – delusional jealousy, pathological jealousy, psychotic jealousy, the erotic jealousy syndrome, and the Othello Syndrome (after the Shakespeare play "Othello," a man who falsely suspected his wife of sexual betrayal). Men and women sometimes harbor false suspicions that a partner is unfaithful when he or she is in fact the paragon of loyalty. The bias appears to become activated in contexts that historically have been linked to infidelity – when a partner is sexually dissatisfied, displays a sudden decline in sex drive, or where there is an increasing gap in the mate value of the two partners [33]. Of course, verifying with certainty that jealous suspicions are false is extremely difficult, given the clandestine nature of infidelity. Nonetheless, the logic of Error Management Theory suggests that a jealousy bias is likely to have evolved; future empirical research is needed to test this hypothesis directly.

Error Management Theory offers a fresh perspective on human mating problems by suggesting that certain types of errors reflect functional adaptations rather than actual flaws in the psychological machinery. It provides new insights into why men and women get into certain types of conflict – for example, why partners sometimes get falsely suspected or accused of infidelity, and why there are numerous psychiatric cases of individuals diagnosed with delusional jealousy.

Behavioral Tactics of Mate Guarding

Inputs that trigger jealousy may tell us little about the actual behavioral output that follows from the perception of a threat. The first attempts to study behavioral tactics of human mate guarding took place occurred in the late 1980's [34]. Researchers identified 19 different tactics of mate guarding, ranging from vigilance to violence. Examples of *vigilance* include: *He called her at unexpected times to see who she was with; She had her friends check up on her; He dropped by unexpectedly to see what she was doing; At the party, she did not let him out of her sight.* Examples of *violence* include: *He hit the guy who made a pass at her; She slapped the woman who made a pass at her partner; He got his friends to beat up the guy who was interested in her.*

Other tactics of mate guarding include the *concealment of mate* (e.g., He did not take her to the party when other males would be present), *monopolization of mate's time* (e.g., He spent all his free time with her so that she could not meet anyone else), *verbal threats* (e.g., She threatened to break up with him if he ever cheated on her), *derogation of competitors* (e.g., He pointed out to her the other guy's flaws), *resource display* (e.g., He bought her an expensive gift), *appearance enhancement* (e.g., He made himself "extra attractive" for her), *sexual inducement* (e.g., She performed sexual favors to keep him around), *physical signals of possession* (e.g., He held her hand when other guys were around), and *possessive ornamentation* (e.g., She asked him to wear a ring signifying that he was taken). It is noteworthy that two of the major strategies commonly found among insects – the concealment of mates and the physical repulsion of rivals – are also found in humans, suggesting a particularly successful region of adaptive design space.

Men and women differ in how frequently they perform these mate guarding tactics [35, 36]. Men are more likely than women to attempt to conceal their mates, use possessive markings (e.g., asking her to wear his jacket), display resources, threaten intrasexual rivals, and use physical violence toward intrasexual rivals as tactics of mate guarding. Women are more likely than men to enhance their physical appearance and flirt with other men as tactics of mate guarding.

Another critical issue centers on what predicts the intensity of effort a person allocated to mate guarding. Given that energy and effort are always finite, effort allotted to one adaptive problem cannot be allotted to others. Mate guarding is theoretically predicted to

increase in intensity to the degree that (1) one is mated to a valuable partner, and so a relaxation in mate guarding might result in a large reproductive loss, and (2) there are interested rivals, and hence an increased threat of mate poaching and the possibility of defection. Other things being equal, the higher the mate value of one's partner, the higher the probability that there will be rivals interested in poaching one's partner.

A study of 107 newlywed married couples explored predictors of the intensity of effort a person allocated to mate guarding [37]. Men married to young and physically attractive women, that is those high in reproductive value, mate guarded them most intensely. They were more likely than other men to conceal their mates, display emotional outbursts at the slightest signals of infidelity, and threaten other men with violence. Examples of the specific actions these men performed include:

- *Refusing to take her to the party where other men were present.*
- *Insisting that she spend all her free time with him.*
- *Yelling at her for talking to another man.*
- *Telling her that he would die if she ever left him.*
- *Derogating another man's intelligence.*
- *Staring coldly at the other guy who was looking at her.*

Just as a woman's youth and physical attractiveness figure heavily in men's initial mate preferences, they also determine the intensity of effort men devote to holding on.

Women's mate guarding, in contrast, was not at all influenced by her husband's physical appearance or his age. It was affected by his income and how determined he was to climb the status hierarchy. Women married to men with abundant resources and men higher on status striving were more likely than other women to display increased levels of vigilance, express emotional distress at the slightest hint of a partner's wandering eye, put extra effort into enhancing their appearance, and show more submissiveness in the service of holding on to their partner. Specific acts by these mate guarding women include:

- *Staying close by his side when they were at the party.*
- *Threatening to break up if he ever cheated on her.*
- *Making herself "extra attractive" to maintain his interest.*
- *Telling him that she would change to please him.*
- *Asking him to wear a ring to signify that he was taken.*

Just as women's desire for men who have status and resources influences initial mate selection, these same qualities continue to influence the effort women devote to keeping the men they have attracted.

Jealousy and the corresponding behavioral strategies of mate guarding are likely to have evolved because of the ever-present possibility of sexual betrayal or emotional defection. In a hazardous mating arena where rivals lurk, partners harbor passions for other people, and infidelity threatens, it is not surprising that evolution has forged elaborate strategies to detect and fend off these threats.

Conclusions

Desirable mates are always in short supply compared to the many who seek them. Because those high in mate value have many mating options and are often heavily courted, they tend to be taken out of the mating market with dispatch. Being already mated, however, does not necessarily deter others who are interested, resulting in the phenomenon of mate poaching, which may have arisen as a distinct mating strategy. Selection would have operated against those who failed to defend against mate poachers. Selection would also have penalized those who let their partner defect, either temporarily or permanently. Mates gained must be retained. Failure to solve this cluster of adaptive problems would have been costly – from genetic cuckoldry to the misdirection of parental effort to reputational damage that would impair future mating opportunities. Thus, counter-strategies evolved to prevent defection, deter poachers, and preserve access to the reproductively relevant resources of an attained mate.

Although both sexes undoubtedly confronted adaptive problems to which mate guarding was an effective solution, the precise nature of these problems differed in several key respects. Because fertilization occurs internally within females and not within males, males historically faced a reproductive risk not faced by females – genetic cuckoldry. The sexes also differed in the qualities of rivals that posed the greater threats. Potential interlopers with better economic resources or prospects, for example, posed a greater threat to men than to women mate guarders, given the premium that women place on resources in potential mates. Potential interlopers who are physically attractive and young posed a greater threat to women than to men mate guarders because of the premium men place these cues to reproductive value in their mate selections. As a consequence of differences in the precise nature of the adaptive problems women and men faced, the sexes evolved corresponding differences in the underlying psychology of mate guarding. Women more than men become easily distressed by threats of a partner becoming emotionally involved with a potential rival, since emotional involvement predicts the long-term diversion of a man's commitments and resources to another woman. Men more than women become distressed by signs of sexual involvement, since sexual involvement jeopardizes a man's certainty in paternity. Sex differences in the relative weight given to signals of sexual and emotional infidelity have been well documented psychologically, physiologically, and cross-culturally.

The adaptive problems that historically gave rise to jealousy and mate guarding, of course, are not necessarily consciously articulated by the persons experiencing them. A man who discovers his wife in the act of intercourse with another man does not think to himself: "Let me see ... this event jeopardizes my certainty in

genetic paternity in offspring, and hence threatens the successful proliferation of my genes relative to those of my rivals ... that makes me mad!" Rather, jealousy becomes activated, physiology aroused, and consequent mate guarding behavior performed. Successful mate guarding does not require conscious awareness of the adaptive logic of why mate guarding mechanisms evolved.

Precisely how much effort a person allocates to mate guarding is partly a function of the value of the mate being guarded. Men married to young and physically attractive mates invest more effort in mate guarding compared to men married to older and less attractive women. Women married to men higher in income and status striving put more effort into guarding their partners than women married to men who earn less or strive less for status. These patterns presumably reflect the fact that attractive women and resourceful men are higher in mate value than same-sex others lacking these qualities. As a consequence, they experience more frequent sexual or romantic interest from others, and hence have more numerous and more desirable potential mating options. Thus, those mated with desirable partners allocate more effort to mate guarding.

Once a threat is perceived and mate guarding psychology activated, specific mate guarding behavior often follows, ranging from vigilance to violence. At this stage in mating science, precisely which acts of mate guarding a person performs cannot be predicted. One person increases the levels of resources bestowed on a mate, a second verbally derogates a perceived rival, a third starts to stalk the mate surreptitiously, and a fourth explodes in violence. The specific mate guarding acts deployed are undoubtedly a function of many factors, such as the magnitude of the threat, the assets of the interloper, the perceived effectiveness of alternative acts, perceived reputational consequences, and many others. In this sense, many design features of the underlying mate guarding psychology remain to be discovered.

REFERENCES

1 Buss DM. The Evolution of Desire: Strategies of Human Mating (Revised Edition). New York: Basic Books; 2003.
2 Buss DM. Conflict between the sexes: Strategic interference and the evocation of anger and upset. J Pers Soc Psychol, 1989; **56**:735–747.
3 Buss DM. From vigilance to violence: Tactics of mate retention. Ethology and Sociobiology 1988; **9**:291–317.
4 Thornhill R, Alcock J. The evolution of insect mating systems. Cambridge, MA: Harvard University Press; 1983.
5 Thornhill R, Alcock J. The evolution of insect mating systems. Cambridge, MA: Harvard University Press; 1983.
6 Alexander RD. Evolutionary change in cricket acoustical communication. Evolution 1962; **16**:443–467.
7 Thornhill R, Alcock J. The evolution of insect mating systems. Cambridge, MA: Harvard University Press; 1983.
8 Buss DM. The Evolution of Desire: Strategies of Human Mating (Revised Edition). New York: Basic Books; 2003.
9 Schmitt DP, Buss DM. Human mate poaching: Tactics and temptations for infiltrating existing relationships. Journal of Personality and Social Psychology 2001; **80**:894–917.
10 Schmitt DP. Desire for sexual variety and mate poaching experiences across multiple languages and cultures. Paper presented to the Annual Meeting of the Human Behavior and Evolution Society, London, June, 2001.
11 Daly M, Wilson M, Weghorst SJ. Male sexual jealousy. Ethology and Sociobiology 1982; **3**:11–27.
12 Symons D. The evolution of human sexuality. New York: Oxford University Press; 1979.
13 Buss DM, Larsen R, Westen D, Semmelroth J. Sex differences in jealousy: Evolution, physiology, and psychology. Psychological Science 1992; **3**:251–255.
14 Daly M, Wilson M, Weghorst SJ Male sexual jealousy. Ethology and Sociobiology 1982; **3**:11–27.
15 Buss DM. The Dangerous Passion: Why Jealousy is as Necessary as Love and Sex. New York: Free Press; 2000.
16 Buss DM, Larsen R, Westen D, Semmelroth J. Sex differences in jealousy: Evolution, physiology, and psychology. Psychological Science 1992; **3**:251–255.
17 Buss DM. The Evolution of Desire: Strategies of Human Mating (Revised Edition). New York: Basic Books; 2003.
18 DeSteno DA, Salovey P. Evolutionary origins of sex differences in jealousy: Questioning the "fitness" of the model. Psychological Science 1996; **7**:367–372.
19 Buss DM, Shackelford TK, Kirkpatrick, LA, Choe J, Hasegawa M, Hasegawa T, Bennett K. Jealousy and the Nature of Beliefs About Infidelity: Tests of Competing Hypotheses About Sex Differences in the United States, Korea, and Japan. Personal Relationships; 1999; **6:**125–150.
20 Pietrzak R, Laird JD, Stevens, DA, Thompson NS. Sex differences in human jealousy: A coordinated study of forced-choice, continuous rating-scale, and physiological responses on the same subjects. Evolution and Human Behavior 2002; **23**:83–94.
21 Shackelford TK, Buss DM, Bennett K. Forgiveness or breakup: Sex differences in responses to a partner's infidelity. Cognition and Emotion 2002; **16**:299–307.
22 Betzig L. Causes of conjugal dissolution. Current Anthropology 1989; **30**:654–676.
23 Buss DM, Shackelford TK, Choe J, Buunk B, Dijkstra P. Distress about rivals: Reactions to intrasexual competitors in Korea, the Netherlands, and America. Personal Relationships 2000; **7**:235–243.
24 Buss DM. Sex differences in human mate preferences: Evolutionary hypotheses testing in 37 cultures. Behavioral and Brain Sciences 1989; **12**:1–49.
25 Buss DM. The Evolution of Desire: Strategies of Human Mating (Revised Edition). New York: Basic Books; 2003.
26 Kenrick DT, Keefe RC. Age preferences in mates reflect sex differences in reproductive strategies. Behavioral and Brain Sciences 1992; **15**:75–133.
27 Haselton MG, Buss DM. Error Management Theory: A new perspective on biases in cross-sex mind reading. Journal of Personality and Social Psychology 2000; **78**: 81–91.
28 Haselton MG. The sexual overperception bias: Evidence of a systematic bias in men from a survey of naturally occurring events. Journal of Research in Personality in press.
29 Haselton MG, Buss DM. Biases in Social Judgment: Design Flaws or Design Features? In: Forgas J, von Hippel W, Williams K, editors. Responding to the Social World: Explicit and Implicit Processes in Social Judgments and Decisions. Cambridge: Cambridge University Press; in press.
30 Buss DM. The Evolution of Desire: Strategies of Human Mating (Revised Edition). New York: Basic Books; 2003.
31 Paul L, Foss MA, Galloway J. Sexual jealousy in young women and men: Aggressive responsiveness to partner and rival. Aggressive Behavior 1993; **19**:401–420.
32 Buss DM. The Dangerous Passion: Why Jealousy is as Necessary as Love and Sex. New York: Free Press; 2000.
33 Buss DM. The Dangerous Passion: Why Jealousy is as Necessary as Love and Sex. New York: Free Press; 2000.
34 Buss DM. From vigilance to violence: Tactics of mate retention. Ethology and Sociobiology 1988; **9**:291–317.
35 Buss DM. From vigilance to violence: Tactics of mate retention. Ethology and Sociobiology 1988; **9**:291–317.
36 Buss DM, Shackelford TK. From vigilance to violence: Mate retention tactics in married couples. Journal of Personality and Social Psychology 1997; **72**:346–361.
37 Buss DM, Shackelford TK. From vigilance to violence: Mate retention tactics in married couples. Journal of Personality and Social Psychology 1997; **72**:346–361.

REVIEW ARTICLE

Darwinian psychiatry and the concept of mental disorder

Alfonso Troisi [1] & Michael McGuire [2]
1. Department of Neurosciences, University of Rome Tor Vergata, Rome, ITALY.
2. Neuropsychiatric Institute, University of California, Los Angeles, USA.

Correspondence to: Alfonso Troisi, MD,
via Guattani, 14,
00161 Rome, ITALY
EMAIL: alfonso.troisi@uniroma2.it.

Submitted: *August 31, 2002*
Accepted: *September 8, 2002*

Key words: **Darwinian psychiatry; mental disorder; functional impairment; suffering; statistical deviance; lesion.**

*Neuroendocrinology Letters 2002; **23** (Suppl.4):31–38 pii: NEL231002R03 Copyright © Neuroendocrinology Letters **www.nel.edu***

Abstract

In this paper, we discuss the concept of mental disorder from the perspective of Darwinian psychiatry. Using this perspective does not resolve all of the quandaries which philosophers of medicine face when trying to provide a general definition of disease. However, it does take an important step toward clarifying why current methods of psychiatric diagnosis are criticizable and how clinicians can improve the identification of true mental disorders. According to Darwinian psychiatry, the validity of the conventional criteria of psychiatric morbidity is dependent on their association with functional impairment. Suffering, statistical deviance, and physical lesion are frequent correlates of mental disorders but, in absence of dysfunctional consequences, none of these criteria is sufficient for considering a psychological or behavioral condition as a psychiatric disorder. The Darwinian concept of mental disorder builds from two basic ideas: (1) the capacity to achieve biological goals is the best single attribute that characterizes mental health; and (2), the assessment of functional capacities cannot be properly made without consideration of the environment in which the individual lives. These two ideas reflect a concept of mental disorder that is both functional and ecological. A correct application of evolutionary knowledge should not necessarily lead to the conclusion that therapeutic intervention should be limited to conditions that jeopardize biological adaptation. Because one of the basic aims of medicine is to alleviate human suffering, an understanding of the evolutionary foundations of the concept of mental disorder should translate into more effective ways for promoting individual and social well-being, not into the search for natural laws determining what is therapeutically right or wrong.

Introduction

During the past 2 decades, psychiatric epidemiological studies have contributed a rapidly growing body of empirical knowledge on the prevalence data for mental disorders. Two large community surveys conducted in the United States, the National Institute of Mental Health Epidemiologic Catchment Area Program (ECA) [1] and the National Comorbidity Survey (NCS) [2], showed overall 1-year mental and addictive disorder prevalence rates approaching 30% and lifetime rates approaching 50%. This means that, according to current diagnostic criteria, one out of every two persons will suffer from a mental disorder during his or her lifetime. The findings of these epidemiological surveys are even more striking considering that several disorders such as most personality disorders, adjustment disorders and impulse control disorders were not included in the ECA and NCS studies.

These implausibly high prevalence rates have led to concerns about the validity of the current methods of psychiatric diagnosis and have reinvigorated the debate about the concept and definition of mental disorder. According to many, the most basic problem with current criteria of psychiatric diagnosis is that they fail to distinguish mental disorders from "problems in living", that is the vast array of problematic but nondisordered human conditions which reflect "the aches and pains of normal life" [3, p. 119]. Because there is no accepted way to define the boundary between mental disorder and psychological health, current methods of psychiatric diagnosis are overinclusive and produce a high number of false positive [4].

In this paper, we discuss the concept of mental disorder from the perspective of Darwinian psychiatry [5, 6]. Using this perspective does not resolve all of the quandaries which philosophers of medicine face when trying to provide a general definition of disease [7, 8]. However, it does take an important step toward clarifying why current methods of psychiatric diagnosis are criticizable and how clinicians can improve the identification of true mental disorders.

We begin with a brief review of the Darwinian model of mental health and normal functioning. This section is necessarily the first step of a line of reasoning aimed at redefining the concept of mental disorder from an evolutionary perspective. To identify what has gone wrong with the individual's mental and behavioral functioning, one should have a detailed idea of how the individual functions or would function when nothing is going wrong. This section introduces the evolutionary concepts that will be used in the next section of the paper, which consists of a critical analysis of the common criteria of psychiatric morbidity. The limits of suffering, statistical deviance, and organic lesion as criteria for validating psychiatric diagnosis will be discussed. Next we will focus on the concept of functional impairment arguing that (1) it is the best single criterion for distinguishing true mental disorders from pseudo-psychopathologies; (2) the Darwinian concept of functional impairment differs in important ways from other views of this construct that have been previously advanced in the psychiatric literature. A discussion of the clinical and social issues related to the Darwinian concept of mental disorder is the final section of the paper.

Mental health

The evolutionary concept of mental health builds from two basic ideas: (1) The capacity to achieve biological goals is the best single attribute that characterizes mental health. And (2), the assessment of functional capacities cannot be properly made without consideration of the environment in which the individual lives. These two ideas reflect a concept of mental health that is both functional and ecological [9].

During the course of evolutionary history, natural selection favored those psychological and behavioral traits that served a specific function more efficiently than available alternative traits did. Therefore, an evolutionary account of the human mind and behavior is an account of how psychological and behavioral traits function as adaptations and how they vary across persons. In an evolutionary context, individuals can be viewed as a mosaic of evolved traits employing a variety of strategies to achieve biological goals. The term "strategy" refers to a cluster of coevolved anatomical, physiological, psychological, and behavioral traits designed by natural selection to enhance inclusive fitness. When we say that a trait is functional or adaptive, we mean that it enhances the inclusive fitness of the individual. Human beings, like all other organisms, have been designed by natural selection to strive for the achievement of specific short-term goals or experiences, such as acquiring resources, making friends, developing social support networks, having high status, attracting a mate, and establishing intimate relationships. In the ancestral environment, the achievement of these short-term goals correlated consistently with a gene-transmitting advantage, the ultimate goal of any evolved strategy. In many respects, human beings no longer live in the environment for which they were adapted. Because the modern world is so different from the ancestral environment, the ancestral-fitness consequences of evolved strategies may no longer be realized. Nevertheless, the capacity to achieve short-term biological goals remains a valid measure of mental health because it is an indication that the individual possesses those optimal functional capacities that, in the ancestral environment, promoted biological adaptation.

The study of interactions between individuals and their environments (the ecological perspective) is essential to evaluate the efficiency of functional capacities. Optimal functional capacities are sets of coevolved traits that are (or were) best suited to increasing inclusive fitness in specific environments. No trait is adaptive in all environments. The same trait can be highly adaptive in one environment and minimally adaptive in another.

The preceding discussion underscores two important points. (1) The evolutionary concept of mental health is consequence-oriented: what makes a condi-

tion pathological are its consequences, not its causes or correlates. And (2), the degree of efficiency of functional capacities is dependent on features of the environment. Adverse environments can compromise the efficiency of optimal capacities, just as favorable environments can offset or mitigate the inefficiency of suboptimal capacities. In conclusion, the Darwinian view of mental health places functional capacities and biological adaptation at the core of attempts to define mental disorder. As a result, issues of psychological suffering, statistical deviance, and organic lesion are de-emphasized and the issue of functional impairment moves to the center stage.

Criteria for defining morbidity

Suffering

People seek medical advice because they feel ill. The apparent triviality of this statement hides an idea that is deeply rooted in common sense: nociceptive experiences, ranging from discomfort and malaise to severe pain, are a crucial feature of disease [10]. In many European languages, the etymological roots of the word "disease" are terms referring to suffering: *maladie* in French and *malattia* in Italian derive from the Latin *male habitum*, "in a bad state"; *pathos* in Greek means suffering, and *boljezn'* in Russian is derived from *bol'* (i.e., pain); and *disease* in English originally meant disease [11]. The importance of psychological suffering as a criterion for diagnosing the presence of a psychiatric disorder is also emphasized in the definition of mental disorder adopted by the 4th edition of the Diagnostic and Statistical Manual of Mental Disorders (DSM-IV) of the American Psychiatric Association. According to the DSM-IV, a mental disorder is "a clinically significant behavioral or psychological syndrome or pattern that occurs in an individual and that is associated with present distress (e.g., a painful symptom) or disability (i.e., impairment in one or more important areas of functioning) or with a significantly increased risk of suffering death, pain, disability, or an important loss of freedom." [12, p. xxi].

Even though most psychiatric disorders involve unpleasant or painful symptoms at some stage of their course, there are obvious problems with the idea that psychological suffering is an essential criterion for diagnosing mental disorder. First, there are psychiatric disorders in which patients do not complain of psychological suffering: the negative syndrome of schizophrenia, schizoid personality disorder and some forms of antisocial personality disorder are examples. Second, people often experience painful emotions (e.g., anxiety and depression) even though they have no psychiatric diagnosis. Loss of a loved one, poverty, and social ostracism may induce a psychological suffering comparable to that of some psychiatric disorders. Third, some neuropsychiatric disorders produce pleasurable feelings instead of mental distress: ecstatic states in some forms of epilepsy, grandiose delusions in some psychoses, hypomania, and intoxication induced by alcohol and drugs are examples. In other words, the association between psychological suffering and mental disorder is complex and includes several possible combinations (mental disorder with suffering, mental disorder without suffering, suffering without mental disorder, mental disorder with pleasure). Such a complexity not only questions the validity of suffering as an essential criterion of psychiatric morbidity but also requires an explanation. An evolutionary analysis of the design features of both the nociceptive warning system and the brain reward system may help clarify the complex relationships between mental disorders and mental pain and pleasure.

When examined from an evolutionary perspective, the fact that mental disorder is often associated with psychological suffering can be easily reconciled with the fact that many forms of psychological suffering do not qualify as mental disorders. Suffering is an evolved response to maladaption. Under minimally adaptive circumstances, individuals experience mental pain that functions in part as a warning system that one's goal seeking efforts are failing and in part as a social signal to others to elicit their assistance in achieving goals [13]. Because true mental disorders are, by definition, maladaptive patterns of behavior, it is usual for psychiatric disorders to be associated with mental distress.

However, in a person with intact functional capacities, psychological suffering often correlates with the implementation of alternative strategies. Focusing the individual's attention on impending or actual obstacles to the achievement of biological goals, negative emotions may stimulate adaptive reactions. If the alternative strategies are effective, a negative cost-benefit situation may be offset, and the negative mood may dissipate. Thus, emotions function as a source of information about short-term goal achievement. Mood regulates the allocation of effort and resources toward strategies likely to give a high payoff and away from unprofitable enterprises and times when efforts will likely be wasted or dangerous [14]. Negative affect has evolved as an emotional indicator that biological goals have not been or are not being achieved, that is, that one's fitness has been or is being compromised.

Sometimes, the functional significance of negative emotions is evident only if the context of occurrence is evaluated from an evolutionary perspective [15, 16]. For this reason, current methods of psychiatric assessment can occasionally mistake adaptive psychological distress for pathological response. Commenting on their implausibly high prevalence rates, Regier *et al*. [17] have acknowledged such a possibility: "it is reasonable to assume that some syndromes in the community represent transient homeostatic responses to internal or external stimuli that do not represent true psychopathologic disorders… many people with currently defined mental syndromes (in particular among the affective and anxiety disorders)… may be having appropriate homeostatic responses that are neither pathologic nor in need of treatment." (p. 114).

Also the fact that some neuropsychiatric disorders are associated with pleasurable feelings is better understood when examined from the perspective of Darwin-

ian psychiatry. The achievement of adaptive goals often depends on a long chain of events and requires the implementation of complex behavioral strategies. In species characterized by behavioral plasticity and flexibility, natural selection has favored the evolution of brain reward systems as a means to guide behavioral choices and to address the individual toward the achievement of biological goals. The neuroscientist Jaak Panksepp has succinctly expressed this concept with these words: "Pleasure is nature's way of telling the brain that it is experiencing stimuli that are useful." [18].

In humans, the brain reward system and the positive emotions originating from its stimulation play a central role in controlling the correct execution of adaptive behaviors. The capacity to experience mental pleasure helps the individual to pursue goals relevant to biological adaptation [19]. In addition, pleasant emotions associated with adaptive behavior increase the probability that one will engage in similar behavior in the future. In this context, it is clear why mental pleasure and adaptive behavior are so strictly associated. Then, how is it possible that maladaptive conditions such as certain mental disorders are associated with pleasurable feelings?

The conventional explanation derives from the biomedical model of psychiatric disorders and postulates the existence of a structural or physiological dysfunction in the neural mechanisms that modulate mental pleasure. This is certainly the case in some forms of epilepsy and bipolar disorder. However, the association between pleasurable feelings and maladaptive patterns of behavior may also result from the artificial and voluntary manipulation of the brain reward system, as in the case of drug abuse.

Under natural conditions, the brain reward system was activated when (and only when) the individual was pursuing or achieving a goal relevant to biological adaptation. In contrast, drugs of abuse directly interact with specific receptors in the brain that normally help mediate feelings of satisfaction and pleasure associated with the execution of adaptive behaviors. Direct chemical stimulation of these receptors creates a signal in the brain that indicates, falsely, the achievement of biological goals [20]. The individual who uses drugs such as opiates or psychostimulants no longer needs the presence of natural rewards to experience the positive emotions that, under normal conditions, are the psychic reflections of doing the "right thing" biologically. The behavior of some drug addicts resembles that of rats implanted with electrodes located in the septal area and allowed to self-stimulate through lever pressing [21]. These animals stop drinking, eating, and mounting estrous females because they continuously engage in bar pressing to receive electrical stimulation in the brain reward system. When viewed from an evolutionary perspective, drug use and abuse qualify as psychiatric disorders because of their disruptive impact on different aspects of adaptive behavior [22]. In accord with such a view, clinical reports have described the adverse effects of drug abuse on the capacity to search for and enjoy natural rewards associated with a variety of adaptive behaviors.

Statistical deviance

Sir Henry Cohen's [23] definition of disease as "a quantitative deviation from the normal" (in which by normal he meant the statistical norm) exemplifies the statistical approach to the problem of defining mental disorder. Traditional critiques to such an approach have discussed a number of problems that complicate the use of statistical deviance as a valid criterion of morbidity [24, 25]. There are diseases which are extremely frequent or normal in the statistical sense, yet abnormal for an individual from a clinical viewpoint. There are many behavioral profiles that are statistically deviant and undesirable but are not disorders (e.g., criminality or extreme shyness). And there are some socially valued traits such as excellence in intelligence, artistic talent or physical strength that are statistically deviant but are not disorders. An evolutionary analysis goes beyond these objections and helps to better understand the complexity of the relationship between statistical deviance and mental disorder.

Individual variability is important to evolutionary processes. Natural selection occurs only when differences in some phenotypic characteristic result in consistent differences in rates of survival and reproduction. There are different modes of selection, however, and they produce different types of interindividual variation [26]. Continuous variation in physical and mental traits is the most common situation in nature. If intermediate phenotypes are most fit, selection is stabilizing and the resulting variation is continuous. In continuous variation, the individuals do not fall into sharp classes but are almost imperceptibly graded between wide extremes. Because the phenotypes that deviate in either direction from an optimal value are selected against, the extremes constitute only a small percentage of the total population with the far larger percentage clustering around the middle. Thus, if a trait is subject to stabilizing selection, it is not surprising that health (to the extent that it depends on the optimal functioning of that specific trait) coincides with the statistical norm [9].

However, not all psychological or behavioral traits are distributed on a continuum. Variability between individuals can be discontinuous: if two or more phenotypes have high fitness, but intermediates between them have low fitness, selection is diversifying; that is it acts in favor of two or more modal phenotypes and against those intermediate between them. Diversifying selection produces discontinuous variation which divides the individuals of a population into two or more sharply distinct forms. Not only may this occur at the anatomical and physiological levels, but also at the behavioral level.

Ethological studies have documented the existence of alternative strategies in many animal populations. Alternative strategies are the product of diversifying selection. Even though statistically deviant, these behavioral strategies are employed to compete success-

fully with rivals and reflect the normal operation of adaptive mechanisms. Primate studies offer nice examples of alternative strategies in species phylogenetically close to humans.

In mandrills, there are two morphological and behavioral variants of adult males that differ in terms of secondary sexual adornments and reproductive strategies [27]. "Fatted" males have highly developed sex skin coloration, large testes, high plasma testosterone levels, and fat rumps, whereas "nonfatted" males have paler sex skin, smaller testes, lower plasma testosterone, and slimmer rumps. While "fatted" males mate-guard fertile females, less developed males remain in the periphery of the group and mate sneakily with females. Similar intermale differences have been observed in orangutans [28]. In the presence of many dominant males, adolescent male orangutans undergo a developmental arrest: They become fertile but do not develop fully adult secondary sexual features, such as cheek flanges, laryngeal sac, beard and mustaches, large body size, and a musky odor. Developmental arrest is associated with a distinct hormonal profile [29]. Arrested males lack levels of luteinizing hormone (LH), testosterone, and dihydrotestosterone (DHT) necessary for development of secondary sexual traits. However, they have sufficient testicular steroids, LH, and follicle stimulating hormone (FSH) to fully develop primary sexual function and fertility. Like in mandrills, the two morphological variants of male orangutans use different mating strategies [30]. Developed males are frequently involved in male-male aggression, are attractive to females and typically consort with them, and may sire many offspring over a relatively short period of time. In contrast, being inconspicuous and less attractive to females, arrested males adopt a low-cost, low-benefit reproductive strategy based on sneaky matings and forced copulations.

In the short period, the reproductive success of "nonfatted" male mandrills and arrested male orangutans is lower than that of fully developed males. However, there are advantages associated with the use of the "sneak and rape" mating strategy. While the "combat and consort" strategy imposes costs on dominant males in terms of metabolic energy and exposure to intermale aggression, the suppression of secondary sexual traits allows subordinate males to minimize aggression and injury from dominant, fully mature males, while still being able to sire. Both the strategies are maintained by natural selection because the disadvantages associated with each strategy are balanced by advantages in a different context. In both mandrills and orangutans, subordinate males can rapidly switch over to the "combat and consort" strategy if the density of dominant males decreases. Arrested male orangutans develop into flanged males if a more favorable reproductive situation occurs, and subordinate male mandrills develop secondary sexual traits when they become dominant. Such a flexibility is a further indication that the "sneak and rape" strategy is an adaptive alternative strategy based on a continuous assessment of reproductive opportunity and risk of intermale aggression.

How do these findings relate to the concept of mental disorder? Darwinian psychiatry suggests that some statistically-deviant behavioral profiles currently classified as psychiatric disorders may be in fact evolved alternative strategies. This hypothesis has been tentatively advanced to explain the interpersonal behavior of individuals with antisocial personality disorder [31] and chronic somatization [32]. More compelling evidence has been gathered on different patterns of attachment. According to attachment theory, individual differences in the organization of the attachment system emerge from caregiving interactions with attachment figures and subsequently have numerous influences on personality and social behavior. The traditional perspective views "secure" attachment as the healthy pattern and the insecure patterns as psychological maladaptations [33]. In contrast, Belsky [34] has advanced the argument that the principal evolutionary function of early social experience is to provide children with diagnostic information about the kinds of social and physical environments they are most likely to encounter during their lifetime. This information would permit individuals to facultatively adopt an appropriate reproductive strategy in future environments. Data on the relationships between social experience in childhood and sexual and parental behavior in adulthood support the interpretation of insecure patterns of attachment as alternative strategies.

Lesion

Anyone familiar with the evolution of the concept of disease in medicine would take it for granted the intrinsic "weakness" of the criteria of suffering and statistical deviance and would probably consider as scarcely original the evolutionary critique delineated in the previous sections. In fact, since the 18th century, in medicine the "strong" criterion of morbidity is the presence of organic lesion.

To most of the schools of medicine of the ancient world, symptoms and signs were themselves diseases. In the 17th century, the English physician Thomas Sydenham introduced the view that symptoms must be distinguished from one another, that common clusters of symptoms (i.e. syndromes) must be recognized, and that the natural course of these clusters should be appreciated. Even though the syndromal approach contributed greatly to the advance of medical nosology in the two centuries that followed, linking symptoms together does not provide the physician with any causal explanation of the disease process.

The next advance in the definition of disease owed a great deal to the work of Giovanni Battista Morgagni, an eighteenth-century Italian physician who introduced the method of clinical-pathological correlation which consists in tracking down in the organs and tissues the clinical manifestations of disease. The view that "a disease entity is an altered part of the body" [35] came to dominate medical thinking because its apparent objectivity and strict relationship with causal

explanations of the patient's symptoms. During the last fifty years the development of new techniques of investigation has expanded the concept of lesion to include physiological, biochemical, and molecular abnormalities, without relinquishing the basic assumption that illness necessarily involves a demonstrable physical abnormality of some sort [24].

Until recently, the Virchowian revolution had not invested psychiatry because of the methodological problems in unveiling the neurobiological bases of mental disorders. However, the recent years have witnessed major advances in the study of neuroscience which have increased our understanding of the relationship between cerebral processes and behavioral, cognitive and emotional disorders. The search for neurobiological explanations for psychiatric disorders is in full flow, spurred on by the same reductionist philosophy and technological advances that are proving so dominant in the study of human psychology and behavior. As a consequence, the old idea [36, 37, 38] that the findings emerging from neurobiological research will ultimately solve the problem of distinguishing between sanity and insanity has been recently reformulated in more sophisticated terms by many representatives of mental health disciplines who seem to embrace the Virchowian view that organic lesion is the essential criterion of psychiatric morbidity [39, 40, 41].

Evolutionary reasoning suggests that such a distinction cannot be based on the demonstration of organic pathology because there is no definitive criterion for sorting out altered brain functioning from normal inter- and intraindividual variability, unless we judge a condition in terms of functional consequences. Ascertaining the pathological nature of a somatic change is relatively straightforward as long as one is concerned with a departure from a recognized and standard pattern. The problem is that it is not always apparent where normal variation ends and pathology begins. Thus, the objectivity of the criterion of lesion is only apparent. Defining lesion is as difficult as defining disease, and the risk of circular reasoning is always present. For example, the 15th edition of the Encyclopedia Britannica defines lesion as "a structural or biochemical change in an organ or tissue produced by disease processes". In logical terms, this means that the definition of lesion is dependent on the definition of disease, not vice versa. Starting with the search for somatic changes in absence of an agreed upon diagnosis of morbidity can yield confusing results, as shown by the following examples selected from recent neurobiological studies.

Studies using positron emission tomography (PET) have demonstrated that cerebral blood flow in orbital frontal areas is higher in patients with obsessive-compulsive disorder (OCD) than in controls [42]. However, blood flow increase in orbital frontal regions has been reported to occur also in healthy subjects during self-induced dysphoria [43]. Several studies have reported that, in homosexual compared to heterosexual men, three brain structures are different: one hypothalamic nucleus, INAH 3, is smaller, while another, the SNC, is larger, as is one of the connecting pathways between the cerebral hemispheres, the anterior commissure [44]. Subjects who are in the early romantic phase of a love relationship are not different from OCD patients in terms of density of the platelet 5-HT transporter, which proves to be significantly lower than in the normal controls [45]. Using PET during the continuous performance task, murderers have been found to have significantly lower glucose metabolism in both lateral and medial prefrontal cortex relative to controls [46].

Are these data sufficient to conclude that transient dysphoria, homosexuality, romantic love, and murder are psychiatric disorders? Are the brains of individuals with these conditions "lesioned"? Are these neurobiological findings likely to influence the judgment about disorder attribution to the same extent for each of these conditions? The complexity of these questions and the fact that different clinical psychiatrists are likely to give different answers show that the concept of lesion is all but objective and that its use as criterion of psychiatric morbidity requires the reference to other factual elements.

How Darwinian psychiatry conceptualizes functional impairment

The preceding discussion shows that the validity of the conventional criteria of psychiatric morbidity is dependent on their association with functional impairment. Suffering, statistical deviance, and physical lesion are frequent correlates of mental disorders but, in absence of dysfunctional consequences, none of these criteria is sufficient for considering a psychological or behavioral condition as a psychiatric disorder.

At this point, a brief clarification of how Darwinian psychiatry conceptualizes the criterion of functional impairment is needed. Evolutionary definitions of mental disorder based on the functional approach have been suggested by a number of authors [7, 24, 47, 48]. For example: (1) A disease is composed of phenomena which are not only abnormal by their species norm, but also place the living organisms displaying the disease at a biological disadvantage. (2) A person is healthy if his body functions with at least species-typical efficiency. And (3), disorders are the results of things that have gone wrong with evolved structures that allow for adequate functioning. These definitions have attracted many criticisms, such as the concept of biological disadvantage is too vague and that it is seldom possible to demonstrate that a difference in behavior affects fertility or mortality. Critics emphasize that defining as abnormal anything that does not function according to its design is useful in instances of somatic illness; however, it is less helpful in behavior disorders because the function of many behavior pattern is unknown.

These criticisms, which reflect the fact that the problem of measuring adaptation in the study of human behavior has proven to be difficult, may be addressed in the following ways: (1) The achievement of short-term biological goals is a valid measure of behavioral adaptation; and (2), the assessment of functional capacities is

the best predictor of future goal achievement [5, 9]. The focus on functional capacities and short-term biological goals allows clinicians to make cross-sectional functional assessments of individual patients which would be impossible to make by applying the lifetime criteria of fertility and mortality. In addition, it excludes from the category of mental disorders those conditions that involve the failure to achieve ultimate biological goals even if a person's functional capacities are intact (e.g., infertility due to rational use of birth-control measures).

Being based on the most recent theoretical advances of evolutionary psychology with its emphasis on evolved psychological mechanisms rather than on longevity and fertility, Wakefield's definition of mental disorder as "harmful dysfunction" is extremely similar to the one proposed here. However, there is an important difference. Wakefield [25] argues that "disorder cannot be simply identified with the scientific concept of inability of an internal mechanism to perform a naturally selected function. Only dysfunctions that are socially disvalued are disorders." (p. 384). We disagree because the reference to social values reintroduces the risk of cultural relativism in the definition of mental disorder, a long-standing problem in the history of psychiatry. In our opinion, the important question raised by Wakefield (i.e., that clinicians should be interested only in those functions that people care about and need within the current social environment) can be adequately addressed by distinguishing between diagnosis of mental disorder and need for treatment, as explained in the next section.

Clinical and social issues

We wish to conclude with a note of clarification about the clinical and social implications of the ideas expressed in this article. A major problem with the application of evolutionary theory to human behavior is the risk of misinterpretation. In the field of ethics and morality, the term naturalistic fallacy has been used to denote the erroneous translation of evolutionary explanations of human behavior into normative or prescriptive terms. The naturalistic fallacy consists in offering some supposedly neutral descriptive statement about what is allegedly natural, as if it could by itself entail some conclusion about what is in some way commendable. The risk of committing the naturalistic fallacy is high when the Darwinian concept of mental disorder is used to decide what conditions should be treated.

A correct application of evolutionary knowledge should not necessarily lead to the conclusion that therapeutic intervention should be limited to mental and behavioral conditions that jeopardize biological adaptation. In contemporary medicine, many therapeutic interventions address problems that are not diseases but that are associated with subjective suffering or undesirable consequences. Cosmetic surgery and anti-aging therapies are just two examples. It is unrealistic to think that psychiatry will remain extraneous to this process that is changing cultural expectations toward medical therapies. Because one of the basic aims of medicine is to alleviate human suffering, an understanding of the evolutionary foundations of the concept of mental disorder should translate into more effective ways for promoting individual and social well-being, not into the search for natural laws determining what is therapeutically right or wrong.

However, Darwinian psychiatry dictates some ethical rules that the reflecting clinician should follow to minimize the risk of inappropriate interventions. The patient should take the decision to be treated on the basis of detailed information concerning the possible adaptive significance of his/her symptoms and their evolutionary origin. In addition, patients who seek treatment for undesirable psychological or behavioral traits that are not pathological should be warned of not confusing medical intervention with medical diagnosis (similarly to what happens today to persons who seek surgical correction for undesirable physical traits). It is not a contradiction that a clinical psychiatrist embracing the Darwinian view of mental disorder informs the patient that his/her condition is not a true mental disorder and, at the same time, accepts to help the patient with the therapeutic means that are used to treat true psychopathologies. Redefining an undesirable condition as a normal variant is more than an academic exercise. Labeling a psychological or behavioral condition as sick may have serious individual and social consequences, including self-reproach and social stigmatization. Since a major contribution of Darwinian psychiatry is the insight that diversity and individual differences are core evolutionary features of any animal species, including *Homo sapiens*, the clinician should share such an information with the patient, not underestimating its reassuring and emancipating potential.

REFERENCES

1 Regier DA, Myers JK, Kramer M, Robins LN, Blazer DG, Hough RL *et al*. The NIMH Epidemiologic Catchment Area program: historical context, major objectives, and study population characteristics. Arch Gen Psychiatry 1984; **41**:934–941.
2 Kessler RC, McGonagle KA, Zhao S, Nelson CB, Hughes M, Eshleman S *et al*. Lifetime and 12-month prevalence of DSM-III-R psychiatric disorders in the United States. Arch Gen Psychiatry 1994; **51**:8–19.
3 Frances A. Problems in defining clinical significance in epidemiological studies. Arch Gen Psychiatry 1998; **55**:119.
4 Spitzer RL. Diagnosis and need for treatment are not the same. Arch Gen Psychiatry 1998; **55**:120.
5 McGuire MT, Troisi A. Darwinian psychiatry. New York: Oxford University Press; 1998.
6 McGuire MT, Troisi A. Evolutionary biology and psychiatry. In: BJ Sadock, VA Sadock, editors. Kaplan & Sadock's comprehensive textbook of psychiatry, VII ed., vol. 1. Philadelphia: Lippincott Williams & Wilkins; 2000. pp. 484–492.
7 Boorse C. On the distinction between disease and illness. Philosophy and Public Affairs 1975; **5**:49–68.
8 Hesslow G. Do we need a concept of disease? Theor Med 1993; **14**:1–14.
9 Troisi A, McGuire MT. Evolution and mental health. In HS Friedman, editor. Encyclopedia of mental health, vol. 2. San Diego: Academic Press; 1998. pp. 173–181.

10 Taylor FK. The medical model of the disease concept. Br J Psychiatry 1976; **128**:588–594.
11 Wulff HR, Andur Pedersen S, Rosenberg R. Philosophy of medicine: An introduction. Oxford: Blackwell; 1986.
12 American Psychiatric Association. Diagnostic and statistical manual of mental disorders, Fourth Edition (DSM-IV). Washington, DC: American Psychiatric Association, 1994.
13 McGuire MT, Troisi A, Raleigh MM. Depression in evolutionary context. In S Baron-Cohen, editor. The maladapted mind: Classic readings in evolutionary psychopathology. Hove, UK: Psychology Press; 1997. pp. 255–282.
14 Nesse RM. Is depression an adaptation? Arch Gen Psychiatry 2000; **57**:14–20.
15 Troisi A, McGuire MT. Evolutionary biology and life events research. Arch Gen Psychiatry 1992; **49**:501–502.
16 Troisi A. Gender differences in vulnerability to social stress: A Darwinian perspective. Physiol Behav 2001; **73**:443–449.
17 Regier DA, Kaelber CT, Rae DS, Farmer ME, Knauper B, Kessler RC *et al*. Limitations of diagnostic criteria and assessment instruments for mental disorders: Implications for research and policy. Arch Gen Psychiatry 1998; **55**:109–115.
18 Panksepp J. Affective neuroscience. The foundations of human and animal emotions. New York: Oxford University Press; 1998.
19 Nesse RM. Evolutionary explanations of emotions. Hum Nature 1990; **1**:261–289.
20 Nesse RM, Berridge KC. Psychoactive drug use in evolutionary perspective. Science 1997; **278**:63–66.
21 Olds J, Milner P. Positive reinforcement produced by electrical stimulation of the septal area and other regions of rat brain. J Comp Physiol Psychol 1954; **47**:419–427.
22 Troisi A. Harmful effects of substance abuse: a Darwinian perspective. Funct Neurol 2001; **16**:237–243.
23 Cohen H. The evolution of the concept of disease. In AL Caplan, HT Engelhardt, Jr., JJ McCartney, editors. Concepts of health and disease: Interdisciplinary perspectives. Reading, MA: Addison-Wesley; 1981. pp. 209–220.
24 Kendell RE. The role of diagnosis in psychiatry. Oxford: Blackwell; 1975.
25 Wakefield JC. The concept of mental disorder: On the boundary between biological facts and social values. Am Psychologist 1992; **47**:373–388.
27 Setchell JM, Dixson AF. Arrested development of secondary sexual adornments in subordinate adult male mandrills (*Mandrillus sphinx*). Am J Phys Anthropol 2001; **115**:245–252.
26 Futuyma DJ. Evolutionary Biology, 2nd edn. Sunderland, MA: Sinauer Associates, Inc.; 1986.
28 Maggioncalda AN, Czekala NM, Sapolsky RM. Growth hormone and thyroid stimulating hormone concentrations in captive male orangutans: implications for understanding developmental arrest. Am J Primatol 2000; **50**:67–76.
29 Maggioncalda AN, Sapolsky RM, Czekala NM. Reproductive hormone profiles in captive male orangutans: implications for understanding developmental arrest. Am J Phys Anthropol 1999; **109**:19–32.
30 Galdikas B. Adult male sociality and reproductive tactics among orangutans at Tanjung Puting. Folia Primatol 1985; **45**:9–24.
31 Mealey L. The sociobiology of sociopathy: An integrated evolutionary model. Behav Brain Sci 1995; **18**:523–599.
32 Troisi A, McGuire MT. Deception and somatizing disorders. In CN Stefanis, AD Rabavilas, CR Soldatos, editors. Psychiatry: A world perspective, vol. 3. Amsterdam: Excerpta Medica; 1991. pp. 973–978.
33 Sroufe LA. The role of infant-caregiver attachment in development. In J Belsky, T Nezworski, editors. Clinical implications of attachment. Hillsdale, NJ: Erlbaum; 1988. pp. 18–38.
34 Belsky J. Modern evolutionary theory and patterns of attachment. In J Cassidy, PR Shaver. Handbook of attachment: Theory, research, and clinical applications. New York: The Guilford Press; 1999. pp. 141–161.
35 Virchow R. Hundert Jahre Allgemeiner Pathologie. Berlin: August Hirschwald; 1895.
36 Schneider K. Klinische Psychopathologie (3rd edn). Stuttgart: Thieme; 1950.
37 Szasz TS. The myth of mentall illness. Foundations of a theory of personal conduct (rev. ed.). New York: Harper & Row; 1974.
38 Ludwig AM. The psychiatrist as physician. J Am Med Ass 1975; **234**:603–604.
39 Guze SB. Why psychiatry is a branch of medicine. New York: Oxford University Press; 1992.
40 Andreasen NC. The validation of psychiatric diagnosis: New models and approaches. Am J Psychiatry 1995; **152**:161–162.
41 Detre T, McDonald MC. Managed care and the future of psychiatry. Arch Gen Psychiatry 1997; **54**:201–204,.
42 Schwartz JM, Stoessel PW, Baxter LR, Martin KM, Phelps ME. Systematic changes in cerebral glucose metabolic rate after successful behavior modification treatment of obssessive-compulsive disorder. Arch Gen Psychiatry 1996; **53**:109–113.
43 Pardo JV, Pardo Pj, Raichle ME. Neural correlates of self-induced dysphoria. Am J Psychiatry 1993; **150**:713–719.
44 Harrison PJ, Everall IP, Catalan J. Is homosexual behaviour hard-wired? Sexual orientation and brain structure. Psychol Med 1994; **24**:811–816.
45 Marazziti D, Akiskal HS, Rossi A, Cassano GB. Alteration of the platelet serotonin transporter in romantic love. Psychol Med 1999; **29**:741–745.
46 Raine A, Buchsbaum MS, Stanley J, Lottenberg S, Abel L, Stoddard J. Selective reductions in prefrontal glucose metabolism in murderers. Biol Psychiatry 1994; **36**:365–373.
47 Scadding JG. Diagnosis: the clinician and the computer. Lancet 1967; **2**:877–882.
48 Klein DF. A proposed definition of mental illness. In RL Spitzer, DF Klein, editors. Critical issues in psychiatric diagnosis. New York: Raven Press; 1978. pp. 41–71.

Neuroendocrinology Letters Special Issue, Suppl.4, Vol.23, December 2002
Copyright © Neuroendocrinology Letters ISSN 0172–780X **www.nel.edu**

REVIEW ARTICLE

Psychopathology or Adaptation? Genetic and Evolutionary Perspectives on Individual Differences and Psychopathology

Charles Crawford & Catherine Salmon

Correspondence to: Charles Crawford PhD *or* Catherine Salmon PhD
Department of Psychology
Simon Fraser University
Burnaby, B.C. V5A 1S6, CANADA
PHONE: +1 (604) 291-3660
FAX: +1 (604) 291-3427
EMAIL: crawford@sfu.ca

Submitted: *August 8, 2002*
Accepted: *September 9, 2002*

Key words: **evolutionary psychology; adaptation; genetics; environment; psychopathology**

Neuroendocrinology Letters 2002; ***23****(Suppl.4):39–45 pii: NEL231002R04* *Copyright © Neuroendocrinology Letters* ***www.nel.edu***

Abstract A greater understanding of psychopathology will be found in the integration of genetic and evolutionary perspectives on adaptation and function. Evolutionary theory proposes that adaptive traits are reproduced more successfully than maladaptive ones. However, some traits, while contributing to fitness in the ancestral environment, may contribute to fitness no longer. This is known as mismatch theory. Evolutionarily informed research into various "pathologies" has yielded interesting results, some based on this theory. This paper serves to distinguish between genetic and evolutionary perspectives on psychopathology as well as to examine some recent research on the selective forces that may be implicated in psychopathy, anorexic behavior, and ADHD. We suggest that research into psychopathy in general would benefit from an evolutionary perspective and an examination of the assumptions behind past research.

Of all the facts of life, the most important is evolution. If psychology is to take its legitimate place among the family of life sciences, it must eventually integrate its basic theories and facts with those of evolution. If we are to understand abnormal behavior, we must do so in the context of a psychology so conceived and so formulated.

Rosenthal [1]

Introduction

This powerful statement, used by David Rosenthal to introduce one of the classic books on psychopathology and genetics, emphasizes the importance of the theory of evolution for understanding both normal and abnormal behavior. But after the introductory chapter, there is very little about evolution in his book. Important concepts such as fitness, stabilizing selection, preadaptation, or speciation appear neither in the glossary nor the index. The concept of adaptation, which Rosenthal [1] defines as "the adjustment of an organism or population to an environment", which is essential to understanding the role of natural selection in the shaping of anatomy, physiology, and behavior, is given only cursory treatment.

Genetic Theory and Abnormal Behavior is exactly what its title suggests it is – a book on genetics and human psychopathology. As such, it is an excellent book, but why did Rosenthal introduce it with a statement about Darwin's theory of evolution by natural selection if evolutionary theory was not to play an important part in it? He apparently assumed that since the science of genetics is concerned with the transmission of hereditary information from generation to generation, and that since the theory of evolution depends on the transmission of hereditary information from generation to generation, that therefore, the genetic and evolutionary perspectives on psychopathology are synonymous. Many psychologists, anthropologists, sociologists, and biologists seem to share this view. It is a view that is incorrect. Moreover, it is a view that has retarded the development of bio-cultural explanations of human psychopathology.

When evolutionary theory is applied to current human behavior, we are concerned, not with the processes of natural selection, but with adaptations, the products of natural selection. In this article, we will take a brief look at the genetic perspective, followed by a review of the evolutionary approach and some current evolutionarily informed research on psychopathology. Our focus is on how evolutionary theory can be used to understand how the products of evolution function in the current environment. Readers desiring additional reading on evolution by natural selection should consult extensive reviews, such as Williams [2], or Buss [3].

The Genetic Perspective

The science of genetics is concerned with how hereditary information encoded in DNA is transmitted from generation to generation, and how that information is involved in the development of the anatomy, physiology, and behavior of individuals. The search for the genetic components of a pathology usually begins with the search for a single locus or chromosome effects. The objective is: (1) to discover the mode of inheritance (dominant, recessive, sex-linked, etc.), (2) to describe the details of the metabolic pathway, (3) to explain its disruptive effect on physiological and anatomical development, and finally, (4) to show how the abnormalities of development affect behavior. Using precisely controlled breeding experiments on non-human animals, geneticists have done a magnificent job of elucidating the principles of the hereditary transmission of information. Progress has been much slower with humans because experimental crosses cannot be performed, environmental control cannot be imposed, the generation interval is relatively long, and the number of offspring per family is small [4]. When Mendel's laws don't work, geneticists may postulate gene-environment interactions or the actions of genes at multiple loci.

The Evolutionary Perspective

Evolutionary theory is concerned with the evolution of species-typical traits, traits that are shared by all members of a species. It thus seems that evolutionary theory may have little practical value in explaining how or why different types of behavior occur. But an explication of the concept of adaptation reveals how the theory of evolution by natural selection can provide some powerful concepts for understanding the role of the environment in producing individual differences in general, and in normal and abnormal behavior in particular.

Biological adaptations that enabled our relatively recent ancestors to deal with their environment must now help us deal with an environment that may differ in many ways from the Pleistocene environment where *Homo Sapiens*' adaptations were shaped. In most cases, these adaptations are adequate. If they were not, our species would be extinct. In some cases, however, their operation may result in behaviors that are maladaptive or even pathological when viewed in the present context. In other words, there may be mismatch between adaptations and their environments.

It must be emphasized that it is not necessary to assume that a behavior is currently adaptive in order to use the theory of evolution by natural selection to help understand it. However, if the theory of evolution is to be used in developing explanations of human behavior, then it must be assumed that adaptations that evolved in prehistoric times can still affect our behavior in some way [5].

Adaptation and natural selection are the central ideas of evolutionary theory. An adaptation is any anatomical structure, physiological process, or behavior pattern that contributed to an ancestral individual's ability to survive and reproduce in competition with other members of its species [6]. The teeth of lions, the hooves of horses, the hands of humans, the cub killing behavior of male lions [7], and love in humans [3] provide examples of adaptations that evolved through natural selection.

Behavioral Adaptation

The mating behavior of male scorpionflies (Figure 1) provides a very instructive example of a behavioral adaptation. Males have three strategies for acquiring a mate [8]. A male may find a dead insect, present it to a female and copulate with her while she eats it. If he

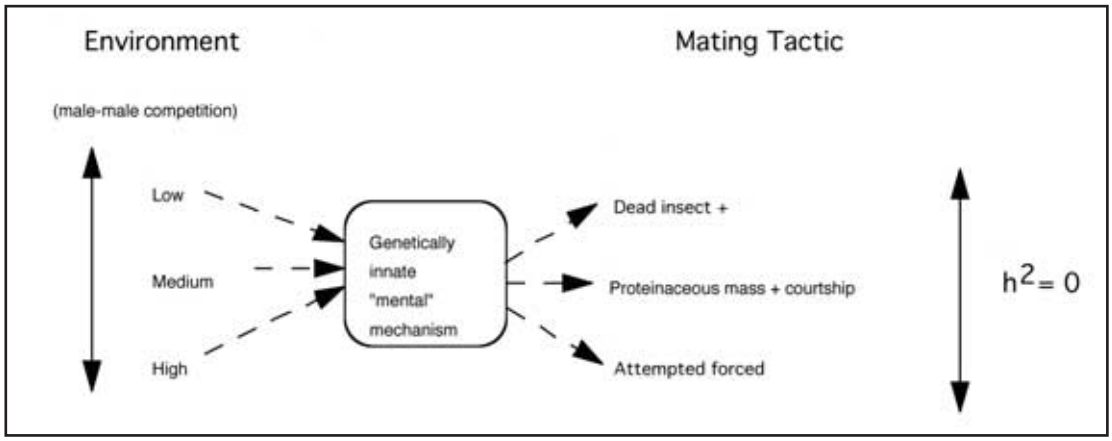


Figure 1: Mating tactics in scorpionflies (*Panorpa sp.*). The level of male-male competition determines the reproductive tactic used. Heritability of the tactics is zero because all males have alleles for all tactics. From "The Theory of Evolution: Of What Value to Psychology?" by C.B. Crawford, 1989. Copyright © 1989 by the American Psychological Association. Adapted with permission.

cannot obtain a dead insect, he may produce a proteinacious mass and feed it to the female and copulate with her as she eats it. Males who cannot obtain an insect or produce the proteinacious mass attempt to copulate forcibly with females. Males also possess an organ that assists them in forcible copulation, helping to restrain an unwilling female. It is not necessary when females are willing.

Thornhill [8] has shown that the strategy employed depends on a male's success in male-male competition. Even dominant males become vigorous forcible copulators if their resources are restricted. The alternate mating tactics of the male scorpionflies are an example of concurrently contingent behavioral programs [9]. Species-typical genetic information, in conjunction with information from the current environment, determines which tactic from a limited repertoire of tactics is produced. In other words, the expression of mating tactics in scorpionflies is contingent on environmental conditions.

Adaptations as Sets of Decision Rules

From a scientific view, an adaptation can be described in terms of a set of decision rules that enabled an ancestral individual to deal with contingencies in its environment. These decision rules are assumed to be instantiated in the neural hardware [10] and can be conceptualized as managing the activities of the organism. But if the rules that are instantiated in the neural hardware were shaped by natural selection, then they can only be changed by natural selection. Since natural selection can only change the frequencies of alleles that code for proteins, we can not consider these rules as completely independent of the physiology in which they are instantiated.

Although most psychologists are willing to admit that physical features and processes may have been shaped by natural selection, they are often reluctant to admit that mental processes are the result of ancestral selection pressures. Although cognitive science and the computer model currently provide the paradigm that most psychologists employ in their work, the assumption of the tabula rasa, the general problem solver, remains dominant. However, this view is untenable if we assume that human beings evolved by natural selection [11, 12]. These authors argue that the theory of evolution requires that the human mind is a highly structured and organized organ that evolved to deal with Pleistocene environmental conditions. From an evolutionary perspective, the mind is a collection of specific mechanisms that each contribute to solving the problems facing it, in the same way that a collection of specific mechanisms is necessary to the digestive functioning of the stomach.

Possible Outcomes when Natural Selection Meets Genetic Variation

There are four possible outcomes from the interaction of natural selection with genetic variation. Imagine that there is an ancestral adaptation X in which there is genetic variation. Natural selection acts upon it. The two possible affects of selection are that a) variability in X is exhausted or b) variability in X is not exhausted. As a result, there are four possible remaining genetic influences on the development of X. If variability in X has been exhausted, development could be freed from genetic influences or genetic influences on development could remain. If variability in X is not exhausted, genetic variation remains and could affect X's functioning or genetic variation remains but it not related to X's functioning.

In general, natural selection acts to eliminate genetic variance. But if variability is exhausted, how likely is it that development is completely freed of genetic influences? This is the tabula rasa, or blank slate, view, and in many ways it is quite unsatisfactory. Imagine a tabula rasa creature living in a variable environment. There are many problems that it will face and solutions to these problems must be learned in order to survive and reproduce. Organisms whose brains make them somewhat prepared to learn something may survive better than those not prepared to learn these things. For example, eating rotten meat can lead to disease and death. It would be adaptive to learn very quickly

that meat with a certain smell or appearance should be avoided. Individuals who were predisposed to avoid certain smells or those that could easily learn to avoid them would have had a better chance of surviving.

It seems more likely that when variability is exhausted, genetic influences on behavior remain. Under such conditions, there would be zero heritability for a trait. This could also be referred to as the pure innate view, the trait will always be expressed. Examples might be that humans all have two eyes, or that scorpionsflies all have the same set of mating strategies, but express them variably depending on the environment they find themselves in. But in fact, empirical evidence suggests that some genetic variation almost always exists [4]. Which raises the question of why such variation exists if natural selections acts, in general, to eliminate it. Many have suggested that the answer is parasites. Or rather parasite protection [13].

Genetic Variation and Evolution

The science of genetics is concerned with how gene differences are involved in the production of phenotype differences. Without these heritable differences in fitness related traits, natural selection cannot shape or change adaptations. Thus, for an adaptation to come into existence, there must have been genetic variation with respect to that adaptation in the ancestral population in which it evolved. However, genetic variation need not remain once the adaptation has been formed. Tooby and Cosmides [10] have argued that genetic variation may, in fact, disrupt the functioning of an adaptation, and therefore, that genetic variation associated with an adaptation should be the exception rather than the rule. They argue that most genetic variation is not related to the adaptiveness of the organ that manifests it, but that it is the result of selection to vary the structure of the organ at the protein level to help the organism to avoid the attacks of parasites.

Consider the following problem. Suppose it was found that identical twins raised in markedly different environments differ as adults on a particular trait, such as extroversion-introversion. Can this finding be interpreted as meaning that genes are not acting on the development of the trait?

To provide an answer, consider the behavior of identical triplet male scorpionflies reared in three different environments. The first triplet is raised in an environment with many dominant males. Since he loses in male-male competition, he attempts to copulate forcibly with females. The second triplet is raised in an environment with moderate male-male competition. Although he is not successful enough to obtain a dead insect to use as a nuptial gift, he can obtain enough resources to generate the proteinacious mass to attract a willing female. The third triplet is reared in an environment populated by subordinate males. He obtains a dead insect and uses it in his courtship. If the heritability of male courtship behavior were computed, it would be zero because the scorpionflies are genetically identical triplets, and therefore all variation between their behaviors is environmental in origin. However, the behavior employed within each environment is determined genetically.

Although gene differences do not produce the differences in behavior, the genes that all scorpionflies possess, in conjunction with varying environmental conditions, determine the behavior that is expressed. The primary focus of the evolutionary perspective is on the genetic architecture that all members of a species possess that guides the development of the adaptations enabling them to interact successfully with their environment.

From an evolutionary perspective, the critical question is not whether the observed behavioral differences are associated with genetic differences, but whether they are correlated with reproductive success in the environment in which they are observed, or if the environment of the species has changed, the environment in which they evolved. An understanding of evolutionary ecology is leading us to a new kind of environmentalism: all individuals in a given species may have genes for a number of strategies, and the one used depends on the environmental conditions encountered [14]. Such a perspective focuses attention on traits: (1) that have zero or low heritability, (2) that were closely related to reproductive function in an ancestral environment, and (3) for which sensitivity to environmental conditions would have been adaptive in an ancestral population.

There are two reasons for the interest in traits with low or zero heritability. First, such traits are likely to have been important in the ancestral environment. If a trait was important in mediating survival, growth, and/or reproduction, it is likely that natural selection would have acted strongly on it, and thereby eliminated most of its additive genetic variance [15]. Second, by focusing on traits with minimal genetic variation, it is possible to get a clearer picture of how variations in these traits are involved in facilitating the organism's interactions with varying environmental conditions. Just as geneticists are interested in reducing the effects of environmental variation so that they can more clearly discern the rules governing the transmission of genetic information, those involved in the study of adaptation are interested in reducing the genetic differences between individuals so that they can more easily perceive how a putative adaptation enables its possessor to deal with varying environmental conditions. For example, Baker and Bellis [16] are unraveling the exquisite way that the human female manages sperm in response to a variety of contingencies.

The focus on traits closely related to reproductive function is because the costs of ancestral reproduction would have been very high, and naturally, natural selection is likely to have shaped adaptations for adjusting it to varying conditions in the environment. The focus on traits that were sensitive to variations in ancestral circumstances is because such traits are also likely to be sensitive to present environmental circumstances. They are therefore traits that can help us to understand how we deal with current environmental contingencies.

Finally, evolutionary psychologists are interested in innate behavioral mechanisms that produce differences in behavior as a function of differing environmental circumstances. Although genetic variation is essential for the evolution of adaptations, it is not essential to the functioning of the adaptation once the adaptation has been produced [10].

Psychopathology as Disease or Adaptation?

One can think of two views of psychopathology. According to one, psychopathology is due to non-adaptive errors, breakdowns, or malfunctions. According to the other, psychopathology may represent the activation of (previously) adaptive strategies. An evolutionary approach points out that, based on natural selection, traits are selected, not on the basis of arbitrary definitions of happiness, well-being, or social conformity, but by their effects on reproduction rates in subsequent generations. Evolutionary explanations and theories have been advanced for many "pathologies" including: mood disorders [17, 18], psychopathy [19, 20], and rape [21]. Nesse and Williams [22] note that diseases and disorders can be perpetuated by genes that have been retained by natural selection either because their effects were beneficial in ancestral environments (fondness for sweets and diabetes) or because the same genes that influence the disease have benefits in some other sphere (sickle-cell anemia and protection against malaria).

The decision rules discussed previously can be seen as the means by which goals are achieved. They are context dependent and entrained to the presence or absence of certain signals. Their flexibility and signal dependence helps individuals to avoid pursuing goals that cannot be obtained or would decrease fitness is pursued regardless of cost [23]. Not only are many sets of decision rules designed to be flexible, but this flexibility is subject to developmental influences. For example, adverse rearing experiences can significantly affect maturation and functioning [24, 25]. As children mature in certain environments, some behavioral strategies will become elaborated while others will be less developed into the individual's personality [26]. A child whose parents are unresponsive to distress may learn that others are unreliable and focus on self-reliance, while a boy who grows up in an environment surrounded by individuals with low life-expectancy may become a risk-prone individual, discounting his future.

Psychopathology and Developmental Instability

Gangestad, Yeo and colleagues [27] have explored the idea of a link between developmental instability and schizophrenia. They define developmental instability as the imprecise expression of a genetic plan for development due to the introduction of developmental noise and suggest that it contributes to individual variations in handedness, functional hemispheric asymmetries for cognitive tasks, and cortical asymmetries. Lalumiere and colleagues [20] have also used developmental instability in focusing on psychopaths.

Psychopaths are deceitful, selfish, manipulative, irresponsible, impulsive and aggressive individuals who have no concern for the welfare of others and experience little remorse or guilt as a result of their antisocial behavior [28]. Compared to other criminals, the crimes psychopaths commit are more goal-oriented and violent. Their behavior has an early onset in life and while they tend to exhibit less cerebral lateralization than nonpsychopaths, there is no evidence of lesions or brain damage [29]. This appears to be a trait in which genetic variation remains and affects development under certain conditions.

There are two views on the development of psychopthy. The first, psychopathy as psychopathology, sees it as a serious personality disorder, a brain-based pathology, or a virulent strain of conduct disorder, [30, 31]. According to this view, the development of psychopathic individuals has been disturbed so that they are unable to experience moral sentiments such as empathy or remorse, cannot appreciate the consequences of their actions and therefore cannot behave in prosocial ways.

The second view is one particularly informed by evolutionary psychology. It is psychopathy as special design [20]. This view is that psychopaths are different by design, not as a result of a deficit. Instead, the behavioral, emotional, cognitive and neuropsychological characteristics of psychopaths are seen as a set of organized, functional and specialized features that formed a viable reproductive social strategy during human evolutionary history. Harpending and Sobus [32] used game theory research to demonstrate that a cheater (nonreciprocator) could achieve reproductive success when: cheaters are difficult to detect, highly mobile, verbally skilled, and skilled at persuading females to mate. Quinsey, Harris, Rice and Cormier [33] have suggested that "psychopathy can be considered to be a life-history strategy consisting of short-term mating tactics, an aggressive and risky approach to achieving social dominance, and frequent use of nonreciprocating and duplicitous tactics in social exchange." These ideas suggest that the defining features of psychopaths are not pathological outcomes of impaired development but instead features of an adaptation designed to thrive in an interpersonal environment dominated by social cooperators.

Lalumiere *et al*. [20] used the concept of developmental instability to examine whether adult psychopathy is the result of pathological or non-pathological development. They looked for signs of developmental perturbations in non-psychopathic and psychopathic offenders and measured fluctuating asymmetry (random deviations from bilateral symmetry) or FA in psychopathic and non-psychopathic offenders as well as non-offenders. The psychopathic offenders showed less evidence of developmental instability than non-psychopathic offenders. Interestingly, the psychopathic offenders had higher FA than non-offenders except for offenders who met the highest psychopath criterion. Those psychopaths had the lowest FA measures of all.

Anorexic Behavior and Reproductive Suppression

Understanding the ultimate causation of a psychological phenomenon can enrich proximate hypotheses, suggesting whole new areas of related inquiry. For example, Polivy & Herman [34] present a model of the proximate causation of several eating disorders, which involves cognitive cues overriding the normal physiological cues of satiety and hunger. This is hypothesized to occur in response to strong societal pressure to be thin. It is an elegant model but leaves unanswered the following questions: 1) What is it about industrialization that encourages a thin standard of beauty? 2) Why do some girls progress to levels of emaciation far thinner than the accepted standard of beauty? 3) Why do we not see "pathologies" associated with other aspects of attractiveness (pathological drives for shiny thick hair, etc.) and 4) What environmental variables are likely to drive the passion for a thin form?

The reproductive suppression hypothesis (RSH) answers these questions. Industrialization is particularly problematic for the reproductive prospects of adolescent girls because it is associated with early menarche and a long period before marriage during which girls may receive attention from large numbers of young men without much adult supervision. Thus, sexual activity is difficult to avoid though pregnancy is very costly. Therefore, most girls experience a desire for thinness related unconsciously to the need to slow down their rate of sexual maturation. As well, individual girls in industrialized societies may experience menarche even earlier than their peers, or lack the social skills appropriate for their age, so that they experience the reproductive stresses even more strongly [35]. As for "pathologies" associated with other aspects of beauty, we do not see them because only fatness is directly linked to fertility.

Finally, the RSH [36, 37] enables us to make predictions about two types of environmental variables associated with the desire for thinness. First, environmental stressors that would have made reproductive suppression adaptive in an ancestral population are likely to be associated with the desire for thinness, such as high female competition or unwanted male attention. Second, any current environmental variable, such as a rich diet, that lengthens the period between sexual maturity and social, intellectual, and emotional maturity brings girls into situations in which they are likely to become pregnant without the adequate resources to raise a child. Unconscious perception of such a situation is also hypothesized to activate the reproductive suppression mechanisms and, hence, a desire for thinness. The mechanism itself has no genetic variation, but there is variation in susceptibility, due perhaps to a combination of genetic variation and environmental influences.

ADHD as a Disorder of Adaptation

Some mental disorders can be viewed as an adaptive response to early pathogenic environments (trauma or neglect) while others reflect the optimization of brain function to some (often early) environments at the cost of poorer response to the demands of other environments [38]. As a result, symptomatic descriptions, as in the DSM-IV, ignore the importance of adaptation in general and, in particular, disregard the shaping of human brains and behaviour by experience [39].

ADHD (attention-deficit/hyperactivity disorder) is characterized by three general symptoms: inattention, hyperactivity, and impulsivity. ADHD may reflect the effects of maternal smoke exposure in utero, brain injury, child abuse, or a combination of environmental experiences coupled with predisposing genes. But an evolutionary model of ADHD may be better able to explain discrepant findings in the literature, provide testable hypotheses, and clarify the relationship between health and disease.

What adaptive problems might these traits have been designed to solve in an ancestral environment?

Ancestral environments would have varied in several characteristics relevant to ADHD, including safe versus not safe, resource-rich versus impoverished, and time-optional versus time-critical [38]. At one extreme environment, human survival would have depended on being, hypervigilant, rapid-scanning, quick to pounce or flee, and motorically hyperactive (foraging, etc.), a response-ready individual. This type of individual would have been advantaged under the harsh conditions of the frozen steppe or humid jungle. However, not all environments would be that harsh, and as societies have become more industrialized and organized, the advantage has moved towards those who display problem-solving and analytic strategies, restraint of impulsivity, and the controlled deployment of energies, a problem-solving individual. Genetic variation in the trait remains in the population and affects the development of this behavior.

This has serious implications for our school system which provides an environment that favors the problem-solving child. Alterations in the environment may reduce the adaptive strain on a child's nervous system whose set point may be at the other extreme from the environment they find themselves in. Further study, including cross-species comparisons of the traits, is needed on the individual components of ADHD (attention, motor activity, and impulsivity) and how they may be beneficial in some settings while non-adaptive in others.

Conclusions

In many ways, it is difficult, and yet important, to integrate genetic and evolutionary perspectives. The genetic perspective focuses on a constant environment, examining genetic variation, as opposed to evolutionary psychology holding genes constant, looking at the impact of the environment. But both views are crucial to a complete understanding of psychopathology. One can see anorexic behavior as a single life history, all women possess the reproductive suppression mechanism but it is only activated in some women who encounter exaggerated ancestral cues and who may also have some type of personal susceptibility. ADHD and

psychopathy are examples of multiple life history strategies in which two genetic strains exist. In the case of ADHD this genetic variation has likely been maintained by different environments, though it is likely that the ADHD strain will decrease over time in our more "problem solving" modern world. On the other hand, the psychopathy life history may actually be increasing. In general, it is only a successful strategy when there are very few in the population, but in our highly mobile big city world, they have advantages they never would have had in small face-to-face populations. We hope that an evolutionary perspective will continue to shed more light on the ultimate causes of various psychopathologies and assist in their management.

REFERENCES

1 Rosenthal D. Genetic theory and abnormal behavior. New York: McGraw-Hill; 1970.
2 Williams GC. Adaptation and natural selection. Princeton, NJ: Princeton University Press. 1966.
3 Buss DM. Evolutionary Psychology: The New Science of the Mind. Needham Heights, MA: Allyn & Bacon. 1999.
4 Plomin R, DeFries JC, McClearn GE. Behavioral genetics: a primer (2nd ed.). New York: Freeman. 1990.
5 Alexander RD. Darwinism and human affairs. Seattle: University of Washington Press. 1979.
6 Wilson EO. Sociobiology: the new synthesis. Cambridge, MA: Harvard University Press. 1975.
7 Schaller G. The Serengeti lion: a study of predator-prey relations. Chicago: University of Chicago Press. 1972.
8 Thornhill R. *Panorpa* (Mecoptera: Panorpidae) scorpionflies: systems for understanding resource-defense polygyny and alternative male reproductive efforts. Annual Review of Ecological Systems 1981; **12**:355–386.
9 Crawford CB. The theory of evolution: of what value to psychology? Journal of Comparative Psychology 1989; **103**:4–22.
10 Tooby J, Cosmides L. On the universality of human nature and the uniqueness of the individual: the role of genetics and adaptation. Journal of Personality 1990; **58**:17–68.
11 Symons D. If we're all Darwinians, what's the fuss about? In: CB Crawford, M Smith, D Krebs, editors. Sociobiology and psychology: Ideals, Issues and Applications. Hillsdale, NJ: Erlbaum. 1987. p. 121–146.
12 Cosmides L, Tooby J. From evolution to behavior: evolutionary psychology as the missing link. In: J Dupre, editor. The latest on the best: essays on evolution and optimality. Cambridge, MA: MIT Press. 1987. p. 277–306.
13 Ridley M. The red queen: sex and the evolution of human nature. New York: Penguin Books. 1993.
14 Crawford CB, Anderson J. Sociobiology: An environmentalist discipline? American Psychologist 1989; **44**:1449–1459.
15 Falconer D & Mackay F. Introduction to quantitative genetics. Essex: Longman's Group. 1966.
16 Baker RR, Bellis MA. Human sperm competition. London: Chapman & Hall. 1995.
17 Nesse RM. Evolutionary explanations of emotions. Human Nature 1990; **1**:261–289.
18 Price J. The adaptive function of mood change. British Journal of Medical Psychology 1998; **71**:465–477.
19 Mealey L. The sociobiology of sociopathy: an integrated evolutionary model. In: S Baron-Cohen, editor. The Maladapted mind: classic readings in evolutionary psychopathology. Hove: Psychology Press. 1997. p. 133–188.
20 Lalumiere ML, Harris GT, Rice ME. Psychopathy and developmental instability. Evolution and Human Behavior 2001; **22**:75–92.
21 Thornhill R, Palmer CT. A natural history of rape: biological bases of sexual coercion. Cambridge, Massachusetts: MIT Press. 2000.
22 Nesse RM, Williams GC. Evolution and healing: the new science of Darwinian medicine. London: Weidenfeld & Nicolson. 1995.
23 Gilbert P. Evolutionary psychopathology: why isn't the mind designed better than it is? British Journal of Medical Psychology 1998; **71**:353–373.
24 Surbey MK. Anorexia nervosa, amenorrhea, and adaptation. Ethology and Sociobiology 1987; **8**:47S–61S.
25 Rosenblum LA, Coplan JD, Friedman S, Bassoff T, Gorman JM, Andrews MW. Adverse early experiences affect noradrenergic and serotonergic functioning in adult primates. Biological Psychiatry 1994; **35**:221–227.
26 Belsky J. Etiology of child maltreatment: a development analysis. Psychological Bulletin 1993; **114**:413–434.
27 Yeo RA, Gangestad SW, Edgar C, Thoma R. The evolutionary genetic underpinnings of schizophrenia: the developmental instability model. Schizophrenia Research 1999; **39**:197–206.
28 Gacono C. The clinical and forensic assessment of psychopathy: a practitioner's guide. Mahwah, NJ: Erlbaum. 2000.
29 Hart SD, Hare RD. Performance of criminal psychopaths on selected neuropsychological tests. Journal of Abnormal Psychology 1990; **99**:374–379.
30 Hart SD, Hare RD. Psychopathy and antisocial personality disorder. Current Opinion in Psychiatry 1996; **9**:129–132.
31 Lapierre D, Braun CM, Hodgins S. Ventral frontal deficits in psychopathy: neuropsychological test findings. Neuropsychologia 1995; **33**:139–151.
32 Harpending HC, Sobus J. Sociopathy as an adaptation. Ethology and Sociobiology 1987; **8**:63s–72s.
33 Quinsey VL, Harris GT, Rice ME, Cormier CA. Violent offenders: appraising and managing risk. Washington, DC: American Psychological Association. 1998.
34 Polivy J, Herman CP. Causes of Eating Disorders. Annu. Rev. Psychol. 2002; **53**:187–213.
35 Anderson JL, Crawford CB, Nadeau J, Lindberg T. Was the Duchess of Windsor right? A cross-cultural review of the socioecology of ideals of female body shape. Ethology and Sociobiology 1992; **13**:197–227.
36 Wasser SK, Barash DP. Reproductive suppression among female mammals: implications for biomedicine and sexual selection theory. Quarterly Review of Biology 1983; **58**:513–538.
37 Salmon C, Crawford CB, Dane L, Zuberbier O. Reproductive suppression, body image, and dieting: the impact of female competition and stress. In prep.
38 Jensen PS, Hoagwood K. The book of names: DSM-IV in context. Developmental Psychopthology 1997; **9**:231–249.
39 Depue RA, Collins PF, Luciana M. A model of neurobiology-environment interaction. In: MF Lenzenweger, JF Haugard, editors. Frontiers of Developmental Psychopathology. New York: Oxford University Press. 1996. p. 44–77.

REVIEW ARTICLE

Marriage: An Evolutionary Perspective

Glenn E. Weisfeld & Carol C. Weisfeld
Department of Psychology, Wayne State University and Department of Psychology, University of Detroit Mercy, USA.

Correspondence to: Glenn E. Weisfeld, Ph.D.
Department of Psychology
Wayne State University
Detroit, MI 48207, USA
PHONE: 1-313-577-2835
FAX: 1-313-577-7636
EMAIL: weisfeld@sun.science.wayne.edu

Submitted: *September 3, 2002*
Accepted: *September 4, 2002*

Key words: **pair bonding; mate choice; dominance; wealth; divorce; marriage; infidelity; industrialization; extended family; fecundity**

Neuroendocrinology Letters 2002; ***23****(Suppl 4):47–54 pii: NEL231002R05 Copyright © Neuroendocrinology Letters* ***www.nel.edu***

Abstract Marriage is universal, and pair bonding is found in other species too with highly dependent young. So marriage functions as a reproductive social arrangement that traditionally involved the extended family. The sexes are not identical in their biological contributions to children's survival, so they seek somewhat different attributes in a mate. Men seek a young, attractive, sexually faithful bride. Women seek a man who is older, taller, and (as in many other species) socially dominant. Both sexes prefer a kind, healthy, attractive, similar mate who is emotionally attached to them. A spouse who fails to maintain sufficiently high mate value is vulnerable to divorce. Infertility and sexual dissatisfaction predict divorce, as does death of a child, but the more children, the stabler the marriage. Cross-cultural data suggest that cruel or subdominant men (e.g., poor providers) and unfaithful women are prone to divorce. Marriages in which the wife dominates the husband in economic contributions, nonverbal behavior, and decision making tend to be less satisfying. In societies in which wives are economically independent of husbands, divorce rates are high. As women's economic power has risen with industrialization, divorce rates have climbed. Economic and fitness considerations also help explain cultural differences in polygyny, age at marriage, arranged marriage, concern with the bride's sexual chastity, and marriage ceremonies. Other factors also affect marital dynamics, such as state subsidies to families, the sex ratio, and influence of the couple's parents.

The purpose of this article is to present a brief survey of theory and research on marriage. Quale, in her *History of Marriage Systems* [1], characterized this topic as follows:

> This is a worldwide history of marriage systems. It goes back to the earliest generations of human life to seek the roots of why and how human beings came to marry, to form lasting, mutually helpful offspring-raising relationships…(p. xi).

Quale's focus on the raising of offspring is consonant with the evolutionary perspective. Evolutionists have recognized that marriage is a human universal and therefore probably has an evolved basis. This conclusion is confirmed by evidence that hormones play a role in the capacity for amorousness [2, 3]. To understand the function of marriage, evolutionists have noted that other species also form adult male-adult female associations that raise young together. Thus, the function of this pair-bonding behavior was hypothesized to be to raise young with the aid of the father as well as of the mother. Pair bonding evolved to keep the father socially attached to the mother so that he would be positioned to help with parental care and to ensure his paternity of his mate's offspring. This functional hypothesis has been confirmed by the observation that pair bonding tends to occur in species with highly dependent young – young that usually require the efforts of both parents to enhance survival [4]. Indeed, children's development is enhanced in every conceivable way by being raised by both biological parents rather than by any other combination [5]. Children of stepparents are at elevated risk of abuse, neglect, low parental investment, and even homicide [6]. Consistent with the notion that human pair bonding has an evolved basis, hormones contribute not only to maternal care [7–10], but also to paternal care. Men, like males of other pair-bonding mammalian species, undergo a rise in prolactin, which promotes parental care, when their mates are pregnant [11].

This biologically functional approach stands in contrast with the perspective of most social scientists, who view marriage as a social or economic partnership of attempted self-fulfillment. This hedonistic view of marriage is especially prominent among U.S. marriage researchers [12]. A content analysis of recent journal articles on marriage reveals that the leading U.S. marriage journal contained many articles on marital satisfaction, whereas journals that covered marriage, among other topics, in non-Western societies had none at all (Table I). A follow-up additional analysis of the content of Spanish-language marriage journals revealed only one article on marital satisfaction.

We believe that this difference in journal content reflects societal differences in viewing marriage. The U.S. is a highly individualistic society in which personal happiness is of great, even paramount, concern. By contrast, more collectivistic societies consider the family to be a social vehicle for nurturing all family members, not just the children but the married couple's parents as well. The U.S. stands at perhaps the extreme point in stressing individual happiness rather than successful child rearing and harmonious relations within the extended family [1, 13].

The mainstream social science literature on marriage, especially in the U.S., focuses on correlates of marital satisfaction and stability. This literature has led to some important conclusions. Marriages tend to be contracted between neighbors and individuals of similar background. Marital satisfaction and stability are correlated with similarity, income, education, health, sexual satisfaction, sexual fidelity, not being parents before marriage, mutual respect and affection, duration of courtship, and age at marriage [14]. Missing from these conventional analyses is a theoretical explanation for why these factors should be important, and especially of why marriage occurs in all human societies. These analyses are also highly culture-bound. For example, an emphasis on spousal companionship would be of relatively little concern in polygynous marriages, in which there is more interest in reproduction [1]. Another shortcoming is a de-emphasis on sex differences in factors in mate choice and marriage maintenance. But the main limitation seems to be a disinclination to consider biological factors that affect reproductive success. Marriage is a reproductive adaptation. Couples that failed to reproduce successfully would have been selected out, along with their marital values and behavior.

We believe that a cross-cultural, cross-species, functional approach can be fruitful in understanding marriage and the family. By viewing marriage as a form of pair bonding, insight can sometimes be gained into why human couples behave as they do. So we begin with a brief discussion of how marriage evolved. Many scenarios have been offered for this evolutionary transition from the mainly promiscuous proclivities of our chim-

Table I. Content Analysis of Research on Marriage in Five Journals in the 1990s.

Journal Title	Marriage	Marital Satisfaction	Marriage & Extended Family
J of Modern African Studies	30	0	2
Modern Asian Studies	57	0	6
J of Latin American Studies	23	0	2
Comparative Studies in Sociology & History	74	0	6
J of Marriage & the Family	200	148	107

Source: JSTOR

panzee-like ancestors to the pair bonding that arose in the hominid line [e.g., 15, 16]. Suffice it to say for our purposes that human pair bonding became evolutionarily stable because it enhanced certainty of paternity, thereby rewarding paternal effort, and because the labors of husband and wife complemented each other. The husband hunted game and defended the family; the wife gathered plant food and nursed the children. Recently the role of the couple's parents has received attention from functionalists. In traditional cultures, grandparents and other family members provide important support to the parents and grandchildren. This multiplication of caretakers is thought to have been responsible for the unusually low inter-birth interval of humans, their high rate of child survival, and their consequent extraordinary success as a primate species [e.g., 15, 17]. Another recent development is Miller's [18] idea that intelligence and artistic ability were sexually selected in hominids, leading to strong selection pressure for those aptitudes and the appreciation thereof. Miller and others have also suggested that the emotions that surround pair bonding behavior, such as feelings of jealousy and infatuation, offer clues to our hominid mating strategies.

In this article we will attempt a brief evolutionary analysis of these aspects of marriage: criteria of mate choice, occurrence of divorce, variations in marriage across cultures, and modern trends in marriage.

Criteria of Mate Choice

The problem faced by the prospective parent is to find and keep a mate who will contribute maximally to one's own reproduction. However, to attract such a mate, one must offer appealing mate qualities oneself. These considerations help account for the fact that spouses tend to be similar in physical attractiveness, intelligence, and other salient background factors. Presumably, spouses are usually similar in mate value [18, 19]. Spouses also tend to be similar in background factors, thus presumably enhancing compatibility. Courtship consists in part of assessing the degree of similarity, in that less similar couples tend to break up [reviewed in 20].

However, spouses also are similar in seemingly irrelevant but highly heritable traits, such as eye color and height. In order to understand why spouses tend to be genetically similar, it is necessary to note that this is true of other species as well, including some insects, birds, and simians [21]. (Extreme genetic similarity is avoided because of inbreeding depression effects, but moderate similarity is sought.) Consequently, a very general functional explanation must be invoked. Various explanations have been offered. The offspring of moderately similar parents may have especially high fitness. The rate of miscarriage in such marriages is relatively low [22], and cousin marriages sometimes have especially high fertility [23]. This benefit of homogamy (or positive assortative mating) may occur through preservation of adaptive gene combinations. Another possibility is that the offspring of similar, or homogamous, parents will share more genes with the parent, thereby providing a boost in passing on one's genes. A related possibility is that sibling cooperation would be greater with closer consanguinity between siblings. In any case, humans seem to exhibit a preference for mates of moderate genetic similarity in various cultures, including contemporary forager cultures [24]. This preference is mediated in part by pheromones [25] but also by cultural rules of exogamy/endogamy [23]. Sexual aversion to first-degree kin develops through proximity during childhood, and recent data suggest that this aversion may be pheromonally mediated [26].

Some additional mate selection criteria are the same for males and females. Both sexes seek a healthy, reproductively competent, kind mate who is emotionally bonded to them [27]. Full sex differentiation is a sign of reproductive maturity and competence; accordingly, both sexes prefer mates who are somewhat more sexually differentiated than average [28]. Both sexes seek signs of genetic quality, i.e., physical attractiveness.

However, some mate choice criteria differ systematically between the sexes. Ultimately, this is because the sexes contribute somewhat differently to their common offspring. Men seek a young bride, who will have all of her reproductive years ahead of her [27]. Women in traditional societies usually marry about the time fertility begins [28]. Their reproductive value is highest then, and so, presumably, is their mate value. Women, on the other hand, seek a man who is a few years older than they [27]. Men continue to be fertile after their wives have reached menopause, so women need be little concerned with their husband's declining fertility. But why should women prefer an older husband? This preference is actually stronger than men's preference for a younger wife. The usual explanation is that older men are wealthier, and women seek the economic resources of a wealthy man. A more comprehensive explanation may be that age is a sign of social dominance, and women, like females of many other species, seek dominant males. This interpretation is supported by the fact that women seek dominance in men even when dominance is defined in terms other than economic ones. Women tend to prefer a taller, more athletic, more self-assured, socially dominant man who exhibits nonverbal signs of dominance [28]. Dominance is generally a sign of superiority over male competitors and would have been a useful indicator of potential as a provider and protector in hominid evolution, and probably a more compelling indicator than culturally defined and variable indicators of wealth such as ownership of many cattle. However, indications of wealth or earning power presumably came to be sought, and were selected for on a cultural basis. Similarly, industriousness and skill at women's tasks are generally sought in a bride. Marriage is in part an economic partnership, and individuals would be well advised, as they often are by their parents, to seek an economic contributor in a spouse. But marriage is much more than an economic partnership. Economic

resources are important to the success of a marriage, but apparently because they enhance the survival of children. In functional terms, resources are a means to the end of reproductive success.

Marriage Maintenance

Mate choice continues after the marriage begins. Divorce or abandonment is always theoretically possible, and it would pay for spouses to consider that option. The predictors of divorce tend to make adaptive sense and, consequently, resemble the criteria of mate choice. Cross-cultural surveys have identified these factors as important in divorce: infertility, refusing sex, sexual infidelity especially by the wife, cruelty especially by the husband, and economic failure especially by the husband [29]. (Note the close parallels to mate choice criteria such as apparent fertility, kindness, emotional commitment, and male dominance.) In no society can men marry if they cannot afford to do so, and destitute men seldom remain married for long. In most societies studied (e.g., Turkey, the U.S., England, Sweden, Australia), marriages in which the husband is moderately dominant in decision making are happiest [30–33]. Marriages in which the wife dominates the husband in nonverbal behavior when the two interact tend to be the least satisfactory [31, 34, 35]. Perhaps the most objective and truest measure of a mate's desirability is reproductive success itself. Accordingly, infertility is an acceptable grounds for divorce in many cultures, and around the world the likelihood of divorce declines with increasing fecundity [36]. Divorce is also more likely in the event of sexual difficulties, rape [37], or death of a child [38]. Finally, societies in which the labor of husband and wife are interdependent, so that neither could thrive economically without the other, tend to have low divorce rates [39]. In light of this, the modern trends toward obliteration of sex role division of labor and toward purchasing what formerly were domestic services may bode ill for the future of marriage.

The frequency and timing of divorce can also be fruitfully interpreted in functional terms. In traditional societies, divorce is fairly rare – about equal to that in the U.S. in the 1950s [40]. One may seek another spouse, but in doing so, one must expend mate search time that might otherwise be utilized in reproduction. Also, if divorce has occurred after the birth of children, one's mate value has declined and one may have difficulty finding a suitable new spouse; this is especially true for women. Furthermore, parental assistance from the father will be less available, and assistance from a stepparent will probably be much less valuable. Accordingly, divorce disproportionately occurs early in marriage when there are few if any children [41]. The peak in divorce at around four years into marriage [42] may be explained in proximate terms by a waning of infatuation after 2 or 3 years into a romantic relationship [43]. This decline in amorousness may be adaptive in allowing dissolution of a marriage that has been barren, and alternatively in allowing couples with a child to divert more emotional investment away from each other and toward their helpless infant. The marriage will then be sustained partly by the parents' attraction to their infant.

Variation in Marriage Across Cultures

Armed with this functional perspective, we can proceed to try to understand some of the variable forms that human marriage takes. About 14% of marriages occur in matrilineal societies [23]. Most of these practice the avunculate, meaning that a woman's brother plays a major parental role for her children. Infidelity is generally common, so that men have little certainty of paternity for their wife's children. Consequently, most men invest mainly in their sisters' children, who they can be certain are their blood kin. Because of infidelity and low paternal investment, divorce rates are high. Thus, this variant on the usual patrilineal form of the family makes functional sense. Matrilineality tends to arise in societies in which women cooperate across generational lines to a high degree, which favors matrilocalism, and in which men leave for long periods on warmaking expeditions and thus risk cuckoldry. By contrast, patrilineality is associated with patrilocalism, which in turn is the rule where kinsmen cooperate in herding, farming, or fighting [1].

Another important economic factor for explaining variability in marriage is wealth. In societies where some men can afford more than one wife at a time, polygyny usually arises [23]. Even in modern societies in which the Christian tradition has rendered polygyny illegal, wealthy men sometimes petition for divorce and then remarry [44, 45]. Such cases of "serial polygyny" are more likely if the husband is still relatively young [46]. Similarly, in many birds, a male that commands a large territory often attracts multiple mates. A female may do better sharing a prosperous male than monopolizing a single but destitute one. Women in polygynous marriages tend to have almost as many surviving children as women in monogamous ones in the same society [47]. Male wealth also affects how marriages are contracted. Arranged marriage, the usual form in traditional societies, is associated with large bride prices [1]. Parents care about the transfer of wealth and also about establishing political and economic alliances with other families through marriage. Parents employ various tactics to maintain control over their children's amorous inclinations, including sex segregation, claustration of women, veiling of women, early marriage, and condemnation of premarital sex. (After marriage, wives are often controlled sexually by surveillance by patrilocal kin and other measures.) However, in no society do parents succeed completely in overriding their children's mate preferences. Arranged marriage is unusual in forager societies, the economic form of our hominid ancestors, so we can assume that young people would have evolved strong and elaborate mate choice criteria of their own, as certainly seems to be the case. Marriages are usually arranged in societies with appreciable bride prices; parents have an economic stake

in the outcome. Bride price or bride service occurs in about 71% of cultures, especially patrilineal ones [48]. Where property stakes are high at marriage, prospective brides will maximize their mate value by enhancing their apparent sexual fidelity. In these societies, genital mutilation (and, very rarely, dowry) sometimes occur, presumably to sweeten the pot for a rich suitor [1]. Genital mutilation is viewed as a means of reducing a woman's sexual desire and thus her tendency to sexual infidelity [23]. It is a remarkable testament to the importance of paternity certainty that families would submit their daughters to this gruesome and often lethal operation. Then again, sexual jealousy is the most common cause of murder around the world [49].

Economic factors also affect the age of marriage. Men must meet an economic test in order to marry, and in societies in which many years are needed to accumulate the skills or property in order to qualify, marriage is delayed. During prosperous times, men's age at marriage tends to fall [1]. On the other hand, men marry early where their economic skills develop early, as among farmers and laborers in contemporary society. To some extent, women's age at marriage tracks men's in the society. Divorce rates tend to be higher when the age gap between spouses is great. However, women always marry at younger average ages than men. This is because of men's need for time to become dominant economically and interpersonally, and because of women's more sharply declining fertility with age. Where women are in short supply, men tend to marry late because they require more time to qualify economically. Women, on the other hand, usually marry when young, as soon as they become marriageable. For example, women tend to marry at earlier ages in polygynous societies than in monogamous ones, because they are more in demand in the former. Lastly, when life expectancies are short, marriage occurs early, just as short-lived animals begin to reproduce at young ages.

Public marriage ceremonies occur in the majority of traditional societies, especially where bride prices are high [1]. A public marriage commitment tends to lower the likelihood of divorce. Also, at marriage ceremonies the two families become acquainted and often establish economic or alliance ties that they would lose in the event of a divorce. Alliances are especially important as a consideration in marriage arrangements in feudal societies in which defense depends greatly on strength of number.

Trends in Modern Marriage

The Industrial Revolution brought profound changes in marriage and the family. Some of these trends continue today. With industrialization, husbands often moved their families to cities to take factory jobs [1]. They usually left their parents and other relatives behind, on the family farm, and became less committed to the financial support of those now distant kin. Wives also sometimes took factory jobs, thus distancing themselves from their children who, in turn, spent many hours away from home while being schooled for the technical jobs required by industry. In short, family members became most distant from one another. Arranged marriage began to die out. Perhaps because of this isolation of the nuclear family from other relatives and weakened ties to in-laws and because spouses met lovers at work, divorce rates began to rise. A steady rise in divorce has occurred wherever industrialization has taken place [36].

In recent decades disintegration of the family has continued, especially in the U.S. [50]. Divorce rates in the U.S. are about triple those in Western Europe, probably in part because of the strong individualism ethic noted previously. A survey found that U.S. and British couples were very similar in values except that the former placed greater importance on individual self-fulfillment and the latter on having a good marriage [51]. More and more U.S. women with young children are working outside the home. Contact hours between parents and children are declining [50]. "Reform" of the welfare system has resulted in even less contact with children as mothers are obligated to have full-time jobs. Adolescent girls often drop out of school to stay home with their younger siblings while the mother is at work, a phenomenon now referred to as the no-parent family.

In Europe the availability of paid parental leave allows most mothers to remain at home with their young infants, and with universal health care mothers can work part-time without losing medical coverage. Some European countries also offer financial incentives for couples to care for aged relatives in the home, thus keeping extended families intact.

However, the low birth rate in these prosperous societies, referred to as the demographic transition, is mystifying. One possible explanation is that parturient women evolved a tendency to evaluate their prospects for raising their newborn successfully. This judgment is made on the basis of the newborn's perceived viability and the availability of assistance from other caretakers. Unmarried, impoverished girls are at elevated risk to abandon or kill a newborn. However, the absence of additional family members due to the breakdown of the extended family may also trigger an aversion to raising children, thereby contributing to the demographic transition [52]. Even when both parents are present, marital satisfaction tends to decline with the birth and development of children, and recovers when the children grow up and leave home [53, 54]. However, this seems to occur only in Western societies such as the U.S., England, and Sweden. It has not been observed in more collectivistic societies with stronger extended-family relationships, Turkey and China [12, 55]. Consistent with the suggestion [52] that the demographic transition reflects breakdown of the extended family, marital satisfaction in Western and Eastern societies seems to depend more on relations with the couple's parents than on the impact of children [56].

Divorce rates continue to rise in all industrialized societies. Another factor is the increased earning power

of women. It is a troubling but well-established fact that divorce rates are high where women are economically independent of their husbands. This is true of traditional societies and modern ones [reviewed in 28]. Husband's income stabilizes marriage, whereas wife's income usually destabilizes it, especially if her income rivals or exceeds his [57]. Similarly, women are seldom willing to marry a man who earns less than they do. High-income women desire a high-income man more strongly than do low-income women, despite being less needy themselves [58, 59]. Marriage is not a simple economic partnership in which marital success is correlated with family income; marital success depends greatly on which spouse earns how much.

Nowhere are these dynamics more apparent than in the African American population. The vast majority of Black births are to unwed mothers. Black adolescent girls may be realistic in despairing of finding a marriageable man, and proceeding to get pregnant and deliver without the aid of a husband [60]. Many black men are effectively unmarriageable because they are poor, imprisoned, alcoholic, mentally ill – or homicide victims. Black women now gain far more education than Black men. The remedy advocated by Wilson [60] is to offer well-paying jobs to impoverished men of any race so they can help support a family. One would, of course, want to make similar jobs available to women too, but these would not strengthen families without concomitant paid parental leave. The availability of marriageable men would indirectly benefit women economically by making marriage more accessible for those who sought it. Women, like men, would have more options in balancing work and family life. Marriage benefits all family members, not just children. People are generally healthier and happier being married [61]. Married men are less prone to alcoholism, mental illness and criminality, including rape, than single men.

It is important to emphasize that these mating dynamics of Blacks are a special case only because of the extraordinary dearth of marriageable Black men. The same effects have occurred in other populations when men are in short supply, such as following military defeat [36]. Where men are scarce, marriage rates fall and sexual promiscuity increases because men can get sex without marriage. Where women are scarce, their rate of marriage tends to be high. Another consequence of a low marriage rate is that sibling relations tend to be more acrimonious between half-siblings and stepsiblings than between full siblings, who are more closely related genetically [62].

In attempting to compensate for the decline in the family, the welfare state may actually undermine marriage by offering incentives to reproduce outside of marriage. The availability of generous child care allowances for unwed mothers has been shown to increase the likelihood of carrying a fetus to term as opposed to getting an abortion [63]. In effect, the state competes with men to assume the paternal role. However, fathers offer more than just economic assistance to children. Cross-culturally, the father typically serves as a protector of the family, an adult model, a playmate especially for weanlings, and a tutor of the sons in masculine pursuits [64]. It seems obvious that family law needs to take each family member into account. Failure to do so can lead to results such as that observed in Czechoslovakia around 1980. State-provided benefits lowered the average age of marriage, but this in turn raised the divorce rate [1].

In sum, it seems that deviation from the species-typical pattern of the extended family can be perilous. In traditional cultures, extended families invariably reside together – if not under the same roof than within easy walking distance. This means that children are raised by multiple kin, and spouses are not solely dependent on each other for emotional and practical support. Grandparents can offer not only tangible assistance such as child care, but also advice on resolving marital difficulties – or advice to terminate a marriage. We found that in the U.S., England, China, and Turkey parental approval of the child's choice of a spouse was associated with marital love [56, 65]. If, however, the couple's parents divorce, their assistance is less feasible and their advice more suspect. Couples with divorced parents are more likely to divorce themselves, so that marital success is passed on across generations. This is true in another sense as well, since the tendency to divorce has appreciable heritability [66]. Thus, even if we have abandoned arranged marriage – which, indeed, usually results in less satisfaction than free-choice marriage – we may still benefit from the advice and involvement of the extended family. A network of kin not only provides emotional security and tangible assistance, it also allows young people to learn how to be parents themselves by observing loving parental care by their elders [67]. In this way too, successful family relations can be passed on.

Acknowledgements

We are grateful to our research colleagues Olcay Imamoğlu, Todd Lucas, Yobany Pardo-Rincon, Michele Parkhill, Robin Russell, Jiliang Shen, Pamela Wells, and Craig Wendorf for their assistance with this interpretation of the marriage literature.

REFERENCES

1 Quale GR. A history of marriage systems. New York: Greenwood; 1988.
2 Higham E. Variations in adolescent psychohormonal development. In: Adelson J, editor. Handbook of adolescent psychology. New York: Wiley; 1980.
3 Richards MH, Larson R. Pubertal development and the daily subjective states of young adolescents. J Research on Adolescence 1993; **3**:145–169.
4 Baker RR, & Bellis MA. Human sperm competition: copulation, masturbation and infidelity. London: Chapman & Hall; 1995.
5 Amato PR. Children's adjustment to divorce: Theories, hypotheses, and empirical support. J Marriage & Family 1993; **55**:23–38.

6 Daly M, Wilson M. Homicide. Hawthorne (N.Y.): Aldine de Gruyter; 1988.
7 Fleming AS. Hormonal and experiential correlates of maternal responsiveness. In: Krasnegor NA, Bridges, RS, editors. Mammalian parenting: biochemical, neurobiological, and behavioral determinants. New York: Oxford University Press; 1990.
8 Goldberg S, Blumberg SL, & Kriger A. Menarche and interest in infants: biological and social influences. Child Development 1982; **53**:1544–1550.
9 Money J, Ehrhardt AA. Man and woman, boy and girl. Baltimore (Md.): Johns Hopkins University Press; 1972.
10 Warren MP, Shortle B. Endocrine correlates of human parenting: A clinical perspective. In: Krasnegor NA, Bridges RS, editors. Mammalian parenting: biochemical, neurobiological, and behavioral determinants. New York: Oxford University Press; 1990.
11 Storey AE, Walsh CJ, Qutinton RL, Wynne-Edwards KE. Hormonal correlates of paternal responsiveness in new and expectant fathers. Evolution & Human Behavior 2000; **21**:79–95.
12 Weisfeld CC, Weisfeld GE, Lucas TW Pardo-Rincon Y, Parkhill MR. What's important – marital satisfaction or reproductive success? Paper presented at the congress of the International Society for Human Ethology, Montréal; August 2002.
13 Brislin, R. Understanding culture's influence on behavior. New York: Harcourt; 2000.
14 Brehm SS, Miller RS, Perlman D, Campbell SM. Intimate relationships (3rd ed.). New York: McGraw Hill; 2002.
15 Hrdy SB. Mother nature: a history of mothers, infants, and natural selection. New York: Pantheon; 1999.
16 Schlegel A. The origin of the family. Paper presented at the convention of the Human Behavior and Evolution Society, New Brunswick (N.J.); June 2002.
17 Zeller AC. A role for children in hominid evolution. Man 1987; **22**:528–557.
18 Miller G. The mating mind. London: Vintage; 2001.
19 Mealey L. Sex differences: developmental and evolutionary strategies. New York: Academic Press; 2000.
20 Weisfeld GE, Russell RJH, Weisfeld CC, Wells PA (1992). Correlates of satisfaction in British marriages. Ethology & Sociobiology 1992; **13**:125–145.
21 Andersson M. Sexual selection. Princeton (N.J.): Princeton University Press; 1996.
22 Rushton JP. Genetic similarity, mate choice, and fecundity in humans. Ethology & Sociobiology 1988; **9**:329–333.
23 van den Berghe PL. Human family systems: an evolutionary view. New York: Elsevier; 1979
24 Coon CS. The hunting peoples. Boston: Little, Brown; 1971.
25 Jacob S, McClintock MK, Zelano B, Ober C. Paternally inhibited HLA alleles are associated with women's choice of male odor. Nature Genetics 2002; **30**:175–179.
26 Czilli T, Weisfeld GE, & Lichtman C. Recognition of parents, children, and siblings by olfaction. Paper presented at the congress of the International Society for Human Ethology, Montréal; 2002.
27 Buss DM. Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. Behavioral & Brain Sciences 1989; **12**:1–49.
28 Weisfeld GE. Evolutionary principles of human adolescence. New York: Basic Books; 1999.
29 Betzig, L. Causes of conjugal dissolution: a cross-cultural study. Current Anthropology 1989; **30**:654–676.
30 Corrales RG. Power and satisfaction in early marriage. In: Cromwell RE, Olson DM, editors. Power in families. New York: Wiley; 1975.
31 Gray-Little B, Burks N. Power and satisfaction in marriage: a review and critique. Psychological Bulletin 1983; **93**:513–538.
32 Kotlar SL. Middle-class marital role perceptions and marital adjustment. Sociology & Social Research 1965; **49**:283–294.
33 Shen J, Wendorf C, Lucas T, Parkhill M. Correlates of satisfaction in Chinese marriages. Poster presented at the congress of the International Society for Human Ethology, Montréal; August 2002
34 Noller P. Nonverbal communication and marital interaction. Oxford: Pergamon Press; 1984.
35 Schell NJ, Weisfeld CC. Marital power dynamics: a Darwinian perspective. In: van der Dennen JMG, Smillie D, Wilson DR, editors. The Darwinian heritage and sociobiology. Westport (Conn.): Praeger; 1999.
36 Goode WJ. World changes in divorce patterns. New Haven (Conn.): Yale University Press; 1993.
37 Thornhill R, Thornhill N. Human rape: an evolutionary analysis. Ethology & Sociobiology 1983; **4**:63–99.
38 Littlefield CH, Silverman I. Marital dissatisfaction following the death of a child: The influence of genetic factors at cause in the death. J Marriage & Family 1991; **53**:799–804.
39 Friedl E. Women and men: an anthropologist's view. New York: Holt, Rinehart & Winston; 1975.
40 Stephens WN. The family in cross-cultural perspective. New York: Holt, Rinehart & Winston; 1963.
41 Brown NM, Amatea ES. Love and intimate relationships: journeys of the heart. New York: Brunner/Mazel; 2000.
42 Fisher H. The anatomy of love: the mysteries of mating, marriage, and why we stray. New York: Fawcett Columbine; 1992.
43 Tennov D. Love and limerence: the experience of being in love (2nd ed.). Lanham (Md.): Scarborough House; 1999.
44 Buckle L, Gallup GG, Rodd ZA. Marriage as a reproductive contract: patterns of marriage, divorce, and remarriage. Ethology & Sociobiology 1996; **17**:363–377.
45 Gottman JM, Levenson RW. The timing of divorce: Predicitng when a couple will divorce over a 14-year period. J Marriage & Family 2000; **62**:737–745.
46 Hiedermann B, Rand OO, Source AM. Economic independence, economic status, and empty nest in midlife marital disruption. J Marriage & Family 1998; **60**:219–231.
47 Daly M., Wilson M. Sex, evolution, and behavior (2nd ed.) Belmont (Calif.): Wadsworth; 1983.
48 Murdock GP. Ethnographic atlas. Pittsburgh, Pa.: University of Pittsburgh Press; 1967.
49 Freedman DG. A biological view of man's social behavior. In: Etkin W, editor. Social behavior from fish to man. Chicago: University of Chicago Press; 1967.
50 Popenoe D. American family decline, 1960–1990: a review and appraisal. J Marriage & Family 1993; **55**:527–555.
51 Perkins HW, Spates JL. Mirror images? Three analyses of values in England and the United States. International J Comparative Sociology 1986; **27**:31–51.
52 Waynforth S, Waynforth D. Minding the baby and demographic transition. Paper presented at the convention of the Human Behavior and Evolution Society, New Brunswick (N.J.); June 2002.
53 Argyle M., Henderson, M. The anatomy of relationships. Harmondsworth (England): Penguin; 1985.
54 Stattin H, Klackenberg G. Discordant family relations in intact families: developmental tendencies over 18 years. J Marriage & Family 1992; **54**:940–956.
55 Pimentel EE. How do I love thee? marital relations in urban China. J Marriage & Family 2000; **62**:32–47.
56 Wendorf CA, Imamoglu EO, Shen J, Weisfeld GE, Lucas TW. Marriage within the extended family in four cultures. Paper presented at the congress of the International Society for Human Ethology, Montréal; August 2002.
57 Cready DM, Fosset MA, Kiecolt KJ. Mate availability and African American family structure in the U.S. metropolitan South, 1960–1990. J Marriage & Family 1997; **59**:192–203.
58 Townsend JM. Mate selection criteria: a pilot study. Ethology & Sociobiology 1989; **10**:241–253.
59 Wiederman MW, Allgeier ER. Gender differences in mate selection criteria: Sociobiological or socioeconomic explanation? Ethology & Sociobiology 1992; **13**:115–124.

60 Wilson WJ. The truly disadvantaged. Chicago: University of Chicago Press; 1987.
61 Argyle M. The psychology of happiness (2nd ed.). New York: Taylor & Francis; 2001.
62 Weisfeld GE, Aytch DM. Biological factors in family violence. Michigan Family Review 1996; **2**:25–39.
63 Chilman CS. Some psychological aspects of adolescent sexual and contraceptive behaviors in a changing American society. In: Lancaster J & Hamburg BA, editors. School-age pregnancy and parenthood: biosocial perspectives. New York: Aldine de Gruyter; 1986.
64 Mackey W C. The American father: biocultural and developmental aspects. New York: Plenum; 1996.
65 Weisfeld GE, Weisfeld CC, Imamoglu EO, Wendorf CA. Cultural differences in the impact of number of children on marital satisfaction. Paper presented at the convention of the Human Behavior and Evolution Society, London; June 2001.
66 McGue M, Lykken DT. Genetic influence on the risk of divorce. Psychological Science 1992, **3**:368–373.
67 Richer J. The rise of psychosocial problems, attachment and mismatch. Paper presented at the congress of the International Society for Human Ethology, Montréal; August 2002.

Neuroendocrinology Letters Special Issue, Suppl.4, Vol.23, December 2002
Copyright © Neuroendocrinology Letters ISSN 0172–780X ***www.nel.edu***

REVIEW ARTICLE

(Evolutionary) Theories of Warfare in Preindustrial (Foraging) Societies

Johan M.G. van der Dennen
Department of Legal Theory, Section Political Science, University of Groningen, THE NETHERLANDS

Correspondence to: Johan M.G. van der Dennen, Ph.D.
Department of Legal Theory, Section Political Science
University of Groningen
Oude Kijk in 't Jatstraat 5,
9712 EA, Groningen, THE NETHERLANDS
PHONE: +31 50 3635649
FAX: +31 50 3635635
EMAIL: j.m.g.van.der.dennen@rechten.rug.nl

Submitted: *September 19, 2002*
Accepted: *October 15, 2002*

Key words: **war causation; evolution; 'primitive' warfare; (pitched) battle; lethal male raiding; kin selection; sexual selection**

Neuroendocrinology Letters 2002; ***23*** *(Suppl.4):55–65 pii: NEL231002R06 Copyright © Neuroendocrinology Letters* ***www.nel.edu***

Abstract I present an inventory of theories of war causation (and on the origin of war) in preindustrial (traditional, foraging, 'primitive', hunter-gatherer, band- and tribe-level) societies, with emphasis on the roles of natural selection, sexual selection and kin selection. Also the school of sociocultural evolution is briefly discussed.

Many anthropologists do not acknowledge a (bio)evolutionary background to war, adhering to Mead's [1] famous dictum 'War is only a cultural invention' (e.g., Harris [2 to 10], Ferguson [11 to 20], Keeley [21]). Many students of war do not consider an evolutionary approach useful or relevant, even though the prevailing cultural-materialist theory is highly compatible with the evolutionary paradigm (Sanderson [22]).

A variety of scholars associate the origin of war with the Mesolithic way of life. Ferguson [17] is the most outspoken advocate of this position: "In sum, the evidence is fully consistent with the conclusion that war first became a social institution in Mesopotamia some 8,000 years ago, and has been reinvented in many times and places since, and flatly inconsistent with the idea that war has been a regular occurrence throughout human history".

In its most general terms, the rationale of warfare, genocide, and other forms of collective violence may be epitomized as 'getting rid of the competition' or eliminating the sources of fear and terror. "War is obviously one way of gaining access to needed resources - and of eliminating potential threats to your own population or resources" (Corning [23]).

(An abbreviated version of this article appeared in Pagel M. (*Editor-in-Chief*) The Oxford encyclopedia of evolution. Vol. 2. Oxford: Oxford Univ. Press; 2002. p.1146-1149).

Natural selection does not, of course, favor destructiveness as such, but reproductive success; violent interactions, including warfare, make evolutionary sense only if they serve reproduction (Meyer [24] to [27]), Low [28, 29], Van der Dennen [30]).

A great number of disciplines have traditionally studied war in contemporary as well as 'primitive' or preliterate, preindustrial, nonstate, band-level and tribal (hunter-gatherer and horticulturalist) societies, but always with the implicit assumption that war was (a) uniquely human, and (b) a one-time cultural invention spread by diffusion, or a number or series of independent inventions (e.g., Cioffi-Revilla [31]).

The discovery of male coalitional aggression and 'lethal male raiding' in free-ranging chimpanzees (Goodall [32], Manson & Wrangham [33], Wrangham [34], Wrangham & Peterson [35]) and battle-type intergroup violence in social carnivores and a great number of primates (Cheney [36], van der Dennen [30]) makes the conventional view of warfare as a singularly human 'cultural invention' of some few thousand years old increasingly untenable. Instead, a view of phylogenetic continuity, as first proposed by Darwin [37], Bigelow ([38], [39]), Corning [23, 40, 41] among others, and elaborated by many others (Meyer [24] to [27]), Low [28, 29], Slurink [42], van Hooff [43], van der Dennen ([30], [44] to [49]), Gat ([50] to [52]) is worth exploring.

Phylogeny refers to the 'ultimate' dimension of causality: "Why has warfare, or propensities for warfare, evolved in the first place?" and "Why has warfare evolved in only so few species?"; which should be distinguished from the proximate causative factors, e.g., "What are the motives or conditions that led to this particular war?". Ultimate and proximate causes are complementary rather than mutually exclusive.

The evolutionary (or selectionist or Darwinian) paradigm proceeds from the assumption that all organisms, including Man (*Homo sapiens sapiens*), have evolved; that all living organisms descend from other organisms that successfully mated and reproduced in past environments, and that – ultimately – all organisms have come in one uninterrupted chain from the first simple multiplying cells, and thus are phylogenetically related to one another. Ultimately, all organisms are the products of the former strategies of their genes.

Darwinian (bio)evolution: natural selection, sexual selection and kin selection

In general, two types of warfare (broadly defined as organized intergroup or intercommunity contest competition) in animals and man have been distinguished: Raiding ('lethal male raiding' or ambush or dawn surprise attack), and battle (confrontation of two opposing lines or phalanxes). When a battle is prearranged it is called a 'pitched battle'. In 'primitive' societies raiding is the most bloody and lethal form of warfare due to small but rapidly accumulating casualties, and occasional near-genocidal routing (e.g., Davie [53], Turney-High [54], Divale [55], Cheney [36], Bigelow ([38], [39]), Manson & Wrangham [33], Low ([28], [29]), van der Dennen [30], Keeley [21], Gat [50], Wrangham [34], Wrangham & Peterson [35], Otterbein [56]).

Lethal male raiding has been explained by Wrangham's 'imbalance-of-power' hypothesis, Tooby & Cosmides' [57] 'risk-contract' theory (see also Malagon-Fajar [58]), and Low's [28, 29] and van der Dennen's [30] sexual selection approach (*vide infra*). Wrangham [34] has also suggested the distinct possibility that the chimpanzee-hominid common ancestor already had this lethal male raiding pattern in its behavioral repertoire (panid-hominid synapomorphy) some 6 million years ago.

Battle-type warfare occurs in many primate species and some other group-territorial mammals, such as social carnivores. Battles result mainly from chance encounters by primate groups, failed raids or failed surprise attacks and chance encounters in 'primitive' peoples, and among standing armies in historical and contemporary warfare when the armies are too big to operate undetectedly. Turney-High [54] has illuminated the 'biomechanics' of the line which develops more or less automatically when two groups meet in an agonistic encounter and every individual organism strives to have its vulnerable flanks protected by its neighbors. In social carnivores and 'female bonded' (or female philopatric) primate species, female participation in these – more noisy than bloody – battles commonly exceeds male participation. Tournament-like 'ritualized' combat is generally found among 'advanced' tribal societies with fairly dense populations (e.g., New Guinea), and is supposed to test the (numerical) strength of the opponent while leaving room for a more peaceful solution of the conflict by mediators – but the ritual battle can easily develop into a rout and a massacre if a substantial imbalance of power is detected by one of the parties involved (Divale, Durham [59, 60], Otterbein, van der Dennen). Some Australian tribes practiced so-called 'expiatory combats' (comparable to medieval duels) for settling disputes (van der Dennen [61]).

The contention that war must have existed before mankind is based on (a) the Phylogenetic Continuity argument (Bigelow, Low, van der Dennen, Otterbein, Wrangham): continuity between humans and nonhuman primates, as opposed to the mostly implicit assumption of Man's uniqueness and the conviction that war is a one-time cultural invention; (b) the Multimale (or Polyadic) Coalition argument: as soon as a species has solved the problem of coordinated cooperative action by more than two individuals, it has solved the problem of warfare because this kind of 'selfish cooperation' (Corning) is an excellent instrument for escalated and violent intercoalition and intergroup contest competition. "Cooperation-for-conflict has probably always been the key to human survival" as Bigelow put it. Until now, at least two (brainy) species have accomplished this: Man (*Homo s. sapiens*) and the common chimpanzee (*Pan troglodytes*); male bottle-nosed dolphins (*Tursiops truncatus*), who are capable of 'super-

coalitions' for the purpose of forcefully monopolizing females, are a serious third candidate. Additionally, some ethnocentric xenophobia between groups would be selectively favored in a potentially hostile and violently competitive environment (e.g., Bigelow, van den Berghe [62], Reynolds, Falger & Vine [63], van der Dennen, Shaw & Wong [64], Hamilton [65 to 67], Irwin [68], Wilson [69, 70]), exacerbated by the sharply decreasing (genetic) kinship at the groups' boundaries: "At the boundary of the local group, there is usually a sharp drop in relatedness; this drop may be such as to promote active hostility between neighbouring groups" (Hamilton [67]). It has been noted by many scholars that intergroup competition can be a potent and relentless selective force without high levels of violence and killing (e.g., Bigelow, Wilson). "By current theory, genocide or genosorption strongly favoring the aggressor need take place only once every few generations to direct evolution. This alone could push truly altruistic genes to a high frequency within the bands" (Wilson [69]).

The question why males are the warriors in raiding-type warfare has been addressed by Symons [71], Trivers [72], Dow [73], Tooby & Cosmides, Low, van der Dennen, Wrangham, and Ghiglieri [74 to 76], among others. Their answers are remarkably compatible: raiding-type warfare evolved as a high-risk/high-gain male-coalitional reproductive strategy (or, arguably, even as a parental investment strategy). To understand this – for some undoubtedly extravagant – claim, the following observations are relevant. Reproductive success is the only criterion in the currency of evolution. Male and female organisms have evolved different strategies for the optimalization of their reproductive success because what for the one sex is a highway to genetic immortality is for the other sex a one-way ticket to genetic oblivion (paraphrasing Symons). For male organisms females are generally the limiting resource: for human males women are the highly strategic 'good' (always in short supply) that can convert the other resources controlled by the males into offspring (Borgia [77], Melotti ([78] to [81]), Symons). Accordingly, among chimpanzees (a male philopatric species), the ultimate benefit of lethal male raiding has been hypothesized to be increased access by raiding males to reproductively valuable females, via either incorporation of neighboring females or encroachment on the territory of neighboring groups and elimination of numerically weaker males.

Wrangham [34] presents the principal adaptive hypothesis for explaining the species distribution of intergroup coalitional killing. This is the imbalance-of-power hypothesis, which suggests that coalitional killing is the expression of a drive for dominance over neighbors. Two conditions are proposed to be both necessary and sufficient to account for coalitional killing of neighbors: (1) a state of intergroup hostility; (2) sufficient imbalances of power between parties that one party can attack the other with impunity. Under these conditions, it is suggested, selection favors the tendency to hunt and kill rivals when the costs are sufficiently low. Given the chimpanzee evidence, Manson & Wrangham proposed that such imbalance-of-power mechanism must have been an important factor favoring the evolution of lethal male violence in humans also – and even before the evolution of weapons. This strategy may be a pattern common to the chimpanzee-bonobo-human (or HUCHIBO) clade: "Unlike gorillas and orangutans, males of the chimpanzee-bonobo-human clade retain their male offspring predominantly, live in closed social groups containing multiple females, mate polygynously, restrict their ranging to a communal territory, are cooperatively active in territorial defence, and, apparently, when a neighbouring community weakens, the males of some communities make a concerted strategic effort to stalk, attack, and kill their rivals as do men" (Ghiglieri [74]), although in the bonobo (*Pan paniscus*) some intergroup agonistic behavior but no lethal raiding (nor communal hunting) has been observed. Especially, the combination of male-male cooperation, 'proto-ethnocentrism', group-territoriality and female transfer has been singled out as the starting condition for lethal intergroup violence (Goodall, Ghiglieri, Alexander [82 to 90], Manson & Wrangham, Slurink, Van der Dennen, Wrangham & Peterson, Wrangham). Wrangham & Peterson note that the underlying psychology of 'male bonding' is no different for chimpanzee raiding parties, human urban gangs, pre-state warrior societies, and contemporary armies.

Tooby & Cosmides enumerate some significant implications of their Risk Contract of War: (1) men, but not women, will have evolved psychological mechanisms ('Darwinian algorithms'), designed for coalitional warfare; and (2) sexual access to women will be the primary benefit that men gain from joining male coalitions. Or, in Low's words: "Through evolutionary history, men have been able to gain reproductively by warring behavior; women have almost never been able to do so" (Low [28]).

This contrasts, as we have seen, with most other primate (and social carnivore) species in which the females have more 'vested interests' in the defense of their lineage and the integrity of their group territory.

The rationale for groups to compete *as groups* has been illuminated by Pitt [91], McEachron & Baer [91] and Baer & McEachron [92]. Several scenarios can be pictured in intergroup contest competition: (a) peaceful coexistence or merging of the groups; (b) peaceful competition between groups with the losers starving; (c) violent conflict between individuals; (d) scramble competition; and (e) violent group conflict, i.e., warfare. Warfare would be the best alternative for the group that practiced it successfully, assuming it to have been within their biological reach. If conflict is inevitable, it makes better evolutionary sense for the troops to determine ownership of the resources *as groups*, rather than having both conflict and decreased inclusive fitness (which would accompany a merger). Assuming that different groups tended towards one or another of these strategies, in varying degrees, it is easy to see that the warprone group would be the most successful, and

could indeed overrun any group attempting to practice one of the other strategies. Plainly, it will be the warmongers whose genes are represented in the next generation. Indeed, the only possible competitive strategy for survival in competition with a group practicing warfare, is warfare itself, either defensive or offensive.

Richerson [94] advances what he calls the 'evolutionary tragedy' hypothesis: Warfare is liable to evolve even if it makes everybody worse off. It is the perversion of the situation (the logic of the war 'game') rather than that of the actors involved.

Humans thus became quintessentially first-strike creatures. Unlike other animal species, they were able to kill adult conspecifics by surprise, when their adversaries were unarmed and vulnerable, and from a substantial distance by throwing projectiles (Pitt, Baer & McEachron, Bingham [95], Gat).

Most of the many factors that favor the reproductive potential of cooperative people and good warriors can be grouped under two categories: (1) the genetic effects of increased *Lebensraum* (territory and resources) and (2) the genetic effects of polygyny (Bigelow, Hamilton, Wilson, Low, van der Dennen).

Among many hunting-gathering peoples a man's quality as a warrior and his hunting prowess is directly related to the number of wives he can obtain, and/or his access to nubile women (e.g., Symons, Chagnon, Low, Hawkes [102], van der Dennen).

Van der Dennen's investigation of the evolutionary origins of intergroup conflict in social carnivores and primates identified (a) the capability to form polyadic coalitions (selfish and opportunistic cooperation with more than one conspecific) as the necessary precondition, which in turn required (b) sociality (intergroup conflict will occur only in long-lived social species: Low [28]); (c) Machiavellian (opportunistic) intelligence; and (d) proto-ethnocentrism. Proto-ethnocentrism is supposed to imply some kind of group identity, that is, the ability to recognize ingroup versus outgroup members, to discriminate between these categories, and to preferentially treat ingroup members to positive reciprocal (altruistic) interactions such as protection, nepotism, and sharing of resources. Van der Dennen's evolutionary scenario or 'evolutionario' also outlines the phylogenetic and socio-ecological principles governing group formation, ingroup altruism, outgroup antagonism, and intergroup agonistic behavior (i.e., war and its non-human equivalent).

Sociocultural evolution: stages in sociopolitical complexity

The basic motives and practices of 'primitive' war were already known to the classical historians such as Herodotus and Tacitus (Turney-High, van der Dennen). One of the first accounts in Europe of 'primitive' cannibalism and warfare was Hans Staden's [103] story of his life among the Brazilian Tupinamba (though some doubt has risen about its authenticity).

In 1767 Adam Ferguson [104] published *An Essay on the History of Civil Society* (the first attempt at an empirical cross-cultural study), in which he concluded: "We had occasion to observe that in every rude state the great business is war; and that in barbarous times, mankind, being generally divided into smaller parties, are engaged in almost perpetual hostilities". War, intergroup antagonism, "has been the great business of mankind since time immemorial". This conclusion neatly confirmed Hobbes' [105] gloomy view of the war-ridden condition of primitive society (the causes of which he identified as "competition, diffidence, and glory"). Diametrically opposed views were espoused by Rousseau [106] in his *Le Contrat Social*, in which he introduced the concept of the 'Noble Savage' who did not wage war simply because there were no (material) benefits to be gained by waging war (This so-called Hobbes-Rousseau controversy, a persistent and irreconcilable one, has dominated the anthropological literature until today).

The concept of evolution as an ordering principle in cultural anthropology was proposed about 1840, even before Darwin's *Origin of Species* [107]. But this referred to (Lamarckian, Spencerian) sociocultural evolution, not to Darwinian (bio)evolution, which Darwin himself liked to call "descent with modification". (The terms 'evolution', 'function', and 'adaptation' are used by both bio-evolutionists and sociocultural evolutionists, but these refer to altogether different phenomena and may cause considerable confusion).

Evolutionism, the predominant school to the end of the 19th century, assumed a linear and progressive conception of evolution and history: human societies advance from the simple to the complex, from the 'savage' primitive horde, through a barbarian stage, to civilization (Spencer [108], Morgan [109], Tylor [110]; Steward [111] and some others saw in cultural evolution a multilineal phenomenon). A century later Sahlins [112 to 115] and Service [116 to 118] proposed a scheme of social evolution in four stages: the band, the tribe, the chiefdom, and the state, with concomitant changes in warfare patterns and motives (from what Muehlmann [119] and Meyer called endemic feuds and wars of retaliation to war as an instrument of predation and plunder, territorial expansion, conquest, subjugation and genocide).

Also Fried [120 to 122] and Hunter & Whitten [123] identified four stages or levels of 'sociopolitical' evolution: egalitarian society, rank society, stratified society, and state-level society (more or less equivalent with the band, tribe, chiefdom and state stages). This sequence is assumed to represent a cultural-evolutionary development. The nature of warfare as it is conducted at each of these levels appears to differ in a systematic way. Similarly, Quincy Wright [124] distinguished social, economic, and political warfare as distinct progressive social-evolutionary stages.

To these levels of sociopolitical organization correspond the levels of military organization as distinguished by Feest [125]: (a) War-chiefs on the basis of reputation; (b) Dual leadership: formal peace- and war-chiefs; (c) Hereditary chiefs and primordial warrior society; (d) Full-blown military societies (or fraterni-

ties); and finally (e) Standing armies (see also Andreski [126], [127]).

Carneiro [128 to 131] noted that whereas small-scale band-level and tribal societies are usually capable of putting together warrior bands of a few dozen at most, chiefdoms can put together fighting forces in the hundreds or thousands. Carneiro studied chiefdom-level warfare in the Cauca Valley of Colombia and in Fiji. He notes that warfare among chiefdoms in these regions was nearly constant. Fiji was seldom without war, and in the Cauca Valley "warfare was universal, acute, and unending" [131], a perpetual struggle for territory and power. This is *a fortiori* the case of states and empires; it has been observed time and again that states make war and war makes states. The formation of the state in codified history represents a remarkable process of parallel evolution, beginning in Mesopotamia around 5,100 years ago (Sanderson [22]). "Conquerors have usually been very generous with their genes. Also, they have frequently killed off or enslaved the males of their vanquished opponents and preempted the women" (Corning [40]).

Hobhouse, Wheeler & Ginsburg [132], van der Bij [133], and Quincy Wright were the first to apply crude statistics to their cross-cultural sample of some 650 distinctive 'primitive' societies, as well as distinguishing levels of 'economic culture', i.e., lower and higher hunters, lower, middle, and higher agriculturists, and lower and higher pastorals. Wright concluded that 95% of his sample were warlike peoples (which seems the confirm the notion of universal belligerence). Other important conclusions were: "Neither territorial conquest, nor seizure of slaves nor plunder of economic goods is characteristic of primitive warfare" and "the more primitive the people the less warlike it tends to be". The absence of 'economic' motives in the warfare patterns of primitive societies (at least the hunter-gatherers) was also emphasized by Turney-High, who thought that primitive warfare was so desultory because it was so thoroughly uneconomic. Few primitive societies had reached what he called the 'military horizon'.

Quite a different tradition was started by Steinmetz [134, 135] (who retorted to van der Bij's finding that primitive peoples are unwarlike by stating that primitive peoples are primitive precisely *because* they are unwarlike) and especially Davie [53] who emphasized sanguinary war for plunder, territorial conquest, abduction of women, etc., although also acknowledging 'non-economic' motives such as revenge, the obligations of the blood feud and other 'magico-religious' motives (cf. Ferguson [11, 13]).

The contemporary schools of (multi)functionalism and (eco)materialism (Vayda [136 to 143], Leeds [144], Harris, Ferguson) also postulate realistic group conflict about material interests; warfare is depicted as a strategy to secure scarce, vital or strategic resources such as land and game (high-quality protein). The roots of the materialist school sprouted in the 1940s when a number of anthropologists reinterpreted Plains Indian, Iroquoian, and Zulu warfare in thoroughly economic terms, i.e., as conscious, deliberate and violent struggles over material resources.

Revenge, women, territory, and scarce resources (including the never-ending search for security) are the main proximate causes or motives of war and feuding in 'primitive' societies reported in the literature, closely followed by status, prestige and glory, and supernatural or magico-religious motives (such as headhunting, trophy taking, scalping, cannibalism, human sacrifice, placating ancestral spirits, etc.) (Davie, Turney-High, Chagnon, Divale, Otterbein, Ferguson, van der Dennen, Keeley, Gat). As Gat reasoned: "The interconnected competition over resources, status and prestige, and reproduction is the *root* cause of conflict and fighting in humans as in all other animal species. Other causes and expressions of fighting in nature, and the motivational and emotional mechanisms associated with them, are derivative of, and subordinate to, these primary causes, and *originally* evolved this way in humans as well".

In a 1978 paper Carol Ember [145] (definitively?) shattered "the myth about peaceful hunter-gatherers". Van der Dennen, Keeley, and Gat could confirm recently that 'primitive' warfare (among hunter-gatherers, horticulturalists, simple agriculturalists) and prehistoric warfare is generally a lethal, bloody, and sometimes even genocidal business: *guerre à l'outrance* (due to rapidly accumulating casualties in raiding and routing). Group extinctions due to chronic warfare between (horticultural) village communities are quite common in New Guinea, Amazonia, and other regions where feuds and wars are endemic.

Broch & Galtung [146] reanalyzed Wright's data by multivariate analysis techniques, and found quite unambiguously that "belligerence is a concomitant of civilization". Though their data are synchronic rather than diachronic, they strongly suggest that there is a process involved, in the sense that increasing civilization would lead to increasing warlikeness or bellicosity.

A concomitant (mainly social-Darwinist) theory in this connection is the view that struggle, war and intergroup conflict have been the principal factors of human progress, or that war is the prime mover of human (cultural, moral, spiritual) evolution: the Agent of Progress.

Among contemporary scholars, the role played by war in the creation of more complex societies is divided between those who see it as a prime mover (e.g., Carneiro), as secondary and only reinforcing other trends (e.g., Fried), or as one of a set of interacting variables (e.g., Ferguson).

See Table I for the main theories of 'primitive' war.

The evolution of historical war may be succinctly described as the transformation of armed men into manned arms, while the reproductive rewards have become increasingly 'unhooked' from the warring behavior, as Low suggested.

Turney-High repeatedly emphasized that the evolution of warfare is not simply a matter of (weapons) technology, but one of social organization. "The military horizon depends, then, not upon the adequacy

Table I: Theories of 'primitive' warfare
The main theories of 'primitive' warfare can be categorized (more or less arbitrarily and overlapping) as follows:

(1) Warfare as cultural invention and macroparasitism. This is the prevailing paradigm among cultural anthropologists, sociologists, and macrohistorians. 'Warfare is only a cultural invention' (Mead [1]) and 'War is not in our genes' are the best known adages of this inventionist (Boasian) school which begins with Boas [149] and his students Dewey [150], Benedict [151] and Mead. Warfare as one-time invention (or series of inventions, and spread mainly by cultural diffusion), and warfare as plunder written-large concomitant with the rise of the first states and empires some 5,000 years ago are the common themes in all general history textbooks: e.g., McNeill [152], Boulding [153], Leakey & Lewin [154], Schneider ([155] to [157]), White [158], Bronowski [159], Starr [160], Dyer [161], Dawson [162] Cioffi-Revilla, Wittfogel [163], the diffusionists, and the Marxist-Leninists.

(2) (Eco)materialist and related (multi)functionalist theories. Most or all theorists of these school acknowledge sociocultural evolution but do not see any special role for 'biology' (which is usually conceived of as 'genes and hormones', without taking the ultimate dimension into consideration), and thus (bio)evolution is commonly rejected as irrelevant (e.g., Ferguson, Keeley). A great number of these theorists are true heirs of Malthus in emphasizing the demographic factor (overpopulation, population pressure in relation to ecological and/or climate changes) in the causation of war: Sumner [164], [165] Sumner & Keller [166], Davie, Bernard, Andreski, Bouthoul, Lathrap [167], Steward, Harris, Ferguson, Keeley. (Multi)functionalists are Vayda, Leeds [168], Vayda & Leeds, Leeds and Vayda [169]. A typical proposition of this school is: "Primitive warfare arose as part of a complex system that prevented human populations from exceeding the carrying capacity of their habitats" (Harris, [3]), or in Vayda's terminology: War functions to adjust the man/land ratio. Multifunctionalists envisage not only the adjustment of the man/land ratio due to warfare, but also the regulation of psychological, economic, and sociopolitical variables. The most caustic, and sarcastic, critic of this school is Hallpike [170]. One offshoot of this school tries to relate population regulation, preferential female infanticide, warfare, and the so-called 'male supremacist complex' (Harris, Divale [171], [172], Divale & Harris [173], [174], Divale *et al*. [175]).

(3) Sociocultural selection and evolution of warfare theories (Evolutionism for short). A typical proposition of this school is: As societies compete, "the less well adapted tend to fall by the wayside, leaving outstanding those best able to withstand the competition" (Carneiro, [129]): White [158], Malinowski [176], Turney-High, Otterbein ([177] to [181]), Meyer, Muehlmann, Fried, Hunter & Whitten, Feest, Andreski, Steward, Naroll & Divale [182], Sahlins, Service, Knauft ([183] to [185]), Boehm [186], among others. White (cf. Newcomb [187]) claimed that "Warfare is a struggle between social organisms, not individuals. Its explanation is therefore social or cultural, not psychological". This programmatic and dogmatic rigor has done more harm than good (e.g., Chagnon, [101]). General criticisms by Hallpike and Robarchek [188], [189]. Most students of this school adhere to the band, tribe, chiefdom, state sequence of sociocultural stages (see text). Muehlmann and others (e.g., Kelly [190]) proposed that war probably originated in and evolved from the blood feud. Meyer envisaged a sociocultural development from endemic war (for metaphysical power) to its instrumentalization (for material power). Meyer and Wilson regard warfare as well as ethnocentrism as cultural hypertrophications of biological predispositions. Lopreato's [191] 'biocultural' approach roots war and general human nastiness in evolved behavioral predispositions of self-enhancement. These last approaches form a transition to the (bio)evolutionary theories.

(4) (Bio)evolutionary theories. This body of theories is predicated upon the assumption of phylogenetic continuity, and gene-culture co-evolutionary or 'dual inheritance' models, meaning that both our biological and sociocultural evolution are acknowledged. These theorists are a heterogeneous lot, ranging from strictly genic selectionists (Durham) to group selectionists, with sexual selectionists and kin selectionists somewhere in between. Intimate relationships have been proposed between

- Warfare and group territoriality: Tinbergen [192], [193], Holsti [194], Davie, Pitt, Turney-High, Bigelow, Alcock [195]. Hamilton and Wilson envisaged a 'stepping stone' model of territorial aggrandizement and genosorption.
- Warfare and hunting (or 'Carnivorous Psychology') theories: James [196], [197], Frobenius [198], Washburn & Lancaster [199], Lee & DeVore [200], Corning, Pfeiffer [201], Melotti, van Hooff. War as (evolved from the) man hunt: Frobenius; 'Killer Ape' popularizations: Dart [202], [203], Ardrey [204]; and related early 'Instinct of Pugnacity' formulations by James and McDougall [205]. Scott [206] proposed that early hominids did not evolve as formidable hunters and warriors but as timid scavengers and 'fear biters'. The masculine 'hunting mystique' has lost much of its appeal lately.
- Warfare and human (ultra)sociality and balance-of-power theorists (human groups as predators upon one another, after the rise of human groups to ecological dominance): Alexander, Andreski, Lorenz [207], Slurink, van der Dennen. "Fear of hostile foreigners has probably always been the most effective promotor of social unity among related bands of people" (Bigelow, [38]).
- Warfare and hominid/human brain evolution (trebling of human brain due to relentless groups competition): Darwin, Keith [208], Bigelow, Pitt, Alexander, Alexander & Tinkle, Baer & McEachron, McEachron & Baer.
- Warfare and group selection (during specifically *human* evolution, human groups have continuously replaced, incorporated, subjugated, or eliminated other human groups): Darwin, Bigelow, Corning, Masters [209], Wilson, Eibl-Eibesfeldt ([210] to [214]), Alexander, Melotti, Boyd & Richerson [215], Richerson & Boyd [216]. Eibl-Eibesfeldt particularly emphasizes the role of indoctrination in creating the 'warrior-type' personality.
- Warfare and kin selection (ethnocentrism-cum-xenophobia): van den Berghe, Goodall, Shaw & Wong, Wilson, Lumsden & Wilson [217], [218], Meyer, Reynolds *et al*., Falger [219], van der Dennen, Thienpont & Cliquet [220].
- Warfare and sexual selection (sexual – or reproductive – competition and the evolution of a 'male coalitional psychology'; war for women); Chagnon, Tooby & Cosmides, Low, van der Dennen, Alexander, Borgia, Symons, Tiger [221], [222], Tiger & Fox [223], Trivers, Wilson, Gat (Goldstein [224] discusses 'War and Gender' without invoking the evolutionary dimension; cf. Adams [225], Ehrenreich [226], Kroeber & Fontana [227]). The warrior-type personality may be viewed as a product of sexual selection. Goodall, Ghiglieri, Manson & Wrangham, van der Dennen, Wrangham, Wrangham & Peterson have taken chimpanzee 'lethal male raiding' into account in explaining human raiding. "Group aggression confers such a huge winning edge against single competitors that, once it entered the arms race of sexual selection, kin selection instantly forged it into the most serious weapon in any male's behavioral arsenal" (Ghiglieri [76]).

of weapons but the adequacy of team work, organization, and command working along certain simple [tactical] principles". Thus armies have been characterized by increasing hierarchization of command structure, fighting phalanx-type battles of ever increasing size, and campaigns for plunder, territorial aggrandizement, and political subordination: power, supremacy, and empire.

Discipline and coordination in battle provide the watershed between warrior and soldier. The psychology of the warrior gave way in western history when warfare changed from guerrilla-like raids and ambushes to massive battle formations: "The first phalanx might have comprised a small elite group of fighting men and assured these specialists in warfare of success in the works of Ares. But the phalanx implies a radical transformation of the warrior ethos: Collective discipline takes the place of individual exploits and *sophrosune*, self-discipline takes the place of *menos*, the state of warrior frenzy" (Vernant [147]). But if contemporary terrorism, guerrilla warfare, warlordism and 'low-level conflict' would prove to be indeed the threats they are said to constitute since World War II, and especially since September 11, 2001, then we may be going 'back to the future'.

War has become an increasingly maladaptive and cost/benefit suboptimal solution to political problems, but will in this century probably be waged for scarce resources, particularly sweet water, oil, 'security' and 'ethnic nationalism' (secessionist, irredentist and ethnonational or ethnopolitical wars are, and probably will be, mainly intranational).

Thus, the means of production, the means of reproduction, and the means of destruction have largely shaped, and will continue to shape human sociocultural evolution (Schmookler [148], Ehrenreich, Sanderson).

BIBLIOGRAPHY

1 Mead M. Warfare is only an invention, not a biological necessity. Asia 1940; **40**:402–5.
2 Harris M. (1971) Ecology, demography and war. Chapter in: Harris M. Culture, man and nature. New York: Thomas Crowell; 1971.
3 Harris M. Warfare old and new. Nat. Hist. 1972; **81**:18–20.
4 Harris M. Cows, pigs, wars and witches: the riddles of culture. New York: Random House, 1974.
5 Harris M. (1975) Culture, man and nature. 2nd ed. New York: Thomas Crowell; 1975.
6 Harris M. Cannibals and kings: the origins of cultures. New York: Random House; 1977. New York: Vintage Books; 1978.
7 Harris M. The Yanomamö and the cause of war in band and village societies. In: Margolis M Carter W, editors. Brazil: an anthropological perspective. essays in honor of Charles Wagley, New York: Columbia Univ Press; 1979. p.121–32.
8 Harris M. Culture, people, nature: an introduction to general anthropology. 3rd ed. New York: Harper & Row; 1980.
9 Harris M. A cultural materialist theory of band and village warfare: the Yanomamo test. In: Ferguson RB, editor. Warfare, culture and environment. New York: Academic Press; 1984. p.111–40.
10 Harris M. Animal capture and Yanomamö warfare: retrospect and new evidence. J Anthropol Res 1984; **40**:183–201.
11 Ferguson RB. Introduction: studying war. In: Ferguson RB, editor. Warfare, culture and environment. New York: Academic Press; 1984. p.1–81.
12 Ferguson RB. Do Yanomamo killers have more kids? Amer Ethnol 1989; **16**:564–5.
13 Ferguson RB. Explaining war. In: Haas J, editor. The anthropology of war. Cambridge: Cambridge Univ Press; 1990. p.26–55.
14 Ferguson RB. A savage encounter: Western contact and the Yanomami war complex. In: Ferguson RB Whitehead NL, editors. War in the tribal zone: expanding states and indigenous warfare. Santa Fe: School of American Research; 1992. p.199–228.
15 Ferguson RB. The general consequences of war: an Amazonian perspective. In: Reyna SP Downs RD, editors. Studying war: anthropological perspectives. New York: Gordon & Breach; 1994. p.85–112.
16 Ferguson RB. Yanomami warfare: a political history. Santa Fe: School for American Research Press; 1995.
17 Ferguson RB. Anthropological perspectives on war. Paper for 'Study of War' volume, Triangle Inst for Security Studies, 1998.
18 Ferguson RB. The causes and origins of 'primitive warfare': on evolved emotions for war. Anthropol Quart 2000; **73**:159–64.
19 Ferguson RB. Materialist, cultural and biological theories on why Yanomami make war. In: Reyna SP Wilson RA, editors. Anthropological theory. Vol. 1, Sage; 2001. p.99–116.
20 Ferguson RB, Whitehead NL, editors. War in the tribal zone: expanding states and indigenous warfare. Santa Fe: School of American Research; 1992.
21 Keeley LH. War before civilization: the myth of the peaceful savage. New York: Oxford Univ Press; 1996.
22 Sanderson SK. The evolution of human sociality: a darwinian conflict perspective. Lanham: Rowman & Littlefield; 2001.
23 Corning PA. An evolutionary paradigm for the study of human aggression. In: Nettleship MA Givens RD Nettleship A, editors. War, its causes and correlates. The Hague: Mouton; 1975. p.359–87.
24 Meyer P. Kriegs- und Militärsoziologie. München: Goldmann; 1977.
25 Meyer P. Evolution und Gewalt. Ansätze zu einer bio-soziologischen Synthese. Hamburg: Parey Verlag; 1981.
26 Meyer P. Human nature and the function of war in social evolution: a critical review of the naturalistic fallacy. In: Van der Dennen JMG Falger VSE, editors. Sociobiology and conflict: evolutionary perspectives on competition, cooperation, violence and warfare. London: Chapman and Hall; 1990. p.227–40.
27 Meyer P. The evolution of warfare: origins of cultural variation. In: Cauchy V, editor. Violence and human coexistence. Montréal: Editions Montmorency; 1995. p.16–22.
28 Low BS. An evolutionary perspective on war. In: Zimmerman W Jacobson HK, editors. Behavior, culture, and conflict in world politics. Ann Arbor: Univ. of Michigan Press; 1993. p.13–56.
29 Low BS. Why sex matters: a darwinian look at human behavior. Princeton: Princeton Univ Press; 2000.
30 Van der Dennen JMG. The origin of war: the evolution of a male-coalitional reproductive strategy. Groningen: Origin Press; 1995.
31 Cioffi-Revilla C. Origins and evolution of war and politics. Internat Stud Quart 1996; **40**:1–22.
32 Goodall J. The chimpanzees of Gombe: patterns of behavior. Cambridge (MA): Harvard Univ Press; 1986/1987.
33 Manson JH, Wrangham RW. Intergroup aggression in chimpanzees and humans. Current Anthropol 1991; **32**:369–77.
34 Wrangham RW. Evolution of coalitionary killing. Yearbook Phys Anthropol 1999; **42**:1–30.

35 Wrangham RW, Peterson D. Demonic males: apes and the origins of human violence. Boston: Houghton Mifflin; 1996.
36 Cheney DL. Interactions and relationships between groups. In: Smuts BB Cheney DL Seyfarth RM Wrangham RW Struhsaker TT, editors. Primate societies. Chicago: Univ Chicago Press; 1987. p.267–81.
37 Darwin CR. The descent of man, and selection in relation to sex. London: Murray; 1871.
38 Bigelow R. The dawn warriors: man's evolution towards peace. Boston: Little, Brown; 1969.
39 Bigelow R. The role of competition and cooperation in human aggression. In: Nettleship MA Givens RD Nettleship A, editors. War, its causes and correlates. The Hague: Mouton; 1975. p.235–61.
40 Corning PA. The synergism hypothesis: a theory of progressive evolution. New York: McGraw-Hill; 1983.
41 Corning PA. Synergy goes to war: an evolutionary theory of collective violence. Paper Conference Association for Politics and the Life Sciences; Oct 18–21, 2001; Charleston, USA.
42 Slurink P. Ecological dominance and the final sprint in hominid evolution. Human Evol 1993; **8**:265–73.
43 Van Hooff JARAM. Intergroup competition and conflict in animals and man. In: Van der Dennen JMG Falger VSE, editors. Sociobiology and conflict: evolutionary perspectives on competition, cooperation, violence and warfare. London: Chapman and Hall; 1990. p.23–54.
44 Van der Dennen JMG. Ethnocentrism and in-group/out-group differentiation: a review and interpretation of the literature. In: Reynolds V Falger VSE Vine I, editors. The sociobiology of ethnocentrism: evolutionary dimensions of xenophobia, discrimination, racism and nationalism. London: Croom Helm; 1987. p.1–47.
45 Van der Dennen JMG. Origin and evolution of 'primitive' warfare. In: Van der Dennen JMG Falger VSE, editors. Sociobiology and conflict: evolutionary perspectives on competition, cooperation, violence and warfare. London: Chapman and Hall; 1990. p.149–88.
46 Van der Dennen JMG. Of badges, bonds and boundaries: in-group/out-group differentiation and ethnic conflict revisited. In: Thienpont K Cliquet R, editors. In-group/out-group behaviour in modern societies: an evolutionary perspective. Brussels: NIDI GBGS Publ; 1999. p.37–74.
47 Van der Dennen, JMG. The origins of war: evolution and intergroup violence in animals and man. Westport CT: Greenwood Press; f.c.
48 Van der Dennen JMG, Falger VSE, editors. Sociobiology and conflict: evolutionary perspectives on competition, cooperation, violence and warfare. London: Chapman and Hall; 1990.
49 Van der Dennen JMG, Smillie D, Wilson DR, editors. The darwinian heritage and sociobiology. Westport CT: Praeger/Greenwood Press; 1999.
50 Gat A. The pattern of fighting in simple, small-scale, pre-state societies. J Anthropol Res 1999; **55**:563–83.
51 Gat A. The human motivational complex: evolutionary theory and the causes of hunter-gatherer fighting. Part 1: Primary somatic and reproductive causes; Part 2: Proximate, subordinate, and derivative causes. Anthropol Quart 2000; **73**:20–34; **73**:74–88.
52 Gat A. The causes and origins of 'primitive warfare': reply to Ferguson. Anthropol Quart 2000; **73**:165–8.
53 Davie MR. The evolution of war: a study of its role in early societies. New Haven: Yale Univ Press; 1929.
54 Turney-High HH. Primitive war: its practice and concepts. Columbia: Univ. South Carolina Press; 1949/1971.
55 Divale WT. Warfare in primitive societies: a bibliography. Santa Barbara: Clio Press; 1973.
56 Otterbein KF. Clan and tribal conflict. In: Kurtz LR, editor. Encyclopedia of violence, peace, and conflict. Vol. 1. San Diego: Academic Press; 1999. p.289–96.
57 Tooby J, Cosmides L. The evolution of war and its cognitive foundations. Proc Inst Evol Studies 1988; **88**:1–15.
58 Malagon-Fajar M. Hubris, warriors and evolution. Paper US Army War College, Carlisle Barracks, 1999.
59 Durham WH. Resource competition and human aggression. Part 1: A review of primitive war. Quart Rev Biol 1976; **51**:385–415.
60 Durham WH. Towards a coevolutionary theory of human biology and culture. In: Chagnon NA Irons W, editors. Evolutionary biology and human social behavior: an anthropological perspective. North Scituate: Duxbury Press; 1979. p.39–58.
61 Van der Dennen JMG. The politics of peace in preindustrial societies: the adaptive rationale behind corroboree and calumet. In: Falger VSE Meyer P van der Dennen JMG, editors. Sociobiology and politics. Research in biopolitics, Vol. 6. Stamford CT: JAI Press; 1998. p.159–192. Also in: Eibl-Eibesfeldt I Salter FK, editors. Indoctrinability, ideology and warfare: evolutionary perspectives. New York: Berghahn Books; 1998. p.151–185.
62 Van den Berghe PL. The ethnic phenomenon. New York: Elsevier; 1981.
63 Reynolds, V, Falger VSE, Vine I, editors. The sociobiology of ethnocentrism: evolutionary dimensions of xenophobia, discrimination, racism and nationalism. London: Croom Helm; 1987.
64 Shaw RP, Wong Y. Genetic seeds of warfare: evolution, nationalism, and patriotism. London: Unwin Hyman; 1989.
65 Hamilton WD. Selection of selfish and altruistic behavior in some extreme models. In: Eisenberg JF Dillon WS, editors. Man and beast: comparative social behavior. Washington DC: Smithsonian Inst Press; 1971. p.57–92.
66 Hamilton WD. Innate social aptitudes of man: an approach from evolutionary genetics. In: Fox R, editor. Biosocial anthropology. London: Dent; 1975. p.133–55.
67 Hamilton WD. The evolution of social behaviour: Vol. 1. Narrow roads of gene land. Oxford: Freeman; 1996.
68 Irwin CJ. The Inuit and the evolution of limited group conflict. In: Van der Dennen JMG Falger VSE, editors. Sociobiology and conflict: evolutionary perspectives on competition, cooperation, violence and warfare. London: Chapman and Hall; 1990. p.189–226.
69 Wilson EO. Sociobiology: the new synthesis. Cambridge (MA): Harvard Univ Press; 1975.
70 Wilson EO. On human nature. Cambridge MA: Harvard Univ. Press; 1978.
71 Symons D. The evolution of human sexuality. Oxford: Oxford Univ Press; 1979.
72 Trivers RL. Social evolution. Menlo Park: Benjamin/Cummings; 1985.
73 Dow J. Women capture as a motivation for warfare: a comparative analysis of intra-cultural variation and a critique of the male supremacist complex. In: Dyson-Hudson R Little M, editors. Rethinking human adaptation: biological and cultural models. Boulder: Westview Press; 1983. p.97–115.
74 Ghiglieri MP. Sociobiology of the great apes and the hominid ancestor. J Human Evol 1987; **16**:319–58.
75 Ghiglieri MP. War among the chimps. Discover 1987; **8**:67–76.
76 Ghiglieri MP. The dark side of man: tracing the origins of male violence. Reading (MA): Perseus Books; 1999.
77 Borgia G. Human aggression as a biological adaptation. In: Lockard JS, editor. The evolution of human social behavior. Amsterdam: Elsevier; 1980. p.150–85.
78 Melotti U. The origin of human aggression: a new evolutionary view. The Mankind Quart 1984; **24**:379–92.
79 Melotti U. Competition and cooperation in human evolution. The Mankind Quart 1985; **25**:323–51.
80 Melotti U. On the evolution of human aggressiveness. In: Wind J Reynolds V, editors. Essays in human sociobiology. Brussels: VUB Press; 1986. p.69–82.

81 Melotti U. War and peace in primitive human societies. In: Van der Dennen JMG Falger VSE, editors. Sociobiology and conflict: evolutionary perspectives on competition, cooperation, violence and warfare. London: Chapman and Hall; 1990. p.241–46.
82 Alexander RD. The search for an evolutionary philosophy of man. Proc Roy Soc Victoria 1971, **84**:99–120.
83 Alexander RD. The evolution of social behavior. Ann Rev Ecol & Syst 1974; **5**:325–83.
84 Alexander RD. Natural selection and the analysis of human sociality. Changing Scenes in the Natural Sciences 1977; **12**:283–337.
85 Alexander RD. Darwinism and human affairs. Seattle: Univ Washington Press; 1979.
86 Alexander RD. The biology of moral systems. New York: Aldine; 1987.
87 Alexander RD. How did humans evolve: reflections on the uniquely unique species. Michigan Mus Zool, Spec Publ, 1, 1990.
88 Alexander RD, Borgia G. Group selection, altruism, and the levels of hierarchical organization of life. Ann Rev Ecol & Syst 1978; **9**:449–74.
89 Alexander RD, Tinkle DW. A comparative review. Biosci 1968; **18**:245–8.
90 Alexander RD, Tinkle DW, editors. Natural selection and social behavior: recent research and new theory. Ann Arbor: Univ Michigan Press; 1981.
91 Pitt R. Warfare and hominid brain evolution. J Theoret Biol 1978; **72**:551–75.
92 McEachron DL, Baer D. A review of selected sociobiological principles: application to hominid evolution II: The effects of intergroup conflict. J Soc & Biol Structures 1982; **5**:121–139.
93 Baer D, McEachron DL. A review of selected sociobiological principles: application to hominid evolution I: The development of group social structure. J Soc & Biol Structures 1982; **5**:69–90.
94 Richerson PJ. Warfare. Ch. 19 of Richerson's Human Ecology course at the Univ of California at Davis, 1995.
95 Bingham PM. Human uniqueness: a general theory. Quart Rev Biol 1999; **74**:133–69.
96 Chagnon NA. Yanomamö: the fierce people. New York: Holt, Rinehart & Winston; 1968.
97 Chagnon NA. Response to Marvin Harris 'Protein theory of warfare'. Psychol Today 1975; **8**:6–7.
98 Chagnon NA. Yanomamö: the fierce people (2nd and 3rd expanded eds). New York: Holt, Rinehart & Winston; 1977/1983.
99 Chagnon NA. Life histories, blood revenge, and warfare in a tribal population. Sci 1988; **239**:985–92.
100 Chagnon NA. Reproductive and somatic conflicts of interest in the genesis of violence and warfare among tribesmen. In: Haas J, editor. The anthropology of war. Cambridge: Cambridge Univ Press; 1990. p.77–104.
101 Chagnon, NA. Chronic problems in understanding tribal violence and warfare. In: Bock GR Goode JA, editors. Genetics of criminal and antisocial behavior. New York: Wiley; 1996. p.202–36.
102 Hawkes, K. (1991) Showing off: tests of an hypothesis about man's foraging goals. Ethol & Sociobiol 1991; **12**:29–54.
103 Staden H. Wahrhaftige Historia und Beschreibung eyner Landtschafft der wilden nacketen grimmigen Menschfresser Leuthen in der Newenwelt Amerika gelegen, etc. (facsimile of original 1557). Frankfurt a.M.: Verlag Wuesten, 1925.
104 Ferguson A. An essay on the history of civil society. Reprint ed (orig 1767). Chicago: Aldine, 1966.
105 Hobbes T. Leviathan; or, the matter, form and power of a commonwealth, ecclesiastical and civil. London: Crooke; 1651.
106 Rousseau JJ. Le contrat social ou principes du droit politique. Amsterdam: MM Rey; 1762 (The Social Contract. New York: Harper, 1957).
107 Darwin CR. The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. London: Murray; 1859.
108 Spencer H. The principles of sociology. 3 Vols. London: Williams & Norgate; 1876/1885. New York: Appleton, 1912.
109 Morgan LH. Ancient society: or researches in the lines of human progress from savagery through barbarism to civilization. New York: Holt; 1877 (reprint: Tucson: Univ Arizona Press).
110 Tylor EB. Primitive culture; Part 1: The origins of culture. London: Murray; 1871/1874.
111 Steward JH. Theory of culture change: the methodology of multilinear evolution. Urbana: Univ Illinois Press; 1955.
112 Sahlins MD. The segmentary lineage: an organization of predatory expansion. Amer Anthropol 1961; **63**:22–45.
113 Sahlins MD. On the sociology of primitive exchange. In: Banton M, editor. The relevance of models for social anthropology. London: Tavistock; 1965. p.139–237.
114 Sahlins MD. Tribesmen. Englewood Cliffs: Prentice Hall; 1968.
115 Sahlins MD, Service ER, editors. Evolution and culture. Ann Arbor: Univ Michigan Press; 1960.
116 Service ER. The Hunters. Englewood Cliffs: Prentice Hall; 1966.
117 Service ER. War and our contemporary ancestors. In: Fried MH Harris M Murphy R, editors. War: the anthropology of armed conflict and aggression. New York: Natural History Press; 1968. p.160–67.
118 Service ER. Origins of the state and civilization: the process of cultural evolution. New York: Norton; 1975.
119 Muehlmann WE. Krieg und Frieden. Ein Leitfaden der politischen Ethnologie. Heidelberg: C.Winters Universitätsbuchhandlung; 1940.
120 Fried MH. Warfare, military organization, and the evolution of society. Anthropologica 1961, **3**:134–47.
121 Fried MH. The evolution of political society: an essay in political anthropology. New York: Random House; 1967.
122 Fried MH, Harris M, Murphy R, editors. War: the anthropology of armed conflict and aggression. New York: Natural History Press; 1968.
123 Hunter DE, Whitten P. The study of anthropology. New York: Harper & Row; 1976.
124 Wright Q. A study of war. Chicago: Univ of Chicago Press; 1942.
125 Feest CF. The art of war. London: Thames & Hudson; 1980.
126 Andreski S. Military organization and society. London: Routledge & Kegan Paul; 1954. Berkeley: Univ California Press; 1968.
127 Andreski S. Origins of war. In: Carthy JD Ebling FJ, editors. The natural history of aggression. New York: Academic Press; 1964. p.129–36.
128 Carneiro RL, editor. The evolution of society. Chicago: Univ Chicago Press; 1967.
129 Carneiro RL. A theory of the origin of the state. Sci 1970; **169**:733–8.
130 Carneiro RL. Political expansion as an expression of the principle of competitive exclusion. In: Cohen R Service ER, editors. Origins of the state: the anthropology of political evolution. Philadelphia: Inst. Study Human Issues; 1978. p.205–23.
131 Carneiro RL. Chiefdom-level warfare as exemplified in Fiji and the Cauca Valley. In: Haas J, editor. The anthropology of war. Cambridge: Cambridge Univ Press; 1990, p.190–211.
132 Hobhouse LT, Wheeler G, Ginsberg M. The material culture and social institutions of the simpler peoples. London: London School of Economics Monogr on Sociol 3, 1915.
133 Van der Bij TS. Ontstaan en eerste ontwikkeling van den oorlog [Origin and initial development of war]. Groningen: Wolters; 1929.
134 Steinmetz SR. Philosophie des Krieges. Leipzig: JA Barth; 1907.
135 Steinmetz SR. Soziologie des Krieges. Leipzig: JA Barth; 1929.
136 Vayda AP. Expansion and warfare among swidden agriculturists. Amer Anthropol 1961; **63**:346–58.

137 Vayda AP. Research on the functions of primitive war. Peace Res Soc (Internat) Papers 1967; **7**:133–8.
138 Vayda AP. Hypotheses about functions of war. In: Fried MH Harris M Murphy R, editors. War: the anthropology of armed conflict and aggression. New York: Natural History Press; 1968. p.85–91.
139 Vayda AP. Phases of the process of war and peace among the Marings of New Guinea. Oceania 1971; **42**:1–24.
140 Vayda AP. Warfare in ecological perspective. Ann Rev Ecol & Syst 1974; **5**:183–93.
141 Vayda AP. War in ecological perspective: persistence, change, and adaptive processes in three Oceanian societies. New York: Pergamon Press; 1976/1979.
142 Vayda AP. Explaining why Marings fought. J Anthropol Res 1989; **45**:159–77.
143 Vayda AP, Leeds A. Anthropology and the study of war. Anthropologica 1961; **3**:131–4.
144 Leeds A. The functions of war. In: Masserman JH, editor. Violence and war with clinical studies. New York: Grune & Stratton; 1963. p.69–82.
145 Ember CR. Myths about hunter-gatherers. Ethnol 1978; **17**: 439–48.
146 Broch T, Galtung J. Belligerence among the primitives: A reanalysis of Quincy Wright's data. J Peace Res 1966; **3**:33–45.
147 Vernant JP. Myth and society in ancient Greece. New York: Zone Books; 1990.
148 Schmookler AB. The parable of the tribes: the problem of power in social evolution. Berkeley: Univ California Press; 1984.
149 Boas F. An anthropologist's view of war. International conciliation pamphlet No. 52, 1912.
150 Dewey J. Human nature and conduct. New York: Holt; 1922.
151 Benedict R. Patterns of culture. New York: Mentor Books; 1934.
152 McNeill WH. Plagues and peoples. Garden City: Anchor/ Doubleday; 1976.
153 Boulding KE. Ecodynamics: a new theory of societal evolution. Beverly Hills: Sage; 1978.
154 Leakey RE, Lewin R. Origins: what new discoveries reveal about the emergence of our species and its possible future. New York: Dutton; 1977.
155 Schneider J. Primitive warfare: a methodological note. Amer Sociol Rev 1950; **15**:772–7.
156 Schneider J. On the beginnings of warfare. Social Forces 1952; **26**:68–74.
157 Schneider J. Is war a social problem? J Confl Resol 1959; **3**:353–60.
158 White LA. The science of culture: a study of man and civilization. New York: Farrar, Straus & Cudahy; 1949.
159 Bronowski J. The ascent of man. Boston: Little, Brown; 1973.
160 Starr CG. A history of the ancient world. New York: Oxford Univ Press; 1974.
161 Dyer G. War. New York: Crown; 1985.
162 Dawson D. The origins of war: biological and anthropological theories. History & Theory 1996; **35**:1–28.
163 Wittfogel KA. Oriental despotism: a comparative study of total power. New Haven: Yale Univ Press; 1957.
164 Sumner WG. Folkways: a study of the sociological importance of usages, manners, customs, mores and morals. Boston: Ginn; 1906.
165 Sumner WG. War and other essays. New Haven: Yale Univ Press; 1911.
166 Sumner WG, Keller AG. The science of society. 4 Vols. New Haven: Yale Univ Press; 1927.
167 Lathrap DW. The upper Amazon. New York: Praeger; 1970.
168 Leeds A. Capitalism, colonialism and war: An evolutionary perspective. In: Nettleship MA Givens RD Nettleship A, editors. War, its causes and correlates, The Hague: Mouton; 1975. p.483–514.
169 Leeds A, Vayda AP. Man, culture and animals. Washington: Publ Amer Assoc Adv Sci 78, 1965.
170 Hallpike CR. Functionalist interpretations of primitive warfare. Man 1973; **8**:451–70.
171 Divale WT. An explanation for primitive warfare: population control and the significance of primitive sex ratios. The New Scholar 1970; **2**:173–92.
172 Divale WT. Migration, external warfare, and matrilocal residence: an explanation for matrilineal residence systems. Behav Sci Res 1974; **9**:75–133.
173 Divale, WT, Harris M. Population, warfare, and the male supremacist complex. Amer Anthropol 1976; **78**:521–38.
174 Divale WT, Harris M. The male supremacist complex: discovery of a cultural invention. Amer Anthropol 1978; **80**:668–71.
175 Divale WT, Chamberis F, Gangloff D. War, peace, and marital residence in pre-industrial societies. J Confl Resol 1976; **20**:57–78.
176 Malinowski B. An anthropological analysis of war. Amer J Sociol 1941; **46**:521–50.
177 Otterbein KF. The anthropology of war. In: Honigmann JJ, editor. Handbook of social and cultural anthropology. New York: Rand McNally; 1973, p.923–58.
178 Otterbein KF. Warfare, territorial expansion, and cultural evolution. Amer Ethnol 1976; **3**:825–7.
179 Otterbein KF. The evolution of war: a cross-cultural study. 2nd. ed. New Haven: HRAF; 1985.
180 Otterbein KF. The anthropology of feuding and warfare: selected works by Keith F. Otterbein. New York: Gordon & Breach; 1994.
181 Otterbein KF. The origins of war. Critical Rev 1997; **11**:251–77.
182 Naroll R, Divale WT. Natural selection in cultural evolution: warfare versus peaceful diffusion. Amer Ethnol 1976; **3**:97–128.
183 Knauft BM. Reconsidering violence in simple human societies: homicide among the Gebusi on New Guinea. Current Anthropol 1987; **28**:457–500.
184 Knauft BM. Violence and sociality in human evolution. Current Anthropol 1991; **32**:391–409.
185 Knauft BM. Culture and cooperation in human evolution. In: Sponsel LE Gregor T, editors. The anthropology of peace and nonviolence. Boulder: Lynne Rienner; 1994. p.37–68.
186 Boehm C. Hierarchy in the forest: the evolution of egalitarian behavior. Cambridge MA: Harvard Univ Press; 1999.
187 Newcomb WW. A re-examination of the causes of Plains warfare. Amer Anthropol 1950; **52**:317–30.
188 Robarchek CA. Primitive warfare and the ratomorphic image of mankind. Amer Anthropol 1989; **91**:903–20.
189 Robarchek CA. Motivations and material causes: on the explanation of conflict and war. In: Haas J, editor. The anthropology of war. Cambridge: Cambridge Univ Press; 1990. p.56–76.
190 Kelly RC. Warless societies and the origin of war. Ann Arbor: Univ Michigan Press; 2000.
191 Lopreato J. Human nature and biocultural evolution. Boston: Allen & Unwin; 1984.
192 Tinbergen N. On war and peace in animals and man. Sci 1968; **160**:1411–8.
193 Tinbergen N. On the history of war. In Valzelli L Morgese L, editors. Aggression and violence: a psychobiological and clinical approach. Saint Vincent: Edizioni Centro Culturale; 1981, p.31–38.
194 Holsti R. The relation of war to the origin of the state. Helsingfors: Annales Academiae Scientiarum Fennicae 1913; **13** (whole issue).
195 Alcock N. The war disease. Oakville: Canadian Peace Research Inst Press; 1972.
196 James W. Principles of psychology. New York: Holt; 1890.
197 James W. The moral equivalent of war. In: James W. Memories and studies. New York: Longmans, Green & Co; 1910. Reprinted in: Bramson L, Goethals G, editors. War: studies from psychology, sociology, anthropology. New York: Basic Books; 1968. p.21–31.

198 Frobenius L. Menschenjagden und Zweikämpfe. Jena: Thüringer Verlagsanstalt; 1914.
199 Washburn SL, Lancaster CS. The evolution of hunting. In: Lee RB DeVore I, editors. Man the hunter, Chicago: Aldine Atherton; 1968. p.293–303.
200 Lee RB, DeVore I, editors. Man the hunter. Chicago: Aldine; 1968.
201 Pfeiffer JE. The emergence of man. New York: Harper & Row; 1972.
202 Dart RA. The predatory transition from ape to man. Internat Anthropol Linguist Rev 1953; **1**:201–19.
203 Dart RA. Adventures with the missing link. New York: Harper & Brothers; 1959.
204 Ardrey R. The hunting hypothesis. New York: Atheneum; 1976.
205 McDougall W. An introduction to social psychology. London: Methuen; 1908. Boston: Luce; 1915.
206 Scott JP. The relationship between hunting, predation, and agonistic behavior. Paper Conference International Society for Research on Aggression (ISRA); July, 1980; Haren, the Netherlands
207 Lorenz K. On aggression. London: Methuen; 1966. New York: Bantam Books: 1967 (orig. Das sogenannte Böse. Zur Naturgeschichte der Aggression. Wien: Borotha-Schoeler Verlag, 1963).
208 Keith A. A new theory of human evolution. London: Watts; 1948.
209 Masters RD. The biological nature of the state. World Politics 1983; **35**:161–93.
210 Eibl-Eibesfeldt I. Liebe und Haß, Zur Naturgeschichte elementarer Verhaltensweisen. München: Piper Verlag; 1970.
211 Eibl-Eibesfeldt I. Krieg und Frieden aus der Sicht der Verhaltensforschung. München: Piper Verlag; 1975.
212 Eibl-Eibesfeldt I. Die Evolution der destruktiven Aggression aus der Sicht der Verhaltensforschung. Beiträge zur Konfliktforschung 1978; **8**:87–111.
213 Eibl-Eibesfeldt I. Warfare, man's indoctrinability and group selection. Z f Tierpsychologie 1982; **60**:177–98.
214 Eibl-Eibesfeldt I, Salter FK, editors. Indoctrinability, ideology, and warfare: evolutionary perspectives. New York: Berghahn; 1998.
215 Boyd R, Richerson PJ. Culture and the evolutionary process. Chicago: Univ. Chicago Press; 1985.
216 Richerson PJ, Boyd R. The evolution of human ultra-sociality. In: Eibl-Eibesfeldt I Salter FK, editors. Indoctrinability, ideology and warfare: evolutionary perspectives. New York: Berghahn Books; 1998, p.71–98.
217 Lumsden CJ, Wilson EO. Genes, mind, and culture: the coevolutionary process. Cambridge (MA): Harvard Univ Press; 1981.
218 Lumsden CJ, Wilson EO. Promethean fire: reflections on the origin of mind. Cambridge (MA): Harvard Univ. Press; 1983.
219 Falger VSE. Evolution and politics: biopolitical essays. Groningen: Origin Press; 1994.
220 Thienpont K, Cliquet R, editors. In-group/out-group behaviour in modern societies: an evolutionary perspective. Brussels: NIDI CBGS Publ; 1999.
221 Tiger L. Men in groups. London: Panther; 1971.
222 Tiger L. The cerebral bridge from family to foe. In: Van der Dennen JMG Falger VSE, editor. Sociobiology and conflict: evolutionary perspectives on competition, cooperation, violence and warfare. London: Chapman and Hall; 1990. p.99–106.
223 Tiger L, Fox R. The imperial animal. New York: Holt, Rinehart & Winston; 1971. 2nd rev ed; 1989.
224 Goldstein JS. War and gender: how gender shapes the war system and vice versa. Cambridge: Cambridge Univ Press; 2001.
225 Adams DB. Why are there so few women warriors? Behavioral Science Research 1983; **18**:196–212.
226 Ehrenreich B. Blood rites: origins and history of the passions of war. New York: Metropolitan Books; 1997.
227 Kroeber CB, Fontana BL. Massacre on the Gila: an account of the last major battle between American Indians, with reflections on the origin of war. Tucson: Univ Arizona Press; 1986.

Sex Hormones Influence Human Cognitive Pattern

Doreen Kimura
Department of Psychology, Simon Fraser University, CANADA.

Correspondence to: Doreen Kimura
Department of Psychology, Simon Fraser University
Burnaby BC, CANADA V5A 1S6
PHONE: (604) 291-3356
FAX: (604) 291-3427
EMAIL: dkimura@sfu.ca

Submitted: *August 28, 2002*
Accepted: *September 5, 2002*

Key words: **sex hormones; cognition; spatial; verbal; motor**

Neuroendocrinology Letters 2002; ***23****(Suppl.4):67–77 pii: NEL231002R07 Copyright © Neuroendocrinology Letters* ***www.nel.edu***

Abstract The major sex differences in cognitive skills are summarized, and the role of sex hormones in early organization and possible maintenance of these differences is discussed. Using animal models and human hormonal anomalies, a good case can be made that prenatal androgens strongly influence adult cognitive pattern, though the relation between baseline androgens and spatial ability, for example, need not be linear. Moreover, men and women remain sensitive to variation in hormonal state, as evidenced in the fluctuations in cognitive and motor performance across natural diurnal, menstrual and circannual rhythms. Evidence from administration of exogenous hormones in humans is more equivocal, though this field ultimately should yield useful information.

Overview of Cognitive Sex Differences

Sex differences in human problem-solving behaviour have been reliably found across many studies over the past few decades, and in several cultures. The major findings are summarized in Table I. The list is not exhaustive, but men and women clearly display different cognitive strengths, hence different *patterns* of ability. It must be kept in mind that these are *average* differences, and that the overlap between the sexes on many tests is extensive. Predicting an individual's performance level based on sex alone would be highly inaccurate.

Table I. Some abilities favouring men and women, respectively

PROBLEM-SOLVING TASKS FAVOURING MEN	PROBLEM-SOLVING TASKS FAVOURING WOMEN
SPATIAL ORIENTATION – making a correction for a change in orientation of an object, e.g., "mental rotation"	**OBJECT LOCATION MEMORY** – recall of the location of objects in an array
VISUALIZATION – determining how a depicted object will appear when manipulated, e.g. folded	**PERCEPTUAL SPEED** – rapid identification of matching or designated items
LINE ORIENTATION – matching the slope of a line	**VERBAL MEMORY** – recall of a story, paragraph or list of unrelated words
MATHEMATICAL REASONING – solving a novel mathematical problem	**NUMERICAL CALCULATION** – adding, subtracting, etc., of given numbers
THROWING ACCURACY – hitting a distant target	**DEXTERITY** – manual tasks involving precision

REVIEW ARTICLE

Spatial Skills

Spatial skills on which men excel include both simple and complex abilities. Ability to match line orientations would generally be regarded as a simple task, in contrast to the ability to mentally rotate a complex figure [100]. The latter yields the largest currently known sex difference on a paper-and-pencil test. The average difference between men and women across many studies employing the test approaches a full standard deviation, or an "effect size" of approximately 1.0. [59, 67]. Effect size is calculated as the difference between two groups, divided by a measure of the variability within the groups (standard deviation). It is indirectly a measure of overlap between groups – the larger the effect size, the less the overlap. On most other spatial tests that favour males, such as tests of spatial visualization, the effect size is modest, nearer .5.

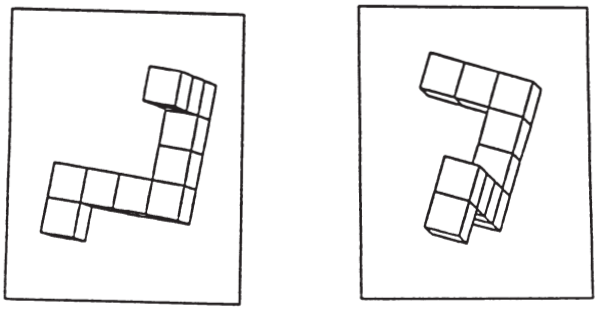


Figure 1. An example of a complex task requiring rotation in "three" dimensions. The subject must decide whether the two figures are the the same figure rotated, or are two different figures.

The Vandenberg Mental Rotations test, based on the Shepard and Metzler designs [91] (Figure 1), depicts complex 3-dimensional figures on a 2-dimensional page. However, the mental rotation of a figure in *three* dimensions is not a prerequisite for producing a large sex difference. Difficult figures requiring imaginal rotation in only two dimensions may yield an equally large effect size [14]. Performance on a mental rotation test has been found to be significantly related to performance on a route-finding task [23] and a computerized labyrinth [78], suggesting that such ability may contribute substantially to navigation.

A quite different spatial task, favouring women, is depicted in Figure 2. The subject is asked to indicate, from memory, which objects have changed locations from the first to the second array [18]. Other studies have confirmed a female advantage in processing the locations of multiple objects in an array [46, 69, 83]. However, when the task emphasizes location *per se*, regardless of object identity, women perform less well than men [43, 83], leading to the suggestion that women may use a common system to process object identity and location, whereas men do not [43, 46]. Such an interpretation would be consistent with findings that females tend more often to employ landmarks in navigating, in contrast to males' employment of geometric cues [105, 109].

Mathematical Abilities

School marks on mathematics tests may not show sex differences, or girls may even do better, as they do on most school subjects on average. However, when mathematical *aptitude* tests are given which are not simply variations of previously learned problems, and which therefore emphasize math reasoning, there is a consistent male advantage [60, 66]. On strictly calculation tests, females more often perform better.

The male advantage appears to increase with increasing difficulty or complexity of the problems; and males are over-represented at the high end of most math aptitude tests. In an extensive study in the United States spanning decades that identified mathematically talented youth, males have always outnumbered females [4, 61]. However, the preponderance of males is especially marked at the upper end of this population on the Scholastic Aptitude Test-Mathematics (SAT-M), by more than 10 to one.

On another very demanding mathematical reasoning test available to math-oriented North American undergraduates, the Putnam competition, male and female scores are also very divergent. In 1999, of the top 138 contestants, only five could be unequivocally identified (by name) as female. In a more recent competition in which sex of contestants was identified, there were again four times as many men as women taking the test, but 84% of women and 54% of men failed the test completely, that is, they got no score. 37.4% of men but only 11% of women got passing scores of 10 and higher.

So for many tests of ability, we must look not merely at the average difference, but at the extremes of the scores. Even when the average sex difference on any test is small, the extremes of the distribution may show a sharp divergence. For most professions, it is the upper end which is critical.

Verbal Skills

Although popular opinion holds that women are superior on most verbal tasks, this is not the case. The assumption probably stems from the earlier onset of fluent articulate speech in young girls [see 64 for an early review, 68]. In adults, however, reliable differences to date favouring women are found primarily on tasks of verbal memory [7, 55] and verbal fluency [19], not on vocabulary or verbal reasoning. Verbal fluency tests usually require the generation of words or sentences which have some constraint on the letters they contain, e.g., listing words that begin with a particular letter. Verbal memory taps the recall of material employing words, whether in lists or meaningful paragraphs, and whether the words are abstract or concrete. Verbal memory tests have shown the largest effect sizes so far of tests favouring women, in one study from .58 to .97 on recall of a word list [13].

Perceptual Skills

Women usually obtain better scores on tests which require rapid matching or identification of designated

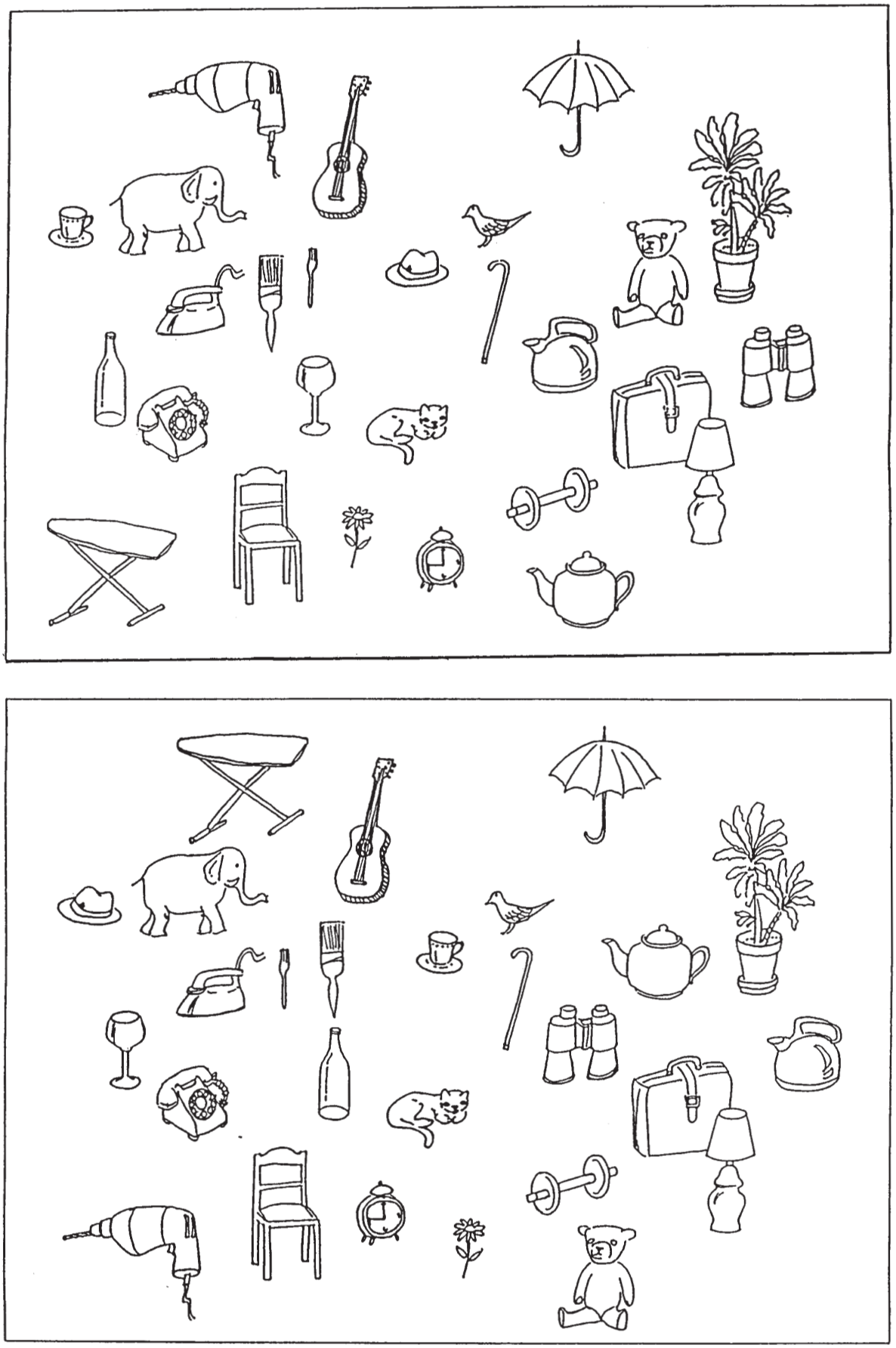


Figure 2. The object location memory task, from Silverman and Eals, 1992. Reproduced by permission of the authors. The top array is shown first and studied for one minute, followed by the bottom array. S indicates which objects have changed location.

Table II. Prepubertal sex differences in cognitive and motor function.

AUTHOR/ YEAR	AGES	FINDINGS
Rosser *et al.*, 1984	4–5	Boys better at spatial rotation
Vederhus & Krekling, 1996	9	Boys better on spatial tasks
Lunn, 1997	3–4	Boys better on targeting
Levine *et al.*, 1999	5–6	Boys better on spatial transformations, mazes
Denckla & Rudel, 1974	5–11	Girls faster at colour naming
Ingram, 1975	3–5	Girls better at copying hand postures
McGuinness *et al.*, 1990	7–10	Girls better memory for words

stimuli, labelled as "perceptual speed". Examples are Identical Pictures, and Finding a's from the ETS battery [19]. The differences between men and women are generally small, less than .5 effect size.

Motor Skills

A very large advantage for men is found on tasks that require hitting a target with a missile, or intercepting a moving target [48, 106, 107]. This advantage does not appear to depend simply on men's greater strength, nor on the their more active sports history. It appears to depend on the accurate co-ordination of spatial targets with large-amplitude aiming movements, but it is not significantly related to scores on paper-and-pencil spatial tasks on which men also excel [107]. The fact that homosexual men, whose physical build, sex of rearing and gender identity is male, throw less accurately on average than heterosexual men [31, 89] suggests that the male advantage is founded on a distinctive cognitive ability, rather than being reducible to somatic characteristics.

In contrast, women do better than men on small-amplitude fine motor skills, such as required on the Purdue Pegboard. Some studies have found this advantage to be related to women's smaller finger size but this is not so in other studies [e.g., 31]. Women also tend to be better at performing manual sequences, relative to their speed on the individual movements [80]; and this advantage is enhanced when performing without vision [12], suggesting that women's motor skills may be more closely related to intrapersonal than to extrapersonal neural systems.

Origins of Cognitive Sex Differences

Most researchers into cognitive sex differences view them as a product of our long evolutionary history as hunter-gatherers, in which men's and women's roles and hence their problem-solving abilities, became quite distinctive and complementary [18, 25,26, 51, but see 58 for an alternative view]. Men were assumed to be responsible for long-and-short-distance hunting and scavenging, travelling farther from the home base than women. They were also responsible for defence. Women, in contrast, were indispensable for infant and child care, and were active in caring for the home. Their contribution to foraging was generally limited to gathering or gleaning near the home.

These complementary roles are assumed to have put different selection pressures on the abilities of the two sexes. Men would be selected for navigational skills which employed geometric cues such as distance and direction (including the ability to correct for changes in direction), and to evolve motor skills directed more at distant targets. Women might be expected to evolve navigation skills employing local landmarks, and motor and perceptual skills appropriate to domestic activities and child care.

There are some nonhuman parallels to human cognitive sex differences, which bolster evolutionary interpretations. In polygynous vole species, in which the male's territory is larger than in monogamous species, males perform better than females on a maze learning task [24]. Male rats make fewer errors than females in a radial arm maze, and moreover the sexes employ different methods of solution [109]. Male baboons perform better on a mental rotation task [102], consistent with their navigational role in guiding the troop.

Whatever the ultimate determinants for human cognitive sexual differentiation, the evidence suggests that the proximate mechanisms have relied heavily on sex hormones, discussed later.

Sociological Hypotheses

In the past, social scientists have attributed cognitive differences between men and women almost entirely to differences in lifetime experience; and given our prior lack of knowledge of the effects of sex hormones, this may have been a defensible point of view. However, it has since emerged that some of these sex differences appear well before puberty and before large differences in experience (Table II); and they appear across cultures that differ in the activities available to men and women (Table III).

It might be expected, to the extent that sex differences are determined by lifetime experiences, that they should have declined in the last few decades. Such claims have indeed been made [21], but there are difficulties in comparing the heterogenous tests and heterogeneous populations over time. For example, the samples of people taking the tests over time has probably changed [32]. Moreover, some tests have been deliberately altered to dilute sex differences, by removing some items that differentiate the sexes.

We are on firmer ground comparing sex differences over different time periods when we know that the

same test has been used throughout, and that the samples we are comparing are equivalent. For example, sex differences on the Vandenberg Mental Rotation test have remained quite stable over the last three decades. We have already noted that this task shows a large sex difference, the effect size hovering around 1.0. Masters and Sanders [67] reviewed 14 studies employing the task between 1975 and 1992, nearly all on college students. Effect sizes varied from .69 to 1.27 across samples, but there was no systematic change across time. The 1975 study showed an effect size of 1.0, and the two most recent papers they cited found effects sizes of 1.27 and 1.14. We can add to that from our own studies – in 1997 we found an effect size of .86 [14], and in 1999, effect sizes of .98 and .90 in two samples [13]. In 2001 Geary and DeSoto found an effect size of approximately 1.06 [27].

Alternative methods of evaluating experiential contributions to sex differences in cognition have employed attempts at relating past activities which were rated as more spatial (e.g., skiing, building model planes), to current scores on a spatial visualization test [79]. A small but significant correlation was found. However, this kind of result does not allow us to determine whether life activities influence spatial ability, or the reverse. A review of studies in which men and women were given intensive practice on a variety of spatial tasks, to see whether women might be differentially advantaged by such practice (as might be expected if lack of past experience were the critical factor), reported negative findings. The sex differences were not erased with short-term intensive practice in adulthood [3].

Of course we would not conclude that life experience plays no role in the appearance of sex differences in cognition. However, it seems inevitable that such experience will manifest itself within the context of nervous systems already differently predisposed at birth.

Early Organizational Effects of Sex Hormones

Sexual Differentiation

Sex differences in cognitive pattern may be interpreted within the general context of mammalian sexual differentiation. The principles of differentiation of male and female structure and behaviour, derived primarily from non-human research, can also be applied, and tested, in the sphere of cognitive or problem-solving behaviours in humans.

The "simple" version of mammalian sexual differentiation [see 30] is that the undifferentiated or default form is the female, and that active processes, largely under control of androgens and their derivatives, are needed to produce a male. The story appears to be very well established for formation of genitalia and general physical type, and for some reproductive behaviours. It has also been convincingly applied to some non-reproductive behaviours, including rough-and-tumble-play and certain problem-solving activities.

Within this framework it has been proposed that there are critical developmental periods, prenatal and immediately postnatal, during which the action of androgens irreversibly masculinizes the brain. Some of these actions depend on the aromatization of testosterone to estrogen; hence the female brain is thought to be protected from such influence by the sequestering of estrogen by a substance called alpha-fetoprotein. Such early developmental influence is called "organizational". In adulthood, sex hormones are again required to activate the hormonally predisposed brain along male or female lines, as appropriate – called an activational influence. Some behaviours organized by androgens, such as rough-and-tumble play, need no further activational influence to appear.

Table III. Cross-cultural studies of sex differences.

AUTHOR/ YEAR	GROUPS COMPARED
Males better at math reasoning:	
Engelhard, 1990	USA & Thailand
Lummis & Stevenson, 1990	USA, China & Japan
Campbell, 1991	USA– Asian & Caucasian
Females better at computation:	
Jensen, 1988	USA – Blacks, Asians and Caucasians
Engelhard, 1990	USA & Thailand
Males better at spatial tasks:	
Chang & Antes, 1987	USA & Taiwan
Mann *et al*., 1990	USA & Japan
Owen & Lynn, 1993	South Africa – Blacks, Indians & Caucasians
Silverman *et al*., 1996	Canada & Japan
Geary & DeSoto, 2001	USA & China
Females better at verbal memory:	
Mann *et al*., 1990	USA & Japan
Owen & Lynn, 1993	South Africa – Blacks, Indians & Caucasians

Since this pioneering schema, the story has inevitably become more complex:

1) The line between organizational and activational influence has become less distinct, with suggestions that these phases overlap in their mechanisms of operation, if not in time [110].
2) Doubts have been raised about assumptions concerning the negligible role of ovarian hormones in organizing female behaviour [see 22 for review].
3) There is clearly variation in the critical hormone-sensitive time period for different behaviours [29], raising the possibility that early individual variation in timing of hormone surges also influences cognitive patterns.
4) It is unclear whether the demonstrated contribution to sexual differentiation by aromatization to estrogen in rodents, is as important in primates [99], including humans [98].
5) In addition to the genomic effects of hormones, acting through the cell nucleus to bind to DNA, and slowly taking effect, there are more immediate non-genomic effects acting on the cell membrane [70].

These considerations may all have a bearing on the interpretation of the role of sex hormones in human cognition. Generalizing from non-humans has provided useful models, but these must ultimately be assessed in humans. Such models can usually only be tested in people by means of naturally-occurring hormonal variation, or in hormonal anomalies, since the opportunity for manipulation of hormones for other than therapeutic purposes is very limited. However, since such anomalies are often the result of a genetic variant, it is sometimes difficult to rule out non-hormonal genetic influences.

Some of the naturally occurring hormonal anomalies studied in the context of cognitive makeup include congenital adrenal hyperplasia (CAH), androgen insensitivity (AI), idiopathic hyogonadotropic hypogonadism (IHH), and Turner's syndrome. Cognitive pattern has also been studied in relation to individual hormone levels across normal men and women, the underlying assumption being that there is a stable base which can vary from person to person.

Evidence for Organizational Hormone Effects on Cognition

The rodent model for organizational effects on problem-solving spatial abilities was presented in a study on rats [109]. Employing a radial maze with 12 arms, open at the top, with food placed consistently in eight of the 12 arms, normal males were found to locate all the food, over many trials, with fewer wrong choices than females. However, males that had been castrated right after birth, and thus had no or little circulating androgens, made more errors as adults than normal males; whereas females that had been injected with estradiol within 10 days of birth performed better than normal females. The authors suggest that the superior performance of males is related to early exposure of the brain to testosterone, presumably by conversion to estrogen. (In later work [108] it was demonstrated that similar hormonal manipulations after day 10 had no such effects.)

If after training the maze was surrounded by a circular curtain, so that the geometry of the room could no longer be used as a cue, the performance of normal males and hormone-treated females, but not of the other two groups, was negatively affected. Conversely, if after training no curtain was used, but the landmarks (pictures on the wall, furniture, etc) around the maze were moved, then the performance of only the normal females and the castrated males was negatively affected. Thus not only the overall performance, but also the cues that were used, were influenced by early hormonal manipulation.

Such studies can be performed in rodents because the brain continues to be susceptible to hormone influences in the first few days after birth, even though the genitals are already formed. No precisely analagous preparations, in whom hormonal disruption is limited to a period right after birth, exist in humans. Several human hormonal anomalies have resulted in prenatal, but due to surgical or therapeutic intervention, minimal anomalous postnatal influence of sex hormones (CAH, cloacal exstrophy, DES exposure). Others have had anomalies throughout their lives (IHH, AI). The former would of course be more informative about any early organizing effects on cognition.

The most compelling evidence for prenatal androgenic influences on cognition in humans comes from CAH cases, in whom high levels of androgens are produced by the adrenals before birth. The androgen overproduction is stopped by cortisol therapy after birth and any virilization of the genitals in females is repaired by surgery. The latter are raised as girls, and most of them are heterosexually oriented and marry men, though their interest in infants is lower than is the case in unaffected women [see 5 for review].

Of interest for cognitive processes is the fact that spatial ability has often been reported to be better in CAH girls than unaffected girls [6, 36, 86]. This advantage appears selective, that is, so far, other abilities are not enhanced. In fact, Hampson *et al*. [36] report that perceptual speed, an ability favouring women, is reduced in CAH girls. Boys may also suffer from CAH and the consequent overproduction of androgens; but their spatial skills are reduced relative to unaffected boys [36]. The reasonable inference, that the optimal level of androgens for the expression of spatial ability is in the low normal male range, is consistent also with studies on normal young adults described below. No cognitive effects of prenatal exposure to diethylstilbestrol (DES), which has some behavioural effects that mimic androgens, have so far been found in humans [41, 42].

Boys born with cloacal exstrophy may have normal prenatal levels of androgens but because they are born without a penis they have in the past usually been castrated within days of birth and raised as girls. An astonishingly high number of them opt to live as males when they reach adolescence [85], in which case one might

speculate that their gender identity was determined prenatally. We do not yet have information on their cognitive patterns.

Hypogonadal men who have lower than normal levels of testosterone throughout their lives, with syndromes like Kallmann's, Klinefelter's, and Idiopathic Hypogonadotropic Hypogonadism (IHH), have poorer spatial ability than normal males even though their Vocabulary scores may not differ from normal [1, 40]. Another study found poorer performance not only on a visuo-constructional task, but also on several verbal tasks [81]. In order to rule out current hormonal environment as the causative factor in these studies, we would need to know the cognitive profile of men who had only recently experienced androgen deficiency. Hier and Crowley [40] provide data on five such men and report that their spatial scores are normal, but more data are needed.

Androgen insensitivity (AI) is a syndrome in which genetic males have testes (hidden in the body cavity), and produce testosterone, but the body's cells do not have androgen receptors. Hence, the androgens are ineffective, the external genitalia are female, and the "girls" are raised as such without any indication of their male genetic makeup until they fail to menstruate. Information on cognitive pattern is incomplete, studies to date employing standard intelligence tests, which generally yield no or small sex differences. Even if AI individuals resembled females, as claimed [44], it would be difficult to evaluate the relative contribution of hormonal influences and of being reared as girls.

Testosterone Levels Across Individuals

Variations in testosterone (T) across seasons, time of day, etc., presumably occur on an underlying stable baseline. We do not yet have information on the relation between T levels early and late in life in the same individuals, but correlations between individuals' T levels across a year, calculated from Smals at al. data [97], are highly significant. There is also evidence from a twin study that a large proportion of the variation in T from person to person is genetically based [74]. These facts suggest that some part of the relationship of T to cognitive function reflects a lifelong or "organizational" effect, particularly when chronological factors are controlled.

It is generally found that levels of testosterone are non-linearly related to cognitive function, in particular to spatial abilities of the kind favouring men [28, 76, 92]. Normal young men with lower levels of T perform better than young men with higher levels; but young women with higher levels perform better than those with lower levels. Such findings are consistent with the idea that spatial ability is enhanced in the low normal male range, at least in the 20–30 age group.

One study found a similar trend for math reasoning, for low–T men to have better scores than high–T men [28]. This result has not yet been confirmed.

Fluctuations in Sex Hormones and Cognitive Function

Sex hormones vary naturally across the monthly cycle in women, and across season of the year and time of day in men. In addition, some cognitive functions have been studied in persons undergoing hormone therapy, as in post-menopausal women, older men, and people undergoing a sex change.

Natural Fluctuations in Estrogen

The earliest demonstrations of cognitive pattern affected by natural fluctuations in sex hormones came from the study of women across the menstrual cycle [9, 54]. The level of estrogen peaks briefly in mid-cycle, and, along with progesterone, rises again for several days prior to the next menstruation, beginning about 10 days before. Earlier studies suffered from inadequate estimations of the appropriate phase for testing, lack of hormonal assays for verification, or a conceptualization of cognitive function which did not take sufficient account of major sex differences in cognition. Later studies that satisified all these requirements found that women were negatively affected during high estrogen levels (compared to low) primarily on male-favouring spatial tasks, while female-favouring tasks such as fluency and fine motor skill were positively affected [33, 34, 35].

Thus, variations in estrogen appear to *selectively* affect cognitive pattern. Such effects have been confirmed by others [37, 88, 94]. Further evidence for the specificity of the effects of estrogen in the motor sphere comes from a report that in the high-estrogen midluteal phase, performance on a manual sequencing task was predictably enhanced, whereas on a male-favouring throwing accuracy task, there was no overall effect on performance [90]. Several studies measuring behavioural asymmetry have also suggested that right-hemisphere cerebral function is depressed, relative to left, in high-estrogen phases [72, 73, 88, 90].

Natural Fluctuations in Androgens

Testosterone levels vary systematically within men depending on season and time of day [15, 52, 76, 77, 97]. Levels in men, at least in the northern hemisphere, are higher in autumn than in spring. Autumnal peaks in T levels have corresponded to increases in sexual activity [84], which would increase the likelihood of late autumn conception. Conceivably, this could be a holdover from our evolutionary past, when infants born in winter months might have been disadvantaged. T levels are also higher in early morning than later in the day [2, 15, 76].

Since we know from across-subject studies that men with T levels in the low normal range perform best on certain spatial tasks, it might be expected that we would see both seasonal and diurnal fluctuations in spatial ability. We found, as expected, that men performed better on a composite spatial measure in spring, when T levels were lower, than in fall [52]. Similarly, Moffat and Hampson [76] found performance on either

a mental rotations task or a composite spatial measure to be worst in men in early morning, when T levels are highest. Note that not all "masculine" tests need be similarly affected. In our seasonal study, neither math reasoning nor throwing accuracy were substantially influenced by the season. This does not of course preclude early organizing effects on these skills.

Obviously, the size of the sex difference would also be expected to vary with time of day or season of the year, with sex differences smaller in the high–T phases. What little data we have suggests that this might be so. In the one study comparing time of day, scores on a mental rotation task did not differ between the sexes early in the day, but was significant later in the day [76]. These effects were not accounted for by changes in cortisol levels. In our data on seasonal changes on a spatial composite score, although the sex difference was significant in autumn, it was smaller than in spring [52]. Were seasonal and diurnal changes in men, combined with menstrual changes in women, studied *systematically*, there might be other extreme situations where sex differences are diminished or even disappear. However, this would not be expected to happen on a random basis.

Effects of Hormonal Manipulations

Studies on natural fluctuations in hormones, insofar as they yield correlational data, are subject to some reservations concerning attribution of causality, which manipulations are not. However, because hormone manipulations are nearly always carried out for therapeutic purposes, generalizing to non-clinical samples must be done cautiously. Also, hormone therapies are typically carried out in subjects older than those in whom natural fluctuations are studied. Most studies in which exogenous sex hormones are administered do not have measures of the resultant levels of hormones. Nonetheless, such data may be useful in confirming or raising questions about the inferences made from looking at natural fluctuations.

Estrogens

Postmenopausal women experience a sharp decline in production of ovarian hormones, chief of which is estrogen. In the last three decades it has been common for such women to undergo hormone replacement therapy, consisting of estrogens and usually progesterone, to combat hot flashes and dryness of skin. Many physicians also advise therapy to prevent osteoporosis. Hormone replacement therapy has been reported to reduce the probability of dementia after menopause [38], but later reports are equivocal [39, 111]. Many studies evaluating the effects of hormone therapy have emphasized memory function, but Duff and Hampson [17] argue that it is *working memory*, not simply short-term memory of any kind, which may benefit from estrogen. Working memory requires some manipulation of the information in short-term store.

Women on hormone replacement therapy usually have been taking it for prolonged periods, so it is not clear whether any beneficial effects are due to the immediate or long-term influence. In one study comparing medicated women during on-therapy and off-therapy phases, it was found that women performed better in the on-therapy phase on tests of manual sequencing and perceptual speed (both of which normally favour women), but not on two spatial tasks [53]. Yet the same women showed a more generalized cognitive advantage when compared with women not on therapy [50], suggesting that the immediate and long-term effects of estrogen therapy may be somewhat different.

Estrogen therapy, combined with anti-androgen therapy, is common in cases of transsexuals seeking sex re-assignment from *male to female*. This research is in its early stages, and further controls are needed, but there is some indication that male-favouring spatial ability may not be impaired by the treatment combination [75, 96], suggesting that in men such ability may be largely determined early in life. Neither were female-favouring tasks such as verbal fluency or perceptual speed enhanced. However, Miles *et al*. [75] report that scores on a verbal memory task (Paired Associate Learning) were better in the hormone-treated group than in a similar transsexual group who had not yet undergone hormone therapy.

Androgens

The interpretation of the effects of testosterone administration in men is complicated by the fact of differences in T levels across ages, with gradual declines from the 20's to the 70's [104]; and by the fact that the relation of T to spatial test scores is not linear, normal young men with lower levels performing better than those with higher levels (see above). One study reported that testosterone treatment in healthy men over 60 selectively improved performance, relative to a placebo group, on a visuo-constructional task (Block Design) in which blocks must be assembled to match a specified pattern [47]. Almost certainly, these men before treatment had T levels well below the mean of younger men, and thus below the "optimal" level.

In contrast, administration of T to a younger group of men, perhaps raising them to above-optimum levels, *depressed* scores on Block Design relative to a placebo group, at least in the initial weeks of treatment [81]. Verbal fluency and manual dexterity, however, usually better in women, were both improved. The interpretation of another study showing apparent improvement on a mental rotation task after T administration [1] is complicated by the fact that the T levels of the treated group appear lower initially than the comparison group. Since different studies use different assay methods and cite different measures, the elusive "optimal level" is usually difficult to determine.

Androgen treatment is also given to *female-to-male* transsexuals. Investigations into cognitive function so far have not used control groups who did not undergo therapy. Some studies [96, 101] report that F–M transsexuals showed improved scores on male-favouring mental rotation tasks, but female-favouring verbal fluency in one study was unchanged, and in the other got worse.

It would of course be of interest to demonstrate even short-lived cognitive effects of T administration in genetic females, since this might indicate an extension of the role of androgens in cognition into adulthood. However, apart from the lack of control subjects, we should also be cautious about the generalizability of such findings to the non-transgendered population. One study reported that the level of androgens was higher in F–M transsexuals than in control females [8], before any hormone treatment. It is reasonable to assume that individuals of either sex who wish to have their sex re-assigned have a somewhat different brain from those who do not. Some recent anatomical evidence to this effect also exists [56]. Thus, F–M individuals may have brains more susceptible to androgenic influences. Nevertheless, the transsexual population is potentially a rich source of information on the effects of sex hormones on cognition in adults.

Conclusions

There are consistent differences between men's and women's cognitive skills, indicating, whatever the source, that their nervous systems also differ. Cognitive sex differences appear well before puberty, are present across cultures, and to some extent parallel differences seen in nonhuman mammals. Nonetheless, we must keep in mind that in the larger comparative context, the similarities beween men's and women's brains far outweigh the differences.

There is substantial evidence in humans that androgens present before birth influence human cognitive abilities into adulthood, at least for certain spatial abilities of the kind at which men excel. Prenatal androgens may also depress certain functions on which women typically excel, but this is not well established. Across young adults, current levels of both androgens and estrogens are systematically related to cognitive pattern, apparently due in part to a stable individual baseline of these hormones. As well, fluctuations in sex hormones across daily, monthly and yearly cycles are accompanied by changes in several cognitive tests, especially those that are sexually differentiated – suggesting a continuing sensitivity of the nervous system to hormonal changes in the adult. The administration of exogenous hormones, usually for therapeutic purposes, at present provides modest support for such a proposition, but this is still a rich field of information to be tapped.

Acknowledgements

Supported by a grant from the Natural Sciences and Engineering Research Council, Canada.

REFERENCES

(For more detailed discussion of sex differences in cognition, and their putative brain mechanisms, see Kimura D. Sex and Cognition 2000; MIT Press)

1 Alexander GM, Swerdloff RS, Wang C, Davidson T, McDonald V, Steiner B, Hines M. Androgen-behavior correlations in hypogonadal and eugonadal men. Hormones & Behavior 1998; **33**:85–94.
2 Aschoff J, Ceresa F, Halberg F, editors. Chronobiological Aspects of Endocrinology, FK Schattauer Verlag, Stuttgart 1974.
3 Baenninger M, Newcombe N. The role of experience in spatial test performance: a meta-analysis. Sex Roles 1989; **20**:327–344.
4 Benbow CP. Sex differences in mathematical reasoning ability in intellectually talented preadolescents: their nature, effects, and possible causes. Behavioral & Brain Sciences 1988; **11**: 169–182.
5 Berenbaum SA. Psychological outcome in congenital adrenal hyperplasia. In: B Stabler, BB Bercu. Therapeutic outcome of endocrine disorders: efficacy, innovation and quality of life. Springer-Verlag, New York, 2000; pp.186–199.
6 Berenbaum SA, Korman K, Leveroni C. Early hormones and sex differences in cognitive abilities. Learning & Individual Differences 1995; **7**:303–321.
7 Bleecker ML, Bolla-Wilson K, Agnew J, Meyers DA. Age-related sex differences in verbal memory. J of Clinical Psychology 1988; **44**:403–411.
8 Bosinski HAG, Schroder I, Peter M, Arndt R, Wille R, Sippell WG. Anthropometrical measurements and androgen levels in males, females, and hormonally untreated female-to-male transsexuals. Archives of Sexual Behavior 1997; **26**:143–157.
9 Broverman DM, Vogel W, Klaiber EL, Majcher D, Shea D, Paul V. Changes in cognitive task performance across the menstrual cycle. J of Comparative & Physiological Psychology 1981; **95**:646–654.
10 Campbell JR. The roots of gender inequity in technical areas. J of Research in Science Teaching 1991; **28**:251–264.
11 Chang K, Antes JR. Sex and cultural differences in map reading. The American Cartographer 1987; **14**:29–42.
12 Chipman K, Hampson E, Kimura D. A sex difference in reliance on vision during manual sequencing tasks. Neuropsychologia 2002; **5**:910–916
13 Chipman K, Kimura D. An investigation of sex differences on incidental memory for verbal and pictorial material. Learning & Individual Differences 1998; **10:**259–272.
14 Collins DW, Kimura D. A large sex difference on a two-dimensional mental rotation task. Behavioral Neuroscience 1997; **111**: 845–849.
15 Dabbs JM. Age and seasonal variation in serum testosterone concentration among men. Chronobiology International 1990; **7**:245–249.
16 Denckla MB, Rudel R. Rapid "automatized" naming of pictured objects, colors, letters and numbers by normal children. Cortex 1974; **10**:186–202.
17 Duff SJ, Hampson E. A beneficial effect of estrogen on working memory in postmenopausal women taking hormone replacement therapy. Hormones & Behavior 2000; **38**:262–276.
18 Eals M, Silverman I. The hunter-gatherer theory of spatial sex differences: proximate factors mediating the female advantage in recall of object arrays. Ethology & Sociobiology 1994; **15**:95–105.
19 Ekstrom RB, French JW, Harman HH, Dermen D. Kit of factor-referenced cognitive tests. Educational Testing Service, Princeton, NJ, 1976.
20 Engelhard G. Gender differences in performance on mathematics items: evidence from the United States and Thailand. Contemporary Educational Psychology 1990; **15**:13–26.
21 Feingold A. Cognitive gender differences are disappearing. American Psychologist 1988; **43**:95–103.
22 Fitch RH, Bimonte HA. Hormones, brain and behavior: Putative biological contributions to cognitive sex differences. In A McGillicuddy-DeLisi, R DeLisi, editors. Biology, Society and Behavior:

The Development of Sex Differences in Cognition, Ablex, Westport Conn 2002; pp. 55–91.
23 Galea LAM, Kimura D. Sex differences in route-learning. Personality & Individual Differences 1993; **14**:53–65.
24 Gaulin SJC, FitzGerald RW, Wartell MS. Sex differences in spatial ability and activity in two vole species. J of Comparative Psychology 1990; **104**:88–93.
25 Gaulin SJC, Hoffman HA. Evolution and development of sex differences in spatial ability. In: LL Betzig, MB Mulder, PW Turke. Human Reproductive Behaviour: A Darwinian perspective, Cambridge University Press, Cambridge, England 1987; pp. 129–152.
26 Geary DC. Sexual selection and sex differences in spatial cognition. Learning & Individual Differences 1995; **7**:289–301.
27 Geary DC, DeSoto MC. Sex differences in spatial abilities among adults from the United States and China. Evolution & Cognition 2001; **7**:172–177.
28 Gouchie C, Kimura D. The relationship between testosterone levels and cognitive ability patterns. Psychoneuroendocrinology 1991; **16**:323–334.
29 Goy RW, Bercovitch FB, McBrair MC. Behavioral masculinization is independent of genital masculinization in prenatally androgenized female rhesus macaques. Hormones & Behavior 1988; **22**:552–571.
30 Goy RW, McEwen BS. Sexual Differentiation of the Brain, MIT Press, Cambridge, Mass, 1980.
31 Hall JAY, Kimura D. Sexual orientation and performance on sexually dimorphic motor tasks. Archives of Sexual Behavior 1995; **24**:395–407.
32 Halpern DF. The disappearance of cognitive gender differences: what you see depends on where you look. American Psychologist 1989; **44**:1156–1158.
33 Hampson E. Estrogen-related variations in human spatial and articulatory-motor skills. Psychoneuroendocrinology 1990a; **15**:97–111.
34 Hampson E. Variations in sex-related cognitive abilities across the menstrual cycle. Brain & Cognition 1990b; **14**:26–43.
35 Hampson E, Kimura D. Reciprocal affects of hormonal fluctuations on human motor and perceptual-spatial skills. Behavioral Neuroscience 1988; **102**:456–459.
36 Hampson E, Rovet JF, Altmann D. Spatial reasoning in children with congenital adrenal hyperplasia due to 21-hydroxylase deficiency. Developmental Neuropsychology 1998; **14**:299–320.
37 Hausmann M, Slabbekoorn D, Van Goozen SHM, Cohen-Kettenis PT, Gunterkun O. Sex hormones affect spatial abilities during the menstrual cycle. Behavioral Neuroscience 2000; **114**:1245–1250.
38 Henderson VW, Paganini-Hill A, Emanuel CK, Dunn ME, Buckwalter JG. Estrogen replacement therapy in older women. Archives of Neurology 1994; **51**:896–900.
39 Henderson VW, Paganini-Hill A, Miller BL, Elble RJ, Reyes PF, Shoupe D, McCleary CA, Klein RA, Hake AM, Farlow MR. Estrogen for Alzheimer's disease in women. Randomized, double-blind, placebo-controlled trial. Neurology 2000; **54**:295–301.
40 Hier DB, Crowley WF. Spatial ability in androgen-deficient men. New England J of Medicine 1982; **306**:1202–1205.
41 Hines M, Sandberg EC. Sexual differentiation of cognitive abilities in women exposed to diethylstilbestrol (DES) prenatally. Hormones & Behavior 1996; **30**:354–363.
42 Hines M, Shipley C. Prenatal exposure to diethylstilbestrol (DES) and the development of sexually dimorphic cognitive abilities and cerebral lateralization. Developmental Psychology 1984; **20**:81–94.
43 Hoesing JM, Lewine JD, Yeo R, Edgar C. Sex differences, spatial working memory and event-related potentials. Society for Neuroscience Abstracts 1994; **20**:1424.
44 Imperato-McGinley J, Pichardo M, Gautier T, Voyer D, Bryden MP. Cognitive abilities in androgen-insensitive subjects: comparison with control males and females from the same kindred. Clinical Endocrinology 1991; **34**:341–347.
45 Ingram D. Motor asymmetries in young children. Neuropsychologia 1975; **13**:95–102.
46 James TW, Kimura D. Sex differences in remembering the locations of objects in an array: location-shifts versus location-exchanges. Evolution and Human Behavior 1997; **18**:155–163.
47 Janowsky JS, Oviatt SK, Orwoll ES. Testosterone influences spatial cognition in older men. Behavioral Neuroscience 1994; **108**:325–332.
48 Jardine R, Martin NG. Spatial ability and throwing accuracy. Behavior Genetics 1983; **13**:331–340.
49 Jensen AR. Sex differences in arithmetic computation and reasoning in prepubertal boys and girls. Behavioral & Brain Sciences 1988; **11**:198–199.
50 Kimura D. Estrogen replacement therapy may protect against intellectual decline in postmenopausal women. Hormones & Behavior 1995; **29**:312–321.
51 Kimura D. Sex differences in the brain. Scientific American 1992; **267**:119–125.
52 Kimura D, Hampson E. Cognitive pattern in men and women is influenced by fluctuations in sex hormones. Current Directions in Psychological Science 1994; **3**:57–61.
53 Kimura D, Hampson E. Neural and hormonal mechanisms mediating sex differences in cognition. In PA Vernon, editor. Biological Approaches to the Study of Human Intelligence, Ablex Publishing Corp., New Jersey, 1993; pp. 375–397.
54 Komnenich P, Lane DM, Dickey RP, Stone SC. Gonadal hormones and cognitive performance. Physiological Psychology 1978; **6**:115–120.
55 Kramer JH, Delis DC, Daniel M. Sex differences in verbal learning. J of Clinical Psychology 1988; **44**:907–915.
56 Kruijver FPM, Zhou J-N, Pool CW, Hofman MA, Gooren LJG, Swaab DF. Male-to-female transsexuals have female neuron numbers in a limbic nucleus. J. Clinical Endocrinology & Metabolism 2000; **85**:2034–2041.
57 Levine SC, Huttenlocher J, Taylor A, Langrock A. Early sex differences in spatial skills. Developmental Psychology 1999; **35**:940–949.
58 Levy J, Heller W. Gender differences in human neuropsychological function. In AA Geroll, H Moltz, IL Ward, editors. Handbook of Behavioral Neurobiology, Sexual Differentiation, Plenum, New York, 1992; pp. 245–274.
59 Linn MC, Petersen AC. Emergence and characterization of sex differences in spatial ability: a meta-analysis. Child Development 1985; **56**:1479–1498.
60 Low R, Over R. Gender differences in solution of algebraic word problems containing irrelevant information. J Educational Psychology 1993; **85**:331–339.
61 Lubinski D, Benbow CP. The study of mathematically precocious youth: the first three decades of a planned 50-year study of intellectual talent. In: RF Subotnik, KD Arnold. Beyond Terman: Contemporary Longitudinal Studies of Giftedness and Talent, Ablex, Norwood NJ, 1994; pp. 255–281.
62 Lummis M, Stevenson HW. Gender differences in beliefs and achievement: a cross-cultural study. Developmental Psychology 1990; **26:**254–263.
63 Lunn D. Foot Asymmetry and Cognitive Ability in Young Children, Unpublished Master's Thesis, University of Western Ontario, London, Canada 1987.
64 Maccoby EE. The Development of Sex Differences. Stanford: Stanford Univ. Press, 1966.
65 Mann VA, Sasanuma S, Sakuma N, Masaki S. Sex differences in cognitive abilities: a cross-cultural perspective. Neuropsychologia 1990**; 28**:1063–1077.
66 Marshall SP, Smith JD. Sex differences in learning mathematics: a longitudinal study with item and error analyses. J of Educational Psychology 1987; **79**:372–383.
67 Masters MS, Sanders B. Is the gender difference in mental rotation disappearing? Behavior Genetics 1993; **23**:337–341.
68 Matheny AP, Bruggemann CE. Children's speech: hereditary components and sex differences. Folia Phoniatrica 1973; **25**:442–449.
69 McBurney DH, Gaulin SJC, Devineni T, Adams C. Superior spatial memory of women: stronger evidence for the gathering hypothesis. Evolution & Human Behavior 1997; **18**:165–174.
70 McEwen BS. Our changing ideas about steroid effects on an ever-changing brain. Seminars in the Neurosciences 1991; **3**:497–507.

71 McGuinness D, Olson A, Chapman J. Sex differences in incidental recall for words and pictures. Learning and Individual Differences 1990; **2**:263–285.

72 Mead LA, Hampson E. Asymmetric effects of ovarian hormones on hemispheric activity: evidence from dichotic and tachistoscopic tests. Neuropsychology 1996; **10**:578–587.

73 Mead LA, Hampson E. Turning bias in humans is influenced by phase of the menstrual cycle. Hormones & Behavior 1997; **31**: 65–74.

74 Meikle AW, Bishop DT, Stringham JD, West DW. Quantitating genetic and nongenetic factors that determine plasma sex steroid variation in normal male twins. Metabolism 1987; **35**: 1090–1095.

75 Miles C, Green R, Sanders G, Hines M. Estrogen and memory in a transsexual population. Hormones & Behavior 1998; **34**: 199–208.

76 Moffat SD, Hampson E. A curvilinear relationship between testosterone and spatial cognition in humans: possible influence of hand preference. Psychoneuroendocrinology 1996; **21**: 323–337.

77 Moffat SD, Hampson E. Salivary testosterone concentrations in left-handers: an association with cerebral language lateralization? Neuropsychology 2000; **14**:71–81.

78 Moffat SD, Hampson E, Hatzipantelis M. Navigation in a virtual maze: sex differences and correlation with psychometric measures of spatial ability in humans. Evolution & Human Behavior 1998; **19**:73–87.

79 Newcombe N, Bandura MM, Taylor DG. Sex differences in spatial ability and spatial activities. Sex Roles 1983; **9**:377–386.

80 Nicholson KG, Kimura D. Sex differences for speech and manual skill. Perceptual & Motor Skills 1996; **82**:3–13.

81 O'Connor DB, Archer J, Hair WM, Wu FCW. Activational effects of testosterone on cognitive function in men. Neuropsychologia 2001; **39**:1385–1394.

82 Owen K, Lynn R. Sex differences in primary cognitive abilities among blacks, Indians and whites in South Africa. J of Biosocial Science 1993; **25**:557–560.

83 Postma A, Izendoorn I, De Haan EHF. Sex differences in object location memory. Brain & Cognition 1998; **36**:334–345.

84 Reinberg A, Lagoguey M. Circadian and circannual rhythms in sexual activity and plasma hormones (FSH, LH, Testosterone) of five human males. Archives of Sexual Behavior 1978; **7**:13–30.

85 Reiner W. The genesis of male gender identity. Paper presented to Lawson Wilkins Pediatric Endocrine Society, Boston, May, 2000.

86 Resnick SM, Berenbaum SA, Gottesman II, Bouchard TJ. Early hormonal influences on cognitive functioning in congenital adrenal hyperplasia. Developmental Psychology 1986; **22**:191–198.

87 Rosser RA, Ensing SS, Glider PJ, Lane S. An information-processing analysis of children's accuracy in predicting the appearance of rotated stimuli. Child Development 1984; **55**:2204–2211.

88 Sanders G, Wenmoth D. Cerebral asymmetry and cognitive performance show complementary fluctuations across the menstrual cycle. In L Ellis, L Ebertz, editors. Males, Females, and Behavior: Towards Biological Understanding, Praeger, Westport, Conn, 1998. pp. 165–175.

89 Sanders G, Wright M. Sexual orientation differences in cerebral asymmetry and in the performance of sexually dimorphic cognitive and motor tasks. Archives of Sexual Behavior 1997; **26**: 463–480.

90 Saucier DM, Kimura D. Intrapersonal motor but not extrapersonal targeting skill is enhanced during the midluteal phase of the menstrual cycle. Developmental Neuropsychology 1998; **14**:385–398.

91 Shepard RN, Metzler J. Mental rotation of three-dimensional objects. Science 1971; **171**:701–703.

92 Shute VJ, Pellegrino JW, Hubert L, Reynolds RW. The relationship between androgen levels and human spatial abilities. Bulletin of the Psychonomic Society 1983; **21**:465–468.

93 Silverman I, Eals M. Sex differences in spatial abilities: evolutionary theory and data. In JH Barkow, L Cosmides, J Tooby, editors. The Adapted Mind, Oxford, New York 1992, pp. 533–549.

94 Silverman I, Phillips K. Effects of estrogen changes during the menstrual cycle on spatial performance. Ethology & Sociobiology 1993; **14**:257–270.

95 Silverman I, Phillips K, Silverman LK. Homogeneity of effect sizes for sex across spatial tests and cultures: implications for hormonal theories. Brain & Cognition 1996; **31**:90–94.

96 Slabbekoorn D, Van Goozen SHM, Megens J, Gooren LJG, Cohen-Kettenis PT. Activating effects of cross-sex hormones on cognitive functioning: a study of short-term and long-term hormone effects in transsexuals. Psychoneuroendocrinology 1999; **24**:423–447.

97 Smals AGH, Kloppenborg PWC, Benraad ThJ. Circannual cycle in plasma testosterone levels in man. J of Clinical Endocrinology & Metabolism 1976; **42**:979–982.

98 Smith EP, Boyd J, Frank GR, Takahashi H, Cohen RM, Specker B, Williams TC, Lubahn DB, Korach KS. Estrogen resistance caused by a mutation in the estrogen-receptor gene in a man. New England J. Medicine 1994; **331**:1056–1061.

99 Thornton J, Goy RW. Female-typical sex behavior of Rhesus and defeminization by androgens given prenatally. Hormones & Behavior 1986; **20**:129–147.

100 Vandenberg SG, Kuse AR. Mental rotations, a group test of three-dimensional spatial visualization. Perceptual & Motor Skills 1978; **47:**599–601.

101Van Goozen SHM, Cohen-Kettenis PT, Gooren LJG, Frijda NH, Van de Poll NE. Activating effects of androgens on cognitive performance: causal evidence in a group of female-to-male transsexuals. Neuropsychologia 1994; **32**:1153–1157.

102 Vauclair J, Fagot J, Hopkins WD. Rotation of mental images in baboons when the visual input is directed to the left cerebral hemisphere. Psychological Science 1993; **4**:99–103.

103 Vederhus L, Krekling S. Sex differences in visual spatial ability in 9-year-old children. Intelligence 1996; **23**:33–43.

104 Vermeulen A. Androgens in the aging male. J of Clinical Endocrinology & Metabolism 1991; **73**:221–224.

105 Ward SL, Newcombe N, Overton WF. Turn left at the church or three miles north: A study of direction giving and sex differences. Environment & Behavior 1986; **18**:192–213.

106 Watson NV, Kimura D. Right-hand superiority for throwing but not for intercepting. Neuropsychologia 1989; **27**:1399–1414.

107 Watson NV, Kimura D. Nontrivial sex differences in throwing and intercepting: relation to psychometrically-defined spatial functions. Personality & Individual Differences 1991; **12**:375–385.

108 Williams CL, Meck WH. Organizational effects of gonadal hormones induce qualitative differences in visuospatial navigation. In: M Haug *et al,* editors. The Development of Sex Differences and Similarities in Behavior, Kluwer Academic Publishers, The Netherlands, 1993; pp. 175–189.

109 Williams CL, Barnett AM, Meck WH. Organizational effects of early gonadal secretions on sexual differentiation in spatial memory. Behavioral Neuroscience 1990; **104**:84–97.

110 Williams CL. A reevaluation of the concept of separable periods of organizational and activational actions of estrogens in development of brain and behavior. In: BR Komisaruk, HJ Siegel, MF Cheng, HH Feder, editors. Reproduction: A Behavioral and Neuroendocrine Perspective, New York Academy of Sciences, New York, 1986; pp. 282–292.

111 Yaffe K, Sawaya G, Lieberburg I, Grady D. Estrogen therapy in postmenopausal women. J. American Medical Association 1998; **279**:688–695.

Neuroendocrinology Letters Special Issue, Suppl.4, Vol.23, December 2002
Copyright © Neuroendocrinology Letters ISSN 0172–780X **www.nel.edu**

REVIEW ARTICLE

Female Mate Value at a Glance: Relationship of Waist-to-Hip Ratio to Health, Fecundity and Attractiveness

Devendra Singh
Department of Psychology, University of Texas at Austin, USA.

Correspondence to: Devendra Singh
Department of Psychology
University of Texas at Austin, USA
Austin, TX 78712
EMAIL: singh@mail.utexas.edu

Submitted: *September 9, 2002*
Accepted: *October 4, 2002*

Key words: **waist-to-hip ratio; body mass index; female attractiveness; mate value; mate selection**

Neuroendocrinology Letters 2002; ***23****(Suppl.4):81–91 pii: NEL231002R08* *Copyright © Neuroendocrinology Letters* ***www.nel.edu***

Abstract A fundamental assumption of adaptive explanations of female attractiveness is that bodily features that males judge as attractive reliably signal youthfulness, healthiness, and fertility or female mate value. One of the bodily features, waist-to-hip ratio (WHR), is a reliable indicator of a female's reproductive age, sex hormone profile, parity and risk for various diseases. Systematic variation in the size of WHR also systematically affects the judgment of female attractiveness, healthiness, and youthfulness. This article summarizes recent findings about the relationship between female's WHR and various factors affecting reproductive capability and risk for diseases. Research on the relationship between attractiveness and WHR is discussed in light of some methodological objections to previous research. Finally, cross-cultural and historical data are presented that suggest that the relationship between WHR and female attractiveness is not culture-specific and not inculcated by modern Western fashion dictates or media.

According to evolution based theories of mate selection, one of the adaptive problems faced by human ancestral males was to assess a woman's mate value, or the degree to which she would enhance his reproductive success. Women's mate value is determined by numerous variables such as hormone profile, reproductive age, fecundity, parity and resistance to diseases, none of which can be directly observed. It has been proposed that information about some of these variables was reliably conveyed by specific characteristics of female bodies and that selection therefore produced psychological mechanisms in men to attend to bodily features in assessing a woman's mate value [1,2]. It is the fundamental assumption of evolutionary mate selection theories that physical attractiveness is largely reflective of reliable cues to a woman's mate value [3–5].

Two different research approaches have been used to demonstrate the link between physical attractiveness and mate value. First are the studies in which people identify those features they find attractive; it is then ascertained whether such features are correlated with variables comprising mate value. Early research of categorizing various facial features that people find attractive [6], recent research by Johnston and his associates on computer generated beautiful faces [7,8] and research by Perrett

and his associates on composite faces [9,10] illustrate this approach. The second approach is to identify bodily features that are known to be related to components of fitness or genetic quality and capacity to cope with environmental stress or health and then to investigate whether people judge such features as attractive. The research of Thornhill, Gangestad and their associates on fluctuating asymmetry (FA) – a marker of developmental stability – and its effect on judgments of attractiveness exemplify this approach [4,11,12].

Another bodily feature that reliably signals hormonal status, susceptibility to endocrinological disorders and fertility is sex-specific fat distribution as measured by the ratio of waist to hip circumference (WHR) [13,14]. This link between health and fertility and WHR should affect the judgment of attractiveness, which should in turn reinforce the assumption that attractiveness conveys information about mate value.

In this paper I will review and summarize the evidence that WHR is a sexually dimorphic feature which reliably tracks women's reproductive capabilities and is related to risks from various diseases. The link between WHR and reproductive capability and healthiness is so precise that minor variations in the size of WHR reflect significant changes in these components of fitness. Most of such research, however, has appeared in highly specialized journals, so many readers may not be familiar with this literature. Next, I will summarize research studies which demonstrate as well as those that dispute that systematic variations of the size of female WHR also systematically affect the judgment of women's attractiveness. Finally, I will present historical and cross-cultural data which suggest that the link between WHR and female attractiveness is due to adaptive design rather than caused by the cultural influence of modern Western societies.

General Characteristics of WHR

Overall body weight gain is the most noticeable change caused by pubertal onset in women. The most popular technique for estimating body weight is body mass index [BMI (weight in kilograms divided by height in meters squared)]. The increase in BMI observed in women during puberty does not take into account the sex-dependent anatomical distribution of fat deposits [15,16]. The deposit and utilization of fat from various anatomical areas is regulated by sex hormones. Simply stated, estrogen inhibits fat deposit in the abdominal region and maximally stimulates fat deposit in the gluteofemoral region (buttocks and thighs) more in than any other region of the body. Testosterone, in contrast, stimulates fat deposit in the abdominal region and inhibits deposits in the gluteofemoral region [17]. It is this sexually dimorphic body fat distribution which primarily sculpts typical body shape differences between the sexes that becomes noticeable after pubertal onset; women have greater amounts of body fat in the lower part of the body (gynoid body fat, or pear shape), whereas men have greater amounts of fat in the upper body (android body fat, or apple shape). This sexually dimorphic body fat distribution is most commonly quantified by measuring and computing the ratio of the waist to hips (WHR) circumference.

WHR has a bimodal distribution with relatively little overlap between the sexes [18]. The range of WHR for the healthy premenopausal Caucasian women has been shown to be .67–.80 and in the range of .85–.95 for healthy Caucasian men [19]. Women typically maintain a lower WHR than men throughout adulthood, although after menopause WHR approaches the masculine range [20,21]. The increase in the size of WHR in menopausal women is due to the reduction of estrogen levels [22]. This interpretation is justified by the observation that premenopausal women suffering from polycystic ovary syndrome (PCOS), which is marked by impaired estrogen production, have higher WHRs than age-matched non-patients [23,24], Additionally, when women suffering from PCOS are administered an estrogen-progestagen compound, their WHRs become lower over time in the absence of any reduction of their BMI [23]. There is no other visible morphological feature which so reliably tracks the level of estrogen.

The size of WHR also has a genetic-heritable component. Data on identical female twins show that additive genetic effects account for 48% of variance, unique environmental effects for 46% and 6% by the effect of age [25]. Recently, segregation analysis has provided evidence for the presence of a major gene for age and BMI adjusted WHR [26]. This interplay of genetic and lifestyle variables may be responsible for population-specific variations in the size of WHR in both men and women [18]. However, it is notable that despite such variations, average male WHR is found to be greater than average female WHR in all the populations studied so far.

WHR and Health Status

There is accumulating clinical and epidemiological evidence that risk for various diseases depends not only on the degree of obesity as commonly measured by BMI, but on anatomical location of fat deposits as well [27–29]. Sex hormones and glucocorticoids regulate adipose (fat) tissue differentiation, function and distribution, but in excess, they cause abdominal or central obesity [30]. Abdominal fat or central obesity is commonly measured by WHR and recently by the size of waist circumference [31,32]. WHR is an independent predictor for cardiovascular disorders, adult-onset diabetes, elevated plasma lipids, hypertension, cancer (endometrial, ovarian and breast), gall bladder disease and premature mortality [13,33]. The clearest support for the relationship between WHR and health is provided by a recent study which conducted forensic autopsies on premenopausal women and found the highest coronary lesions in women with 0.87 or greater WHR after controlling for age and BMI [34].

WHR also significantly predicts poor stress-coping skills and prevalence of various personality disorders. For example, women with higher WHR perform poorly in stressful situations and lack habituation to stress

(defined as significantly greater secretion of cortisol) than women with low WHR [35]. Women with a high WHR compared to those with lower WHR score higher on Cluster c (characterized by anxiety and fear) as determined by the structured clinical interview schedule [36]. A longitudinal study reports that women with high WHR exhibit greater cynicism, anxiety and depression than women with low WHR [37]. Thus susceptibility to various major physical diseases and psychological disorders is reliably conveyed by the size of WHR.

It should, however, be noted that while WHR and BMI are positively correlated, they measure overlapping, yet distinctly different aspects of body fat deposits. BMI reflects the degree of thinness/fatness without differentiating whether fat is centrally located or peripherally located (on the limbs), whereas WHR measures upper central (android) and lower (gynoid) body obesity. Although BMI is most frequently used by epidemiologists because of the ease of this measure, there is considerable variability in body composition for any BMI; some individuals with low BMI have as much fat as those with higher BMIs [38]. Additionally, BMI is not appreciably affected by certain parasitic infestations, whereas WHR is. For example, schistosomiasis and Leishmania (Kala-Azar), which are quite prevalent in non-industrialized, non-western countries (and undoubtedly prevalent in the environment of evolutionary adaptiveness, or EEA), affect liver function and induce large bellies in infected individuals. The pathogen infestation does not cause immediate mortality and infected individuals remain asymptomatic and survive 10–15 years, but have low energy levels. The enlargement in the belly size would affect the size of WHR without any readily noticeable change in BMI [39].

The degree of overall obesity, as measured by BMI ,does affect the size of WHR especially in instances of very low and high BMI. For example, low BMI leads to typical gynoid pattern of fat distribution (i.e., low WHR), whereas excess weight or high BMI results in android (high WHR) pattern of fat distribution in women [40]. It is, therefore, common practice in clinical research to measure both BMI and WHR if the subject population represents a wide range of BMI. For accurately evaluating the role of WHR, BMI is divided into lower, middle and upper terciles [15]. The World Health Organization (WHO) defines BMI of 18.5 as thin, or underweight, 19–24 as normal weight, 25–29.9 as overweight and 30 or greater as obese. Frequently, the effect of WHR size on risk for diseases is found to be significant for normal weight range; BMIs representing overweight and obesity overshadows the impact of WHR [41].

The relevant issue from a mate selection perspective is whether people can accurately judge differences in the health of women who differ from each other only in the size of WHR and BMI. To explore this issue, male and female physicians (health experts) were given 12 line drawings of women representing three levels of BMI (all figures had identical height, but different depictions of body weight – underweight, normal and overweight) and within each BMI group four levels of WHR (0.7, 0.8, 0.9, 1.0). Both male and female physicians rated the 0.7 WHR figure in the normal weight category as most healthy and attractive; the underweight figure with low WHR (0.7) was not judged to be healthy or attractive but was judged as younger than normal weight low WHR figure. Body weight did affect the judgment of healthiness as the overweight figure even with low WHR was judged to be less healthy, less attractive and older than underweight and normal weight figures of the same WHR [42]. When young and older laymen and women were asked to rate the same 12 figures, their judgments of healthiness, attractiveness and youthfulness were practically identical to those of the physicians. It should be stressed that ***within*** *each body weight category*, physician and lay people both judged the figures with lower WHR as more attractive, healthy and youthful [14].

This inverse relationship between WHR and judgments of healthiness and youthfulness has now been replicated using silhouette photographs of women with known BMIs and WHRs [41]. Silhouettes with low BMI and low WHR were judged as more likely to be healthy and to live longer than silhouettes of the same BMI but higher WHR, independent of the observers' own BMI, age or sex. When high BMI silhouettes (BMI of 29) were used, the size of WHR was less influential in the judgment of health and age. Women with high BMI, independent of WHR, were judged to be 15–18 years older than figures with low WHR and low BMI.

Thus, it is this interaction between WHR and BMI that affects health status and healthiness, and no valid conclusion can therefore be drawn if the interaction between BMI and WHR is ignored.

WHR and Reproductive Capability

WHR reliably signals practically all the conditions that affect women's reproductive status. Prior to puberty and again after menopause, females have WHR which is quite similar to that of males; only during reproductive age do women maintain a WHR lower than that of men [20]. The onset of puberty and resultant activation of the menstrual cycle is related to the size of WHR. Females with a high WHR have more irregular cycles [43] and have significantly fewer ovulatory cycles than women with a low WHR [44]. Changes in the size of WHR also track ovulatory phases; WHR becomes significantly lower during ovulation compared to the non-ovulatory phases of the menstrual cycle [45]. Thus, WHR is a reliable indicator of a woman's fecundability. For successful conception, however, it is essential that the chemical environment within the reproductive track facilitate sperm viability. After sperm insemination, the endocervical mucus pH determines viability of sperm; if endocervical mucus has high pH it impairs mucus-sperm interaction and reduces fertility. Endocervical mucus pH has been shown to be inversely related to serum androgen levels and WHR in women who have a BMI in the normal range [46]. The probability of successful pregnancy induction is also affected

by WHR. Women participating in a donor insemination program have a lower probability of conception if their WHR is greater than 0.8, after controlling for age, BMI and parity [47].

The failure to conceive during artificial insemination could be due either to deficits in gonadotropin hormone release or some variable associated with embryo implantation. The pregnancy rate of *in-vitro* fertilization embryo transfer, however, bypasses this problem, as gonadotropin hormones are regulated prior to embryo transfer. Women with high WHR (0.80 or higher) have significantly lower pregnancy rates than women with lower WHRs (0.70–0.79), independent of their BMIs [48]. Therefore, it appears that the lower pregnancy rate in women with high WHR, compared to women with low WHR, is due to a problem with embryo development and its viability. Currently, there is no information available about the incidence or frequency of spontaneous abortion and WHR.

One of the significant problems affecting the reproductive success of ancestral population males would have been to assess whether a potential mate was nulliparous or not, and more critically (due to paternal uncertainty), whether the woman was in the early stage of a pregnancy induced by another male. WHR provides reliable information about both of these conditions. The fat deposits in early pregnancy are primarily localized in the pelvic girdle regions and, hence, an increase in WHR in the absence of any significant weight gain is one of the first signs of pregnancy [49]. Reproductive history such as parity or lactation can also increase the size of a woman's WHR, independent of age and BMI. Nulliparous Dutch women have a mean WHR of 0.74 but it increases to 0.76 after two births and to 0.79 after seven births [50]. The increase in the size of the WHR related to parity cannot be explained by abdominal muscle stretching caused by pregnancy. Indeed, magnetic resonance studies have shown that successive pregnancies tend to localize more adipose tissue in the abdominal area [51].

WHR and Attractiveness Judgments

To establish that WHR allows males to solve the adaptive problem of identifying a female's mate value, it needs to be demonstrated that males possess perceptual mechanisms to detect and use information conveyed by WHR in determining a woman's attractiveness as a potential mate. If this is so, it should be possible to systematically change men's evaluations of women's attractiveness by manipulating the size of WHR alone.

To investigate this issue, I developed 12 drawings of female figures, differing solely in the size of their WHR. As there is a positive relationship between BMI and WHR, I used three levels of BMI (underweight, normal and overweight). Within each weight category, line drawings represented four levels of WHR [two typical gynoid WHR (0.7 and 0.8) and two android (0.9 and 1.0) by changing waist size only. The choice to represent various WHRs by changing the size of the waist was based on findings that of all body parts, waist size is clearly positively correlated with altered sex hormonal profile. For instance, postmenopausal women on hormone replacement therapy loose fat selectively from the waist without any significant change in fat deposit on the hip, buttocks or overall body fat [52,53].

Judgments of attractiveness, healthiness and youthfulness were obtained for these 12 figures from men and women of diverse age (18–85 years old), professional (white collar workers, lawyers, physicians), educational (undergraduates and postgraduate degree), and ethnic (Afro-American, Mexican American, Euroamerican) backgrounds [13,14,54]. To summarize the findings:

a) there was a high degree of consensus across sex, educational and ethnic background for the judgment of attractiveness, healthiness and youthfulness;
b) participants judged figures with gynoid WHRs (0.7 and 0.8) as more attractive, healthy, and youthful than figures with android WHRs (0.9 and 1.0); and
c) attractiveness ratings along with ratings of healthiness and youthfulness show a linear drop from WHR of 0.7, followed by 0.8, then 0.9 and then 1.0 in each body weight category.

However, there was a significant interaction between BMI and WHR; within each underweight, normal and overweight category, figures with low WHR were judged as more attractive than figures with high WHR, but across body weight categories, the normal weight figure with low WHR (0.7) had the highest attractiveness rating. Underweight figures with similar WHRs were not judged to be as attractive as normal weight figures with low WHR, and overweight figures, in spite of low WHRs were judged to be less attractive, less healthy and older. Thus, the relationship between WHR and attractiveness was most clearly evident with figures of normal body weight. The impact of WHR on attractiveness judgments is obscured by body weight deviation from the average weight, regardless of whether the weight is extremely low (underweight) or high (overweight). Many researchers have erroneously assumed that WHR and attractiveness hypotheses do not assign any role to BMI, although I had clearly stated the interaction between body weight and WHR in 1993, Viz, "Neither body weight nor WHR alone can explain attractiveness. To be attractive, women must have a low WHR and deviate little from normal weight" [14].

The findings that normal weight female figures with low (0.7) WHR are judged most attractive has been replicated with participants in the U.S., U.K., Germany and Australia using the 12 line drawings developed for the initial study [55–57]. Obviously, the use of line drawings to depict variations in WHR lacks ecological validity. While it allows systematic variation of WHR and holds other bodily features constant, one cannot determine from this if such a manipulation causes people to pay more attention to WHR than usual or how WHR might affect the judgment of female attractiveness when other bodily features, such as breast and facial attractiveness, can also be observed. I have replicated the line drawing findings using photographs of women with altered WHR, but the photographs did not show face

or breasts [58]. Now, Henss has used full frontal photographs that include the face and breasts of different women with computer altered WHR and replicated the findings of the inverse relationship between WHR and attractiveness [59]. This is an exceptionally methodologically sound study as Henss used photographs of six different women and used a between-subjects design, whereas most of the previous studies in this field have used a within-subjects design.

Tovee and his associates [60] have correctly objected to previous research that indicated a relationship between WHR and attractiveness, because none of the previous studies used women with known WHR; it could be that such a relationship may not generalize to an actual population. These researchers, however, incorrectly insist that previous research on WHR and attractiveness did not explore the role of BMI and did not acknowledge the reported interaction between WHR and BMI. To demonstrate that BMI is the more important variable determining female attractiveness, Tovee *et al*. in their first study asked subjects to rate attractiveness of female photographs depicting women with BMI at the 5th percentile (emaciated) to the 95th percentile (morbidly obese) to determine the relative impact of BMI and WHR on attractiveness rating. The results show that when such a BMI range is used, BMI accounts for the majority of the variance, while WHR accounts for very little variance. It should be stressed that *in spite* of the well-established relationship between BMI and WHR, these investigators treated BMI and WHR as independent variables and did not examine their interaction [61,62]. The most appropriate analysis of their data would have been to divide BMI into terciles and to examine the role of WHR within each BMI tercile. Recently, Thornhill and Grammer have examined the effect of BMI and WHR on attractiveness as part of a larger study investigating the relationship of facial attractiveness to BMI and WHR based attractiveness [63]. These investigators used nude full body photographs of young women with known BMI and WHR, but the BMI of these women ranged from 15 to 24. Thornhill and Grammer found a weak effect of WHR and a significant effect of BMI on attractiveness ratings. However, they also did not

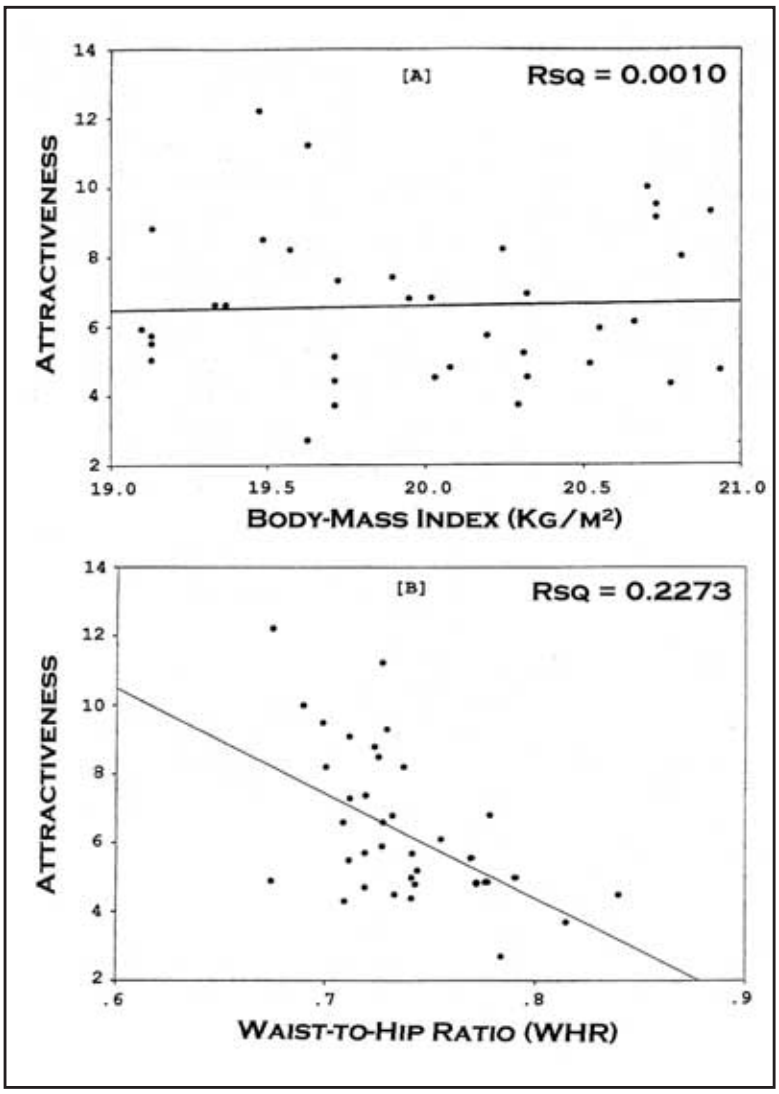


Figure 1. Variance of attractiveness ratings explained by BMI (A) and WHR (B) for data of U.S. and Austrian men analyzed for normal weight BMI range (n=43). When data for the entire sample (n=92) representing BMI range from 15–24 was analyzed, BMI accounts for 23% of variance while WHR accounts for 5% of variance.

examine the role of BMI for the normal population range. Normative data shows that 21 is the 50th percentile for BMI for Caucasian women in the age range of 20–24 [64].

We have recently reanalyzed Thornhill and Grammer's attractiveness data for the photographs showing only the back of the women, head to calf (so as to eliminate any contributions of breast size or facial attractiveness), from the BMI range of 19–22 which represents 50% (n=43) of their sample [65]. Examining the bivariate linear relationships between attractiveness and BMI (in the range of 19–22), and attractiveness and WHR, we found that BMI accounts for virtually no variance, whereas WHR accounts for more than 20% of the variance (Figure 1 here). Clearly, in this BMI range, which represents the majority of normal weight women, WHR is by far the most important for judgment of attractiveness. However, by selecting a greater range of values, BMI can be shown to be more important than WHR in attractiveness. For example, when we use the entire sample of BMI (15–24) used by Thornhill and Grammer, BMI accounts for 23% of the variance in attractiveness, whereas WHR accounts for only 5%. Differences among different BMI ranges account for huge variance overall, but BMI is much less important within a normal weight range. Needless to say, BMI and WHR interact in determining female attractiveness, and treating these two variables as independent would lead to erroneous inferences.

Studies attempting to treat hips or breasts as independent and non-interacting components determining attractiveness face similar problems. For example, in one study, 27 line drawings were developed to systematically represent WHR from 0.5 to 0.9 by either manipulating the size of the waist or the size of the hips within three (underweight, normal and overweight) body weight categories [66]. Results showed that U.S. undergraduate students judge figures with higher WHR as more attractive than figures with low WHR and that body weight and hip size explain more variance than WHR. The authors, however, did not check whether they were successful in changing the size of WHR without affecting perceived body weight. This becomes especially problematic because within any combination of weight category and waist size, a lower WHR can only result from larger hips [59], which makes figures look heavier.

Another recent study [67] has failed to replicate the positive relationship between WHR and attractiveness in U.S. undergraduates reported by Tassinary and Hansen [66]. In this study, color photographs of women were used in which a range of 0.5 to 1.0 WHRs was created by modifying the waist size. These investigators obtained attractiveness ratings and asked participants to estimate the body weight of women in the photographs. Results show that perceived body weight affects attractiveness judgments, and when perceived body weight is statistically controlled, an inverse relationship between WHR and attractiveness is still found to be significant.

It is obvious that isolated changes in different bodily features do not cause independent and isolated changes. The body is perceived as a whole unitary entity (Gestalt) and any morphological trait manipulated beyond a certain point would make the body appear grotesque or unattractive.

Cross-cultural Evidence

The inverse relationship between WHR and female attractiveness has been replicated in various societies, such as the island of Azore, Australia, England, Guinea-Bissau, Greece, Hong Kong, Kenya, India, Indonesia, and Uganda [39,68,69]. These findings are open to the possibility that such a relationship is due to exposure to Western media. Although one would still need to explain why such a relationship exists in Western societies and why Asian and African societies, which are reported to associate fatness with female attractiveness in spite of exposure to Western media, nevertheless attend to and are influenced by WHR.

Obviously, better evidence for a cross-cultural consensus reflective of WHR as an adaptive trait would be to find preferences for low WHR in tribal people who are least exposed to Western influence. There are a few studies that have used this approach. Yu and Shepard [70] report that Peruvian tribe men (n=18, age range 14 – 60 years) living in a reservation and not exposed to European tourists (Gombato group) judge line depicting females of depicting high WHR as more attractive than those with low WHR. However, when these figures were shown to Peruvian tribe men (Shipetiari and Alto Madre groups), who have been exposed to Western tourists for 20–30 years, they judged figures with low WHR as more attractive than figures with high WHR. Preference of the tribes exposed to Western media was identical to that found in Western societies. These investigators therefore concluded that attractiveness of low WHR is a Western phenomenon copied by tribal people in defining their own idea of feminine beauty.

Wetsman and Marlowe [71] tested a hunter gatherer tribe (Hadza) of Tanzania and found that the size of WHR does not affect judgments of attractiveness; Hadza judged heavier figures as more attractive than normal and underweight figures, regardless of their WHRs. These investigators suggest that ecological conditions shape the notion of female attractiveness. They propose that in subsistence-oriented societies, such as hunter-gatherers, women with a greater amount of fat are preferred by men, but in agricultural societies where there is a predictable surplus food supply, preference for lower BMI and low WHR develops.

Another variable that may shape the nature of preferences is the population-typical range of body weight and WHR distribution. As pointed out by Symons [2], psychological mechanisms could instantiate a rule to "prefer WHR somewhat lower than the local female average." As there are population-specific variations in the size of the WHR, it could be that female attractiveness is defined on the basis of being "somewhat lower

than the local female average," rather than some absolute size of WHR. Sugiyama [72] has used this type of logic to investigate the nature of the relationship between WHR and attractiveness and mate preference in the hunter-gatherer Shiwiar tribe of Eastern Ecuador. Sugiyama measured WHRs of Shiwiar men and women and found that the average female WHR was not as low as typically found in Western societies, although average female WHR was significantly lower than average male WHR. Sugiyama used WHR lower and higher than the population average and found that Shiwiar men find female figures depicting lower WHRs attractive and desirable as potential mates. It is worth noting that women of child-bearing age of the Gombato group of Peru have a "high WHR even before final pregnancy and post-childbearing women are thin and have a low WHR" [70]. Therefore, Yu and Shephard should have measured the population average of WHR and investigated if the preferred female WHR was lower than average male WHR, rather than the absolute number of 0.7.

Taking into account the role of population-specific sexual dimorphism in the size of WHR, I and my associates measured the WHRs of isolated herder-gatherer tribes (Sugali and Yanadi) in Southern India as well as those of tribal people (Yanadi) who had moved to the city to work as laborers and would have been exposed to Western media [73]. The argument of Yu and Shephard [70] is that "access to television, cinema and advertising posters displaying exceptionally gynoid females draped over desirable products such as cars and beer" changes the ideals of beauty, and therefore one would expect that a tribe who had moved to the city would have very different notions of what constituted a beautiful woman. The first step was to ascertain the population-specific WHR. Results indicated that all three tribal groups had an average male and female WHR within the range as reported for Caucasian men and women, respectively. Adult males belonging to these three tribes were shown 12 nude female photographs (showing the back side of the body) selected from the set of photographs used by Thornhill and Grammer. As all tribal men were illiterate, they were asked to draw a line (long line for very attractive, and short line for less attractive) on a regular (8.5x11 inch) piece of paper for each figure. This technique allowed us to obtain a score for each photograph rather than obtaining ranking based on the "select the most attractive" technique which generates only nominal data but has been used by two other studies [70,71] of isolated tribes. Results showed that the attractiveness rating was jointly determined by BMI and WHR (Figure 2 here). Photographs were judged to be attractive only if they had normal BMI and a low WHR. There was no difference in the judgment of attractiveness between the tribal group that had moved to the city and the tribal group that had not. As a matter of fact, their judgments were practically identical to those of U.S. participants. To my knowledge, this is the only attractiveness study conducted with a tribal population using photographs of women with known BMI and WHR.

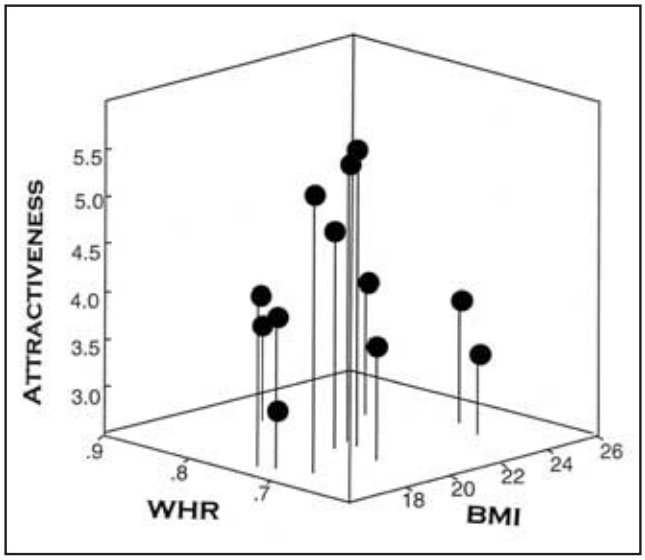


Figure 2. Attractiveness ratings of three groups of adult tribal men (Sugali, rural Yanadi and urban Yanadi) of Southern India (n=103]. It should be stressed that the range of sexual dimorphic difference in size of WHR in these tribal populations is comparable to the range reported for Caucasian populations. There was no significant tribal membership effect and ratings of tribal members who lived in the city responded in the same manner as rural members. Note that, similar to Western men (63], the attractiveness of these tribal men are jointly determined by BMI and WHR.

Cross-generational (historical) Evidence

There is a widespread belief among lay people and many social scientists that people's aesthetic choices are shaped solely by their cultural influences. In the absence of any precise formulation of variables regulating culture and (now) media effect, any similarity across cultures is explained by exposure to a dominant culture media, and lack of similarity is taken as evidence for the uniqueness of culture. Accordingly, Yu and Shepard [70] have argued that culturally isolated indigenous Peruvian men find women with high WHR most attractive, whereas men from the same population exposed to Western media for 20–30 years judge women with low WHR as most attractive. Arguing that even exposure of brief duration (20–30 years) can change the beauty ideals of a culture makes it practically impossible to refute their explanation. Presently, one cannot locate a cultural group in the world for which it can be claimed they have not been exposed to the Western media. Therefore, the issue that a cross-cultural consensus for female attractiveness is due to the design of the psychological mechanism cannot be explored.

One way to assess the role of cultural diffusion versus adaptive design for cross-cultural consensus in attractiveness is to examine the ancient sculptures of various cultures. Artists use naturally occurring responses to biologically significant stimuli. Thus, artistic representations of the female body should invariably be in accord with biological facts. This inference is supported by the evidence that ancient female

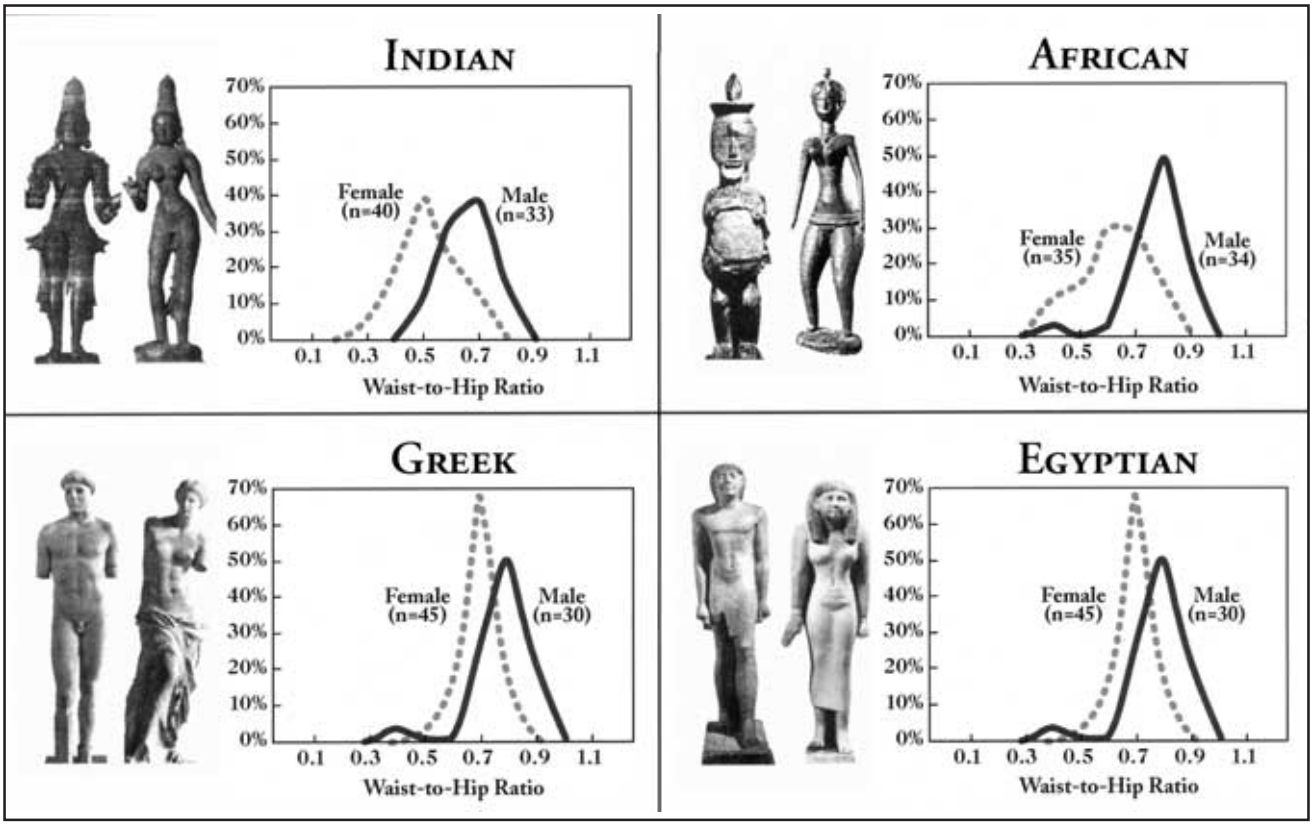


Figure 3. Distribution of male and female WHR in ancient sculptures of three societies and statuettes of African tribes. The source book of these measurements were suggested by art history professors unfamiliar with the WHR hypothesis and contained a broad spectrum from various time periods. All sculptures, whether of mythological or real people, were measured if they were depicted in a frontal (standing or kneeling) pose, unobscured by shadows or objects and with minimal or body hugging clothing. Note that sexual dimorphism is evident in all four groups.

statuettes of venuses of Central Europe and Turkey share a markedly emphasized concentration of lower body fat [74]. Fertility and age related changes in the WHR of a woman would have been observed by artists universally, so the sexual dimorphism in the size of WHR should be evident in artists' depictions of male and female body shapes, in spite of local cannons of aesthetic representation. Consider the ancient sculptures of Rome and India. The archetypical female body form epitomized by Aphrodite, the goddess of beauty and fertility, is, in spite of the difference in representational style remarkably similar to the ancient erotic female sculptures of India. The continued representations of sexual dimorphism among sculptures from Greece, India, and Egypt suggest an almost obsessive and universal interest in specific body parts that depict an alluring body form. Haywood (Personal communication), an art historian, points out that the body form epitomized by Aphrodite was the "ideal" body, whereas the body form of Hera, the goddess of the home and wifely virtues, was sexually less alluring. A cursory examination of these sculptures reveals that the narrow waist of Aphrodite is highlighted, whereas clothing hides the waist and lower body parts of Hera.

If it can be demonstrated that ancient Greek (Greco-Roman), Indian and Egyptian sculptures depict a sexually dimorphic WHR, such a consensus cannot be explained by the influence of modern Western culture. To explore this possibility, I measured WHRs in 286 ancient sculptures from India, Egypt, Greece (Greco-Roman) and some African tribes [73]. In all four cultural groups, distributions of WHR vary but the mean female WHR was significantly lower than the mean male WHR, despite cultural variability (Figure 3 here). Hence, it follows that evolved preferences for female WHR may not be for any absolute size, but rather for lower than average male WHR size evident in a given population.

In a remarkably ambitious study, worldwide WHRs in female depictions dating from the Upper Paleolithic to modern times were analyzed [75]. Measurements of female WHR were obtained from 330 photographs of artworks dating from 32,000 years (B.P.) to 1999 A.D. from Europe, Asia, America and Africa. Results show that, most frequently, WHR was depicted in the range of 0.6 to 0.7. The most important finding of this investigation is that female WHR depictions have remained relatively unchanged from the Upper Paleolithic to the present day. Taken together, this historical cross-cultural information affirms the claim that preference for low WHR is an adaptive design feature rather than an artifact of cultural influence.

General Discussion and Conclusions

The research summarized in this article validates the assertion that selection designed psychological mechanisms in humans to attend to bodily features that convey reliable information about phenotypic and genetic quality and to judge such bodily features as attractive. WHR is a reliable indicator of a woman's various aspects of reproductive capacity (postpubertal premenopausal status, hormonal status and probability of conception and parity), early sign of pregnancy, potential parasite infestation and risk for various diseases. Given that WHR is a heritable trait, an ancestral man selecting a mate with low WHR would have assured his offspring of high quality maternal care (lower risk for diseases) and the genetic gift of good health.

It could be the link between phenotypic quality and WHR that explains the appeal of an hour-glass figure with full breasts and wider hips set against a narrow waist. Women seem to know that the hour-glass figure is sexually appealing to men and attempt to highlight it by manipulating their waist size. When asked how they embellish their appearance around men, young women in the U.S. report "sucking in" their stomachs as the most frequently used tactic after facial makeup and clothing [76]. Similarly, the past popularity of the corset, in spite of the internal injury it caused women, and the currently popularity of abdominoplasty (tummy tuck) are testimonials of the importance of waist size in defining a sexually attractive body. Alternately, women who wish to conceal their sexual attractiveness, such as executive businesswomen, choose clothing that hides rather than highlights their body shape. Nuns' habits, for example, disguise WHR and send a message to males that the women inside the costume are not potential sexual mates.

Women's body shape is affected by both WHR and degree of thinness and fatness (BMI). The amount of body fat is affected by regular availability of food, duration and nature of physical work and certain chronic diseases. In an ancestral hunter-gatherer population, an extremely thin woman (low BMI) would signal malnutrition or sickness; such a woman would have been excluded as a potential mate without any further examination of her WHR. Similarly, an obese woman (high BMI) would arguably be uncommon (due to an unpredictable food supply and physical work) and hence obesity would be a sign of a pathological condition; such a woman would have also been excluded as a potential mate without any further examination of her WHR. From an evolutionary perspective, attractiveness indicators should be examined within the context of an evolutionarily relevant range of occurrence. If the majority of women were within the range of normal weight and if the occurrence extreme thinness or obesity was rare, attending to WHR would have allowed our male ancestors to reliably infer the health and fertility of their potential mates. Moreover, people in ancestral populations would have faced seasons of feast and famine, leading to fluctuations in BMI; however, WHR is not significantly altered until the weight loss or gain exceeds 16.2 pounds [77]. Therefore, small deviations from average body weight (8–10 pounds) would have affected BMI, but such a change would not have been evolutionarily relevant, as such change would have been transitory and tied to feast and famine cycles. However, even a small deviation in WHR would have been indicative of either early pregnancy, pathogen infestation, or parity. It should also be stressed that information about BMI alone, unlike WHR, does not provide any reliable information about the reproductive age of a woman; postmenopausal and prepubertal women can all have an identical BMIs.

Obviously, females with identical WHRs can vary in total body fat, and a maximally attractive amount of total fat may vary from society to society. Human males may have psychological mechanisms designed to adjust certain determinants of attractiveness to local conditions or ecology [2]. Human societies that face frequent food shortage, or must depend on hard labor to acquire and store food, may find strong legs and arms or overall plumpness of body more attractive than narrow waists [71]. Population-specific distribution of BMI and WHR may also influence the size of WHR which is maximally attractive [72]. In some societies where the majority of women have high WHR (e.g. Eskimos of Alaska), men may judge women with high WHR as quite attractive. What is important, however, is the sexually dimorphic size of the WHR rather than the size of women's WHR alone. WHR and attractiveness hypotheses would predict that the maximally attractive size of female WHR should be *lower* rather than equal to or greater than that of men in a population. Cross-cultural studies examining the role of fatness and WHR in determining female attractiveness must obtain information about society-specific distributions of male and female WHR.

Finally, the issue that human females have multiple secondary sexual features of the face and body that affect attractiveness must be addressed. Thornhill and Grammer [63] provide research evidence that suggests that features of a woman's face and body "collectively comprise a single ornament that honestly signals hormonal health and associated variables, such as immunocompetence and possible development health as well" [63, p. 115]. However, the components that constitute a single ornament can convey many overlapping and yet slightly different messages about phenotypic and genetic quality. Facial secondary sexual characteristics convey information about hormonal condition prior to and during puberty and age. These facial characteristics, however, do not provide any readily observable, reliable information about ovulation or early stage of pregnancy. Facial and body asymmetry can be indicative of past parasite infestation or developmental stress on the immune system, but may not be sensitive to current hormone levels and reproductive history. Manning [78] has suggested that developmental stability is signaled by fixed traits such as teeth and other skeletal features, as asymmetry in these traits results from a slow incremental accumulation. Phys-

iological status is signaled by those dynamic soft-tissue traits that are related to some aspect of fertility or metabolic efficiency. For example, Manning and his associates [79] found that women's breasts become more symmetrical during ovulation; WHR also becomes smaller during ovulation [45], so attending to breast shape and the size of WHR can provide information about the fecundability of women. Although not yet incorporated into attractiveness literature, the 2nd and 4th digit (2D:4D) ratio is a reliable signal of sex hormone levels and the fertility of a woman [78]. It may very well be that the 2D:4D ratio influences mate choice to some degree. The main point which I wish to make is that the single but complex ornament of the face and body may contain correlated components that provide overlapping but still different messages about the attractiveness and mate value of a woman.

Thornhill and Grammar [63] have provided a way to integrate the role of face and body in determining attractiveness. A better understanding of the interrelationship between various sexual characteristics (facial, breast, BMI, WHR) that constitute attractiveness and female mate quality could emerge from an examination of these sexual characteristics simultaneously.

REFERENCES

1 Symons D. The Evolution of Human Sexuality. New York, Oxford, 1979.
2 Symons D. Beauty is in the Adaptation of the Beholder: The Evolutionary Psychology of Human Female Sexual Attractiveness. In: Abramson PR, Pinkerton, S D eds. Sexual Nature, Sexual Culture. Chicago: University of Chicago Press; 1995, 80–118.
3 Buss DM. The Evolution of Desire: Strategies of Human Mating. New York: Basic Books; 1994.
4 Gangestad S, Thornhill R. Human Sexual Selection and Developmental Stability. In: Simpson J, Kenrick D, eds. Evolutionary Social Psychology. Mahwah: Elrbaum; 1997. pp. 169–195.
5 Grammer K, Thornhill K. Human (Homo sapiens) Facial Attractiveness and Sexual Selection: The Role of Symmetry and Averageness. J Comp Psychol 1994; **108**:233–242.
6 Cunningham MR. Measuring the Physical in Physical Attractiveness: Quasi-experiments in the Sociobiology of Female Facial Beauty. J Pers Soc Psychol 1986; **50**:925–935.
7 Johnston VS, Franklin M. Is Beauty in the Eye of the Beholder? Ethol Sociobiol 1993; **14**:183–199.
8 Johnston VS. Why We Feel: The Science of Human Emotion. Reading: Perscus Press.
9 Perrett DI, May KA, Yoskikawa S. Facial Shape and Judgment of Female Attractiveness. Nature 1994; **368**:239–242.
10 Perret DI, Burt MD, Penton-voak IS, Lee KJ, Rowland DA, Edwards R. Symmetry and Human Facial Attractiveness. Evol Hum Behav 1999; **20**:295–307.
11 Gangestad SW, Thornhill R, Yeo RA. Facial Attractiveness, Developmental Stability, and Fluctuating Asymmetry. Ethol Sociobiol 1994; **15**:73–85.
12 Thornhill R, Gangestad SW. Facial Attractiveness. Trend Cog Sci 1999; **3**:452–460.
13 Singh D. Adaptive Significance of Female Physical Attractiveness: Role of Waist-to-hip Ratio. J Pers Soc Psychol 1993; **65**:292–307.
14 Singh D. Body Shape and Women's Attractiveness: The Critical Role of Waist-to-hip Ratio. Hum Nat 1993; **4**:297–321.
15 Lev-Ran A. Human Obesity: An Evolutionary Approach to Understanding our Bulging Waistline. Diabetes Metab Res Rev 2001; **17**:347–362.
16 Seidell JC, Flegal KM. Assessing Obesity: Classification and Epidemiology. BMJ 1997; **53**:238–252.
17 Bjorntorp P. Body Fat Distribution, Insulin Resistance, and Metabolic Diseases. Nutr 1997; **13**:795–803.
18 Molarius A, Seidell JC, Sans S, Tuomilehto JR, Kuulasmaa K. Waist and Hip Circumference, and Waist-to-hip Ratio in 19 Populations of WHO MONICA Project. Int J Obes 1999; **23**:116–125.
19 Marti B, Tuomilehto J, Saloman V, Kartovaara L, Korhonen HJ, Pietinen P. Body Fat Distribution in the Finnish Population: Environmental Determinants and Predictive Power For Cardiovascular Risk Factor Level. J Epidemiol Com Hlth 1991; **45**:131–137.
20 Kirschner MA, Samojlik E. Sex Hormone Metabolism in Upper and Lower Body Obesity. Int J Obes 1991; **15**:101–108.
21 Arechiga J, Prado C, Canto M, Carmenati H. Women in Transition-menopause and Body Composition in Different Populations. Coll Anthropol 2001; **25**:443–448.
22 Dewailly D, Cortet-Rudelli C, Deroubaix-Allard D. Markers of Abdominal Adipose Tissue in Women: Relationship to Ovarian Function. TEM 1998; **9**:68–71.
23 Pasquali R, Gambineri A, Anconetani B, Vicennati V, Colitta D, Caramelli E, Casimirri F, Morselli-Labali AM. The Natural History of the Metabolic Syndrome in Young Women with the Polycystic Ovary Syndrome and the Effect on Long-term Oestrogen-progestagen Treatment. Clin Endocrinol (Oxf.) 1999; **50**:517–527.
24 Velazquez HE, Bellabarba GA, Mendoza S, Sanchez L. Postprandial Triglyceride Response in Patients with Polycystic Ovary Syndrome: Relationship with Waist-to-hip Ratio and Insulin. Fert Steril 2000; **74**:1159–1163.
25 Nelson TL, Vogler GP, Pederson NL, Miles TP. Genetic and Environmental Influences on Waist-to-hip Ratio and Waist Circumference in an Older Swedish Twin Population. Int. J Obes 1999; **23**:449–455.
26 Feitosa MF, Borecki I, Hunt SC, Arnett DK, Rao DC, Province M. Inheritance of the Waist-to-hip Ratio in the National Heart, Lung, and Blood Institute Family Heart Study. Obes Res 2000; **8**:294–301.
27 Bjorntorp P. The Association Between Obesity, Adipose Tissue Distribution and Disease. Acta. Med Scand 1988; **723**:121–134.
28 Kissebah AH, Krakower GR. Regional Adiposity and Mortality. Physiol Rev 1994; **74**:761–811.
29 Guo S, Salisbury S, Roche AF, Chumela WC, Siervogel RM. Cardiovascular Disease Risk Factor and Body Composition: A Review Nutr Res 1994; **14**:1721–1777.
30 Bujalska IJ, Kumar S. Does Central Obesity Reflect "Cushing's Disease of the Omentum?" Lancet 1997; **349**:1210–1213.
31 Han TS, Lean ME, Seidell JC. Waist Circumference Remains as Useful Predictor of Coronary Heart Disease. BMJ 1996; **312**:1227–1228.
32 Lean ME, Han TS, Morrison CE. Waist Circumference as a Measure for Indicating Need for Weight Management. BMJ 1995; **311**:158–161.
33 Folsom AR, Kaye SA, Seller TA, Hong C, Cerhan JR, Potter JD, Prineas RJ. Body Fat Distribution and 5-year Risk for Death in Older Women. J Amer Med Assoc 1993; **269**:483–487.
34 Kortelainen ML, Sarkioja T. Extent and Composition of Coronary Lesions in Relation to Fat Distribution in Women Younger than 50 Years of Age. Arterio Throm Vas Biol 1999; **19**:695–699.
35 Epel ES, McEwen B, Seeman T, Matthews K, Castellazo G, Brownell KD, Bell J, Ickovies JR. Stress and Body Shape: Stress-induced Cortisol Secretion is Consistently Greater Among Women with Central Fat. Psychosom Med 2000; **62**:623–632.
36 Rosmond R, Baghei F, Holm G, Bjorntorp P. Relationship Between Personality Disorders and Anthropometry, Hormones and Metabolism in Women. J Endocrinol Invest 2001; **24**:159–165.

37 Nelson TL, Palmer RF, Pedersen NL, Miles TP. Psychological and Behavioral Predictor of Body Fat Distribution: Age and Gender Effect. Obes Res 1999; **7**:199–207.
38 Baumgartner RN, Heymsfield SB, Roche AF. Human Body Composition and the Epidemiology of Chronic Diseases. Obes Res 1995; **3**:73–95.
39 Singh D. Attractiveness of Body Shape in Cross-cultural Perspective. Biennial Meeting of the Society for Psychological Anthropology, October 9, 1997. San Diego, California.
40 Kirchengast S, Gruber D, Sator M, Knogler, W Huber, J. The Impact of Nutritional Status on Body Fat Distribution Patterns in Pre- and Postmenopausal Females. J. Biosoc. Sci 1998; **30**:145–154.
41 Han TS, Morrison CE, Lean ME. Age and Health Indicators Assessed by Silhouette Photographs. Eur J Clin Nutr 1999; **53**:606–611.
42 Singh D. Waist-to-hip Ratio and Judgment of Attractiveness and Healthiness of Female Figures by Male and Female Physicians. Int J Obes 1994; **18**:731–737.
43 Van Hooff MH, Voorhorst FJ, Kaptein MB, Hirasing RA, Koppenaal C, Schoemaker J. Insulin, Androgen, and Gonadotropin Concentration, Body Mass Index, and Waist to Hip Ratio in the First Years After Menarche in Girls with Regular Menstrual Cycle, Irregular Menstrual Cycles, or Oligomenorrhea. J Clin Endocrinol Metab 2000; **85**:1394–1400.
44 Moran C, Hernandez E, Ruiz IE, Fonseca ME, Bermudez JA, Zarate A. Upper Body Obesity and Hyperinsulinemia are Associated with Anovulation. Gynecol Obstet Invest 1999; **47**:1–5.
45 Singh D, Davis M, Randall P. Fluctuating Ovulation: Lower WHR, Enhanced Self-perceived Attractiveness, and Increased Sexual Desire. Paper presented at Human Evolution and Behavior Society meeting, London, U.K. 2000, June 14.
46 Jenkins JM, Brook P.F, Sargeant S, Cooke ID. Endocervical Mucus pH is Inversely Related to Serum Androgen Levels and Waist-to-hip Ratio. Fert Ster 1995; **63**:1005–1008.
47 Zaadstra BM, Seidell JC, Van Noord PA, te Velde ER, Habbema JDF, Vrieswijk B, Karbaat J. Fat and Female Fecundity: Prospective Study of Body Fat Distribution and Conception Rates. BMJ 1993; **306**:484–487.
48 Waas P. waldenstrom, U Rossner, Hellberg D. An Android Body Fat Distribution in Female Impairs the Pregnancy Rate of *In-vitro* Fertilization-embryo Transfer. Hum Reprod 1997; **12**, 2057–2060.
49 Clapp JF, Seaward BL, Sleamaker RH, Hiser J. Maternal Physiological Adaptations to Early Human Pregnancy. Am J Obstet Gynecol 1988; **159**:1456–1460.
50 Tonkelaar I, Seidell JC, Van Noord PA, Baander-van Halewijn EA, Ouwehand IJ. Fat Distribution in Relation to Age, Degree of Obesity, Smoking Habits, Parity and Estrogen Use: A Cross-sectional Study of 11,825 Dutch Women Participating in DOM-Project. Int J Obes 1990; **14**:753–761.
51 Sohlstrom A, Forsum E. Changes in Adipose Tissue Volume and Distribution During Reproduction in Swedish Women as Assessed by Magnetic Imagery. Am J Clin Nutr 1995; **161**:287–295.
52 Haarbo J, Marslow V, Gottfredsen A, Christiansen C. Postmenopausal Hormone Replacement Therapy Prevents Central Distribution of Body Fat After Menopause. Metab 1991; **40**:323–326.
53 Perrone G, Liu Y, Capri O, Critelli C, Barillaro F, Galoppi P, Zichella L. Evaluation of the Body Composition and Fat Distribution in Long-term Users of Hormone Replacement Therapy. Gynecol Obstet Invest 1999; **48**:52–55.
54 Singh D. Body Fat Distribution and Perception of Desirable Female Shape by Young Black Men and Women. Int J Eating Disorder, 1994; **16**:289–294.
55 Furnham A, Tan T, McManus C. Waist-to-hip Ratio and Preferences for Body Shape: A Replication and Extension. Pers Indiv Diff 1997; **22**:539–549.
56 Henss R. Waist-to-hip Ratio and Attractiveness: Replication and Extension. Pers Ind Diff 1995; **19**:479–488.
57 Connally J, Slaughter V, Mealy L. Children's Preference for Waist-to-hip Ratio: A Developmental Study. (submitted for publication).
58 Singh D. Is Thin Really Beautiful and Good? Relationship Between Waist-to-hip (WHR) Ratio and Female Attractiveness. Pers Ind Diff 1994; **16**:123–132.
59 Henss R. Waist-to-hip Ratio and Female Attractiveness. Evidence from Photographic Stimuli and Methodological Considerations. Pers Indiv Diff 2000; **28**:501–513.
60 Tovee MJ, Reinhardt S, Emery JL, Cornelissen PL. Optimal Body Weight Index and Maximal Sexual Attractiveness. Lancet 1998; **352**:548.
61 Tovee MJ, Maisey DS, Emery JL, Cornelissen PL. Visual Cues to Female Attractiveness. Proc R Soc Lond B Biol Sci 1999; **266**:211–218.
62 Tovee MJ, Cornelissen PL. Female and Male Perception of Female Physical Attractiveness in Front-view and Profile. Br J Psychol 2001; **92**:391–402.
63 Thornhill R, Grammer K. The Body and Face of Women: One Ornament That Signals Quality? Evol Hum Behav 1999; **20**:105–120.
64 Must A, Dallal GE, Dietz W.H. Reference Data for Obesity: 85th and 95th Percentile of Body Mass Index (Wt/Ht^2) and Triceps Thickness. Am J Nutr 1991; **53**:839–846.
65 Singh D, Zambarano RJ, Grammer K, Thornhill R. Body Mass Index, Waist-to-hip Ratio and Women's Body Attractiveness. (unpublished manuscript)
66 Tassinary LG, Hansen KA. A Critical Test of the Waist-to-hip Ratio Hypothesis of Female Physical Attractiveness. Psychol Sci 1998; **9**:150–155.
67 Streeter S.A, McBurney D. Waist-hip ratio and attractiveness: New evidence and a critique for a "critical test," Evol Hum Behav in press.
68 Furnham A, Moutafi J, Baguma P. A Cross-cultural Study on the Role of Weight and Waist-to-hip Ratio on Female Attractiveness. Pers Indiv Diff 2002; **32**:729–745.
69 Singh D, Luis S. Ethnic and Gender Consensus for the Effects of Waist-to-hip Ratio on Judgment of Women's Attractiveness. Hum Nat 1995; **6**:51–65.
70 Yu DW, Shepard GH. Is Beauty in the Eye of the Beholder? Nature 1998; **396**:321–322.
71 Wetsman A, Marlowe F. How Universal are Preferences for Female Waist-to-hip Ratios? Evidence from the Hadza of Tanzania. Evol Hum Behav 1999; **20**:219–228.
72 Sugiyama LS. Beauty is in the Context-sensitive Adaptation of the Beholder: Shiwiar Use of Waist-to-Hip Ratio in Assessment of Female Mate Value. Evol Hum Behav (in press)
73 Singh D. Waist-to-hip Ratio: An Indicator of Female Mate Value. Kyoto Symposium on Human Mate Choice, November 20–24, 2000.
74 Tarui S, Tokunaga K, Fujioka S, Matsuzawa Y. Visceral fat obesity: Anthropological and pathophysiological aspects. Int J Obes 1991; **15**:1–8.
75 Chiappa P. Palencia G, Mondragon-ceballos R. The Everlasting Appeal of Low Female Waist-to-hip Ratio in Works of Art. Submitted for publication.
76 Tooke W, Camire L. Pattern of deception in intersexual and intrasexual mating strategies. Ethol Sociobiol 1991; **12**:345–364.
77 Kissebah A.H, Peiris A, Evans D.J. Mechanisms associating body fat distribution with the abnormal metabolic profile in obesity. In Berry EM, Blondheim SH, Elihau HE, Schafrir E, Eds. Recent Advances in Obesity Research, London: John Libbey; 1987. pp. 54–49.
78 Manning JT. Digit ratio: A pointer to fertility, behavior, and health, New Brunswick, NJ : Rutgers University Press, 2002.
79 Manning JT, Scutt D, Whitehouse GH, Leinster SJ, Walton JH. Asymmetry and menstrual cycle in women. Ethol Sociobiol 1996; **17**:129–143.

Neuroendocrinology Letters Special Issue, Suppl.4, Vol.23, December 2002
Copyright © Neuroendocrinology Letters ISSN 0172–780X **www.nel.edu**

REVIEW ARTICLE

The Neural Mechanisms of Mate Choice: A Hypothesis

Helen Fisher[1], Arthur Aron[2], Debra Mashek[2], Haifang Li[3], Greg Strong[2] & Lucy L. Brown[4]

1. Department of Anthropology, Rutgers Uuniversity, New Brunswick, NJ, USA.
2. Department of Psychology, SUNY Stony Brook
3. Department of Radiology, SUNY Stony Brook
4. Department of Neurology and Neuroscience, Albert Einstein College of Medicine

Correspondence to: Dr. Helen E. Fisher, 4 East 70th Street,
New York City, NY 10021, USA
PHONE: +1 (212) 744-9870
FAX: +1 (212) 772-1637
EMAIL: hefisher@worldnet.att.net.

Submitted: *September 9, 2002*
Accepted: *September 15, 2002*

Key words: **mate choice; attraction; proceptivity; dopamine; fMRI scanning; brain circuits**

Neuroendocrinology Letters 2002; ***23*** *(Suppl.4):92–97 pii: NEL231002R09 Copyright © Neuroendocrinology Letters* ***www.nel.edu***

Abstract Scientists have described many physical and behavioral traits in avian and mammalian species that evolved to attract mates. But the brain mechanisms by which conspecifics become attracted to these traits is unknown. This paper maintains that two aspects of mate choice evolved in tandem: 1) traits that evolved in the "display producer" to attract mates and, 2) corresponding neural mechanisms in the "display chooser" that enable them to become attracted to these display traits. Then it discusses our (in-progress) fMRI brain scanning project on human romantic attraction, what we believe is a developed form of "courtship attraction" common to avian and mammalian species as well as the primary neural mechanism underlying avian and mammalian mate choice. The paper hypothesizes that courtship attraction is associated with elevated levels of central dopamine and norepinephrine and decreased levels of central serotonin in reward pathways of the brain. It also proposes that courtship attraction is part of a triune brain system for mating, reproduction and parenting. 1) The sex drive evolved to motivate birds and mammals to court any conspecifics. 2) The attraction system evolved to enable individuals to discriminate among potential mating partners and focus courtship activities on particular individuals, thereby conserving mating time and energy. 3) The neural circuitry for attachment evolved to enable individuals to complete species-specific parental duties.

Introduction

Charles Darwin distinguished between two types of sexual selection, intrasexual selection, by which members of one sex evolve traits that enable them to compete directly with one another to win mating opportunities; and intersexual selection, by which individuals of one sex evolve traits that are preferred by members of the opposite sex [1]. The second of these two processes for mating success has become known as "mate choice." This paper maintains that two aspects of mate choice evolved in

tandem: 1) traits that evolved in the "display producer" to attract mates and, 2) corresponding neural mechanisms in the "display chooser," the viewer of the display, that enable the viewer to become attracted to these display traits.

It is well established that many creatures have mate preferences and make mate choices. In fact, the phenomenon of mate choice is so common in nature that the ethological literature regularly uses several terms to describe it, including "mate choice," "female choice", "mate preference", "individual preference", "favoritism", "sexual choice" and "selective proceptivity." And in past decades scientists have described many physical and behavioral traits that evolved in birds and mammals by means of mate choice [2, 3]. The peacock's elaborate tail feathers are the standard example. But no one had defined the corresponding neural mechanisms in the display chooser, the brain mechanisms by which the chooser internally processes these display traits, comes to prefer certain traits, rejects other traits, and focusses mating energy on particular conspecifics, thereby making a mate choice. So this paper attempts to define the primary neural mechanisms that facilitate mate preference, the mechanisms by which the chooser prefers and pursues certain conspecifics. We call this neural mechanism "courtship attraction."

We hypothesize that courtship attraction is associated with a specific and distinct constellation of neural correlates, an "attraction system;" that this attraction system operates in tandem with other neural systems, including the sex drive and circuits for sensory perception, discrimination and memory; that courtship attraction is expressed at different times and to different degrees in different species according to each species' specific reproductive strategy; and that this neural attraction circuit evolved to enable display choosers to perform three essential tasks of courtship: 1) discriminate among courtship displays; 2) prefer those displays that advertise superior genes, better resources and/or more parental investment; and 3) motivate the display chooser to focus courtship attention on and pursue particular mating partners, thereby conserving courtship time and energy.

It is hypothesized that in most mammalian and avian species this excitatory state of courtship attraction is brief; attraction lasts only minutes, hours, days or weeks. In humans, the neural mechanisms associated with courtship attraction are more developed, forming the physiological basis of what is commonly known as passionate love, obsessive love, "being in love", and/or romantic love.

Overview Of The Field

Psychologists regularly distinguish between the affective state of romantic attraction (passionate love, obsessive love, or "being in love") and the sex drive [4, 5, 6, 7, 8]. But this motivation-emotion system, courtship attraction, is not clearly described in the ethological literature. Instead, ethologists generally lump attraction with the sex drive and call this behavioral/physiological state "proceptivity." There are exceptions. In 1976 Frank Beach made a distinction between the sex drive and attraction, writing: "The occurrence or non-occurrence of copulation depends as much on individual affinities and aversions as upon the presence or absence of sex hormones in the female…proceptive and receptive behavior may depend upon different anatomical and neurochemical systems in the brain."[9]. More recently Donald Pfaff and colleagues have distinguished between the hormone-dependent elevation of courtship arousal and the expression of approach and other courtship behaviors, regarding these as distinct aspects of mating behavior and physiology [10].

A few scientists have also considered the anatomical and/or neurochemical mechanisms that produce and direct courtship attraction. Darwin proposed that female mate preferences arose from their innate sense of beauty. But he (understandably) offered no suggestion as to how this feminine attraction to beauty operates in the brain. He wrote, "It is, however, difficult to obtain direct evidence of their capacity to appreciate beauty" [11].

Hutchison and Hutchison propose that courtship could entail "a sequence of choices each requiring different mechanisms" and they speculate on some of the underlying neural mechanisms associated with mate preference [12]. They question whether the sex hormones are involved, saying, "Hormones are well known to be closely related to sexual behaviour. But whether sex hormones have any specific role in the establishment and expression of mating preferences… does not appear to be known" [13]. Yet they conclude that testosterone and some of the androgenic metabolites could be involved in some aspects of avian mate choice.

Geoffrey Miller has hypothesized that the endorphins are involved in mate choice. He notes that "display-judgers" must have evolved several faculties to discern and respond to the displays of "display-producers," including aspects of sensory perception, cognition, memory, judgement and feelings of pleasure. He calls this constellation of neural mechanisms in both sexes "mental machinery" and "sexual choice equipment" [14]. Miller then distinguishes between "cold choosers," such as insects that become attracted to ornamental displays without any sensation of pleasure, and "hot choosers," animals whose choice of mates is directed by subjective feelings of pleasure. And he writes, "The hot chooser has a big pleasure-meter in its brain – it may be something like the level of endorphins floating around its nervous system" [15]. Miller maintains that both sexes inherit and pass to their offspring the genes that underlie this mental machinery for mate preference [16].

Frank Beach also recognized that proceptive behavior was a composite of more than one neurochemical system and suggested that the sex hormones may have operated in tandem with the monoamines. As he reported, "The mating behavior of female rats treated with monoamine receptor blocking agents indicates that 'lordotic behavior and soliciting behavior may be mediated by anatomically and possibly neurochemically

separate systems" [17, 18]. Subsequently it has been established that some of the monoamines, specifically dopamine and norepinephrine, play significant roles in regulating aspects of proceptivity [19, 20, 21, 22, 23, 24, 25, 26].

We hypothesize that some of the monoamines, specifically elevated levels of central dopamine and norepinephrine and decreased levels of central serotonin, are the primary neural mechanisms associated with mate choice [27]. We arrived at this hypothesis after launching a three-part investigation of courtship attraction in humans. We chose to study attraction in humans because this motivation-emotion system is universal to human societies, extensively described in the psychological literature, and more easily tabulated and quantified than is courtship attraction in other species. The rest of this paper reports on this in-progress investigation of human courtship attraction, what we regard as the primary neural mechanism underlying mate choice.

Phase I: The Hypothesis

In their survey of 166 societies, Jankowiak and Fischer found evidence of romantic attraction in 89% of these cultures. People sang love songs, composed love poems, practiced love magic, described myths and legends about love, and/or committed suicide or homicide due to unrequited love. The authors found no negative evidence; in the balance of these societies the lack of evidence was attributed to ethnographic oversight. So Jankowiak and Fischer conclude that romantic attraction is a universal affective state [28].

In phase I of the investigation of this neural circuit, the currently available American psychological literature was canvassed and a list of psychophysiological properties regularly associated with this excitatory state was compiled [29, 30, 31, 32]. These primary psychophysiological characteristics of romantic attraction were then compared with the behavioral effects of central dopamine, norepinephrine and serotonin [33]. Several correlations (listed below) suggest that elevated levels of central dopamine and norepinephrine and decreased levels of serotonin are involved in human courtship attraction.

1) Romantic attraction is associated with focussed attention on a specific, preferred other. Elevated concentrations of central dopamine and norepinephrine are associated with heightened and focussed attention [34, 35, 36]. These parallels suggest that elevated levels of central dopamine and norepinephrine contribute to the lover's focussed attention on the beloved.
2) The lover tends to regard the beloved as novel and unique. Elevated concentrations of central dopamine are associated with exposure to novelty [37].
3) The lover tends to remember tiny details of the beloved and their times spent together. Elevated levels of central norepinephrine are associated with increased memory for new stimuli [38].
4) The lover becomes highly motivated to seek affiliation with the beloved and exhibits diverse goal-oriented behaviors designed to achieve affiliative contact. Elevated levels of central dopamine are associated with motivation and goal-directed behaviors [39, 40, 41].
5) Characteristic of the lover is emotional dependence on the relationship with the beloved and longing, even craving, for emotional union with the beloved. Emotional dependency and craving are aspects of addiction associated with dopamine and norepinephrine pathways in the brain [42, 43, 44].
6) When people are "in love," they characteristically express heightened energy, sleeplessness and often loss of appetite, as well as labile emotional states, predominated by euphoria. Elevated levels of dopamine and norepinephrine are associated with hyperactivity [45], sleeplessness [46], loss of appetite [47] and feelings of euphoria [48, 49].
7) Adversity intensifies feelings of attraction. Known as the "Romeo and Juliet Effect," this phenomenon is most likely also associated with elevated levels of dopamine. When a reward is delayed, dopamine-producing cells in the Ventral Tegmental Area of the midbrain increase their activity [50]. (This neural mechanism probably evolved, in part, to drive birds and mammals to work even harder in times of adversity to acquire genetically desirable partners.)
8) The most prominent aspect of romantic attraction is obsessive thinking about the beloved. Obsessive thinking is commonly associated with low levels of central serotonin [51, 52, 53].

Focussed attention, motivation, goal-oriented behaviors, heightened energy, sleeplessness, loss of appetite, feelings of euphoria, obsessive thinking about the beloved, and heightened attraction during adversity in the relationship are all aspects of romantic attraction and all of these traits are associated with elevated levels of central dopamine and norepinephrine and/or decreased levels of central serotonin. These correlated data led to the hypothesis that romantic attraction to a preferred conspecific is associated with elevated levels of central dopamine and norepinephrine and decreased levels of central serotonin in corresponding brain regions. Passionate attraction takes a variety of graded forms, however, ranging from romantic love that is returned to unrequited love. So it is expected that these gradations of attraction are associated with different combinations of central dopamine, norepinephrine and serotonin, as well as with the activities of many other neural systems.

Phase II: Protocol Design

In phase II of this project the authors devised an experiment to establish which of several stimuli would produce feelings of romantic attraction. Eleven female and three male volunteers who reported that they had "just fallen madly in love" were first orally interviewed; data were also collected regarding their romantic rela-

tionship via a series of questionnaires. Then these subjects used a computer-based response device to indicate the intensity of their current feelings of romantic love while being exposed to a series of stimuli, including a visual image of the beloved, a smell, a song, a love note, a memory of the beloved and an anticipated event with the beloved. Their responses were recorded and compared to their responses while reacting to a neutral stimulus in each of the above categories; and a statistical analysis was made. It was established that feelings of romantic attraction are stimulated most effectively by photographs of the beloved, "thinking back" to specific relationship events, and songs relevant to the relationship [54].

These data formed the basis of the protocol for the functional Magnetic Resonance Imaging (fMRI) investigation, Phase III of this project.

Phase III: fMRI Investigation

In Phase III of this project, volunteers between the ages of 18 and 28 who reported that they had "just fallen madly in love" were interviewed to establish the extent of their romantic passion and their appropriateness for fMRI brain scanning. Subjects were then educated regarding the fMRI procedure and the protocol of the experiment and administered several questionnaires; then the brain scanning session was scheduled and completed. Among the tasks that each subject was required to do during the brain scanning process was to look at a photograph of the beloved and a photograph of a familiar individual for whom the subject felt no strong positive or negative feelings. During this twelve minute experiment, 3,200 brain images were collected for each subject.

This fMRI study is currently in progress. It is predicted that some of the brain regions associated with the feeling of intense romantic attraction will be those with high concentrations of receptor sites for dopamine, norepinephrine and serotonin, such as the caudate and the putamen and other regions associated with the "reward system" in the brain [55, 56, 57].

Discussion

Bartels and Zeki completed a similar fMRI experiment using 17 men and women who reported being "truly, deeply and madly in love" [58]. These scientists found a specific constellation of brain activity associated with romantic attraction and concluded that "a unique network of areas is responsible for evoking this affective state" [59]. In their study, bilateral activation occurred in the medial insula, the anterior cingulate cortex, the posterior hippocampus, the head of the caudate nucleus and the putamen. Deactivations occurred in the right prefrontal, parietal and middle temporal cortices, the medial prefrontal cortex, the posterior cingulate gyrus and the posterior amygdaloid region.

The caudate nucleus is associated with motivation and goal-oriented behaviors and 80% of receptor sites for central dopamine reside here. These data suggest that our hypothesis is at least partially correct: courtship attraction is primarily a motivation system that arises, in part, from the basal ganglia and is associated with dopamine pathways in the reward system of the brain.

Data from animal studies also support our hypothesis that elevated levels of central dopamine play a primary role in courtship attraction in mammalian species. In rats, blocking the activities of dopamine diminishes proceptive behaviors, including hopping and darting [60]. When a female lab–raised prairie vole is mated with a male, she forms a distinct preference for this partner. This preference is associated with a 50% increase of dopamine in the nucleus accumbens [61]. When a dopamine antagonist is injected directly into the nucleus accumbens, females no longer prefer this partner. And when a female is injected with a dopamine agonist, she begins to prefer a conspecific who is present at the time of infusion, even if the female has not mated with this male [62].

Data on animals also suggest that norepinephrine is involved in the courtship attraction response. When a female prairie vole is exposed to a drop of male urine on the upper lip, norepinephrine is released in parts of the olfactory bulb; this contributes to the release of estrogen and concomitant proceptive behavior [63]. Ovarian hormones, estradiol and progesterone, act to determine the release of norepinephrine in the hypothalamus to produce lordosis behavior in rats, a primary aspect of courtship behavior in this species [64]. And when ovariectomized, sexually receptive female rats receive injections of estrogen and are then permitted to mate, mating produces release of norepinephrine in the lateral ventromedial hypothalamus [65].

Conclusion

Fisher (1998) has hypothesized that avian and mammalian species have evolved three distinct brain systems for courtship, mating, reproduction and parenting [66].

1) The sex drive is characterized by a craving for sexual gratification.
2) Attraction (favoritism, sexual preference, or mate choice) is characterized by focussed attention on a preferred partner, heightened energy, motivation and goal-oriented courtship behaviors.
3) Attachment is characterized by the maintenance of proximity to a mating partner, affiliative gestures and expressions of calm when in social contact with this mating partner, separation anxiety when apart, and parental behaviors such as territory defense, nest building, mutual feeding, grooming and other parental chores [67, 68, 69, 70].

Each of these motivation-emotion systems, lust, attraction and attachment, is associated with a different constellation of brain circuits, different behavior patterns and different affective states. Each varies according to the reproductive strategy of each species. And each motivation-emotion system evolved to play a distinct

role in reproduction [71]. The sex drive evolved principally to motivate individuals to seek sexual union with *any* appropriate member of the species. Attraction evolved to motivate individuals to select among potential mating partners, prefer particular conspecifics, and focus their courtship attention on this/these individuals, thereby making a mate choice. And the neural circuitry for adult male/female attachment evolved primarily to motivate individuals to sustain these affiliative connections long enough to complete species-specific parental duties [72].

This paper focusses on the neural circuitry of the attraction system. It hypothesizes that mate choice in mammalian and avian species is associated with two phenomena that evolved in tandem: 1) traits of the "display producer" and, 2) a corresponding neural mechanism that enables the "display chooser" to prefer certain display traits, an "attraction system." Primary to this neural courtship attraction system in avian and mammalian species is elevated levels of central dopamine and norepinephrine and decreased levels of central serotonin in corresponding brain regions.

Among the brain regions likely to be involved in the neural circuitry of attraction and mate choice are: 1) The caudate nucleus and other regions of the basal ganglia associated with focussed attention, motivation, goal-oriented behavior, craving and addiction. 2) The anterior cingulate cortex and other regions of the Limbic System associated with emotion, feeling and affect. 3) The insular cortex, which processes emotions and bodily states. 4) Structures in the prefrontal cortex associated with reward assessment, planning and monitoring (most likely regions of the dorsolateral prefrontal cortex) and cortical structures associated with emotion processing (most likely regions in the ventromedial prefrontal cortex).

Some of the neural circuits associated with the sex drive have been identified [73, 74, 75]. It is hypothesized that the neural system for courtship attraction is distinct from but closely linked to some of these primary circuits associated with the sex drive and that these two neural systems, attraction and the sex drive, operate in tandem in most avian and mammalian species. This courtship attraction circuit must also operate in tandem with neural systems associated with the discrimination of colors, sizes, shapes, vocal tones, odors, postures, gestures and other brain systems associated with sensory perception, memory, reward assessment, planning and motor activities.

Last, it is hypothesized that this attraction circuit varies in duration and intensity according to each species' reproductive strategy. Yet this neural motivation-emotion system plays a similar role in reproduction across species: It enables both males and females to distinguish among potential mating partners, prefer particular conspecifics, and focus their courtship attention on the pursuit of these favored individuals, thereby conserving mating time and energy by making a mate choice. In humans this motivation-emotion system has evolved into a brain network that has come to be called romantic love.

REFERENCES

1 Darwin C. *The descent of man and selection in relation to sex*. New York: The Modern Library/Random House (1871/n.d.).
2 Andersson M. Sexual Selection. Princeton, NJ: Princeton University Press; 1994.
3 Miller G. The mating Mind: How sexual choice shaped the evolution of human nature. New York: Doubleday; 2000.
4 Aron A, Aron EN. Love and sexuality. *In* K McKinney and S Sprecher, eds. *Sexuality in close relationships*. Hillsdale, NJ: Lawrence Erlbaum; 1991. pp. 25–48.
5 Hatfield E, Rapson RL. *Love and sex: cross-cultural perspectives*. Needham Heights, MA: Allyn and Bacon; 1996.
6 Hatfield E, Sprecher S. Measuring passionate love in intimate relations. *Journal of Adolescelnce* 1986; **9**:383–410.
7 Hatfield E. Passionate and companionate Love: *In* RJ Sternberg and ML Barnes, eds. *The Psychology of Love*. New Haven: Yale University Press; 1988. pp. 191–217.
8 Shaver P, Hazan C, Bradshaw D. Love as Attachment: The integration of three behavioral systems. In Sternberg RJ and Barnes ML, eds. *The Psychology of Love* New Haven: Yale University Press; 1988. pp. 68–99.
9. Beach, FA. Sexual Attractivity, Proceptivity, and Receptivity in Female Mammals. *Hormones and Behavior* 1976; **7**:105–138. p. 131.
10 Pfaff D, Frohlich J, Morgan M. Hormonal and genetic influences on arousal – sexual and otherwise. *Trends in Neuroscience* 2002; **25** (1):45–50.
11 Darwin, C. *The descent of man and selection in relation to sex*. New York: The Modern Library/Random House; 1871/n.d. p. 743.
12 Hutchison JB, Hutchison RE. Hormonal mechanisms of mate choice in birds. In P Bateson, ed. *Mate Choice*. Cambridge: Cambridge University Press; 1983. pp. 389–405. p. 390.
13 Ibid, p. 389.
14 Miller, G. The Mating Mind: How Sexual Choice Shaped the Evolution of Human Nature. New York: Doubleday; 2000. p. 93.
15 Ibid, p. 149.
16 Ibid, p. 72.
17 Beach, FA. Sexual Attractivity, Proceptivity, and Receptivity in Female Mammals. Hormones and Behavior 1976; **7**:105–138. p. 131.
18 Ward IL, Crowley WR, Zemlen FP, Margules DL. Monoaminergic Mediation of Female Sexual Behavior. *Journal of Comparative Physiology and Psychology* 1975; **88**:53–61.
19 Pfaff D, Frohlich J, Morgan M. Hormonal and genetic influences on arousal – sexual and otherwise. *Trends in Neuroscience* 2002; **25**(1):45–50.
20 Pfaff DW. Drive: Neurobiological and Molecular Mechanisms of Sexual Motivation. Cambridge, MA: The MIT Press; 1999.
21 Etgen AM, Chu HP, Fiber JM, Karkanias GB, Morales JM. Hormonal integration of neurochemical and sensory signals governing female reproductive behavior. *Behav Brain Res* 1999; **105**(1):93–103.
22 Etgen AM, JC Morales. Somatosensory stimuli evoke norepinephrine release in the anterior ventromedial hypothalamus of sexually receptive female rates. *J Neuroendocrinology* 2002; **14**(3):213–8.
23 Hull EM, Du J, Lorrain DS, Matuszewich L. Extracellular dopamine in the medial preoptic area: implications for sexual motivation and hormonal control of copulation. *Journal of Neuroscience* 1995; **15**(11):7465–7471.
24 Hull EM, Lorrain DS, Du J, Matuszewich L, Lumley LA, Putnam SK, Moses J. Hormone-neurotransmitter interactions in the control of sexual behavior. *Behavioural Brain Research* 1999; **105**(1):105–16.
25 Wersinger SR, Rissman EF . Dopamine activates masculine sexual behavior independent of the estrogen receptor alpha. *Journal of Neuroscience* 2000; **20**, 110:4248–54.
26 Argiolas A, Melis MR. Neuromodulation of penile erection: an overview of the role of neurotransmitters and neuropeptides. *Progress in Neurobiology* 1995; **47**(4–5):235–255.
27 Fisher H, Aron A, Mashek D, Li H, Strong G, Brown LL. The Neural Mechanisms of Mate Choice. Paper delivered at the annual meet-

ing of the Human Behavior and Evolution Society, 2000.
28 Jankowiak WR, Fischer EF. A cross-cultural perspective on romantic love. *Ethnology* 1992; **31**(2):149.
29 Tennov D. *Love and limerence: the experience of being in Love*. New York: Stein and Day; 1979.
30 Hatfield E, Sprecher S. Measuring passionate love in intimate relations. *Journal of Adolescence* 1986; **9**:383–410.
31 Harris H. Rethinking Polynesian heterosexual Relationships: A case study of Mangaia, Cook Islands. *In* Jankowiak W, ed. *Romantic Passion: A universal Experience?* New York: Columbia University Press; 1995. pp. 95–127.
32 Fisher HE. Lust, attraction and attachment in mammalian reproduction. *Human Nature* 1998; **9**(1):23–52.
33 Ibid.
34 Kiyatkin EA. Functional significance of mesolimbic dopamine. *Neuroscience & Biobehavioral Reviews* 1995; **19**(4):573–98.
35 Salamone JD. The behavioral neurochemistry of motivation: methodological and conceptual issues in studies of the dynamic activity of nucleus accumbens dopamine. *Journal of Neuroscience Methods* 1996; **64**(2):137–49.
36 Scatton B, D'Angio M, Driscoll P, Serrano A. An *in Vivo* voltammetric study of the response of mesocortical and mesoaccumbens dopaminergic neurons to environmental stimuli in strains of rats with differing levels of emotionality. In PW Kalivas & CB Nemeroff, eds. *The Mesocorticolimbic Dopamine System*. New York: The New York Academy of Sciences; 1988. pp. 124–137.
37 Tassin JP, Herve D, Blanc G, Glowinski J. Differential effects of a two-minute open field session on dopamine utilization in the frontal cortices of BALB/C and C57 BL/6 mice. *Neuroscience Letters* 1980; **17**:67–71.
38 Griffin MG, Taylor GT. Norepinephrine modulation of social memory: evidence for a time-dependent functional recovery of behavior. *Behavioral Neuroscience* 1995; **109**(3):466–473.
39 Kiyatkin EA. Functional significance of mesolimbic dopamine. *Neuroscience & Biobehavioral Reviews* 1995; **19**(4):573–98.
40 Salamone JD. The behavioral neurochemistry of motivation: methodological and conceptual issues in studies of the dynamic activity of nucleus accumbens dopamine. *Journal of Neuroscience Methods* 1996; **64**(2):137–49.
41 Scatton B, D'Angio M, Driscoll P, A Serrano. An *in Vivo* voltammetric study of the response of mesocortical and mesoaccumbens dopaminergic neurons to environmental stimuli in strains of rats with differing levels of emotionality. *In* P.W. Kalivas & C.B. Nemeroff, eds. *The Mesocorticolimbic Dopamine System*. New York: The New York Academy of Sciences; 1988. pp. 124–137.
42 Wise RA. Brain dopamine and reward. *Annual Review of Psychology* 1989; **40**:191–225.
43 Wise RA. Neurobiology of addiction. *Current Opinion in Neurobiology* 1996; **6**:243–251.
44 Seiden LS, Commins DL, Vosmer G, Axt K, Marek G. Neurotoxicity in Dopamine and 5 – Hydroxytryptamine Terminal Fields: A regional Analysis of Nigrostriatal and Mesolimbic Projections. In Kalivas PW and Nemeroff CB, eds. *The Mesocorticolimbic Dopamine System*. Annals of the New York Academy of Sciences **537** 1988. pp. 161–172.
45 Post RM, Weiss SRB, Pert A. Cocaine-induced behavioral sensitization and kindling: implications for the emergence of psychopathology and seizures. *In* Kalivas PW and Nemeroff CB, eds. *The Mesocorticolimbic Dopamine System*. New York: The New York Academy of Sciences; 1988. (**537**) pp. 292–308.
46 Kruk AL, CJ Pycock. *Neurotransmitters and drugs*. New York: Chapman and Hall; 1991.
47 Colle LM, Wise RA. Facilitory and inhibitory effects of nucleus accumbens amphetamine on feeding. *In* Kalivas PW and Nemeroff CB, eds. *The Mesocorticolimbic Dopamine System*. New York: The New York Academy of Science; 1988. (**537**) pp. 491–492.
48 Wise RA. Psychomotor stimulant properties of addictive drugs. *In* Kalivas PW and Nemeroff CB, eds. *The Mesocorticolimbic Dopamine System*. New York: The New York Academy of Science; 1988. (**537**) pp. 228–234.
49 Wise RA. Brain dopamine and reward. *Annual Review of Psychology* 1989; **40**:191–225.
50 Schultz W. Multiple Reward Signals in the Brain. *Nature Reviews. Neuroscience* 2000; **1**:199–207.
51 Flament MF, Rapoport JL, Bert CL. Clomipramine treatment of childhood obsessive-compulsive disorder: a double–blind controlled study. *Archives of General Psychiatry* 1985; **42**:977–986.
52 Hollander E, Fay M, Cohen B, R Campeas, Gorman JM, Liebowitz MR. Serotonergic and noradrenergic sensitivity in obsessive-compulsive disorder: Behavioral Findings. *American Journal of Psychiatry* 1988; **145**:1015–1017.
53 Thoren P, Asberg M, Bertilsson L. Clomipramine treatment of obsessive disorder: biochemical and clinical aspects. *Archives of General Psychiatry* 1980; **37**:1289–1294.
54 Mashek D, Aron A, Fisher HE. Identifying, evoking and measuring intense feelings of romantic love. *Representative Research in Social Psychology* 2000; **24**:48–55.
55 Wise RA. Psychomotor stimulant properties of addictive drugs. *In* Kalivas PW and Nemeroff CB, eds. *The Mesocorticolimbic Dopamine System*. New York: The New York Academy of Science; 1988. (**537**) pp. 228–234.
56 Wise RA. Brain dopamine and reward. *Annual Review of Psychology* 1989; **40**:191–225.
57 Martin-Soelch C, Leenders KL, Chevalley AF, Missimer J, Kunig G, Magyar S, Mino A, Schultz W. Reward mechanisms in the brain and their role in dependence: evidence from neurophysiological and neuroimaging studies. *Brain Research Reviews* 2001; **36**:139–149.
58 Bartels A, Zeki S. The neural basis of romantic love. *NeuroReport* 2000; **11**(17):3829–3834. p. 3829.
59 Ibid, p. 3829.
60 Herbert J. Sexuality, Stress and the Chemical Architecture of the Brain. *Annual Review of Sex Research* 1996; **7**:1–44.
61 Gingrich B, Liu Y, Cascio C, Wang Z, Insel TR. D2 receptors in the nucleus accumbens are important for social attachment in female prairie voles (*Microtus ochrogaster*). *Behavioral Neuroscience* 2000; **114**(1):173–183.
62 Ibid.
63 Dluzen DE, Ramirez VD, Carter CS, Getz LL. Male Vole Urine Changes Luteinizing Hormone-Releasing Hormone and Norepinephrine in Female Olfactory Bulb. *Science* 1981; **212**:573–575.
64 Etgen AM, Chu HP, Fiber JM, Karkanias GB, Morales JM. Hormonal integration of neurochemical and sensory signals governing female reproductive behavior. *Behav Brain Res* 1999; **105**(1):93–103.
65 Etgen AM, Morales JC. Somatosensory stimuli evoke norepinephrine release in the anterior ventromedial hypothalamus of sexually receptive female rates. *J. Neuroendocrinology* 2002; **14**(3):213–8.
66 Fisher HE. Lust, attraction and attachment in mammalian reproduction. *Human Nature* 1998; **9**(1):23–52.
67 Carter CS. Oxytocin and sexual behavior. *Neuroscience and Biobehavioral Reviews* 1992; **16**:131–144.
68 Carter CS, DeVries AC, Getz LL. Physiological substrates of mammalian monogamy: the prairie vole model. *Neuroscience and Biobehavioral Reviews* 1995; **19**, 2:303–314.
69 Insel TR. Oxytocin – A Neuropeptide for Affiliation: Evidence from Behavioral, Receptor Autoradiographic and Comparative Studies. *Psychoneuroendocrinology* 1992; **17**(1):3.
70 Winslow JT, Hastings N, Carter CS, Harbaugh CR, Young TR, Li J, Nilsen R, Waymire KG, MacGregor GR, Insel TR. Increased affiliative response to vasopressin in mice expressing the V1a receptor from a monogamous vole. *Nature* 1999; **100**:766–768.
71 Fisher HE. Lust, attraction and attachment in mammalian reproduction. *Human Nature* 1998; **9**:1:23–52.
72 Ibid.
73 Arnow BA, Desmond JE, Banner LL, Glover GH, Solomon A, Polan ML, Lue TF, Atlas SW. Brain activation and sexual arousal in healthy, heterosexual males. *Brain* 2002; **125** (Pt 5):1014–23.
74 Karama S, Lecours AR, Leroux JM, Bourgouin P, Beaudoin G, Joubert S, Beauregard M. Areas of brain activation in males and females during viewing of erotic film excerpts. *Hum Brain Mapp* 2002; **16**(1):1–13.
75 Beauregard M, Levesque J, Bourgouin P. Neural correlates of conscious self-regulation of emotion. *J Neurosci* 2001; **21**(18): RC165.

Neuroendocrinology Letters Special Issue, Suppl.4, Vol.23, December 2002
Copyright © Neuroendocrinology Letters ISSN 0172–780X **www.nel.edu**

REVIEW ARTICLE

Toward an evolutionary psychology of religiosity

Caspar Soeling & Eckart Voland*
Zentrum für Philosophie und Grundlagen der Wissenschaft der Universität Giessen, GERMANY

Correspondence to: *Prof.* Eckart Voland, *Dr. rer. nat.*
Otto-Behaghel-Str. 10C, D-35394 Giessen, GERMANY
PHONE: + (49)-641-99-15550
FAX: + (49)-641-99-15509
EMAIL: c.soeling@bistumlimburg.de
EMAIL: eckart.voland@phil.uni-giessen.de

Submitted: *August 30, 2002*
Accepted: *September 4, 2002*

Key words: **evolutionary psychology; religiosity; Darwinian algorithms; cognitive domains; mysticism; ethics; myths; rituals; adaptations**

Neuroendocrinology Letters 2002; ***23****(Suppl.4):98–104 pii: NEL231002R10* *Copyright © Neuroendocrinology Letters* ***www.nel.edu***

Abstract

How can the evolution of religiosity be explained? To answer this question, we attempt to develop an understanding of the psychological domains underlying religious behaviour. We see four evolved domains, the sum and interaction of which constitute religiosity, namely: mysticism, ethics, myths and rituals. Even if the individual content, accents and implementations differ in each specific religion, they nevertheless derive from evolved Darwinian algorithms that are species-specific adaptations of homo sapiens.

Mysticism. Intuitive ontologies are the basis for mystical experiences. Usually they serve to classify reality into animate and inanimate objects, animals or plants, for example. For a variety of psychological reasons, supernatural experiences result from a mixture of different ontological categories.

Ethics. The basis for ethics lies in the social competency of human beings. Ethics is founded on the concept of social exchange ("social-contract algorithm") with its ideas about reciprocity, fairness, justice, cheater detection, in-group/out-group differentiation, etc.

Myths. The basis for myths is the "language instinct". We interpret myths as the verbal expression of the cognitive content of those individual modules that constitute the belief system. Above all, myths document the experience and processing of contingency and thus help social bonding.

Rituals. Rituals are based on the handicap principle. By making certain symbols and acts more expensive, they signal commitment for a reliable in-group morale.

In conclusion, we argue that human religiosity emerges from a cognitive interaction between these four domains. Religiosity processes contingencies and enhances co-operation through social bonding, norm setting and cheater detection. It fulfils those functions for which the mental modules of its four domains have evolved so that we feel it appears to be justified to attribute to religiosity the evolutionary status of an adaptation.

Introduction

Religiosity is part of the biological constitution of homo sapiens sapiens. Even if the age of human religiosity is not precisely known, its emergence is linked with the cultural explosion of the Upper Palaeolithic [1,2]. However, the question is still unclear of how this unique feature in natural history was able to evolve biologically. Why are people religious? How can a natural organism put questions about the supernatural? Why do living organisms invest so much time and energy in behaviours which do not directly serve maintenance or reproduction? What selective advantage does religiosity offer? Is it a biological adaptation or a functionless byproduct of other biological features? In the following, these questions are going to be pursued with the aid of the heuristics of evolutionary psychology [cf. 3 for more details].

Method

Evolutionary psychology (together with cognitive science, to which it repeatedly refers) assumes that the brain is an information-processing system. Signals from the outside and inside the brain are processed by means of a functional and morphologically structured network of numerous individual, more or less specialised subsystems, which Fodor [4] labelled "modules", while Pinker [5] called them "instincts" and Cosmides and Tooby [6] referred to them as "evolutionary algorithms". Each of these algorithms was shaped by natural selection and is genetically determined. Thus, these are species-specific adaptations, i.e. universals, which have developed and been optimised over the course of evolution.

For Darwin-inspired behavioural researchers, there are fundamentally two heuristic perspectives from which to study biological adaptations in human conduct. Either one starts from an adaptive problem and searches for psychological or ethological mechanisms which could have evolved in adaptation to this problem. Or, one seeks explanations for the evolution of human behaviours by reconstructing adaptive scenarios leading to the biological functionality of the behaviour in question [7]. Of these two proposed paths, this paper takes the second route and thus inquires what is the adaptive problem to which religiosity could be the evolved solution.

Religiosity is a human universal, which offers answers to contingency questions. Religiosity thus can be divided into two issues: namely the questions raised as a result of experience with contingencies, and secondly, the answer to these questions through the idea of transcendence [8].

ad 1. A cognitive dissonance between the understanding of oneself and of the world is experienced as a contingency. Contingency presupposes that humans no longer take reality for granted. Once humans have experienced surprising, non-routine and unexpected events, and once feelings of fear and of hope emerge and possibly the search for an anchor of the contingent event in the well known consistent world commences, this can signal religiosity.

ad 2. There are numerous possible answers to the questions raised by experiences of contingent events. Specific religious answers are characterised by two moments: First of all, by going beyond one's available and familiar world. After that, humans can only find security in what is inaccessible to them. This hereafter remains both invisible and unattainable at the same time. Therefore, in every religion, the unattainable institutions of the hereafter must be linked to relatively true-to-life, concrete and visible ideas and practices such as myths and rituals. This bond to empirically concrete things is what distinguishes religion from all forms of philosophy with which it has a lot in common otherwise.

Beyond this general definition of religiosity, religious behaviour can be viewed in a more differentiated way, because it is constituted from various, differently shaped and accentuated modes of behaviour. In accordance with the opinion held by most religious-scholars, every religion is characterised by four constituting elements (mysticism, myths, ethics and rituals). It therefore seems logical to analytically sub-divide the issue of the evolutionary history and the function of religiosity into four aspects and to begin by first examining each of these four components separately.

Results

1 Mysticism

1.1. THE RELIGIOUS PHENOMENON. Individual and collective experiences form the central role in every religious community. There is no religion which does not have a mystical tradition. Mysticism here is not to be understood as an edifice of teaching, but rather as a path of experience. The term is derived from the Greek "myein", i.e. to close one's eyes. The essence of mysticism is one's very own, internal experience with God. Externally, it is characterised by special modes of behaviour, such as adoration, meditation, silence or even dance, the goal of which is a special internal experience. It enables the pious to experience evidence, clarity, security and happiness, in ways that are frequently unexpected and unanticipated. Mystic contemplation is experienced in the form of visions, auditory experiences, ecstasy, or physical insensitivity or over-sensitivity.

When viewing the supernatural beings, there is often a mixture of knowledge about different types of entities in the real world. The frequently unclear external circumstances (e.g. twilight, sunset, but also the dark atmosphere of Romanesque cathedrals filled by one's imagination) overburden the capability of people to classify an event or an object clearly. Often these are contingency experiences, i.e. experiences, the classification of which demands too much of people. Due to the lack of clarity, it becomes likely to mix known categories, ontologies, and experiences with unsuitable ideas about the unknown.

This mixture is often observed in representations of gods in human form [9]. Hybrids of humans and animals and androgynous divine figures can be found, including their ability to undergo a metamorphosis. The oldest known symbolic representation is such a hybrid: the 33ky old Hohenstein-Stadel lion/man. Even multiple "organs" are found: two or three heads, the possession of three bodies, multiple arms or one hundred eyes. How can these representations and the experiences on which they are based be explained?

1.2. THE UNDERLYING ALGORITHM. Humans have intuitive ontologies [10]. They spontaneously classify their perceptions and experiences into existing categories. As the experiments of Keil [11] show, they do this even when important information allowing a safe categorisation is missing. Keil told his probands stories about imaginary beings which he called hyraxes or throtels and which were never described or defined in more detail. The only thing that was said about hyraxes was, for example, that they occasionally sleep. Or that throtels have to be tied up. Kindergarden children, who could never have seen either throtels or hyraxes, nevertheless tended to surmise, on the basis of the aforementioned information, that hyraxes can be hungry, for example, or that throtels might be made of metal. On the other hand, it was inconceivable to the children that a hyrax could be made of metal. Even though no theoretical knowledge whatsoever nor any other information existed, the children nevertheless communicated about hyraxes and throtels like they would about living organisms and artefacts. They thus ascribed a certain ontological status to these beings without having any further knowledge about them. In this connection, Gelman *et al*. [12] speak of an "essentialist bias".

The assumption of such traits and further descriptions are a consequence of the human disposition to produce precise ontological hypotheses, whenever this appears to be useful in a natural context. This includes, in particular, hypotheses regarding the causes of events that can not be understood otherwise, e.g. spectacular natural phenomena, personal catastrophes or feelings of happiness. Like other hypotheses, the majority of these assumptions can be corrected in light of better knowledge – but some of the hypotheses can not be corrected. This opens the door to "false" applications of natural ontologies, in which for example inanimate objects are compared with animated ones (animism) or natural forces are imputed human intentions (anthropomorphism) [13].

Once incomprehensible natural phenomena have experienced an anthropomorphic reconstruction, however, it is only logical to ascribe anthropomorphic behavioural and social theory to these supernatural entities. Although the gods may be unusual in certain ways, yet at the same time, they are the plane of projection of our intuitive psychology. They harbour intentions, experience desires and perceive emotions, and this precisely makes them mostly calculable despite a transcendental reverie [5, 10, 14]. If there were absolutely no correspondence between the supernatural beings and the intuitive knowledge of the world, humans would not be able to imagine the world of the supernatural.

1.3. THE EVOLUTIONARY BENEFIT. What biological benefit underlies the natural ontologies? It is very obvious, that these ontologies are not only significant with regard to the order and systematisation of the environment within the human mind, but they also have direct consequences for human conduct. Intuitive ontologies serve as a means of orientation in the realm of reality and help to provide quick and adequate reactions to the objects to which they refer. They thus serve the heuristics and the decision-making process of the individual facing adaptive problems in highly uncertain environments. If the perception is not unambiguous and intuitive ontologies undertake an erroneous classification, it is adaptive, however, to avoid possibly risky errors and instead to tolerate low-risk ones. This explains why inanimate objects are more likely to be seen as animate objects than vice-versa [13, 14].

Human rationality is not based on the capability to apply fixed rules, such as logic or probability theory to all possible problems without reference to the content. Instead, human rationality is understood to be the ability to select and apply simple and efficient inherent heuristics that are adequate for dealing with the specific problem [15]. Accordingly, human thinking is not adapted to probability theory or logic, but to the risks and opportunity structures of the environment. In this context, intuitive ontologies have their place.

2 Ethics

2.1. THE RELIGIOUS PHENOMENON. Every religion has a certain understanding of humans and their world, which is reflected in its social practice. This is why religion and morale are so closely linked to one another. In addition to rituals, moral conduct is the manifest expression of a religious attitude. Even if religions can differ considerably with regard to their justifications for morals, they nevertheless show amazingly strong large parallels in their content when issuing ethical instructions. This pronounced similarity in the basic ethical attitudes made possible a joint declaration to be presented to the Parliament of World Religions for the first time in the history in 1993. In the so-called "World Ethics Project", some 6,500 members of numerous religions elaborated the details of which moral values and basic moral convictions are common to all of the religions in the world despite their differences [16]. The so-called "golden rule" assumes a prominent position here. It is very obviously deeply rooted in all ethical traditions of mankind and is a normative precept in most religions. Of course, the "golden rule" very often remains limited to a clearly defined moral "in-group" [17, 18], which at the same time reinforces outward competitiveness.

2.2. THE UNDERLYING ALGORITHM. It is well known that reciprocal systems are not spontaneously stable. Reciprocity constantly runs the risk of being exploited, be it because opportunities for reciprocity are too rare for demographic reasons, or because some cheaters deliberately make an effort to take advantage of the benefits of the system for themselves, but do not bear the costs. In the same degree to which natural selection rewards co-operation, it wil automatically promote at the same time, the development of mechanisms offering the best possible protection against exploitation. This is why there is selective pressure with regard to the detection of fraudulent rule-breakers. In fact, Cosmides und Tooby [6], and Gigerenzer and Hug [19], were able to prove very impressively with the aid of the "Wason selections"-tasks, that our perceptive, recognition and thinking apparatus is very specifically designed to detect social cheaters. Human intelligence is primarily social intelligence, and therefore it is clearly easier for us to detect deviations from social rules as violations of the rules than logically similar deviations from rules that do not have any social component. In short: It is easier to expose cheaters than to think logically. The findings of Mealey *et al*. [20] and Oda [21], according to which we obviously remember the faces of persons of whom we believe that they have a cheating past better than the faces of presumably honest persons, corroborate these insights.

The basis of ethical universals are hence cognitive algorithms, such as the cheater detector mechanism, which evolved hand in hand with a developed co-operative lifestyle. The products of these social-contract algorithms are ideas and concepts, such as reciprocity, fairness, defection, justice, guilt, in-group/out-group differentiation, and other regulatory ideas of human morals, which have in common that they are based on cost/benefit representations of social relationships.

2.3. THE EVOLUTIONARY BENEFIT. The evolutionary benefit of morals originates, as a rule, from the gains from co-operation for all of the members of a moral community, frequently in competition with neighbouring moral in-groups. It should not be overlooked, of course, that morals, as an exploitative instrument, can also lead to an asymmetrical distribution of the pay-offs [18, 22].

3 Myths

3.1. THE RELIGIOUS PHENOMENON. Every religion has its myths. In some cultures, they are transmitted in writing, in others through pictures, and still others through oral traditions. Myths teach about occurrences that transcend space and time in an illustrative, reporting manner. In contrast to a rational and conceptual grasp of reality, myths have their own individual 'logic'. This inherent logic stems from the symbol of the absolute and hereafter as meant in the religious act, the symbol which is constructed of elements of reality. Myths are by-and-large a coherent system of experiences. This system is based on the fundamental ways in which the being and the real are generally perceived, classified and interpreted [23]. It therefore stands to reason that religious myths might be understood as verbal elaborations of religious experiences. However, as religious experiences exceed what is normal or unambiguous, myths are characterised by multilayered meanings. In this sense, myths stand for the typical human irritations due to the experience of the contingencies of chaos and ambiguity. Only myths open up these incomprehensible experiences and fill them with meaning. This process, which has cognitive and emotional aspects, is to be approached as the fundamental function of religion; in this sense, a core value for the religion can be attributed to myths [24].

As the world experienced by human beings is, however, ultimately similar everywhere, myths can be typified in accordance with certain horizons of experience, e.g. genesis myths (cosmogonic myths, creation myths), anthropological myths (creation of man, mortality, sacrifices, tribulations) or myths with a legitimising function for religious ceremonies and service to what is sacred [25].

3.2. THE UNDERLYING ALGORITHM. According to Pinker [26], language is not a cultural artefact, but a clearly defined part of the biological features of the human brain, which he refers to as "language instinct". But how do the contents of what is being communicated come about? According to Pinker [26], they are the product of complex interactions between universal human nature and the conditions under which humans live. Consequently, indications of mental concepts can be found in language. It suggests itself therefore, that this perspective can be transferred to myths. Instead of a structuralist connection of myths to elementary biological modes of behaviour [27] or to elementary developmental psychology experiences [28] from the perspective of a "language instinct", it would also be possible and necessary to examine myths for their cognitive foundations. A corresponding, systematic analysis has yet to be done, however. Such an analysis would have to cover the content comprised by the following mental modules assumed by Cosmides *et al*. [7]:

1. for risks: fear and caution;
2. for impurities: feelings of disgust and the intuition for the risks of contagion and illnesses;
3. for the awareness for current emotional states, such as happiness and sadness, the moods of contentment and restlessness;
4. a mental archive of status and rank as well as criteria for their evaluation;
5. kinship;
6. partnership, including sexual attraction and love, as well as faithfulness and separation.

An initial and unsecured examination makes it clear that, indeed, all of these elementary themes are of central importance in the religions and can be found on the ritual, ethical and mythological levels. To this extent, this approach could form a successful trace.

1. Risks, fear and caution: The significance of dealing with fear is already indicated in the definition of religion as a process for coping with contingencies. Religion absorbs fear and frustrations and simultaneously explains the inevitability of pain. The numerous attempts from the the philosopher Kierkegaard [29] to the biologist Dobzhansky [30] to explain religion as a consequence of imaging time and the knowledge of death have fear as their starting point. Of course, it should not be overlooked, that systems of belief, especially if they have an authoritarian structure, can also generate anxiety and fear.
2. Purity and impurity: Cleansing acts are one of the elementary acts of human life and co-existence. According to Douglas [31], impurities are to be understood as risks to social orders. As an anomaly that breaks social norms, the impurity symbolises the area which drops out of the complex of ordered relationships. It is no wonder, therefore, that ritual cleansing acts, such as baptism when joining a church, or the cleansing acts of the Hindus in the Ganges, are widespread in all religions.
3. Restlessness and happiness: One of the most frequently cited sayings of St. Augustine deals with restlessness: "My heart is restless until it rests in you". This is taken from St. Augustine's biography called Confessions. It is not only a description of a life, but can also be understood as a report from the internal topography of the human soul [32]. Restlessness and the search for happiness are typical for human conduct and thus are mirrored in all religions. Its external expression is found in the motif of the pilgrimage, which is also widespread in all of the great world religions.
4. Status and rank: The term "hierarchy" (from the Greek 'hier-arkhia', sacred rule) shows how firmly status and rank are anchored in religious thought.
5. Kinship: The elementary nature of this theme can be illustrated by the universally widespread religious prohibitions of incest.
6. Partnership: Once again, the importance of this theme is illustrated by the universal religious precepts related to marriage.

Our approach receives further confirmation from the idea discussed above according to which intuitive ontologies slip into religiosity. What is typical for the experience of the supernatural is that it infringes intuitive knowledge. This infringement should also be reflected in the myths of the world. The definitions of myths previously discussed show that this is the case. Accordingly, myths do not report a rational or comprehensible grasp of reality, but they describe precisely what goes beyond all recognition and understanding.

3.3. THE EVOLUTIONARY BENEFIT. In the evolution of primates, the social ability to live in larger social groups has turned out to be a very crucial survival factor. Human evolutionary history has followed this trend to larger and more complex social systems. After the early hominids had asserted themselves as the ecologically dominant species in their African habitat, their survival and their reproduction was mainly jeopardised by competing neighbouring groups. And the larger a group was, the bigger its benefit in the context of between group competition [33].

In order to be able to take advantage of the benefit of larger communities, the development of a social bonding mechanism was necessary, of course. Grooming – the social glue of monkeys and apes – became increasingly unsuitable, due to the necessary time involved, and was therefore replaced. In its stead, we have language [34]. Language binds because it fulfils an eminently important biological function: The exchange of social knowledge about one's fellows – without personal observation, if need be. Nonhuman primates are incapable of this. Although they can regulate their dyadic social relationships by means of grooming, yet they run into efficiency limits, which humans have overcome through the evolution of language. Even without personal contacts, we know about the features and traits of our fellow humans, their reliability, their honesty and even their fraudulent tendencies, their suitability as partners in co-operation and mating, their courage and their drive, their social dominance and willingness to help – in fact, about their social tendencies and character traits in general. Sure, one also occasionally blindly accepts false rumours and slander as being true. But occasional erroneous information is the price which does not outweigh the benefit, which we get by being able to acquire social knowledge faster and more efficiently than our ape ancestors.

If myths document the experience and processing of contingencies, then they serve the same purpose as language: By allowing every member of the group to share in the experiences of another, myths help to cope with what appears to be impossible to master. This way, a bond is created, a sense of community, and thus a social identity. Myths serve the yearnings of humans for wanting to belong to an in-group and to distinguish themselves from the out-groups.

4 Rituals

4.1. THE RELIGIOUS PHENOMENON. Essentially, religious rituals are not solely characterised by repetitions, but by the fact that routines receive a sense of meaning in addition to a sense of purpose [35]. In this way, a certain act or object is symbolically charged up. Rituals only rarely serve an utilitarian purposes, but instead are integrated into other communication structures.

Despite all of the differences between cults, rites can be recognised, that presumably can be found in all religions. It is noticeable that they are closely co-ordinated with biological processes or turning points. Thiel [36] has systemised them as follows:

- Apotropaic rites dispel imminent evil and evil spirits
- Through elimination rites, communities attempt to isolate something evil from themselves, i.e. by transferring their sins to a scapegoat, for example.
- Cleansing rites
- "Rites de passage" accompany a change of place, state, social position or age.

4.2. THE UNDERLYING ALGORITHM. Rituals serve to make certain symbols and acts more expensive, in order to establish reliability between the sender of the signal and its recipient. They are subject to the functional logic of the handicap principle [37] and signal moral commitment [38].

A visit to a village that is squalid as can be, makes us aware of how expensive religious rituals are. As a rule, the church, or the temple, respectively, is the largest building in the village, even though it is only used for a few hours a week. Nevertheless, years or even decades of sacrifice were often necessary, to erect this building. However, the costs of religious rituals lie not only in the financial sector. Almost every sermon and almost every meditation targets the individual believers. It is not merely about putting money into the offertory box, but about sacrificing one's own life. Initiation rituals, in particular, which can frequently be found in rituals of so-called high-religions only in a stylised form, illustrate the costs of being accepted by a religious community: Acceptance involves not only the time which is invested, but also the anxiety and the handling of pain, such as that evoked by circumcision.

Because rituals guarantee the reliability of in-group morals and signal commitment, it can be assumed that the more expensive a religion's rituals are, i.e. the more time, resources or vitality they consume, the more efficiently they help to build up intra-group solidarity. And vice-versa, it is to be expected that the more important co-operation is for the survival and welfare of a group, the more expensive this group's rituals will become [38].

4.3.THE EVOLUTIONARY BENEFIT. Religious rituals coincide with language as they communicate a group code and thus establish conventions. They do not merely contain the symbolic representation of a social contract, but at the same time, they are also its implementation and excecution. Thus, they give conventions expression and acceptance. Accordingly, the ritual is the fundamental social act. Rappaport [39] assumes, that language and the social orders based on language would not have arisen without the support of what is regarded sacred. Since lies and alternative meanings are inherent in language, it cannot establish reliability – as rituals do.

If there are any binding words within a society at all, then it is also necessary to establish such words. "The Word is established by the invariance of liturgy. It may be suggested, furthermore, that it emerged phylogenetically as some expressions drawn from the burgeoning language of earlier hominids were absorbed into, and subordinated to, the invariance of already existing nonverbal rituals which seem to be common in the animal world" [40]. Because those who practice rituals accept high costs, their spoken word has a corresponding importance [41]. Due to the fact that a ritual is visibly expensive, it achieves its own authenticity – therefore it can not cheat, as a matter of principle.

Discussion

In our view, religiosity is characterised by four domains, which have each passed through their own selection history (Table 1). Mysticism is based on intuitive ontologies and serves to cope with contingencies and decision-making in a highly uncertain environment. Ethics increases social competency and enables gains from co-operation. Myths serve to promote social identity in a world that differentiates in-groups from out-groups. Finally, rituals implement hard-to-fake signals to establish reliable moral standards within the group. Thus religiosity represents a biologically functional phenomenon. What remains to be explained of course, is how from an originally domain-specific psychology such a complex system of behaviour as religiosity could arise. Together with Mithen [1,2] we assume that in the evolutionary history of homo sapiens sapiens, for reasons which await further exploration, a cognitive network of originally separate domains emerged. The consequence was an increasingly cognitive fluidity, which finally led to what has been called the "symbolic revolution" – religiosity being part of it.

The interlinkage of the four domains of religiosity has produced numerous and diverse possibilities for interaction. Myths can reproduce the ontologies of the belief system, or carry ethical convictions. Rituals can evoke mystical experiences, and they can in turn draw on ethics in their content. Thus, evolutionarily novel potentials were created, which eventually constitute religiosity. To be sure, this line of argumentation does not address the question of whether God exists or not. However, it attempts to outline a possible research per-

Table 1: Overview of the four constituting domains of religiosity and their evolutionary functions

	Mysticism	Ethics	Myths	Ritual
Adaptation	Intuitive ontologies	Social competency	Language instinct	Handicap principle
Function	Processing of contingencies through categorisation and decision making	Gains from co-operation are possible	Social identity and bonding in the service of an in-group /out-group differentiation	Cheater detection in view of the free-rider problem

spective for what may become a Darwinian theory of human religiosity (Table 1).

With the emergence of religiosity from its four domains, there has no doubt been an increase in complexity of human behaviour, but there has not been any transformation of function. Religiosity *in toto* continues to fulfil those four functions, for which the evolutionary algorithms of the four domains evolved. It processes experiences of contingency and enhances cooperation through social bonding, norm setting and cheater detection. It is our perception that there is no additional function, so that it appears to us be justified, in contrast to Kirkpatrick [14], Mithen [2], Pinker [5] and other authors, to attribute the evolutionary status of an adaptation to religiosity, and not the status of an exaptation, a spandrel or a functionless by-product.

REFERENCES

1 Mithen S. The prehistory of the mind: A search for the origins of art, science and religion. London: Thames and Hudson; 1996.
2 Mithen S. Symbolism and the supernatural. In: Dunbar R, Knight C, Power C, editors. The evolution of culture – An interdisciplinary view. Edinburgh: Edinburgh University Press; 1999. pp. 147–69.
3 Soeling C. Der Gottesinstinkt – Bausteine für eine evolutionäre Religionstheorie [The god instinct – Elements of an evolutionary theory of religion]. Dissertation, University of Giessen, Germany; 2002 (http://bibd.uni-giessen.de/ghtm/2002/uni/d020116.htm).
4 Fodor JA. The modularity of the mind. Cambridge, MA: MIT Press; 1983.
5 Pinker S. How the mind works. New York: Norton; 1997.
6 Cosmides L, Tooby J. Cognitive adaptations for social exchange. In: Barkow JH, Cosmides L, Tooby J, editors. The adapted mind – Evolutionary psychology and the generation of culture. New York and Oxford: Oxford University Press; 1992. pp. 163–228.
7 Cosmides L, Tooby J, Barkow JH. Evolutionary psychology and conceptual integration. In: Barkow JH, Cosmides L, Tooby J, editors. The adapted mind – Evolutionary psychology and the generation of culture. New York and Oxford: Oxford University Press; 1992. pp. 3–15.
8 Pollak D. Was ist Religion? Probleme der Definition [What is religion? Problems of definition]. Z Religionswiss 995; **3**:163–90.
9 Gladigow B. Gottesvorstellungen [Imaginations of God]. In: Cancik H, editor. Handbuch religionswissenschaftlicher Grundbegriffe [Handbook of fundamentals in religious science], Vol 3. Stuttgart: Kohlhammer; 1993. pp. 32–49.
10 Boyer P. The naturalness of religious ideas: A cognitive theory of religion. Berkeley: University of California Press; 1994.
11 Keil F. Concepts, kinds and cognitive development. Cambridge, MA: MIT Press; 1989.
12 Gelman SA, Coley JD, Gottfried GM. Essentialist beliefs in children: The acquisition of concepts and theories. In: Hirschfeld L, Gelman SA, editors. Mapping the mind: Domain specifity in cognition and culture. Cambridge: Cambridge University Press; 1994. pp. 341–65.
13 Guthrie SG. Faces in the clouds: New theory of religion. New York: Oxford University Press; 1993.
14 Kirkpatrick LA. Toward an evolutionary psychology of religion and personality. J Pers 1999; **67**:921–52.
15 Gigerenzer G, Todd PM. Simple heuristics that make us smart. New York: Oxford University Press; 1999.
16 Kueng H, Kuschel K-J. editors. A global ethic – The declaration of the parliament of world's religions. London: SCM Press; 1993.
17 Hartung J. Love thy neighbor: the evolution of in-group morality. Skeptic 1995; **3(4)**:86–99.
18 Ridley M. The origins of virtue: Human instinct and the evolution of cooperation. New York: Viking; 1996.
19 Gigerenzer G, Hug K. Domain-specific reasoning: Social contracts, cheating and perspective change. Cognition 1992; **42**:127–71.
20 Mealey L, Daood C, Krage M. Enhanced memory for faces of cheaters. Ethol Sociobiol 1996; **17**: 119–28.
21 Oda R. Biased face recognition in the prisoner's dilemma game. Evol Hum Behav 1997; **18**:309–15.
22 Cronk L. Evolutionary theories of morality and the manipulative use of signals. Zygon 1994; **29**:81–101.
23 Hübner K. Mythos (philosophisch) [Myth (philosophical) In: Balz HB, Krause G, Müller G, editors. Theologische Real Enzyklopädie [Encyklopaedia of theology], Vol. 23. Berlin: de Gruyter; 1994. pp. 597–608.
24 Stolz F. Grundzüge der Religionswissenschaft [Outline of religious science]. 2nd edition. Göttingen: Vandenhoeck and Ruprecht; 1997.
25 Bürkle H. Mythos (Begriff, religionsgeschichtlich) [Myth (concept, in the history of religion]. In: Kasper W, editor. Lexikon für Theologie und Kirche [Encyclopaedia for theology and church], Vol. 7. Freiburg: Herder; 1998. pp. 597–600.
26 Pinker S. The language instinct. London: Lane; 1994.
27 Burkert W. Creation of the sacred: Tracks of biology in early religions. Cambridge MA: Harvard University Press; 1996.
28 Bischof N. Das Kraftfeld der Mythen [The force field of myths]. München: Piper; 1996.
29 Kierkegaard S. The sickness onto death. In: Hong H, editor. Kierkegaard's writings, Vol. 19. Princeton: Princeton University Press; 1980.
30 Dobzhansky T. On religion, death and evolutionary adaptation. Zygon 1966; **1**:361–80.
31 Douglas M. Purity and danger: An analysis of the concepts of pollution and taboo. London: Routledge; 1966. (Reprint 1995).
32 Flasch K. Augustin: Einführung in sein Denken [Augustin: Introduction to his thinking]. Stuttgart: Reclam; 1980.
33 Alexander R. The biology of moral systems. Hawthorne: Aldine DeGruyter; 1997.
34 Dunbar RIM. Grooming, gossip and the evolution of language. London: Faber and Faber; 1996.
35 Assmann J. Das kulturelle Gedächtnis. Schrift, Erinnerung und politische Identität [Cultural memory: writing, memory and political identity]. München: Piper; 1992.
36 Thiel JF. Religionsethnologie [Ethnology of Religions]. Berlin: Reimer; 1984.
37 Zahavi A, Zahavi A. The handicap principle: A missing piece of Darwin's puzzle. New York: Oxford University Press; 1997.
38 Irons W. Religion as a hard-to-fake sign of commitment. In: Nesse RM, editor. Evolution and the capacity for commitment. New York: Russell Sage Foundation; 2001. pp. 292–309.
39 Rappaport RA. The sacred in human evolution. Ann Rev Ecol Syst 1971; **2**:23–44.
40 Rappaport RA. Ecology meaning and religion. Berkeley: North Atlantic Books; 1979.
41 Knight C. Ritual/speech coevolution: A solution to the problem of deception. In: Hurford JR, Studdert-Kennedy M, Knight C, editors. Approaches to the evolution of language – Social and cognitive bases. Cambridge: Cambridge University Press; 1998. pp. 68–91.

REVIEW ARTICLE

Comparative Approaches in Evolutionary Psychology: Molecular Neuroscience Meets the Mind

Jaak Panksepp[1,2,*], Joseph R. Moskal[2], Jules B. Panksepp[3] & Roger A. Kroes[2]

1. J.P. Scott Center for Neuroscience, Mind & Behavior and Department of Psychology, Bowling Green State University, USA.
2. Falk Center for Molecular Therapeutics and Department of Biomedical Engineering, Northwestern University, USA.
3. J.P. Scott Center for Neuroscience, Mind & Behavior and Department of Biological Sciences, Bowling Green State University, USA.

Correspondence to: Jaak Panksepp
Department of Psychology
Bowling Green State University
Bowling Green, OH 43403, USA
PHONE: (419) 372-2819
FAX: (419) 372-6013
EMAIL: jpankse@bgnet.bgsu.edu

Submitted: *September 7, 2002*
Accepted: *September 18, 2002*

Key words: **evolutionary psychology; neuroevolutionary psychobiology; emotions; cognition; mind; depression, social dominance; play; microarrays; gene chip; psychiatric disorders**

Neuroendocrinology Letters 2002; ***23*** *(Suppl.4):105–115 pii: NEL231002R11 Copyright © Neuroendocrinology Letters* ***www.nel.edu***

Abstract

Evolutionary psychologists often overlook a wealth of information existing between the proximate genotypic level and the ultimate phenotypic level. This commonly ignored level of biological organization is the ongoing activity of neurobiological systems. In this paper, we extend our previous arguments concerning strategic weaknesses of evolutionary psychology by advocating a foundational view that focuses on similarities in brain, behavior, and various basic psychological features across mammalian species. Such an approach offers the potential to link the emerging discipline of evolutionary psychology to its parent scientific disciplines such as biochemistry, physiology, molecular genetics, developmental biology and the neuroscientific analysis of animal behavior. We detail an example of this through our impending work using gene microarray technology to characterize gene expression patterns in rats during aggressive and playful social interactions. Through a focus on functional homologies and the experimental analysis of conserved, subcortical emotional and motivational brain systems, *neuroevolutionary psychobiology* can reveal ancient features of the human mind that are still shared with other animals. Claims regarding evolved, uniquely human, psychological constructs should be constrained by the rigorous evidentiary standards that are routine in other sciences.

Introduction

Evolutionary psychology seeks to explain the evolved, *functional* characteristics of the human mind and thus their past and/or present *adaptive* value. This objective has been typically examined through the lens of an explanatory framework where special-purpose brain 'modules' are postulated to have been critical for hominid survival and reproductive success (herein referred to as the EP approach).

One accomplishment of the EP approach is that it has energized a variety of social psychological experiments that have revealed consistent aspects of the human mind [reviewed in 1, 2, 3]. Moreover, a second success of the EP approach is that most scholars now concede the existence of a core human psyche that is largely a product of biological evolution (specifically a result of natural selection). Disagreement, however, centers on the degree to which these accomplishments are related. For instance, although the validity and testability of determining what aspects of the human mind were designed by natural selection have been entertained [4, 5], there has been little consensus on what criteria should constitute an adequate weight of evidence for identifying evolutionary adaptations.

Constructs such as adaptation, special design, and module figure prominently in these debates and continue to rival competing counterpart concepts such as exaptation, plasticity, and general learning mechanism. Understanding precisely how such evolutionary explanations fit into a comprehensive framework for studying the human brain and mind remains a major challenge for evolutionary psychology. Although some investigators have recently addressed the need to incorporate an understanding of organic systems into the EP approach [e.g., 2,6], rigorous neurobiological and genetic data are not typically included among the standard criteria for falsifying hypotheses in evolutionary psychology.

The proposition that the human brain is constituted of adaptive modules is reminiscent of past approaches to understand human behavior, such as phrenology. The existence of a variety of genetically inherited, adaptive sociobiological modules (unique to the hominid lineage and located in neocortex) is dubious at best when considered simultaneously with our current understanding of mammalian brain organization. For instance, pre-existing genetic constraints and epistatic interactions may impart substantial effects on the polygenic and pleiotropic phenotypic traits with which evolutionary psychologists are concerned. Moreover, the organization of neocortex, which is commonly assumed to be a prime anatomical substrate for unique cognitive modules in the human brain, exhibits no robust signs of localized anatomical specialization above and beyond specific sensory and motor connections, and their polymodal interactions.

Such considerations have previously led us to argue that the human brain can *acquire* a large variety of *epigenetically* derived functions via interactions of a limited number of evolutionarily conserved affective/motivational systems (situated largely in subcortical areas) with a set of plastic general-purpose learning mechanisms in neocortex [7,8]. We do not deny the existence of certain special-purpose learning systems in the brain, such as fear learning, which is shared with other animals. However, the human neocortex includes much more than a conglomeration of special-purpose learning mechanisms. It contains a neural architecture that can generate flexible features which may be best conceptualized as *rewriteable*. There has been little substantive research into how the de novo, evolved functions of the mind can be distinguished from the phenotypic consequences of individual, social, and cultural learning experiences. Until such issues are addressed by evolutionary psychology, a scientifically coherent framework for studying the evolution of human and animal minds will remain elusive.

In the first part of this paper, we will argue that much of human mental activity is driven by the ancient affective emotional and motivational brain systems that are shared with other animals. This is not to deny that propositional thoughts are uniquely efficacious in controlling human behavior, but to suggest that such cognitive activities are often driven by affective urges. Thus, it is suggested that most specialized learning functions are closely linked to, and perhaps critically dependent upon, such affect/motivation generating systems. The present arguments will be framed through a summary of our past concerns with the EP approach [7]. In the latter part of the paper, we will proceed to argue for the utility of examining the human mind with the concept of homology rather than those of analogy or reverse engineering – the perspectives commonly employed by investigators using the EP approach.

Specifically, we will advocate a multidisciplinary approach that aims to 'triangulate' between:

(i) behavioral genetic studies that focus on heritability and individual gene contributions;
(ii) molecular biological studies that directly analyze differential gene expression within the brain in a variety of relevant behavioral contexts; and
(iii) traditional psychobiological and neuroethological studies that can characterize brain-behavior, structure-function relationships.

An example of this strategy will be detailed through a description of our upcoming work on messenger ribonucleic acid (mRNA) expression patterns in rats during social interactions. Examination of mRNA transcription patterns in specific brain areas can begin to provide insight into how individual patterns of gene expression during behavioral, motivational, and affective states relate to dynamic patterns of social organization. If, what might be aptly termed, homologous patterns of gene expression are identified in such experimental paradigms, then the existence of a unique, evolutionary origin for human behavior and underlying mental processes may require re-evaluation.

Similar principles have been guiding biomedical research for years and a parallel strategy can be developed for studying the human mind. Ultimately, the

importance of such gene expression patterns for evolutionary psychology can be evaluated, and we assume demonstrated, by the design of new pharmacological therapies in humans (see *From Brain Molecules to Mind Medicines* section). Molecular biological studies alone, however, will not suffice. Together with approaches such as comparative brain imaging and the phylogenetic analysis of psycho-behavioral traits [9, 10], an evolutionary psychology that incorporates homology and the experimental analysis of neural systems into its explanatory scheme should be scientifically more successful than approaches that are built purely from conceptual perspectives.

A Summary of the 'Seven Sins of Evolutionary Psychology'

Our previous critique of the EP approach [7] was motivated by the following convergent issues:

(i) the general failure of the EP approach to incorporate the many existing lines of behavioral brain research;
(ii) the tendency of the EP approach to generate adaptive scenarios regarding socio-emotional processes in humans without apparent concern for how such processes might be interfaced with brain structure and function; and
(iii) the concurrent claim that the EP approach now provides one of the most robust lines of inquiry for identifying the types of adaptations that actually exist in the human brain. We agreed with the EP approach insofar that it has been premised on the acceptance of evolutionary thought as one of the most important ways to determine the psychological 'natural kinds' that exist within the brains of humans as well as other animals.

We extended our critique by elaborating a general framework through which the origin of many (but certainly not all) aspects of the human mind can be conceptualized: The human brain contains various ancient subcortical systems that foster affective/motivational processes, which interact with neocortex, a tissue comprised of a relatively homogenous field of columnar units which support many of the seemingly unique higher functions of the human brain. We argued that much of the modern human mind arises as a consequence of those subcortical-neocortical interactions operating in various environmental contexts. Although the respective functions of subcortical and neocortical systems may be adaptive in their own right, the phenotypic expressions that resulted from interactions between these brain areas, especially with the massive expansion of neocortex in humans, led to a dramatic shift in the structure of the hominid mind. Importantly, *such changes were not necessarily due to genetic selection and may have emerged culturally and epigenetically because of the mushrooming of general-purpose neocortex* .

In other words, the progressive accumulation of interactions between environment (both physical and social), evolutionary conserved brain systems (e.g., the limbic system, which includes paleocortical zones such as cingulate, insular, orbitofrontal and periamygdaloid cortices), and a new standard for neural plasticity (i.e., via neocortical expansions) gave rise to a qualitatively different shade of mind – one that could communicate not merely with *signs*, but in *symbolic* terms. Our ideas were aimed at serving as a more neurobiologically oriented extension of previous formulations, such as Lumsden and Wilson's [11] gene-culture co-evolution and the role of exaptations in evolution [12]. The time is finally ripe to begin building an evolutionary viewpoint of the mind based on comparative concepts that incorporate the intrinsic systems found in all mammalian brains [10]. To underscore the major points that led to this assertion, we will now briefly summarize the specific 'sins' that were discussed in our previous articles [7, 8].

I. Are there Pleistocene sources of current human social adaptations?

Evolutionary psychologists have generally backed off from this assumption, as they have realized that neocortex was the main type of brain tissue that emerged two million years ago when hominid brains began to diverge from the chimp-sized brains of our ancestral stock. As we noted before, "let us recall that the 'chips' of the human cortex – the columnar structures containing approximately 3,000 neurons each – are very similar throughout the brain and also from one mammalian species to another. These features are suggestive of highly generalized (almost 'random access'), chip-based computational devices" (pp. 116) [7]. Thus, the critical question remains: Did modular, special purpose brain functions result largely from the process of genetically-based natural selection during the homonid cerebral expansion of the past few million years, or rather have most higher *hominid* brain functions become modularized epigenetically and emergently through learning and cultural experiences? The specializations in cortical areas that we share with other animals (i.e., limbic and sensory cortices), that are accepted by most neuroscientists, are not at issue here. In any event, the effects of natural selection must be distinguished from the consequences of epigenetic influences To our knowledge, evolutionary psychologists have yet to tackle such crucial problems.

II. Why focus on one species?

Without a clear understanding of what humans share with other animals, it is difficult to specify the truly unique capacities of the human mind. Neuroanatomical and neurochemical homologies offer a productive way to specify the intrinsic, evolved faculties of the human brain and mind. Many of these homologies will be evident in instinctual behavior patterns which exhibit class-typical ethological resemblances across mammalian species. Likewise, as homologous overlap areas between human and animal brain functions are

characterized, the utilization of anthropomorphic reasoning can become a fertile source of testable hypotheses [13].

III. Which psychological adaptations have been specially designed?

Adaptive brain functions should always be discriminated from phenotypic effects that appear functional, but were actually derived from sources of evolutionary change other than natural selection, such as exaptations, spandrels, genetic drift, and especially the general ability to learn new skills and strategies. As already mentioned in the first item, delineating genetic and epigenetic influences on brain functions remains a major challenge that must be increasingly acknowledged and empirically confronted by evolutionary psychologists. Furthermore, the roles of developmental programs and the cultural transmission of learned traits must be examined through the lens of evolutionary psychology as well.

IV. Are there massive modules for mental traits?

The concept of 'brain centers' was discarded in functional neuroscience several decades ago. There are indeed various special-purpose circuits and systems in subcortical regions of the brain, but such systems are not encapsulated and appear to interact with each other extensively [10]. For instance, Mesulam [14] has described 'channel' and 'state' brain functions. State functions, or the widely ramifying background processes of the brain (e.g., attention, emotions, and motivations), are more likely to exhibit robust genetic controls than the channel functions of the brain which elaborate detailed aspects of information processing in the brain (e.g., specific perceptions, thoughts, or strategies). Moreover, the forces that drove the expansion of heteromodal neocortex during primate brain evolution may have been substantially different than those that shaped sensory and motor processing systems (i.e., internal vs. environmental selective pressures as described in [15]).

V. Why conflate emotions and cognitions?

There is considerable pressure currently to envision emotions largely as a subset of cognitive processes [16], as many scholars have generally failed to consider evolutionary evidence underscoring the traditionally understood distinction between reason and passion, or cognitions and emotions [17]. Clore & Ortony [18] suggested that emotions are best understood with regard to their propositional contents (i.e., what they refer to) rather then considering the possibility that affective states can exist both with and without cognitive contents (albeit they usually do have such contents). The existence of phenomena such as dreaming, psychomotor epilepsy (characterized by emotional auras), and brain stimulation induced emotional states suggests that primitive emotional and motivational systems can generate psychological urgencies (i.e., non-sensory states of consciousness) that exist independently of externally (e.g., perceptually) and internally (e.g., thought) driven cognitive contents. That emotions and cognitions function synergistically in the intact brain is not a compelling rationale to avoid scientific dissection of such interactive albeit evolutionarily distinguishable processes.

VI. Why ignore the brain?

This is a criticism of the general failure to constrain theories of mind with explicit neurobiological criteria. Modern neuroscience has provided a suitable foundation to begin thinking more clearly about the underlying organic basis of mental processes. Molecular biology is now providing equally fruitful approaches for uncovering the functional characteristics of biological systems that are inherited via genetic transmission. The social sciences must deal with such underlying levels of organization and some have started to do so, albeit at a markedly slow pace.

VII. Do anti-organic biases help create a computationalist/representationalist myth?

Evolutionary psychologists have suggested that the underlying operations of mind can be conceptualized adequately as computations carried out by the brain – or rather as functional sets of neural algorithms. An algorithm *is a formal procedure for any mathematical operatio*n. While specific neural algorithms may underpin certain aspects of sensory/perceptual and motor/action, channel functions [e.g., 19], the central neural substrates underlying psychobehavioral states are unlikely to be organized in a similar manner. Such functions are more fundamentally organic and analog, exerting global brain/mind influences. In other words, the brain can produce behavioral and mental phenotypes via neuronal mechanisms that are markedly different in their constitution when compared with mathematical computations, whether manifested at the level of anatomical reorganizations and/or dynamic changes in the elements of individual synapses.

All of the flaws mentioned above ultimately relate to the failure of evolutionary psychology to assume a deeply organic perspective. Historically, the explanatory validity of most biological disciplines has depended on how successfully they were linked to fundamental lower (e.g., molecular) levels of organization. This will be true for evolutionary psychology as well. If such a linkage is not achieved with regard to the study of the human mind, a major negative consequence may be a massively inappropriate conflation of evolved, adaptive specificity with emergent, epigenetic processes. For instance, consider a concrete example: Rats will avoid foods that make them sick. Although they are likely to have evolved mechanisms for generating feelings of sickness and mechanisms to associate such feelings with recently consumed foods – especially novel foods – they probably do not possess adaptations that allow them to instinctually avoid palatable poisons. Such a specific behavioral phenotype may only be achieved thorough a general-purpose, food selection learning mechanism. Due to the power of long-interval associa-

tive learning, animals learn to avoid salient substances that *may* have made them sick. Thus, one might find many genes that affect learning in general, or the pleasures and displeasures of tastes and feelings of well-being and sickness, but not brain mechanisms that generate avoidance of specific foodstuffs.

Considering the large number of specific behavioral tendencies that can arise from a comparatively modest number of interacting adaptations, evolutionary psychology will benefit immensely from a rigorous analysis of the biological underpinnings of psychological traits. For example, Badcock's [2] confrontation with key biological issues addresses how aspects of culture may be related to genetic mechanisms, such as genomic imprinting. The provocative findings of Keverne *et al*. [20], indicating that development of neocortex is disproportionately influenced by maternally imprinted genes while the development of key emotional areas, such as the hypothalamus, are governed by paternally imprinted genes, may have profound implications for understanding sexual selection in evolutionary psychology.

A New Strategy for Evolutionary Psychology

We have thus far argued that comparative analyses of brain and behavior can offer new vistas for understanding the evolution of the mammalian mind, and thereby the mental functions that result exclusively from human brain activity. Identifying homologous brain functions will aid in defining the appropriate null hypotheses for human studies; namely, mental differences between species must be associated with differences in brain structure, connectivity, neurochemistry, and/or patterns of activation. For evolutionary psychologists, this type of approach may initially seem counterintuitive, as the EP approach has been typically concerned with *similarities* in organization of the human mind across individuals. However, unique species-specific traits can be confirmed only through an exclusion of the possibility that a respective trait is shared between phylogenetically related species.

Towards this goal, neurophysiological studies can help elucidate the details of single unit activity and synaptic interactions, but such levels of organization are difficult to translate to human research. It would be better to carry out concurrent investigations of global neurochemical systems (for which there exists much comparative data) and deeper genetic levels (e.g., analysis of DNA polymorphisms or RNA expression patterns). Such a paradigm can be established by employing two general strategies:

(i) investing in carefully selected animal models of basic behavior patterns that can be studied with regard to human psychological constructs and
(ii) taking the previous phase of investigation into the realm of modern neurochemistry and molecular biology.

The major advantage of this particular approach is that it can potentially extend the scope of evolutionary psychology to include levels of organization essential for understanding the evolution of complex organic systems. For instance, *neuroevolutionary psychobiology* has already revealed how separation distress systems and their relevant neurochemical controls (e.g., endogenous opioids) may have emerged from pre-existing pain systems of the brain [10]. One can easily envision how such evolutionary sculpting of new brain functions may have emerged while retaining ancestral neurochemical characteristics. Modern molecular biological analyses should be able to directly evaluate the relatedness of genetic controls in such systems across species.

Although no single approach can validate hypotheses regarding the evolution of the human mind and its relations to ancient brain functions, molecular biological studies can aid in providing a basis for the explanatory constraints that should be utilized by evolutionary psychologists. The remaining aim of this paper is to exemplify how molecular biological tools can be employed in evolutionary psychology. First, we will briefly summarize the overall utility of such technologies.

Gene Expression Arrays

A powerful, recent development in molecular biology has been the emergence of rapid throughput technologies that allow the concurrent evaluation of differential expression of many genes in virtually any tissue of interest. For example, a recent paper highlighted the overlapping and non-overlapping microbial gene expression patterns evoked by three pathogens [21]. Another study identified several new genes related to hemodynamic stress that may arise from hypertension [22]. The potential value of broad genome scans in the study of psychiatric disorders has been well described [23, 24, 25], but the main factor preventing their widespread use are the methodological complexities and comparatively high costs of such technologies.

However, relevant studies are beginning to appear. For instance, Tononi & Cirelli [26] have shared provocative findings that indicate waking-specific and sleep-specific profiles of gene expression. Preliminary results have also emerged for complex brain disorders such as schizophrenia [27]. To our knowledge, this technology has not yet been applied systematically to a behavioral model that would be of direct relevance to evolutionary psychology.

We have recently begun to apply gene expression microarray technology to the study of behavior in rats and for the remainder of this paper we will outline our initial experimental strategies. Such experiments should be of broad interest in fields ranging from neuroethology to biological psychiatry and ultimately, we hope, evolutionary psychology. Considering that molecular screening techniques remain in their infancy, and methodological and conceptual concerns accompany their utilization as well [29], it may be initially as wise to employ a targeted (i.e., selected gene) as more

comprehensive approaches. Indeed, due to incomplete genomic information, a full scan is not yet possible in laboratory rats.

The Neurobiological Sources of Separation Distress

A consistently demonstrated finding regarding subcortical brain systems is that affective responses can be evoked by localized electrical stimulation [10]. A compelling question thus is whether differential, artificial activation of distinct emotional systems (e.g., electrical activation of SEEKING, RAGE, FEAR or PANIC circuits) can generate distinct gene expression profiles at various points in time following activation. If there are indeed selective patterns of gene expression under such conditions, and furthermore if some of the respective gene products (e.g., neuropeptides) can arouse predicted affective responses (monitored by place preference measures), there then emerges an opportunity to evaluate the role of the associated neurobiological substrates in human emotional experiences. In such human studies, there would be an additional interesting opportunity to explore whether certain patterns of cognitive activity accompany distinct states of emotional arousal. Namely, would individuals exhibit characteristic patterns of thought during or following pharmacologically induced shifts in emotional states?

However, since many distinct emotional circuits overlap extensively in the diencephalon and midbrain, electrical brain stimulation studies may not be an optimal initial strategy. Rather, it seems that a study of natural, easily generated instinctual-emotional behaviors (fear, anger, seeking, sex, maternal behavior, separation distress and rough-and-tumble play) might serve as better starting points. Behavioral and neurochemical alterations resulting from such affective states have been studied in animal behavior models, and may be foundational processes for many human mental tendencies and psychiatric disorders [10]. In particular, the psychological stress and depression that results from social subordination and loss in rats is well documented, and thereby serves as one provocative starting point for studies of gene expression changes that result from social-environmental challenges.

Following the seminal work of John Bowlby [30], it was gradually recognized that behaviors related to separation distress were extant throughout most mammalian taxa. Subsequent investigations were targeted at characterizing the anatomical and neurochemical organization of neural circuits related to separation distress [20, 31, 38]. Studies evaluating the effects of electrical brain stimulation on evoked separation calls identified the associated anatomical trajectories in midline diencephalic structures, while the cardinal neurochemistries that inhibited separation distress vocalizations were endogenous opioid, oxytocin, and prolactin systems. These findings have been corroborated by many investigators [reviewed in 10] and they have set the stage for understanding many of the basic socio-emotional processes carried out by the mammalian brain, like those that mediate social attachments [33]. Furthermore, such work has also led to new animal models of depressive disorders [e.g., 34] and has helped stimulate research programs that focus on understanding related behavioral phenomena, such as gregariousness and social bonding [reviewed in 35].

Findings from other research areas complement the initial work on mammalian separation distress circuits. For example, studies examining the neural consequences of social isolation revealed several major neurochemical changes; among the most prominent brain alterations were a reduction in serotonin turnover and increased dopamine receptor sensitivity, both of which can promote elevated aggressive tendencies during social encounters [34]. Moreover, the psychiatric community has increasingly recognized that, in addition to the classical concept of stress [37], there are particularly devastating effects of social loss and chronic social isolation on mental health – especially as an etiological factor in depression. A variety of retrospective studies have documented an increased tendency for depressive disorders to arise following the loss of a loved one [38,39]. However, our understanding of the neurobiological changes associated with the formation and maintenance of social bonds remains in its infancy [40]. A wide ranging screen of gene expression patterns related to social behavioral processes is essential for characterizing the effects of social loss on psychobiological processes, and ultimately may help elucidate the evolutionary derived features of the mammalian brain and mind.

An Ethological Model for Simulating the Depressive Cascade: Social Competition

Animal models have had clear implications for the biomedical sciences and can provide a comparable understanding for evolutionary psychology. For instance, here we suggest that the use of two well-established experimental paradigms for analyzing social dominance in rodents may serve as potential models for the cascade of brain changes that result from depressive disorders, as well as a consequence of adaptive social behaviors. Contemporary psychiatry currently recognizes that the absence of social support and persistent losses in social encounters can serve as major vectors that lead to depressive disorders [e.g., 41] As we will allude to later in this section, the resident-intruder paradigm in rats may be ideally suited for analyzing differential brain gene expression in 'winners' and 'losers'. But, first we will briefly consider the scientific background for making such contrasts.

It is a commonplace observation that there are winners and losers in all forms of social competition. The idea that social defeat, which typically leads to subordination, may be a major contributory factor in the genesis of depression has recently received considerable attention within evolutionarily oriented segments of the psychiatric community [42]. In humans, at an emotional level, social defeat is accompanied by feelings such as hopelessness and helplessness, weakness and tiredness, as well as inferiority and inadequacy.

Such changes in affect are similar to those traditionally deemed to be primary characteristics of depressive disorders. Aside from pharmacological studies, where many antidepressant agents increase confidence [e.g., 43, 44], little is known about the central nervous system changes set in motion by defeat. Possible changes suggested by animal models are an initial arousal of biogenic amines [45], opiates [46], and other stress related neuropeptides, such as Corticotropin Releasing Factor (CRF) [47], and cytokines [48]. Whether alterations in these neurochemical axes are simply due to stress in general or rather to the specific social stresses described above is unknown. It has become widely accepted that stress is a major contributory factor in the etiology of depressive disorders [37, 47]. More recently, with an appreciation that all mammalian brains contain specific emotional systems that mediate social processes [10, 35], it has been recognized that social loss may be the most common type of stress that promotes the cascade of neuro-affective alterations leading to depression [49]. Furthermore, it has been proposed that such responses may reflect adaptive coping responses to a rapid diminution of available social resources [50].

In general, social stress can be categorized into two major types: (i) that which emerges from social loss, such as the loss of a loved one, and (ii) that which emerges from the loss of social status. With a growing recognition that loss in social encounters (submissiveness) can lead to depression [49], it has been increasingly theorized that social competition in animals may model certain aspects of depression in humans. Both types of social loss share certain key physiological features, such as arousal of the hypothalamic-pituitary-adrenal axis [37, 47], and activation of non-specific arousal/attentional circuits like ascending norepinephrine and acetylcholine systems [33, 52]. Use of modern gene expression technologies, such as those described above, should help unravel the neurobiological underpinnings of pathophysiological processes, and thereby offer a new understanding of both the pathogenesis of depression and the pharmacological facilitation of confidence.

Spontaneous acts of aggression commonly ensue when one adult animal intrudes on the living space of a conspecific. Such behavior patterns, which are typically more clearly evident in males than females, have the potential to be a robust animal model for social loss-induced depression. In such resident-intruder paradigms, with all other variables like weight and age controlled, the intruder routinely becomes the loser [53]. Whereas the resident (dominant) animal thrives, the intruder (subordinate) becomes unambiguously defensive and in the severest circumstances becomes physiologically compromised with a loss of weight and chronic elevation of stress indices [54]. Other severe consequences, including long-term disruptions of heart rate and body temperature regulation [55], are especially manifest when social contact with 'friendly' animals is not permitted following defeat [56]. In this last study, intruding animals had been socially housed and following defeat they were either returned to previous social housing conditions or they were kept isolated. Only the animals denied subsequent social housing (i.e., those not allowed resumption of positive social interactions) exhibited a cascade of severe physiological and psychological changes during the three weeks following defeat (e.g., loss of weight, adrenal hypertrophy, testicular regression, and increased fearfulness).

Studies employing *in situ* hybridization highlight major differences in *c-fos* gene expression between winners and losers [57]. The largest effects of losing are evident in the paraventricular nuclei of the hypothalamus, the origin of the pituitary adrenal stress response that is abnormal in depression [37, 47]. Since *c-fos* activation promotes a cascade of alterations in gene expression [e.g., 58], there are bound to be many differentially regulated genes that result from winning and losing social encounters.

An interesting contrast condition to the resident-intruder paradigm is the analysis of outwardly similar play behavior patterns in juvenile animals. This type of social competition is not as stressful as the resident-intruder paradigm. Under comparable conditions juvenile animals exhibit 'play fighting' which can also lead to the establishment of social dominance [59]. Such social engagements, however, are affectively positive for both animals as evaluated by place preference and other instrumental tasks [60]. In such experimental paradigms, social deprivation promotes rough-and-tumble play whereby stable, but friendly, patterns of dominance emerge [10]. Although endogenous brain opioid systems have been demonstrated to change as a result of play [61, 62], little is known about other concomitant alterations in neurochemistry. A scan of differences in gene expression may reveal that aggressive and play dominance have markedly different effects on the brain. Such an expectation stems from a recent demonstration of differential *c-fos* mRNA transcription patterns in winners and losers from adult resident-intruder paradigms [57] and during play between juveniles [63]. The precise identity of the more widespread genetic changes can be identified using gene expression microarrays.

Thus, as has been argued by several evolutionarily-oriented investigators [e.g., 49], the formation of social dominance may reveal genetic alterations that ultimately lead to depressive phenotypes in submissive animals, while the second paradigm (i.e., social play) may reveal possible differences in gene expression that lead to submission, but without negative social stress. Such gene expression patterns may carry considerably different emotional and adaptive consequences. Moreover, since both behavioral paradigms entail comparable amounts of energy use, changes in expression that are due to non-specific behavioral and general arousal processes should be filtered out of the analysis. Although no control can be perfect when it comes to such dynamic social processes, the two models are about as close as they can come to ideal mutual controls for each other. Inclusion of socially housed animals in these studies (that exhibit little robust social

interaction) can provide additional 'social-contact' controls that will permit a clearer interpretation of differences in gene expression that are observed during the two social situations.

Several other naturalistic models of animal behavior offer an opportunity to study potentially key aspects of human behavior. To be fruitful, studies of gene expression patterns must converge with other cross-species approaches, such as brain imaging technologies, the construction of behavioral phylogenies, comparative neuroanatomy, and analyzing the consequences of nucleotide polymorphisms on physiological function. Ultimately the importance of such approaches for evolutionary psychology can be directly evaluated by the development of increasingly specialized pharmacological therapies for treating psychiatric disorders.

From Brain Molecules to Mind Medicines

The most likely place where the evolutionary functions of the brain and mind will find a common, fertile ground for substantive empirical advances is in the neurochemical coding of emotional and motivational behaviors, and the affective processes and thinking tendencies associated with them. This is because homologous brain systems in humans and other animals can be studied with the same neurochemical techniques, and the underlying neurochemical systems can be linked directly to genetic issues. Neuroantomical and neurophysiological correlates are also important, but much less susceptible to such comparative genetic studies. Also, in this context, it is worth noting that the therapeutic applications that may emerge from a detailed understanding of state functions of the brain (e.g., the basic attentional, emotional, and motivational systems of the brain) are much more likely to be fruitful than that which could be achieved through a study of the channel functions of the brain (which presumably mediate the epigenetically divergent individual differences that are abundant in all species). In pursuing such neuroevolutionary psychobiological relationships, it is likely that new therapeutic principles will be discovered that will herald a new and more subtle generation of interventions in biological psychiatry.

Here we would like to briefly summarize the work of Moskal and co-workers [64] on the discovery of a new class of potential therapeutic agents that emerged from a strictly molecular approach to the brain and that furthermore highlights the remarkable power of molecular biological tools to uncover specific, evolved functions of the brain. This research was initiated in the early 1980s with the goal of discovering new brain molecules that may be important in the mediation of complex central nervous system functions, such as learning and memory formation. Since it was already well established that one of the cardinal brain areas involved in translating experiences into long-term memories was the hippocampus, the goal was to discover new memory-related molecules that may exist in tissues derived from that brain structure. Accordingly, a library of monoclonal antibodies (MAbs), directed to the developing hippocampal formation of neonatal rats was created [65]. Promising MAbs were identified first by immunocytochemical methods including identifying those that bound to the cell surfaces of live hippocampal neurons maintained in tissue culture (the assumption being that important functional events would be transpiring at the cell surface), and second by evaluation of functional effects including behavioral changes in various animal models when such antibodies were injected into the ventricular system [66, 67].

This screening led to the identification of an MAb that not only bound relatively selectively to the hippocampus, but which could also facilitate learning. Pharmacological studies indicated that binding was occurring at the glycine co-agonist binding site of the NMDA receptor-ionophore complex [68, 69]. This MAb was used as a template to create, via cloning and sequencing the hypervariable regions of the antibody, a family of peptides that mimicked the antibody itself [64]. Further purification and structure-function activity studies yielded a family of small peptides we now call *Glyxins* which not only have all of the behavioral effects of the parent MAb, but also proved to be effective in inhibiting neuronal damage caused by hypoxic insult to the brain, and also proved to be effective in alleviating neuropathic pain [64, and unpublished data].

The molecular analysis of brain tissues, in conjunction with parallel behavioral studies, can yield insights into the evolved regulatory systems of the brain that cut across species barriers. We believe that with the advent of tools for the analysis of gene expression, especially micorarray technology, one can now go from the analysis of gene activation patterns in the brain to the identification of molecular targets for therapeutic interventions in psychiatry. The success of this enterprise could introduce a powerful new biological foundation for evolutionary psychological thought.

Conclusions

From the perspective of the so called 'hard' sciences, such as physics or chemistry, evolutionary psychology is an emerging discipline that will benefit immensely from a consideration of the underlying, neurobiological substrates of mental processes and behavior that can be modeled in related animals. A historical example of this can be found in the emergence of biochemistry as an independent field of inquiry. Surely biochemistry is currently accepted as a field in and of itself, but it should be remembered that not until early in the twentieth century had chemists begun to apply their knowledge and experimental methods to the study of cell function. As it were, the pioneers of biological chemistry legitimized biochemistry as a field and furthermore ushered in the present age of molecular biology by identifying the chemicals of life (e.g., glycolysis, the tricarboxylic acid pathway, essential vitamins and minerals, etc.). Later concepts such as the allosteric regulation of enzymes, energy storage and transfer in the form of adenosine triphosphate, and signal transduction via cyclic AMP solidified biochemistry as a field that had gone beyond

the mere description of the chemicals of life, to one capable of generating new hypotheses that gave important insights into cell function; concepts not intuitively obvious to chemists, but clearly grounded in basic chemical processes – emergent properties with lives of their own, if you will, but grounded by parent scientific disciplines.

Another important point to be gleaned from the history of physics and chemistry as applied to biology is how crucial model systems have been for the development of new scientific disciplines. Molecular biology would not have been possible if it were not for the use of a prokaryote, *E. coli*, which was used to generate much of the essential data that forms the backbone of the field today. The fact that the genetics of *E.coli* and the biological machinery that coordinates it differs substantially from eukaryotes has done nothing to invalidate the absolute need for having chosen a suitable model species for the investigation of fundamental processes. Moreover, nested in this approach is the key assumption that the study of less complex systems – systems that nonetheless exhibit the core properties under investigation – are the primary way in which parent sciences can lay the needed foundation for the creation of emergent disciplines. Thus, the study of basic psychological processes will benefit enormously from the neuroethological study of instinctual tendencies that all mammals share. Perhaps just as importantly, without the integration of more molar approaches with more molecular ones, newer scientific fields, such as evolutionary psychology, often fail to tap into the richness of thought that has preceded them.

Consider one relevant example in more detail. What is psychoneuroimmunology? In a general sense, disregard that it is a scientific field that has organized important insights into testable models, rather just think about the hybridization of terms! Psychoneuroimmunology studies the impact of psychological constructs on the unconscious aspects of the nervous system that control the immune system and its associated diseases. What was there before the concept of psychoneuroimmunology was coined? How did stress affect immune, neuronal, or mental processes? There were generally no formal hypotheses and thus there was no coherent scientific discipline addressing such questions. As parent disciplines have become progressively integrated, there was a gradual transition from some type of 'hit and miss' approach to a set of principles that allow a variety of psychosomatic abnormalities to be recognized as standard medical disorders. Currently one of the most powerful sub-notions of evolutionary theory is The Medical Model – that is diseases of the body have an organic basis that can be identified, characterized, and medical interventions can be developed based on basic chemical, physical, and biological processes. Moreover, in psychiatry emergent properties of the brain, such as basic affective responses and their accompanying emotional states, are being characterized as etiological agents that intersect with the more clearly biological features of the brain and body. No voodoo or prayer is required, unless you are at the fringes of psychoneuroimmunology!

Likewise, emotional experience and its linkage to cognitive processes is bound to figure prominently into a coherent evolutionary psychology. From this perspective, consciousness and affective experience may have arisen concurrently in neural evolution as a way to elaborate and extend the potential reach of instinctual urges, while new levels of cortico-cognitive processes that serve to increase behavioral flexibility promoted the ability of organisms to efficiently pursue goals essential to survival. Accordingly, affect could not exist independent of consciousness, since in essence it is something that exists as part and parcel of conscious perception. Even in the absence of complex intellectual function, affective experience (an apparently intrinsic brain function) appears to exert a powerful influence on behavior in all mammals, and new models have been developed which allow such issues to be addressed objectively across species [70]. It thus is essential for evolutionary psychologists to investigate how such phenomena relate to the unique human psychological traits about which they are primarily concerned. One example of how this may be achieved is through a description and subsequent dissection of the neuroscientific and molecular biological substrates that foster affective experience within all mammalian brains [10]. These issues need to be linked to the extensive data-base describing the natural behavioral tendencies of animals and humans [71]. These strategies can be directly linked to the rapidly emerging evidence that highlights the extent to which psychiatric disorders are influenced by predisposing genetic factors [72].

In conclusion, lessons from the history of science suggest the following:

(i) You must build a field of scientific inquiry using the robust tools that already exist in related disciplines and from such an approach, emergent, testable ideas can be expected;
(ii) If you are willing to embrace evolutionary theory and the Medical Model of disease, then there must be a genetic basis to many fundamental aspects of human behavior;
(iii) Many of the basic constituents of human behavior are likely to be present in animals other than humans (while at the same time not denying that many additional mental potentials arose from more recent cortico-cognitive developments); and
(iv) As such, the use of animal models to study human behavior using the tools of chemistry, physics, biology, biochemistry, and molecular biology can be fruitfully undertaken.

With the development of new molecular techniques and the subsequent collection of new data sets in model species, a more thorough understanding of the genetically promoted characteristics of human mind and behavior will gradually emerge. This, in no way, denies the special neuro-symbolic and cultural capacities that have emerged which allow humans to have thoughts about

their thoughts and feelings that seem beyond the ken of practically all other species.

This paper has argued for a relatively novel scientific framework that should be considered and debated by the current generation of evolutionary psychologists; namely, that hypotheses regarding the human mind must be tethered to a discipline we call *neuroevolutionary psychobiology*. In the final analysis, from a molecular biological perspective at least, the use of animal models should be – indeed, must be – the approach that is most valuable for unraveling the biological substrates that form the cornerstones of the human mind and behavior. In laying down such solid neuropsychological foundations, we may develop more appropriate intellectual spaces for scientifically understanding even the most subtly evolved functions of the human mind. When these foundations are more fully understood, then we will be able to better address those aspects of the human mind that are truly unique and critically dependent on our vast cortico-cognitive resources–such as our capacity to symbolize and communicate world events in linguistic terms. Such emergent capacities have permitted the emergence of spectacular cultural traditions and our profound interest in the minds of others, as each of us seeks to sustain and improve the inter-subjective fabric of our existence.

Acknowledgements

We are grateful for the helpful criticisms and ongoing discussions that were provided by Robert Huber, Moira van Staaden, and their laboratories at BGSU. Financial support of this work from the Falk Foundation is gratefully acknowledged.

REFERENCES

1 Buss DM. Evolutionary psychology: the new science of the mind. Boston (MA): Allyn and Bacon; 1999.
2 Barret L, Dunbar R, Lycett J. Human Evolutionary Psychology. New York; Palgrave; 2002.
3 Ketelaar T, Ellis BS. Are evolutionary explanations unfalsifiable? Evolutionary psychology and the Lakatosian philosophy of science. Psychol Inquiry 2000; **11**:1–21.
4 Andrews PW, Gangestad SW, Matthews D. Adapationism – how to carry out an exaptationist program. Behav Brain Sci; in press.
5 Badcock C. Evolutionary psychology: a critical introduction. Cambridge (UK): PolityPress; 2000.
6 Duchaine B, Cosmides L, Tooby J. Evolutionary psychology and the brain. Curr Opin Neurobiol 2001; **11**:225–30.
7 Panksepp J, Panksepp JB. The seven sins of evolutionary psychology. Evol Cogn 2000; **6**:108–131.
8 Panksepp J, Panksepp JB. A continuing critique of evolutionary psychology. Sevensins for seven sinners, plus or minus two. Evol Cogn 2001; **7**:56–80.
9 Emery NJ. The eyes have it: the neuroethology, function and evolution of social gaze. Neurosci Biobehav Rev 2000; **24**:581–604.
10 Panksepp J. Affective neuroscience, the foundations of human and animal emotions. New York: Oxford University Press; 1998.
11 Lumsden CJ, Wilson EO. Genes, mind, and culture: The coevolutionary process. Cambridge, Mass: Harvard University Press; 1981.
12 Gould SJ, Vrba ES. Exaptation: a missing term in the science of form. Paleobiol 1982; **8**:4–15.
13 Panksepp J. Affective Neuroscience: A conceptual framework for the neurobiological study of emotions. In K. Strongman, editor, International Reviews of Emotion Research, Chichester, England: Wiley, 1991. pp. 59–99.
14 Mesulam MM. Editor, Principles of Behavior and Cognitive Neurology, 2nd ed. New York: Oxford Univ. Press. 2000.
15 Rapoport SI. 1999. How did the brain evolve? A proposal based on new evidence from *in vivo* brain imaging during attention and ideation. Brain Res Bull **50**(3):149–165.
16 Lane RD, Nadel L, editors. Cognitive neuroscience of emotion. New York: Oxford University Press; 2000.
17 Panksepp, J. At the interface of affective, behavioral and cognitive neurosciences. Decoding the emotional feelings of the brain. Brain Cog 2003; In press.
18 Clore GL, Ortony A. Cogniton in emotion: always, sometimes, or never? In: Lane RD, Nadel L, editors. Cognitive neuroscience of emotion. New York: Oxford University Press; 2000. p. 24–61.
19 Ariff G, Donchin O, Nanayakkara T, Shadmehr R. A real-time state predictor in motor control: Study of saccadic eye movements during unseen reaching movements. J Neurosci 2002; **22**:7721–29.
20 Keverne EB, Fundele R, Narasimha M, Barton SC, Surani MA. Genomic imprinting and the differential roles of parental genomes in brain development. Dev Brain Res 1996; **92**:91–100.
21 Huang Q, Liu DY, Majewski P, Schulte LC, Korn JM, Young RA *et al*. The plasticity of dendritic cell responses to pathogens and their components. Science 2001; **294**:870–75.
22 McCormick SM, Eskin SG, McIntire LV, Teng CL, Lu CM, Russell CG *et al*. DNA microarray reveals changes in gene expression of shear stressed human umbilical vein endothelial cells. Proc Natl Acad Sci (USA) 2001; **98**:8955–60.
23 Marcotte ER, Srivastava, LK, Quiron R. DNA microarrays in neuropsychopharmacology. Trends Phamacol Sci 2001, **22**:426–36.
24 Shilling PD, Kelsoe JR. Functional genomics approaches to understanding brain disorders. Pharmacogenomics 2002, **3**:31–45.
25 Watson SJ, Akil H. Gene chips and arrays revealed: A primer on their power and their uses. Biol Psychiat 1999; **45**:533–43.
26 Cirelli C, Tononi G. Gene expression in the brain across the sleep-waking cycle. Brain Res 2000; **885**:303–21.
27 Mirnics K, Middleton FA, Lewis DA, Levitt P. Analysis of complex brain disorders with gene expression microarrays: schizophrenia as a disease of the synapse. Trends Neurosci 2001 **24**:479–86.
28 Mong JA, Krebs C, Pfaff D. Perspective: micoarrays and differential display PCR-tools for studying transcript levels of genes in neuroendocrine systems. Endocrinol 2002; **143**:2002–6.
29 Brazma A, Hingamp P, Quackenbush J, Sherlock G, Spellman P, Stoeckert C *et al*. Minimum information about a microarray experiment (MIAME) – toward standards for microarray data. Nat Genetics 2001; **29**:365–71.
30 Melges FT, Bowlby J. Types of hopelessness in psychopathological process. Arch Gen Psychiatry 1969; **20**:460–69.
31 Panksepp J, Herman B, Conner R, Bishop P, Scott JP. The biology of social attachments: opiates alleviate separation distress. Biol Psychiatry 1978; **13**:607–18.
32 Panksepp J, Herman BH, Vilberg T, Bishop P, DeEskinazi FG. Endogenous opioids and social behavior. Neurosci Biobehav Rev 1980; **4**:473–87.
33 Nelson EE, Panksepp J. Brain substrates of infant-mother attachment: contributions of opioids, oxytocin, and norepinephrine. Neurosci Biobehav Rev 1998; **22**:437–52.
34 Panksepp J, Yates G, Ikemoto S, Nelson E. Simple ethological models of depression: social-isolation induced "despair" in chicks and mice. In B. Olivier and J. Moss, editors, Animal Models in Psychopharmacology, Holland: Duphar, 1991, pp. 161–181.

35 Carter CS, Lederhendler I, Kirkpatrick B. The integrative neurobiology of affiliation. Annals NY Acad Sci 1997; **807**:13–18.
36 Linnoila M, Charney DS. The neurobiology of aggression. In D.S. Charney, E.J. Nestler & B.S. Bunney, editors Neurobiology of Mental Illness, New York; Oxford University Press; 1999.
37 Lopez JF, Akil H, Watson SJ. Neural circuits mediating stress. Biol Psychiatry 1999; **46**:1461–71.
38 Kobak, R.R., Sudler, N. & Gamble, W. (1991) Attachment and depressive symptoms during adolescence: A developmental pathways analysis. Devel Psychopath 1991; **3**:461–47.
39 Ornish D. (1997). Love & survival: The scientific basis for the healing power of intimacy. New York; HarperCollins; 1997.
40 Panksepp J. The long-term psychobiological consequences of infant emotions: Prescriptions for the twenty-first century. Infant Ment Health J. 2001; **22**:132–173.
41 Price J, Sloman L, Gardner R Jr, Gilbert P, Rohde P. The social competition hypothesis of depression. Brit J Psychiatry 1994; **164**:309–15.
42 Gardner R Jr. Evolutionary perspectives on stress and affective disorder. Semin Clin Neuropsychiatry 2001; **6**:32–42.
43 Raleigh MJ, McGuire MT, Brammer GL, Pollack DB, Yuwiler A. Serotonergic mechansims promote dominance acquisition in adult male vervet monkeys. Brain Res 1991; **559**:181–90.
44 Tse WS, Bond AJ. Serotonergic intervention affects both social dominance and affiliative behaviour. Psychopharmacol (Berl) 2002; **161**:324–30.
45 Tidey JW, Miczek KA. Social defeat stress selectively alters mesocorticolimbic dopamine release: an *in vivo* microdialysis study. Brain Res 1996; **721**:140–9.
46 Thompson ML, Miczek KA, Noda K, Shuster L, Kumar MS. Analgesia in defeated mice: evidence for mediation via central rather than pituitary or adrenal endogenous opioid peptides. Pharmacol Biochem Behav 1988; **29**:451–6.
47 Nemeroff CB. Psychopharmacology of affective disorders in the 21st century. Biol Psychiatry 1998; **44**:517–25.
48 Dantzer R, Gheusi G, Johnson RW, Kelley KW. Central administration of insulin-like growth factor-1 inhibits lipopolysaccharide-induced sickness behavior in mice. NeuroReport 1999; **10**:289–92.
49 Sloman L, Gilbert P, editors. Subordination and defeat: an evolutionary approach to mood disorders and their therapy. Mahwah (NJ): Lawrence Erlbaum; 2000.
50 Nesse RM. Motivation and melancholy: a Darwinian perspective. In: French JA, Kamil AC, Leger DW, editors. Evolutionary psychology and motivation. University of Nebraska Press: Lincoln (NB); 2001. p. 179–204.
51 Hill OW, Price JS. Childhood bereavement and adult depression. Brit J Psychiatry 1967; **113**:743–51.
52 Higley JD, Suomi SJ, Linnoila M. A longitudinal assessment of CSF monoamine metabolite and plasma cortisol concentrations in young rhesus monkeys. Biol Psychiatry 1992; **32**:127–45.
53 Blanchard DC, Sakai RR, McEwen B, Weiss SM, Blanchard RJ. Subordination stress: behavioral, brain, and neuroendocrine correlates. Behav Brain Res 1993; **58**:113–21.
54 Blanchard RJ, McKittrick CR, Blanchard DC. Animal models of social stress: effects on behavior and brain neurochemical systems. Physiol Behav 2001; **73**:261–71.
55 Tornatzky W, Miczek KA. Long-term impairment of autonomic circadian rhythms after brief intermittent social stress. Physiol Behav 1993; **53**:983–93.
56 Ruis MA, te Brake JH, Buwalda B, De Boer SF, Meerlo P, Korte SM *et al*. Housing familiar male wildtype rats together reduces the long-term adverse behavioural and physiological effects of social defeat. Psychoneuroendocrinol 1999; **24**:285–300.
57 Kollack-Walker S, Watson SJ, Akil H. Social stress in hamsters: defeat activates specific neurocircuits within the brain. J Neurosci 1997; **17**:8842–55.
58 Angel P, Karin M. The role of Jun, Fos and the AP-1 complex in cell-proliferation and transformation. Biochimica Biophysica Acta 1991; **1072**:129–57.
59 Panksepp J, Jalowiec J, DeEskinazi FG, Bishop P. Opiates and play dominance in juvenile rats. Behav Neurosci 1985; **99**:441–53.
60 Normansell L, Panksepp J. Effects of morphine and naloxone on play-rewarded spatial discrimination in juvenile rats. Dev Psychobiol 1990; **23**:75–83.
61 Panksepp J, Bishop P. An autoradiographic map of (3H) diprenorphine binding in rat brain: effects of social interaction. Brain Res Bull 1981; **7**:405–10.
62 Vanderschuren LJ, Niesink RJ, Van Ree JM. The neurobiology of social play behavior in rats. Neurosci Biobehav Rev 1997; **21**:309–26.
63 Gordon NS, Kollack-Walker S, Akil H, Panksepp J. Expression of c-fos gene activation during rough and tumble play in juvenile rats. Brain Res Bull 2002; **57**:651–9.
64 Moskal JR, Yamamoto H, Colley PA. The use of antibody engineering to create novel drugs that target N-methyl-D-aspartate receptors. Current Drug Targets 2001; **2**:331–345.
65 Moskal JR, Schaffner AE Monoclonal antibodies to the dentate gyrus: Immunocytochemical characterization and flow cytometric analysis of hippocampal neurons bearing unique cell-surface antigen. J Neurosci, 1986; **6**:2045–2053.
66 Stanton PK, Sarvey JM, Moskal JR Inhibition of the production and maintenance of long-term potentiation in rat hippocampal slices by a monoclonal antibody. Proc Natl Acad Sci USA., 1987; **84**:1684–1688.
67 Thompson LT, Moskal JR, Disterhoft JF. (1992) "Hippocampus-dependent learning facilitated by a monoclonal antibody or D-cycloserine. Nature 1987; **359**:638–641.
68 Haring R, Stanton PK, Scheideler M, Moskal JR. Glycine-like modulation of NMDA receptors by a monoclonal antibody that enhances long-term potentiation. J Neurochem_ 1991; **57**:323–332.
69 Haring R, Stanton PK, Potter PE, Sircar R, Moskal JR. Glycine-like modulation of N-methyl-D-aspartate receptors by a monoclonal antibody to the dentate gyrus. In: JM Kamenka and D.F. Domino, editors. Multiple Sigma and PCP receptor ligands: Mechanisms for neuromodulation and neuroprotection? Ann Arbor: NPP Books, 1991, pp. 879–894.
70 Knutson B, Burgdorf J, Panksepp J. Ultrasonic vocalizations as indices of affective states in rats. Psychol Bull 2002; **128;** 961–977.
71 Eibl-Eibesfeldt I. Ethology, the study of behavior. New York: Holt, Rinehart and Winston; 1975.
72 Tandon K, McGuffin P. The genetic basis of psychiatric illness in man. Eur J Neurosci 2002; **16**:403–407.

Is ADHD adaptive or non-adaptive behavior?

Zdenek Matejcek

Correspondence: Prof. Zdenek Matejcek, Ph.D.
Dept. of Social Psychiatry, Prague Psychiatric Center,
Ustavni 91, 181 03 Praha 8 – Bohnice, CZECH REPUBLIC.
PHONE: +420 266 003 261 FAX: +420 266 003 270
E-MAIL: MATEJCEK@PCP.LF3.CUNI.CZ

Submitted: *July 1, 2003*

Key words: **ADHD; evolutionary psychology; adaptive behavior; non-adaptive behavior**

Neuroendocrinol Lett 2003; ***24****(3/4):148–150 pii: NEL243403L01* *Copyright © Neuroendocrinology Letters* ***www.nel.edu***

Abstract The evolutionary approach to the issue of ADHD derives from the assumption that what is regarded as a pathological phenomenon today was once an adaptive response to the conditions of life in the ancestral stages of human development. The paper argues against this conception on the basis of the clinical picture of ADHD. The author believes that in the previous "natural" conditions the ADHD syndrome was even more of a maladaptation than in the "protective" conditions of present-day life.

The Evolutionary Approach to ADHD

On the pages of this journal (2002; 23 (Suppl.4): 39–45), Charles Crawford and Catherine Salmon have posed the question of whether some nosological units considered to be pathological today should not instead be viewed as the remains of man's purposeful adaptation to life conditions somewhere deep in our evolutionary history. As examples they give psychopathy, mental anorexia and the ADHD syndrome (attention deficit/hyperactivity disorder). For each of the three "disorders" they find an explanation in evolutionary theory. It is ADHD that I would like to comment on from the point of view of a clinical psychologist.

In the case of ADHD the authors hold that the evolutionary model may account for the discrepancies in findings traditionally cited in the literature far better than the symptomatic description given in DSM-IV, that the evolutionary model provides a testable hypothesis and that it elucidates the relationships between health and disease. Their idea is roughly as follows: ADHD is characterized by transient concentration, hyperactivity and impulsiveness. In the extreme conditions of prehistory, man's survival required hypervigilance, rapid-scanning, quickness to move, hyperactivity and response-readiness. This would have been an advantage "under the harsh conditions of the frozen steppe or humid jungle". In different environments however, with societies becoming more industrialized and organized, "problem-solving and analytic strategies, restraint of impulsivity, and the controlled deployment of energies" would more and more become the order of the day. Still the population continues to retain the genetic variation of these original traits, which is reflected in the development of this kind of behavior. Crawford and Salmon's conclusion is that what is adaptive in one type of environment may no longer be adaptive in another.

Symptomatic Diagnosis versus Etiological Diagnosis

Their explanation sounds plausible enough and the last sentence may no doubt be endorsed without reservation. Nonetheless I can't help feeling that there is something amiss. It will do no harm if we first make a short review of the story of ADHD. As a term, ADHD is a relatively recent coinage which replaced the previous MBD or minimal brain dysfunction. It has its advocates, but also many critics, myself included, who point out its disadvantages. To begin with, ADHD, as in fact any descriptive or symptomatic diagnosis, essentially says nothing more than what can be seen at first glance. The International Classification, in order to distinguish a normal condition from a pathological one, then must look for criteria that would express

that only a certain, especially marked type of behavior deserves this particular diagnostic label. It is necessary to section off one extreme (oddly enough not the other one) from some kind of continuum. But why section off anything at all in the first place if a certain behavioral trait represents a continuum distributed in the population according to the Gaussian curve? The point is that things are somewhat different! Clinical experience shows that the extreme described today as ADHD does exhibit certain signs of pathology.

I still believe that the term MBD was factual, pertinent and practical, although it of course could not entirely avoid the difficulties of delimiting (still normal) function and (no longer normal) dysfunction. There will always be fuzzy borderlines. However the term MBD was definitely much easier to use when presenting arguments in front of the lay public (i.e. even teachers). It made it possible to explain that we are dealing with a special (unusual, peculiar) function of the brain, for which neither school nor the parents or the child alone were responsible, and so there is no use blaming anyone, but instead we have to look for help together.

Over a time things have cleared up due to using (as I believe) the clinical finding, including psychological tests, as a starting point and due to taking account of etiology and not only external manifestations. In clinical practice all these cases of encephalopathy, dysfunction and ADHD obviously look different from what they appear to be at the taxonomist's table.

Non-adaptive ADHD

Under normal circumstances the "unknown" equals the "dangerous" for the child. The adaptive mechanism is anxiety which tells the child (from the eighth month of life onwards), "don't go there!", "keep close to your mom!", "watch out for the unfamiliar!" By contrast, children with ADHD are indifferent to dangers – they are difficult to watch over, they will rush toward anything "unknown" without hesitation and this kind of behavior goes way beyond the age limit of three years when in prehistory they presumably must have been largely independent so that the mothers could be free to look after new offspring. Anxiety as a behavioral corrective does not apply to these children – they simply expose themselves to dangers to an exceptionally large degree. Under natural conditions they would have been caught by a leopard, bitten by a snake, got lost in the jungle, drowned in a lake – and even should they have survived all this, their reproduction chances were certainly not very high.

In addition, the "impulsive" child with "transient concentration" coming under the diagnosis of ADHD is anything but hypervigilant. On the contrary, the child habitually "acts before he or she thinks", cannot distinguish a relevant stimulus from an irrelevant one, "has" to respond to everything that his senses "come up against", is "addicted" to stimuli and cannot switch them off, and so is "defenseless" against them. In other words, he or she is at increased risk in this respect. Surely enough, this is true of the harsh natural conditions of our ancestors more than of the civilized conditions of today.

Hyperactivity does not mean fast and precise advance or fast and organized retreat – it involves motor restlessness which is very difficult to keep under control. Such restlessness often deserves the attribute "tremorous". It certainly does not allow one to hide somewhere quietly, to stay silent and motionless, to wait patiently, etc. By contrast, such a child arouses and attracts the attention of his surroundings – as it no doubt would attract that of a predator. In his environment such a child acts as a disturbing element and exhausts those who are there to guard and protect him, even more those who are to teach him something. Hyperactivity does not increase motor efficiency, it serves to decrease it. True, a hyperactive child will climb everywhere, but he will also fall down from there.

The syndrome ADHD does not expressly include physical clumsiness today (which was still part of MBD), but in clinical practice it is of course in evidence. Actually everywhere we look we find difficulties: in motor coordination, in keeping balance, in right-left orientation etc. There are neuropsychological diagnostic schemes in use to measure this. For many of these children walking along a narrow path or throwing and catching something presents an insurmountable difficulty. They are far more prone to accidents and more frequently subject to medical care than other children. Moreover, they exhibit difficulties in articulation as much as in expression and communication – for these problems diagnostic schemes have also been developed. Physically inept individuals with communication problems would hardly have had better chances to succeed in reproduction competition with skilful, able and communicative people.

Finally, the syndrome MBD (and, to a perceptibly increased extent, the symptoms in ADHD children) included strikingly uneven distribution in the efficiency of individual mental components. It is as if, for instance, something has dropped out from the structure of the cognitive abilities, something has not matured, something has atrophied and, on the contrary, something has become overgrown (both in compensation and without it). There are children who cannot cope with verbal tasks, and there are children who are incapable of understanding any visual model. The idea of their finding their bearings in a varied space is absolutely out of question. This certainly does not sound like an adaptive evolutionary advantage. I would again regard it as the very opposite. What is far more likely to be of advantage in the frozen steppe, or a jungle, or today's big city, is a harmonious distribution of all functions and not such chaos in abilities and disabilities.

Clinical experience clearly supports the idea that we are dealing not only with an end section of a continuum, but with something "more", i.e. a certain pathology the cause of which may be looked for in a mild damage of the brain, in genetically conditioned peculiar functioning of the brain, in short somewhere in deep biological structures.

Adaptive ADHD

True, the world is full of "lively" and "highly active" children, inattentive children, or children precipitous in their reactions. We can come across them at every step. That is a different story, though. Anyone who has seen these children and ADHD children will never lump them together. The parents often say that their child cannot concentrate on "anything for a moment". But when we ask how long the child manages to play with something, how long he or she can manage to listen to a story or watch TV, we can see the difference at once. In one child it is a matter of seconds, in another it is half an hour, an hour or even longer. At school, even normal "highly active" children may be a problem, but we have different recommendations, different advice, different protective and supportive measures for them than for children with MBD or ADHD.

These basically healthy, agile and bright children may well be one of the "adaptive" genetic variations surviving from prehistory until today. Why not? But they are not children with ADHD (i.e. ADHD that deserves its place in DSM-IV), for although ADHD children are capable of survival and acceptable social integration in our contemporary refined and "handicap-friendly" environment, their chances in the prehistoric conditions would be rather slim. In sum, I think that we may turn Crawford and Salmon's argument around and say that ADHD is an acceptable adaptive behavior today, whereas in prehistory it was entirely non-adaptive.

Conclusion

Why have ADHD children not disappear altogether over the millennia? (In fact, their number appears to be increasing.) The answer is that although this type of behavior is due to genetic mechanisms, there are other mechanisms at play "over and above" the genetic factor. These other mechanisms, damaging or adversely affecting the function of the brain, are constantly with us. Actually they have been selectively dogging each new human generation from prehistory until today in much the same way, I think, as, for instance, cerebral palsy or congenital blindness and deafness. Also these affections are not just one extreme of the continuum of human agility or sharpness of hearing and vision, but involve something "more". In the Pleistocene period children with such a handicap would have, more often than today, simply not survived – and if they did, it was only thanks to exceptional protective and supportive care for its offspring which human society was so extraordinarily endowed with in its evolution. At present, however, in our contemporary cultural environment these children live a relatively acceptable life on the whole. Compared with children with severe motor or sensory handicaps, ADHD children's "extra" burden is relatively small – but it is not difficult to imagine that in the Pleistocene period even this small non-adaptive "extra" was for its bearers considerably greater burden than is the case today.

REFERENCES

Attention-Deficit/Hyperactivity Disorder. In: Diagnostic and Statistical Manual of Mental Disorders, 4th edition, DSM-IV-TR. Washington: American Psychiatric Association; 2000. pp. 85–98.

Crawford Ch, Salmon C. Psychopathology or Adaptation? Genetic and Evolutionary Perspectives on Individual Differences and Psychopathology. Neuroendocrinology Letters, 2002; **23**(suppl. 4): 39–45.

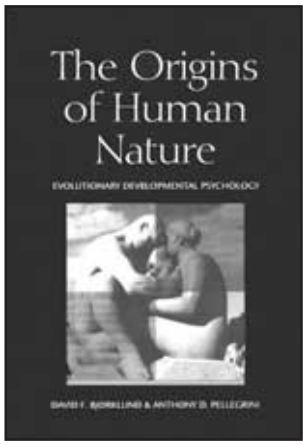
Kucera O, et al. Psychopathological manifestations of mild children's encephalopathy. (In Czech) Prague, SZN 1961.

Recommended Reading

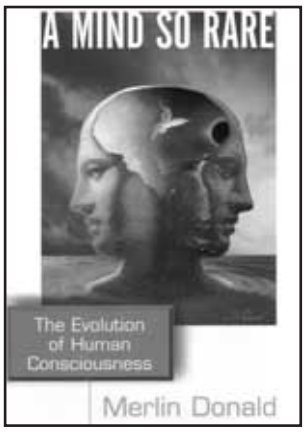
The contributions in the present issue cover several aspects of the study of human behavior from an evolutionary viewpoint. Since the scientific study of human behavior is a growing discipline, it is not possible to discuss the entire range of research directions. The following list of books suggests further readings from topics not discussed in this journal as well as publications for students at an introductory level.



That Complex Whole: Culture and the Evolution of Human Behavior
by *Lee Cronk*,
Westview Press.



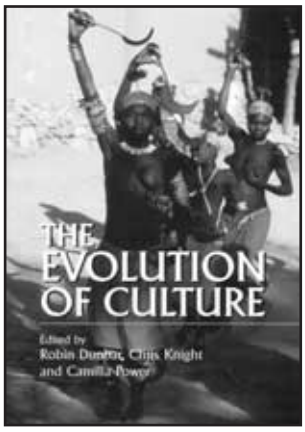
The Origins of Human Nature: Evolutionary Developmental Psychology
by David F. Bjorklund, Anthony D. Pellegrini,
American Psychological Association.



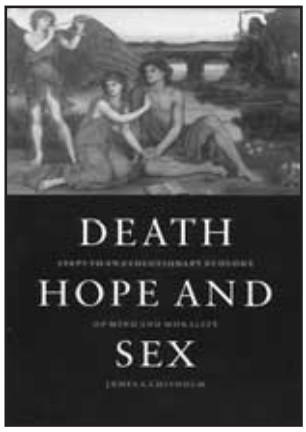
A Mind So Rare: The Evolution of Human Consciousness
by *Merlin Donald*,
W.W.Norton & Company.



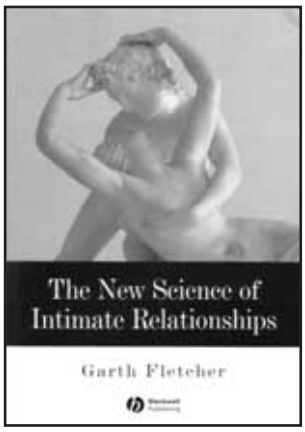
A Mind of Her Own: The Evolutionary Psychology of Women
by *Anne Campbell*,
Oxford University Press.



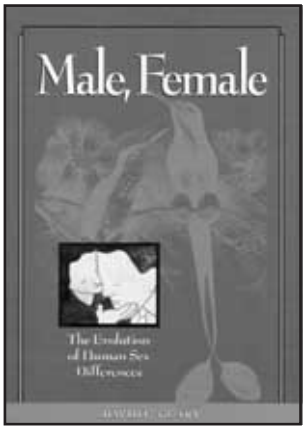
The Evolution of Culture: An Interdisciplinary View
by *R. I. M. Dunbar, Chris Knight, Camilla Power,*
Edinburgh University Press.



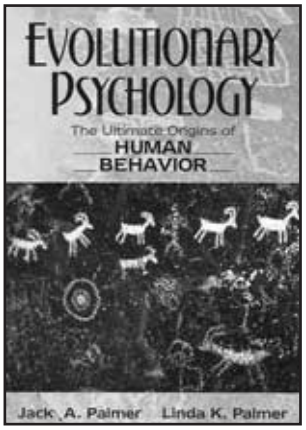
Death, Hope and Sex: Steps to an Evolutionary Ecology of Mind and Morality
by *James S. Chisholm*,
Cambridge University Press.



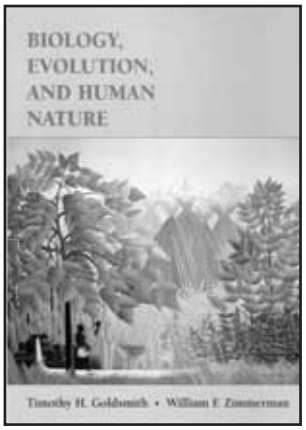
The New Science of Intimate Relationships
by *Garth Fletcher*,
Blackwell Publishing.



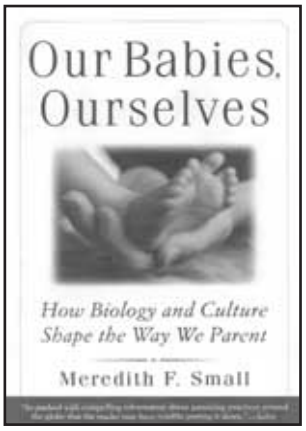
Male, Female: The Evolution of Human Sex Differences
by *David C. Geary*,
American Psychological Association.



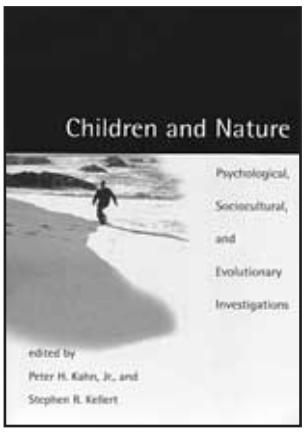
Evolutionary Psychology: The Ultimate Origins of Human Behavior
by *Jack A. Palmer, Linda K. Palmer,*
Allyn & Bacon.



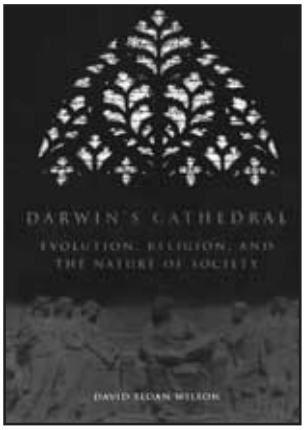
Biology, Evolution, and Human Nature
by *Timothy H. Goldsmith, William F. Zimmerman,*
John Wiley & Sons, Inc.



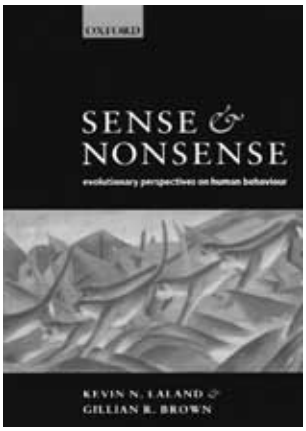
Our Babies, Ourselves: How Biology and Culture Shape the Way We Parent
by Meredith F. Small,
Anchor Books.



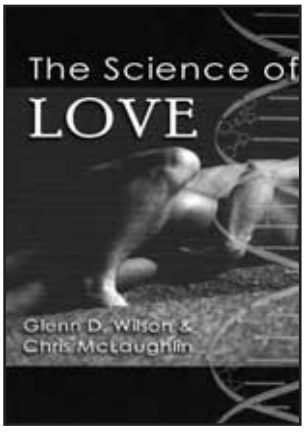
Children and Nature: Psychological, Sociocultural, and Evolutionary Investigations
by *Peter H. Kahn Jr., Stephen R. Kellert*,
MIT Press.



Darwin's Cathedral: Evolution, Religion, and the Nature of Society
by *David Sloan Wilson*,
Chicago University Press.



Sense and Nonsense: Evolutionary Perspectives on Human Behaviour
by *Kevin Laland, Gillian Brown,*
Oxford University Press.



The Science of Love
by *Glenn D. Wilson, Chris McLaughlin,*
Fusion Press.