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J. Decety Y. Christen (Eds.)

New Frontiers in Social Neuroscience

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Jean Decety • Yves Christen
Editors

New Frontiers in Social Neuroscience

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Editors
Jean Decety
Dept. of Psychology
The University of Chicago
Chicago Illinois, USA

Yves Christen
Fondation IPSEN pour la Recherche
Therapeutique
Boulogne Billancourt Cedex
France

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Foreword

The Scope of Social Neuroscience: From Cells to Societies

Traditionally, neuroscience has considered the nervous system as an isolated entity and largely ignored influences of the social environments in which humans and many animal species live. However, there is mounting evidence that the social environment affects behavior (and vice versa) across species, from microbes to humans. Vertebrate species display a remarkable range in social organization, from living relatively asocial and territorial lives, to being socially monogamous and living as bonded pairs, to being highly gregarious and living in large social groups. There is also considerable diversity in social behavior between individuals of a given species, which can be shaped by early social relationships, neuroendocrine state, and genetic factors.

Thus, we were social before we were humans, and as neuroscience matures, it becomes increasingly apparent that the nervous system cannot be considered as an isolated entity, without consideration of the social environments in which humans and many animal species live.

Social neuroscience, the interdisciplinary field devoted to the study of the neural, hormonal, cellular, and genetic mechanisms underlying the emergent organizations beyond the individual that characterize social species, is rapidly growing (Cacioppo and Decety 2011a). This multi-level interdisciplinary endeavor is not limited to humans, even if this is what many of us are ultimately interested in. According to work in evolutionary biology and genetics, we share a lot of genes with other animals, even with simple organisms such as the worm *Caenorhabditis elegans*. Based on the whole genome sequences that have become available for diverse species, we now know that a remarkably large number of protein-coding genes are shared across all animals. Simple animals such as nematodes, flies and bees have simpler behaviors, simpler nervous systems, and often (but not always) smaller genomes, than more complex animals. Yet simple animal models can greatly inform social behavior. Further, many of the social behaviors exhibited by simple animals (e.g., courtship, mating, aggression, parenting, foraging, learning and memory) are reminiscent of social behaviors in more complex animals (Sokolowski 2010). For example, after an inexperienced male watches two males fight, he alters his subsequent behavior accordingly, depending on whether he encounters the loser or winner (Yurkovic 2006).

Social processes influence neuro-hormonal events and neuro-hormonal processes influences social behavior. Examples of such reciprocal influences abound. In monkeys, testosterone levels promote sexual behavior in males, whereas the availability of sexually receptive females, in turn, influences testosterone levels (Bernstein et al. 1983). In a study conducted in Australia, a group of teenage male skateboarders performed two tricks – one that they could do easily, another that they often crashed on – ten times in front of a male experimenter and then repeated the process (Ronay and von Hippel 2010). A second group did the same, first in front of a male experimenter and then in front of an attractive 18-year-old female. When observed by this attractive female, the skateboarders in the second group aborted fewer of their difficult tricks. Saliva samples after the experiment indicated that the second group had higher testosterone levels than the first, suggesting that the young woman's proximity elevated the skateboarders' testosterone and that elevated testosterone may have sparked a drive to mate and demonstrate health and vigor through risk taking.

An interdisciplinary field of study that includes behavioral neuroscience, system neuroscience, behavioral ecology, and social psychology, and which seeks to understand how biological systems implement social behavior allows us to understand how the molecular and cellular mechanisms underpinning social interaction have evolved across species. In addition, non-human animal models allow investigation of neurobiological and cellular mechanisms in ways not available in humans, for obvious ethical reasons. Thus comparative research is extremely important and valuable, and there is much to be learned from sharing our knowledge and work across species and levels of analysis. For instance, homologues of oxytocin and vasopressin have existed for 700 million years and play a general role in the modulation of social behavior and reproduction. Their roles in facilitating species-typical social and reproductive behaviors are as evolutionarily conserved as their structure and expression, although the specific behaviors that they regulate are quite diverse (Donaldson and Young 2008).

Recognizing the continuity of evolution makes clear the futility of selecting any particular time period for the development of human social processing capacities like focusing on the so-called environment of evolutionary adaptedness, from 60,000 to 10,000 years ago, when supposedly humans became what they are today. This is what Marlene Zuk (2013) calls a paleofantasy. Additionally, humans are still evolving as a species. Numerous human genes have changed over just the last few thousand years – a blink of an eye, evolutionarily speaking – while others are the same as they have been for millions of years, relatively unchanged from the form we share with ancestors as distant as worms and yeast.

The 21st Fondation IPSEN *Colloque Médecine et Recherche* in the Neuroscience Series, held in Paris on April 22, 2013, focused on the current state of research of the social brain from a multi-level perspective with scholars from diverse disciplines including, evolutionary biology, anthropology, behavioral ecology, ethology, neurobiology, developmental science, social psychology and clinical and affective neuroscience. This one-day meeting was a wonderful illustration of the range of topics that benefit from this approach. The social brain was examined in multiple species from insects to humans; on multiple levels, from genetic expression to behavior; and from multiple functions such as parental care and empathy, rescue and helping behavior, morality, leadership, deception, racial biases, and social dominance.

Finally, it is important to note that bringing the laws that link different levels of analysis – the goal of social neuroscience – is not synonymous to reducing or eliminating higher levels of analysis (Cacioppo and Decety 2011b). The constructs developed by social scientists (e.g., behavioral economists or sociologists) are valuable in relation to those of biology, but can, and need to be, informed and refined through integration with theories and methods from social neuroscience. Social neuroscience research provides genetic and molecular insights that clearly translate to investigations of social behavior in other species. It is critical that those primarily interested in explaining human behavior begin to validate their hypotheses using animal models, including the study of the behavioral impact of pharmacological modulations and brain lesions that closely mimic some of the lesions found in humans. It is also important for those primarily using animal models to understand the psychological constructs used by scientists studying human mental and behavioral processes. This will allow the former to better develop appropriate behavioral paradigms. By bridging the gap between animal and human studies, social neuroscience contributes much to our understanding of the mechanisms by which the social world (and its disorders) impacts health, life span, and cognition. The translational bridge, however, needs to be built with careful consideration of species differences, based on evolutionary adaptations. While some of the principles may be conserved (i.e. importance of receptor maps and role of gonadal steroids), the details for social organization need to be explored for each species, recognizing the importance of diversity in the neural mechanisms for social cognition (Insel 2010).

Chicago, USA Jean Decety
Boulogne Billancourt Cedex, France Yves Christen

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Contents

Contributors

Peter A. Bos Department of Psychology, Utrecht University, Utrecht, The Netherlands

Department of Psychiatry, University of Cape Town, Cape Town, South Africa

Jakob Bro-Jørgensen Mammalian Behaviour & Evolution Group, Department of Evolution, Ecology & Behaviour, Institute of Integrative Biology, Faculty of Health and Life Sciences, University of Liverpool, Neston, UK

Beatrice de Gelder Faculty of Social Behavioural Sciences, Tilburg University, Tilburg, The Netherlands

Brain and Emotion Laboratory, Maastricht University, Maastricht, The Netherlands

Jean Decety Department of Psychology and Department of Psychiatry and Behavioral Neuroscience, The University of Chicago, Chicago, USA

Robin I.M. Dunbar Department of Experimental Psychology, University of Oxford, Oxford, UK

Craig F. Ferris Psychology Department, Center for Translational NeuroImaging, Northeastern University, Boston, USA

Ilanit Gordon Yale University, New Haven, USA

Leor M. Hackel Department of Psychology, New York University, New York, USA

J. Kiley Hamlin UBC Department of Psychology, University of Columbia, Vancouver, Canada

Ruud Hortensius Faculty of Social Behavioural Sciences, Tilburg University, Tilburg, The Netherlands

Sarah Blaffer Hrdy University of California, Davis, USA

Citrona Farms, Winters, USA

Stephen M. Rogers School of Biological Sciences, University of Sydney, Sydney, Australia

David Terburg Department of Psychology, Utrecht University, Utrecht, The Netherlands

Department of Psychiatry, University of Cape Town, Cape Town, South Africa

Jay J. Van Bavel Department of Psychology, New York University, New York, USA

Jack van Honk Department of Psychology, Utrecht University, Utrecht, The Netherlands

Department of Psychiatry, University of Cape Town, Cape Town, South Africa

Mark van Vugt Department of Social and Organizational Psychology, VU University Amsterdam, Amsterdam, The Netherlands

Institute for Cognitive and Evolutionary Anthropology, University of Oxford, Oxford, UK

Centre for the Study of Group Processes, University of Kent, Kent, UK

Y. Jenny Xiao Department of Psychology, New York University, New York, USA

What's So Social About the Social Brain?

R.I.M. Dunbar

Abstract In trying to understand the neurobiology of sociality, we face a problem over the kinds of behavioural indices we can use in experiments. The focus of most research has been on economic games or the socio-cognitive processes involved in dyadic interactions (e.g., theory of mind or prosocial/altruistic behaviour). These largely reflect causal interactions between strangers. However, the nature of primate (and hence human) sociality, as reflected in the social brain hypothesis, is more complex and involves long-term bonded relationships that allow individuals to maintain several social layers in their network simultaneously. Identifying suitable tests that can be used in either cognitive or neuroimaging experiments is challenging.

Introduction

The last decade has witnessed the dramatic growth of social (sometimes social cognitive) neuroscience. There has been considerable interest, for example, in microeconomic games (mainly various forms of public good games, such as the Prisoner's Dilemma, the Ultimatum Game and Trust Game, among others) in which individuals decide whether or not to act generously towards another individual. On the cognitive side, there has been a longstanding interest focussed on those aspects of cognition thought to underpin autistic spectrum disorders; this has led to the development of a consensus view that there is a mentalising (or theory of mind) network comprising units in the prefrontal cortex, the temporal cortex and the temporo-parietal junction.

The bulk of this research has, however, focussed mainly on dyadic interactions or on cognitive processes thought to be important in dyadic interactions. Economic

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R.I.M. Dunbar (✉)
Department of Experimental Psychology, University of Oxford, South Parks Road, OX1 3UD Oxford, UK
e-mail: robin.dunbar@psy.ox.ac.uk

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games are designed mainly to be played between two players, and most of the work on mentalising has focussed on conventional theory of mind (second order intentionality), which asks whether one individual can understand another's mental state. This research strategy has been perfectly sensible, not least because some aspects of our social behaviour do involve dyadic interactions of this kind. However, both approaches have significant limitations in that, in effect, they focus on the bricks and mortar of sociality and do not address the real complexity of sociality in primates. Their view of sociality is really the kind of dyad-based sociality that we find in many antelope and deer – species that form socially amorphous herds based on rather transient interactions between pairs of individuals. These kinds of social groups contrast radically with the structured groups that we find in primates, where triadic and polyadic relationships, and to some extent the group itself, become important.

The classic approaches are perfectly reasonable in the context of the research on which they are based. Economic games are premised on the assumption that all human relationships are essentially trading relationships: the second-hand car salesman's view of sociality. This view encourages us to be concerned about being cheated, or whether the person with whom we strike a deal is likely to renege on the agreement. Indeed, in many experimental contexts, the odds are deliberately stacked to make free riding an attractive strategy. In most cases, relationships are assumed to be of very short duration: I offer you a commodity or an investment bid, which you can accept or decline in the light of your broad assessment of the risks of being cheated, and after that we seldom meet again. Typically, these games focus on interactions between strangers and almost never concern themselves with other kinds of relationships (friendship, kinship) or with the central aims of sociality (namely, creating functional communities whose purpose is to enable us to solve the larger scale problems that threaten to undermine our ability to survive and reproduce successfully).

Similarly, the principal focus of theory of mind studies has been with the competences of 5- to 6-year-old children. For reasons that remain slightly puzzling, theory of mind (i.e., second order intentionality, as defined by the ability to solve standard false belief tasks) seems to have been taken as the quintessential social cognitive ability, even though adults are capable of handling much higher order intentionality tasks (Kinderman et al. 1998; Stiller and Dunbar 2007). Theory of mind is, of course, a major Rubicon that differentiates humans from all other animals (with the possible exception of great apes: O'Connell and Dunbar 2003; Cartmill and Byrne 2007). Theory of mind requires us to be able to imagine what another individual is thinking, and is, of course, critical in our dyadic interactions, not least because it is fundamental to our being able to hold a conversation with another individual (we speak telegraphically and in metaphors, and these require the listener to figure out what it is the speaker *means* to say). However, a significant proportion of our conversations involve several individuals simultaneously (the average size of conversation groups is around three individuals, often with a fourth person as the object of the conversation; Dunbar et al. 1995; Dezecache and Dunbar 2012), and many examples of culture (e.g., staged drama, novels) require the audience to handle the mind states of several characters at once (Stiller et al. 2004; Krems and Dunbar 2013).

I want to argue that, in effect, these conventional approaches to social neuroscience focus on the bricks and mortar of sociality, the raw components that go towards making the primate (and human) social world as complex as it is. What they do not address is the building that these bricks are used to construct and, to pursue the metaphor, the problem is that the bricks alone do not define the building. I will try to suggest what this complexity actually involves in the hopes that it will stimulate new approaches. I will begin, however, by briefly reviewing the social brain hypothesis and the evidence for it, and will then use this as a platform to explore the nature of primate sociality.

The Social Brain Hypothesis

As a concept, the social brain hypothesis has two distinct origins. The term was originally used in cognitive neuroscience (notably by Brothers 1990) to capture a sense that much of the brain's activity is really geared to steering a way through the complex social world in which we live. This sense was picked up in the comparative literature when it was explicitly used as an explanation for the unusually large brains of primates compared to all other vertebrates (including other mammals). Originally framed as the Machiavellian Intelligence Hypothesis, it argued that primates need large brains because they live in unusually complex societies (Byrne and Whiten 1988). Since there were some concerns about the implication that primates engaged in genuinely political strategies, the name was soon changed and Brothers' term was adopted instead (Dunbar 1992; Barton and Dunbar 1997). In some senses, this was an appropriate development because the Machiavellian Hypothesis seemed to imply that there was simply a qualitative difference between primates and all other species and no difference among the primates themselves. In fact, primates have brains that vary considerably, both in terms of absolute size and relative to body size, and this itself requires an explanation. The social brain hypothesis at least provides the basis for differences between species. It also provides a basis for differences between different mammalian families.

The core evidence adduced in support of the social brain hypothesis is the fact that there is a relationship between social group size in primates (including humans) and the volume of the neocortex (Dunbar 1992; Barton 1996), or better still the frontal lobes of the neocortex (Dunbar 2011; Fig. 1). Subsequent comparative analyses have confirmed and extended this finding in a number of important ways. First, Dunbar and Shultz (2007) undertook a path analysis that explored the intercorrelations between brain size and a number of anatomical and behavioural variables in primates and concluded that the main predictor of neocortex volume was social group size, with other ecological and anatomical variables being either constraints on brain growth or functional consequences of large brains. Second, Shultz and Dunbar (2010a) showed that, across the major mammal families,

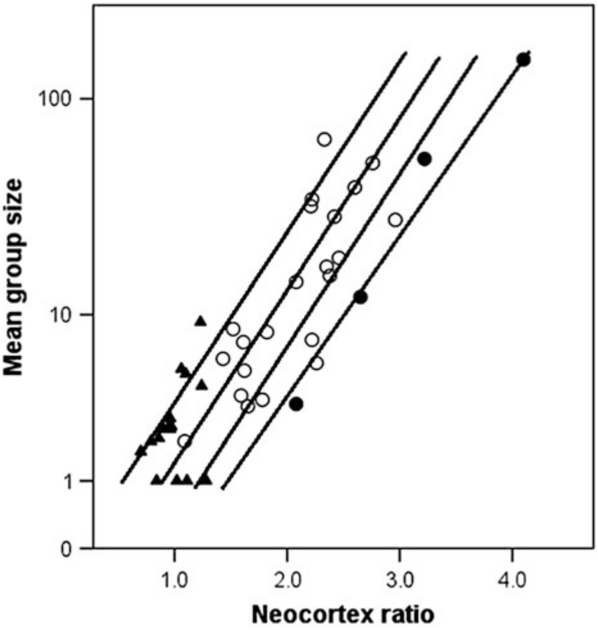

Fig. 1 Mean social group size for a species plotted against its neocortex ratio (volume of neocortex divided by the volume of the rest of the brain), showing four separate socio-cognitive grades (Redrawn from Dunbar 1992, 2011)

encephalisation across evolutionary time (i.e., the rate with which brain size has increased relative to body size across geological time) correlates with the frequency of bonded social systems among the living representatives of each family. Third, the latter relationship broadly reflects the fact that, outside primates, bonded social systems in mammals typically involve pair-bonded monogamy, such that the main driver of the social brain in non-primate mammals is in fact pair-bonding (Shultz and Dunbar 2007) and the cognitive demands of maintaining long lasting pair-bonds (Dunbar and Shultz 2010).

The equation relating neocortex volume and group size in great apes was originally used to predict group size for humans, and it gave a value of ~150 (Dunbar 1993). Evidence to support the claim that this is a 'natural' group size for humans came from quantitative data on both the size of communities in ethnographic societies and the size of personal (i.e., ego-centric) social networks. Subsequent analyses of these data revealed that human social networks are highly structured, such that the community of 150 in fact consists of a series of layers that are scaled with a regular scaling ratio of about three (Zhou et al. 2005). In other words, both ego-centric networks and social organisations consist of layers or groupings that contain, inclusively, about 5, 15, 50 and 150 individuals, with this pattern continuing on through at least two further layers (at 500 and 1,500).

Since these original data were published, a number of neuroimaging studies have confirmed and extended the relationship between social group size (indexed as personal social network size) and brain size at the level of the individual. In a series of analyses, Powell et al. (2010, 2012) demonstrated that, in individual adult humans, social network size (indexed as the 15-layer) correlated with both an individual's mentalising competences and the gross volume of their orbitofrontal cortex. Lewis et al. (2011) demonstrated that network size and mentalising competences also correlated parametrically with the volume of core frontal and temporal regions in the theory of mind network, with the ventromedial prefrontal cortex providing the focus for a uniquely strong three-way correlation. Subsequently, Kanai et al. (2011) found similar correlations between the number of friends listed on subjects' preferred social networking site and the volume of various frontal and temporal cortex regions. Perhaps more importantly, Sallet et al. (2012) demonstrated a similar set of relationships in macaques (with social network size indexed as housing group). In an earlier analysis of humans, Bickart et al. (2010) had used a somewhat idiosyncratic definition of social networks to test for (and confirm) a relationship between the number of friends included in personal networks and the size of the amygdala. Although the amygdala has not featured in either the comparative analyses or other neuroimaging studies, in fact such a relationship is quite plausible: social relationships involve the assessment of emotional cues, and the capacity to interpret these correctly must be important for coping with life in large social groups. More importantly, however, the amygdala does have a direct neural connection with the orbitofrontal cortex and is thus likely to play an ancillary relationship in the extended socialising neural network.

The Primate Social World

The social brain data suggest that large-brained species (and, indeed, individuals with larger prefrontal cortex elements) can manage more relationships simultaneously than smaller-brained species. This finding significantly raises the game in terms of the cognitive mechanisms involved. It is not just a matter of remembering who is who (although memory for faces is obviously an important requirement) but rather one of being able to place these individuals in a multidimensional social space such that an animal can access and manage triadic relationships (how my behaviour towards you will be interpreted by – and affect the behaviour of – a third party), as well as higher order polyadic relationships.

Passingham and Wise (2012) have argued that anthropoid primates have evolved entirely novel regions of the prefrontal cortex that allow them to undertake very fast, one-trial learning, in effect by being able to predict into the future on the basis of very limited information in the past. In contrast, other vertebrates (and this includes prosimian primates) rely on computationally more cumbersome trial-and-error association learning. This prefrontal cortex effect also involves increased capacity to inhibit prepotent responses (Shultz and Dunbar 2010b). The ability to inhibit prepotent responses is central to living in large social groups, both because it enables animals to defer short-term gains in the interests of larger long-term ones (crucial for group-level solutions to ecological problems) and also because it probably allows animals to hold back on punishment in circumstances where punishing defaulters might have negative consequences for the social stability of a group. Since punishment has been viewed as the archetypal social interaction both by economists and by those who have used economic games as an experimental index of sociality, the suggestion that there is a need to *withhold* punishment in the interests of not destabilising relationships potentially places something of a question mark over this whole approach.

I noted above that bonded relationships seem to be important in driving the evolution of large brains in mammals as a whole. We have some difficulty defining exactly what is involved in these kinds of relationships (Dunbar and Shultz 2010), in part because we have no real metric for quantifying them, even though most ethologists have no trouble recognising them in practice – and no more so than we do in everyday social life. This may reflect the fact that relationships have a major emotional content rather than being cognitive phenomena, and we have trouble translating experienced emotions into words. The key, however, is that such relationships are long lasting (they may last an entire lifetime), commonly involve a great deal of very intense social grooming (such that the amount of grooming animals do correlates with the size of the group: Lehmann et al. 2007) and often provide the basis for mutual defence against conspecifics (and occasionally even predators).

The bonded relationships that characterise primate sociality are created through what is, in effect, a two-step process. Monkeys and apes universally use social grooming as the principal means for expressing social relationships. Although grooming certainly serves to maintain the fur by removing debris and skin flakes (and undoubtedly had its evolutionary origins in hygiene), in reality most of these species groom each other for far longer than is minimally necessary to maintain clean fur. Grooming triggers the release of endorphins (specifically β-endorphins; Keverne et al. 1989; Depue and Morrone-Strupinsky 2005), and these seem to create an internal psychopharmacological platform off which a second (cognitive) mechanism creates the long-term, stable relationships of trust and obligation that provide the basis for coalitions and alliances. Although a great deal has been made of the role of oxytocin in creating social bonds in mammals (including humans), in reality its effects are short-lived and lead to rapid habituation (Dunbar 2010), and it may only have these effects in a limited range of contexts that apply broadly across mammals (e.g., limited term pair-bonds and transient interactions). It has been explicitly argued that, because the oxytocin mechanism is relatively weak, the evolution of bonded relationships in primates required a more robust pharmacological mechanism to support this new form of sociality and that this mechanism is the endorphin system (Broad et al. 2006; Machin and Dunbar 2011).

Some evidence that the complexity of relationships varies in a consistent way with neocortex size is provided by the original social brain data: the plot of group size against neocortex volume. These data turn out to consist of several (in fact, four) distinct grades, of which only the ape grade is obvious to the naked eye although the others can be shown statistically (Fig. 1). What this tells us is that the computational demands of sociality increase progressively across the grades, with ape sociality apparently being more cognitively demanding than that of any other simian and prosimian forms of sociality. In a nutshell, apes require a bigger computer to manage a group of a given size than the most social monkeys do, and these in turn require a bigger one that the less social monkeys, etc. We do not know exactly why ape sociality is so much more demanding than monkey sociality, but the fact is that it is. What we do know is that species that have larger neocortices have larger grooming cliques (Kudo and Dunbar 2001), are more likely to use coalitions in mutual defence (Dunbar and Shultz 2007), are more likely to use tactical deception (Byrne and Corp 2004) and are likely to exploit more sophisticated male mating strategies (Pawlowski et al. 1998).

More importantly, the structure of social groups varies systemically with brain size. Using grooming frequencies as an index of social relationships between individuals (a standard metric in primatology), Lehmann and Dunbar (2009) have shown that larger social groups become increasingly substructured in large-brained species of Old World monkeys (Fig. 2), which represents a rather complex relationship between group size, brain size, grooming time and network complexity. In effect, although animals in large groups spend more time engaged in social grooming, this is not because they groom with more individuals. In fact, as group size and grooming time increase, the number of animals groomed actually *decreases*: the additional grooming time becomes concentrated on *fewer* individuals, creating stronger bonds as a result since, as we have shown for humans, the time invested in a relationship directly affects its quality (Roberts and Dunbar 2011a, b). In species with relatively small brains, animals simply try to groom with every new group member, and ultimately this places a limit on the size of group that can be bonded together. In species with relatively big brains, however, individuals don't try to groom with everyone, but instead withdraw from casual interactions to focus more and more of their grooming on their core grooming partners as group size increases. In less intensely social species, this behaviour would result in a reduction in group size, but in these very social species it provides a mechanism that allows them to support ever bigger groups.

In effect, these species somehow manage to create a two-tier form of sociality: they can maintain a larger superficial structure (i.e., a larger group) by investing more heavily in an inner core of relationships *even though* they don't invest directly in the outer layer. In other words, they can manage two different kinds of relationships at the same time – what amount to weak and strong ties in the Granovetter (1973) sense. We know that primates can manage to distinguish, and keep separate, two different dimensions to a relationship (kinship versus rank; Bergman et al. 2003). Our network analyses suggest that they can manage two separate kinds of relationships as well.

All this perhaps makes more sense in light of the function of social groups. In primates, social groups are the principal defence against predators, as they are in many mammals. However, in herd-forming mammals, groups are relatively ephemeral, increasing or decreasing in size as a consequence of the moment-by-moment changes in predation risk and the costs of being in the group. These costs relate in part to stresses created by the proximity of other individuals (which have very

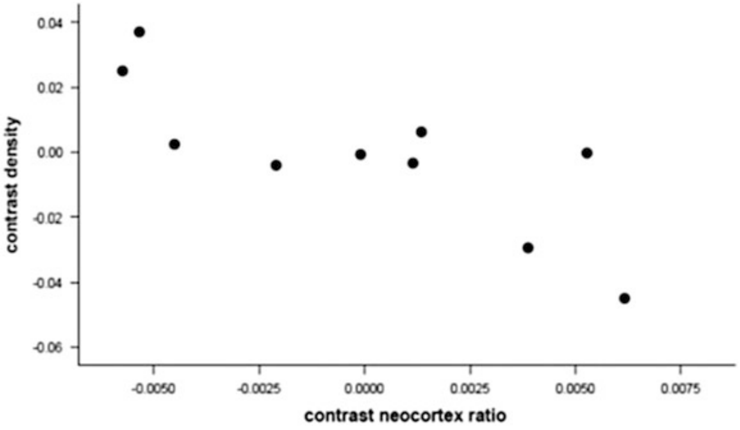

Fig. 2 Network density among females (indexed by dyadic grooming frequencies) as a function of relative neocortex volume for cercopithecine monkey species. Network density indexes the interconnectedness of group members and can be interpreted as showing increased clumpiness when low (Reproduced with the permission of the publishers, the Royal Society of London, from Lehmann and Dunbar (2009))

significant effects on female menstrual endocrinology, resulting in infertility: Abbott et al. 1986; Dunbar 1988) and in part to the fact that living in larger groups forces animals to forage for longer and travel further each day (Dunbar et al. 2009). Such groups lack stability and lack collective defence: animals do not go to each other's defence. Their value as defensive alliances is limited because the members can easily disperse when the stresses become too great: they have no intrinsic 'loyalty' to each other or to the group as an abstract entity (this last being a particular feature of human sociality).

Among the cercopithecine monkeys, there is, in effect, an intrinsic commitment to the group as a group. Females are philopatric (remain in their social group for life), which makes it difficult for an individual to leave or join simply because the costs of being in the group rise. In effect, the individual is locked into an implicit social contract which requires it to put up with short-term costs (the stresses noted above, and the need to resist taking short-term advantage of other group members) in order to benefit from the greater benefits (in terms of protection from predation) provided in the longer run by the group as a whole. This trade-off seems to require quite sophisticated cognitive abilities.

The Challenge

Finding suitable measures that reflect these more complex kinds of sociality is not going to be easy. What is clear, however, is that the kinds of tests that are in wide current use are not satisfactory; they reflect transient interactions between strangers rather than the kinds of long-term, bonded relationships that give primate (and hence human) sociality its peculiar feel. Part of the problem here is that relationships are emotional and it seems that the emotional component of relationships is something we don’t have good cognitive access to and hence have trouble describing in language. The fact that we cannot verbalise about or comment on the emotional component of relationships means that we don’t have a good metric for comparing relationships of different quality (either between species or, within species, between individuals) and this makes it difficult for us to study them (Dunbar and Shultz 2010). As a result, perhaps we tend to focus our attention on low-level cognitive processes or behavioural interactions that may not capture the real underlying nature of human (and primate) sociality. This poses a challenge to which we urgently need to find a solution.

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The Neurobiology of a Transformation from Asocial to Social Life During Swarm Formation in Desert Locusts

Stephen M. Rogers

Abstract Many species display complex social interactions and for such animals other members of their species can form a major or even dominant part of their environment. Social interactions between these animals can induce long-lasting changes in brain function and behaviour that in turn alter the ways in which they respond to each other. Locusts are insects that can change reversibly between an asocial solitarious phase and a social gregarious phase that is driven by changes in population density. Phase change encompasses both a socially driven mechanism and multifaceted changes in behaviour, physiology, neurochemistry, brain morphology and even appearance. At low densities, locusts occur in the solitarious phase. Their biology is governed by the need to be inconspicuous and they actively avoid other locusts, thus maintaining their low population density. When sheer population size and scarce resources force solitarious locusts together despite their aversion to each other, a transformation is triggered that results in the gregarious phase. The stimuli responsible for starting this transformation are provided by other locusts, notably mechanosensory stimulation resulting from inadvertent jostling of each other. After just a few hours these stimuli induce changes in behaviour, including, critically, a change toward a propensity to be attracted towards other locusts. This attraction initiates a positive feedback loop whereby the continual presence of other locusts provides the necessary stimuli to drive the process towards the extreme gregarious phenotype and eventually to swarming. The biology of gregarious locusts is then dominated by the demands of group living. There is intense competition for resources and considerably greater sensory complexity in the environment brought about by living in a constantly moving throng of other animals. These behavioural demands are reflected in the substantially larger brains of gregarious locusts compared with solitarious locusts. Phase differences can also be detected at the level of identified neurons and circuits and in dramatic changes in

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S.M. Rogers (✉)
School of Biological Sciences, University of Sydney, A08- Heydon Laurence Building,
Sydney NSW 2006, Australia
e-mail: stephen.rogers@sydney.edu.au

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neurochemistry, but only serotonin shows a substantial increase during the critical 1–4 h window during which gregarious behaviour is established. Blocking the action of serotonin or preventing its synthesis prevents behavioural gregarization. Applying serotonin or its agonists induces gregarious behaviour even in locusts that have never encountered other locusts. The analysis of phase change in locusts provides insights into a feedback circuit between the environment and the neurobiology of social interaction. Remarkably, there is emerging evidence that the neuronal mechanisms underlying this transformation in locusts show similarities with those underlying social behaviours in other animals.

Introduction

Locusts are grasshoppers (Insecta: Orthoptera: Acrididae) that are most well known for their propensity to undergo periodic mass swarming events, where billions of individuals covering up to hundreds of km^2 erupt from their desert retreats and consume all the available vegetation. Whilst various locust species remain a considerable agricultural problem in many parts of the world, it is perhaps not immediately clear what they have to offer as models for understanding the neurobiology of social interaction. Their usefulness comes from the realisation that swarming is not an inevitable part of the life history of locusts and that they can spend many generations in a form that not only does not swarm but actively avoids other locusts. The swarming and non-swarming forms of the locust are known as the gregarious and solitarious phases (Fig. 1), and the two phases differ so extensively in behaviour, physiology, colouration and morphology (Fig. 1) that until the 1920s they were thought to be different species (Uvarov 1921). All locust species, of which there are only approximately 20 out of $>$10,000 Acridid species, however, are able to transform reversibly from the completely asocial solitarious phase to the highly social gregarious phase, depending upon environmental cues.

Remarkably, there is strong evidence that the neuronal mechanisms underlying the transformation from solitarious to gregarious behaviour in locusts show pronounced similarities to those underlying social behaviours in other animals. We are just beginning to understand the molecular and neuronal mechanisms driving the early stages of this transformation (Rogers et al. 2004; Anstey et al. 2009; Ma et al. 2011; Guo et al. 2011; Wu et al. 2012; Ott et al. 2012). The sheer extent of behavioural change provides a rich substrate with which to perform comparative analyses of how neuronal circuits organise social behaviour. Such research is considerably facilitated by the detailed information already available about the structure and function of the nervous systems of locusts, down to the cellular physiology of individual neurons and circuits (Burrows 1996). The brain and nervous system of the asocial solitarious locust make the ideal control for comparison with the brain and nervous system of the social gregarious locust. Such a facultative switch, between asocial and social forms within the same animal,

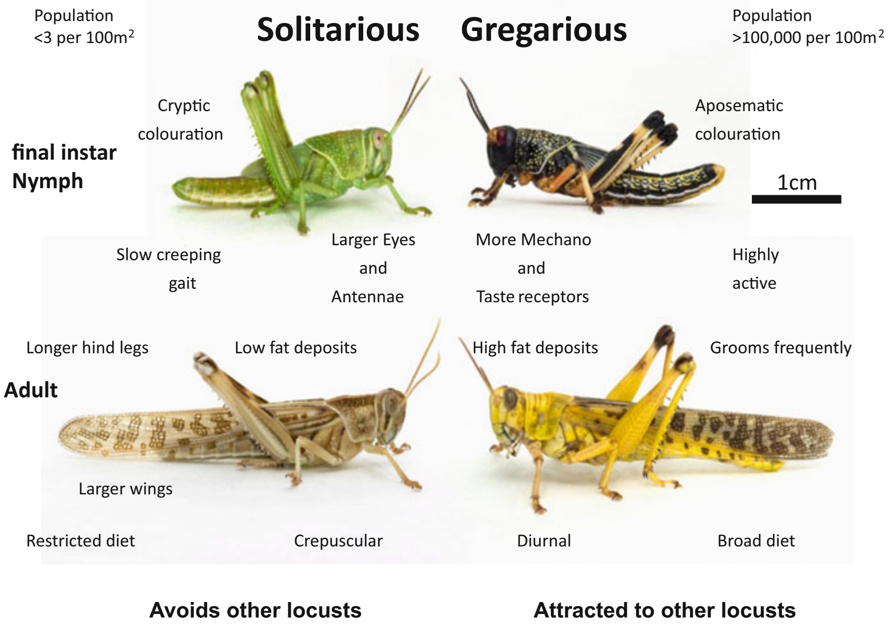

Fig. 1 Last larval instar (*top*) and adult (*bottom*) solitarious (*left*) and gregarious (*right*) phase desert locusts, *Schistocerca gregari a* showing their characteristic differences in appearance and posture. Some of the other key behavioural and physiological features of each phase are listed around the photographs

contrasts strongly with more familiar social insects such as bees and ants, where the degree of sociality is typically fixed for individuals within each species.

Locust Phase Change: Phenotypic Plasticity and Sociality

Locusts show some of the most dramatic examples of phenotypic plasticity, the environmentally driven expression of alternative phenotypes from the same genotype shown by any animal (West-Eberhard 2003). Phase change is driven entirely by changes in population density and is mediated by a socially driven mechanism (Uvarov 1966, 1977; Simpson et al. 1999). At low densities, locusts occur in the solitarious phase. Solitarious locusts are typical grasshoppers in that they rely on being inconspicuous to avoid predators; they are cryptic in both colouration and behaviour. They walk with a slow, creeping gait, fly predominantly at night, have narrow dietary preferences and actively avoid other locusts (unless seeking a mate), thus spreading themselves out thinly in the environment and maintaining their low population density. By contrast, gregarious desert locusts (*Schistocerca gregaria*) walk with a rapid, upright gait, fly during the day, have a broad diet and, most importantly, are attracted to other locusts such that they may eventually aggregate into vast migratory swarms. With inconspicuousness no longer an option, they have bright warning colours, which advertise that they eat small quantities of poisonous plants to make themselves distasteful to predators (Sword 1999). They also have shorter wings and hind legs and smaller eyes and antennae but more close-proximity touch and taste receptors.

Locusts are typically insects of arid environments that have infrequent and unpredictable rainfalls, leading to sparse vegetation growth only capable of supporting low population densities of locusts. Occasionally, perhaps once every decade, more sustained rains lead to brief periods of superabundant vegetation growth, leading to a concomitant rapid rise in the locust population. Sheer population size and increasingly patchy food resources brought about by consumption and the cessation of rain will act to force solitarious locusts together despite their natural aversion to one another (Collett et al. 1998). This forced contact triggers a far-reaching transformation that results in the gregarious phase. This process begins with a rapid change of behaviour, such that after just a few hours of forced crowding, previously solitarious locusts behave in many respects like locusts that have been in the gregarious phase their entire lives (Roessingh et al. 1993; Simpson et al. 1999). This change sets up conditions for a positive feedback loop in which the continual presence of other locusts provides the necessary stimuli to drive the process on to completion with further accumulating changes in behaviour, physiology and colouration. Some of these changes will occur within the life span of an individual; others develop over the course of several generations through epigenetic mechanisms (Uvarov 1966, 1977; Pener and Simpson 2009). Phase change is a fully reversible process that is the product of changes that occur with many different time scales (Roessingh and Simpson 1994; Simpson et al. 1999; Bouaichi et al. 1995; Gray et al. 2009).

The stimuli responsible for starting this transformation are provided entirely by other locusts and not any other indicator of environmental stress. In the Desert Locust, *Schistocerca gregaria*, there are two distinct sensory pathways through which the initial transformation in behaviour can be induced: first, mechanosensory stimulation specifically to the hind femora brought about by locusts jostling each other (Simpson et al. 2001; Rogers et al. 2003); and second, the combined sight and smell of other locusts with neither stimulus on its own being effective (Roessingh et al. 1998; Anstey et al. 2009). In the distantly related Australian Plague Locust (*Chortoicetes terminifera*), the change from solitarious to gregarious behaviour is induced by mechanosensory stimulation of the antennae, not the hind legs (Cullen et al. 2010). The stimuli responsible for inducing behavioural gregarization in the Migratory Locust (*Locusta migratoria*), another major pest species, are still not fully characterised. Other aspects of phase transformation, notably the longer term changes in colouration and morphology, appear to be mediated by separate, parallel pathways with independent induction mechanisms and hormonal control (Lester et al. 2005). For example, the neuropeptide [His^7]-Corazonin mediates the melanisation of gregarious locusts and some morphometric changes in body proportions but has little effect on behaviour (Tawfik et al. 1999; Hoste et al. 2002; Maeno and Tanaka 2004).

Social Behaviour of Gregarious Locusts

The modifications shown by gregarious locusts are not primarily concerned with adapting them for sustained long-distance travel to new feeding areas, because solitarious locusts can also fly for many hundreds of kilometres (Pener and Simpson 2009). Instead, it seems that the extensive adaptations shown by gregarious locusts occur to enable them to cope with the demands of living within a large group of conspecifics. To what extent, therefore, can gregarious locusts be considered social? Locusts display a different kind of social behaviour to that characterising eusocial insects such as bees, ants and termites; there is no reproductive or other division of labour between different individuals in the 'society.' All locusts in a swarm have the same behavioural phenotype, so their sociality arises from the need to engage with and respond to the large numbers of other locusts around them. In a swarm, other locusts form a substantial, even dominant part of the environment of each individual, and they constitute an ever-changing and potentially unpredictable element of it.

The most characteristic manifestation of social interaction displayed by locusts is the formation of coherent marching cohorts of wingless nymphs or flying swarms of adults, with the great majority of individuals moving in the same direction. These highly ordered migratory bands arise spontaneously when local population density exceeds a critical threshold (Buhl et al. 2006). From small nucleation events, hopper bands can expand and recruit all the locusts they encounter until they cover areas measuring kilometres across (Uvarov 1977). Even at their largest expanse, group structure is maintained entirely by local interactions and the implementation of simple behavioural rules of alignment and walking speed between near neighbours in the band (Buhl et al. 2006, 2011). In the Australian Plague Locust, *Chortoicetes terminifera*, the alignment between individuals that determines band cohesion and movement only operates if the distance between locusts is less than 13.5 cm (Buhl et al. 2011).

In addition to alignment and mass migration, there is a more general social dimension within a locust swarm that is generated by the intense competition for resources, particularly food, and necessitates interactions between individuals. At its most extreme, this manifests itself as a propensity to cannibalism, with vulnerable conspecifics being devoured to compensate for protein deprivation (Bazazi et al. 2008, 2011; Hansen et al. 2011). Whilst swarms provide safety in numbers by using a herd strategy to protect against predation, this protection is offset by the risk of falling victim to their own conspecifics. Nevertheless, living in a group, even with the risk of cannibalization, provides survival benefits. This benefit has been termed a 'lifeboat mechanism,' where individuals in the group are on average able to survive longer and travel farther compared to individuals attempting to migrate on their own (Hansen et al. 2011).

Adaptations in the Brain for Social Life in a Swarm

Gregarization requires the acquisition of new behaviours and negotiating new risks, such as the behavioural demands of generalist foraging and intense intraspecific competition. Furthermore, when locusts become gregarious, there is an inherently much greater sensory complexity in the environment brought about by living in the midst of a dense and highly mobile swarm of other animals. How is this reflected by the structure and function of the nervous system (Fig. 2)? The brains of gregarious locusts have very different proportions and are 30 % larger overall than in solitarious locusts (Ott and Rogers 2010). Phase-related differences in brain proportions arise from a combination of allometric growth of different brain regions relative to each other as overall size increases and discrete changes in specific brain regions (grade shifts). In the visual system, gregarious locusts have proportionately larger second (medulla) and third visual neuropiles (lobula) compared to the first (lamina). This expansion of the higher visual centres in gregarious locusts occurs despite the fact that they have smaller eyes than solitarious locusts (Dirsh 1953; Rogers et al. 2010). The increased size of these higher centres is possibly linked to the complex optic flow-fields and increased risk of collision inherent in a swarm (Matheson et al. 2004; see below).

In the olfactory system, gregarious locusts have fewer olfactory sensilla on the antenna than solitarious locusts (*Locusta migratoria*: Greenwood and Chapman 1984; *S. gregaria*: Ochieng' et al. 1998). The antennal lobe, where the olfactory receptor neurons first project, is 10 % smaller in gregarious locusts than in solitarious locusts of matching brain size. This contrasts with the massive expansion of the mushroom bodies, a higher olfactory and multi-modal integration centre, in gregarious locusts. The primary calyx in particular, which is composed mainly of axon terminals of projection neuron from the antennal lobes and intrinsic Kenyon cell dendrites, showed the most dramatic phase-related difference (50 % absolute) of all brain regions investigated. Overall it seems that, in the both the visual and olfactory systems as well as other important integration centres such as the central complex, the larger brains of gregarious locusts prioritize higher levels of integration. Solitarious locusts invest more in low-level sensory processing, having disproportionally larger primary visual and olfactory neuropiles. The reason for this difference may lie in the need to increase sensitivity, since the solitarious lifestyle entails greater activity at lower light levels, and the need to detect stimuli over greater distances, since they are subject to increased individual predation risk.

Phase-related differences in brain function can be shown to occur at the level of individual identified neurons and neuronal circuits, for example, in a circuit that signals the approach of an object on a collision course with the locust (Simmons and Rind 1992; Rind and Simmons 1992). The Descending Contralateral Movement

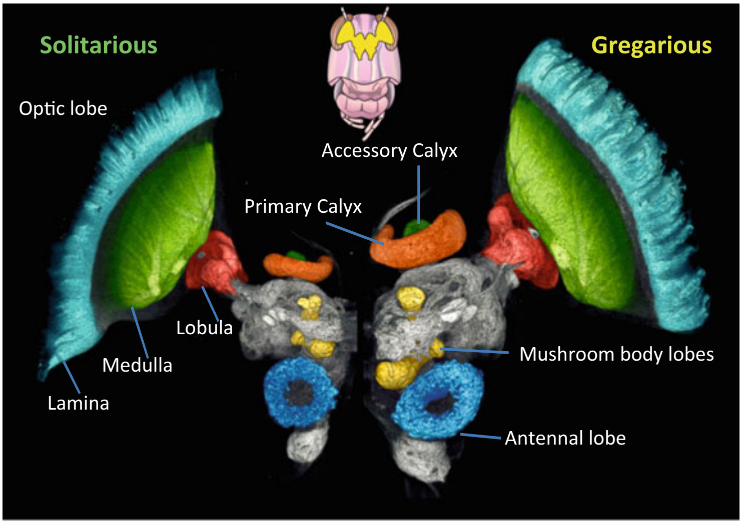

Fig. 2 Solitarious and gregarious locusts differ profoundly in overall brain size and relative development of different brain regions. A composite frontal view of the brain (shown *in situ* in the head in the inset locust head), solitarious on the *left* and gregarious on the *right*, was created from confocal microscope images of brains labelled with fluorescent antibodies against the synaptic protein synapsin. The locusts from which these images were taken had heads of the same size. Different neuropiles in the visual and olfactory processing pathways have been colour-coded (Data are from Ott and Rogers (2010))

Detector (DCMD) is a large intersegmental interneuron that originates in the brain and descends to the motor centres controlling locomotion in the thorax (Fig. 3a; Rowell 1971). It receives a monosynaptic input (1:1 gain) from a large-field visual interneuron, the Lobula Giant Motion Detector (LGMD). The receptive field organization of this neuron is broadly similar in both phases, spanning an entire visual hemisphere (Rogers et al. 2010), and it contains a large central region spanning 120 ° × 60 ° that produces equally strong responses to looming stimuli originating from anywhere within it. The LGMD/DCMD of gregarious locusts, however, generates more action potentials at a higher frequency than those of solitarious locusts when challenged by the same visual stimulus (Fig. 3b). Moreover, gregarious locusts have a small caudolateral focus of even greater responsiveness.

The response of DCMD in gregarious locusts habituates much less to repeated presentations of the same stimulus than in solitarious locusts (Fig. 3b; Matheson et al. 2004). This maintenance of a strong response to repeated stimuli is presumably an adaptation to enable gregarious locusts to avoid colliding with other locusts in a swarm. By contrast, solitarious locusts need to produce infrequent escape behaviours and then effectively disappear, relying on their camouflage and stillness.

The DCMD makes a monosynaptic connection onto an identified leg motor neuron, the fast extensor tibiae (FETi; Fig. 3c; Simmons 1980). The total synaptic

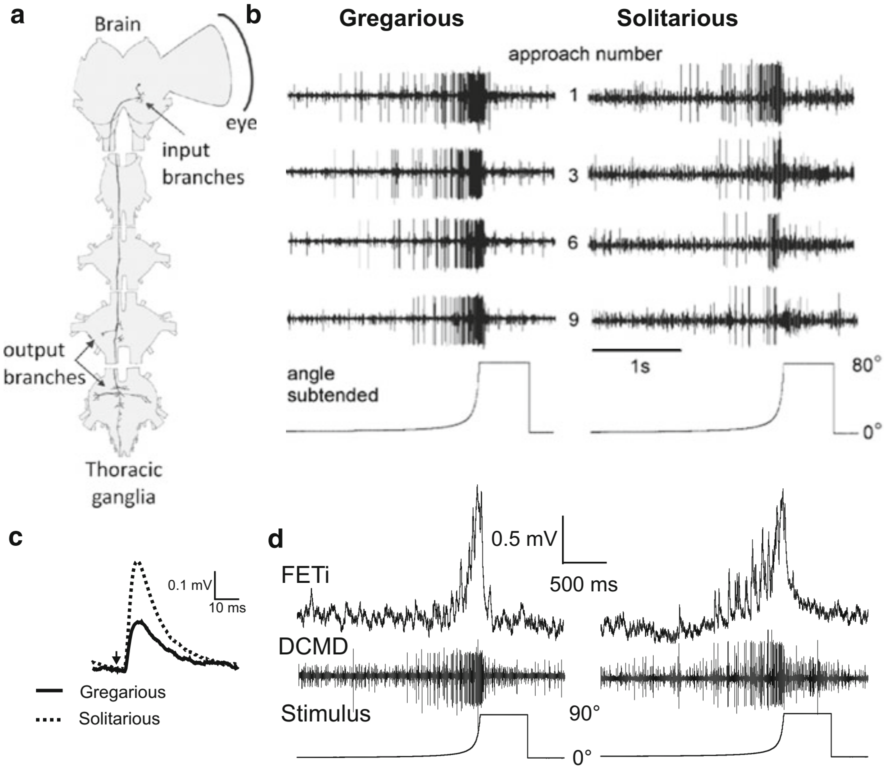

Fig. 3 The Descending Contralateral Motion Detector (DCMD) is a visual interneuron that detects objects on a collision course. (**a**) Anatomy of DCMD; it receives input from the optic lobe of the brain and descends down the nerve cord to the motor control centres located in the thoracic ganglia. (**b**) DCMD habituates to repeated presentations of the same stimulus, but the response in gregarious locusts remains robust. Extracellular recording from DCMD in a gregarious (*left*) and solitarious (*right*) locust repeatedly stimulated by the same looming stimulus (*bottom row* shows the angular expansion of the approaching object) at 1-min intervals. The number and frequency of spikes evoked in DCMD decrease markedly by even the third approach in the solitarious locust but remain strong in the gregarious locust even after nine repeated presentations. (**c**) EPSPs evoked by individual DCMD spikes in FETi are twice the amplitude in solitarious locusts (*dashed line*) compared to those in gregarious locusts (*solid line*) (Data from Matheson et al. (2004)). (**d**) Compound EPSP response in FETi (*upper trace*) evoked by activity in the DCMD (*middle trace*) following exposure to a looming stimulus (angular subtense to 90 °, *lower trace*); the total synaptic drive is similar in both phases, aided by the higher firing rates of DCMD in gregarious locusts and facilitation of the DCMD-FETi synapse, which emphasises the response to true looming stimuli (Data are from Rogers et al. (2007))

drive onto FETi produced by a looming stimulus has the same maximum amplitude in both phases, even though the DCMD spike pattern is stronger in gregarious locusts (Fig. 3d). The equalisation of the postsynaptic response arises in part because the individual excitatory postsynaptic potentials (EPSPs) in FETi evoked by each DCMD spike are only half the amplitude of those in solitarious locusts

(Fig. 3c; Rogers et al. 2007). A sequence of DCMD spikes produced by a looming stimulus produces much stronger facilitation of EPSPs in the FETi of gregarious locusts than in solitarious locusts (Fig. 3d), amplifying the strength of response to genuine looming stimuli over those produced by visual stimuli not on a direct collision course with the locust. This is especially important when dealing with the visually cluttered environment characteristic of a swarm. This nonlinear synaptic transformation of EPSP amplitude also tunes the DCMD-FETi synapse so that gregarious locusts respond earlier than solitarious locusts to small moving objects.

The Tritocerebral Commissure Giant neurons (TCGs) are a pair of neurons that convey signals from wind-sensitive hairs on the head to thoracic flight motor centres (Bacon and Tyrer 1978). A current of air to the head will cause locusts to initiate flight if their tarsi are not in contact with the ground. Gregarious locusts will do this at a lower threshold than solitarious locusts, despite having fewer sensory hairs on their heads (Fuchs et al. 2003). The increased sensitivity instead arises in part from the higher spike frequencies evoked in the sensory neurons by wind stimuli, which offset the lesser number of sensory receptors. There is, however, no difference in the signalling of the TCG neurons in the two phases preceding flight initiation, so that the actions of other interneurons must act to the lower behavioural threshold in gregarious locusts.

The Mechanism of Phase Change

Measuring Behaviour

If we are to understand the underlying mechanisms driving the rapid transformation from solitarious to gregarious behaviour, it is essential to quantify that behavioural change in a controlled setting. We have used a behavioural assay based on the performance of locusts in an arena (Roessingh et al. 1993; Simpson et al. 1999; Cullen et al. 2012). This arena consists of a rectangular space 41 cm long × 31 cm wide × 10 cm high with two clear perforated partitions at each end, behind each of which is a chamber 8 cm long × 31 cm wide × 10 cm high (Fig. 4). A 'stimulus group' of 30 long-term gregarious locusts is placed in one of these chambers so that a locust in the main arena can see and smell this group and is able to approach or avoid it (the other chamber is left empty). An experimental locust is introduced into the arena via a hole in the centre of its floor and detailed observations of its behaviour – both continuous measures of its location, velocity and trajectory as well as discrete events such as head, antennal movements and leg movements – are made for the next 500s.

Observations are made of the performance of 100 locusts that are known to be highly solitarious and of 100 locusts that are known to be highly gregarious to generate a data set of expected behaviour for each phase in this arena. From this basic data set we can develop a multidimensional model of solitarious and

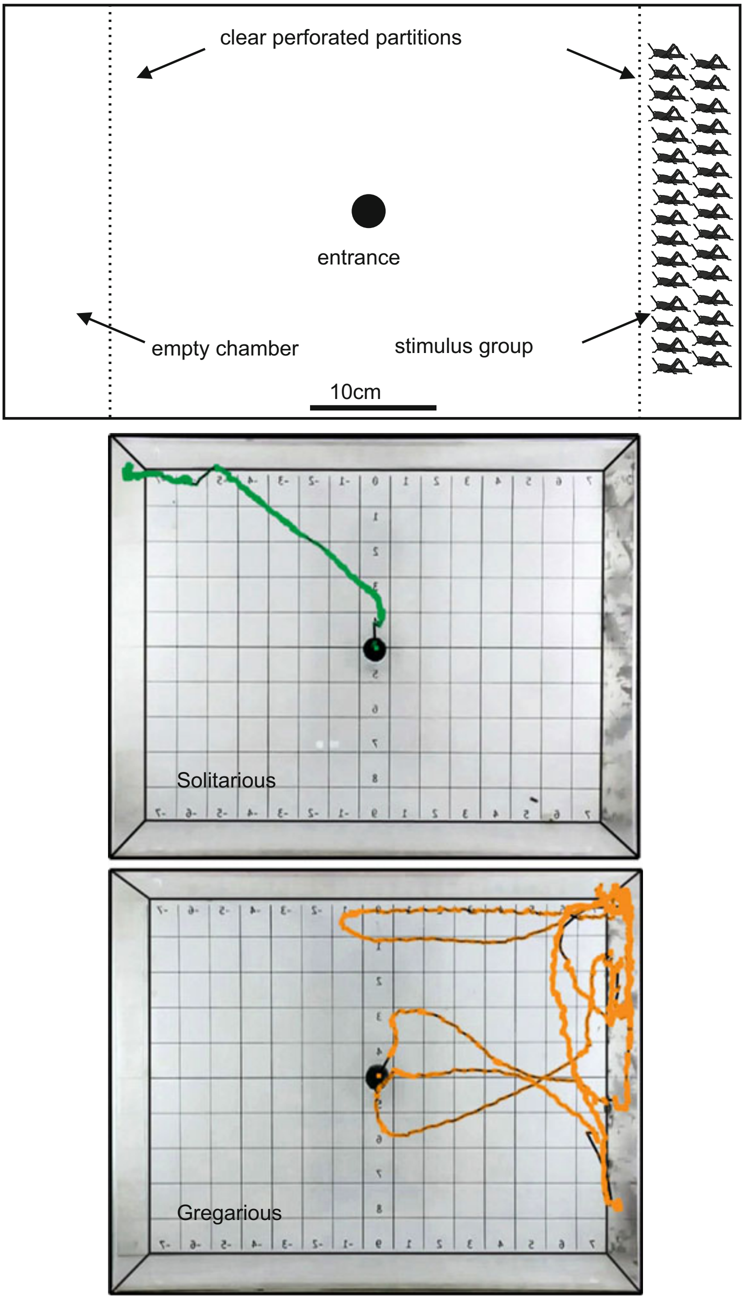

Fig. 4 The design of the behavioural arena (*top*) and representative trajectories of a solitarious (*middle*) and gregarious (*bottom*) locust over the course of a 500-s observation period

gregarious behaviour. We use binary logistic regression to analyse the data, since it is able to condense several discrete behavioural variables into a single metric, P_{greg}, which is the probability that a locust belongs to the gregarious model population on the basis of its performance. This model is typically able to correctly categorise >90 % of locusts as either solitarious or gregarious. A P_{greg} of 0 means that the locust's behaviour is indistinguishable from the solitariously reared model population, whereas a P_{greg} of 1 indicates fully gregarious behaviour. The statistical model can then be applied to locusts of unknown phase state to determine their P_{greg} on the basis of their behaviour when introduced into the arena. Transitional states between the two extremes can be quantified so that a direct link can be made between changes in the central nervous system (CNS) and behaviour, which, in turn, gives us a way to assess quantitatively the effects of pharmacological or other treatments on the propensity of locusts to gregarize or solitarize.

Gregarious and solitarious locusts differ in many aspects of behaviour; the arena only reveals some of these and the logistic regression model uses four different measures that span the gamut of these behavioural differences. Two of the behaviours are related to general activity, walking speed and proportion of time spent totally inactive. Gregarious locusts walk at approximately twice the speed of solitarious locusts and spend much less of their time motionless (60 %) compared to solitarious locusts, which are motionless for about 95 % of the time (Fig. 4; compare the path-lengths of the solitarious and gregarious locusts). Another key measurement in the model is the time spent adjacent to the stimulus group of locusts at one end of the arena. Solitarious locusts avoid this end of the arena and typically move to the opposite end, whereas two-thirds of gregarious locusts will spend at least some time in the arena in close proximity to the other locusts (approximately 20 % of the total time in the arena on average; compare the paths of the solitarious and gregarious locusts in Fig. 4). The final behaviour in the model is the frequency of grooming, with gregarious locusts much more likely to groom than solitarious locusts.

The final value of P_{greg} obtained after observation is derived from a weighted sum of all of these behaviours. Changes in any one of these behavioural variables are insufficient to cause a major change in P_{greg}; only a concerted change in all four of them will cause a pronounced shift towards either end of the solitarious-gregarious axis.

Changes in CNS Neurochemistry During Phase Change

Our own research has largely concentrated on the Desert Locust, *Schistocerca gregaria*. Our first attempt to understand the neurochemical mechanisms driving phase change was to perform a large-scale analysis of changing neurochemistry during the entire process, from solitarious to gregarious and back again (Rogers et al. 2004). The amounts of 13 different neurotransmitters and/or neuromodulators in different parts of the CNS were measured using high-performance liquid chromatography (HPLC). We measured these neurochemicals in both long-term solitarious and long-term gregarious locusts, as well as in locusts undergoing phase transition in both directions. Eight of these substances were more abundant in both the brain and the thoracic ganglia of long-term solitarious locusts than in long-term gregarious ones, and three were less abundant, with only two showing no significant difference (Fig. 5a). Isolating larval gregarious locusts led to rapid changes in seven neurochemicals within 24 h, equal to or in most cases exceeding the differences seen between long-term solitarious and gregarious locusts. Over subsequent generations of isolation, the long-term differences between phases fully established themselves. During the process of gregarization, crowding larval 3rd generation solitarious locusts led to rapid changes in six neurochemicals within the first 24 h, by which time gregarious behaviour was already being fully expressed and presenting many possible targets for further analysis. We also looked, however, at the critical 4 h window during which gregarization is first established. Here the result was clear: only serotonin (5-hydroxytryptamine, 5HT) showed a dramatic increase (Fig. 5b). This increase was confined to the thoracic ganglia and could be induced by either the mechanosensory or the sight + smell gregarizing pathway (Anstey et al. 2009). After crowding solitarious nymphs for the duration of the entire 5th larval instar, the amounts of all chemicals except octopamine were similar to those of long-term gregarious locusts. These measurements show that the expression of many neuroactive substances in the CNS changes and presumably underpins the behavioural and physiological changes that are the hallmarks of phase differences.

The Key Role of Serotonin in Initiating Gregarization

The rapid transient increase in serotonin which accompanied the initial acquisition of gregarious behaviour prompted us to examine its role more closely. In our first experiments, we determined how close a correspondence there was between serotonin titres and the extent of behavioural change (Anstey et al. 2009). We crowded solitarious locusts for 0, 1, or 2 h to generate the entire gamut of behaviour from solitarious to gregarious and measured the amount of serotonin in the thoracic ganglia of each locust; there was a significant positive correlation between the amount of serotonin and the degree of gregarious behaviour (Fig. 6a). Locusts that behaved the most gregariously ($P_{greg} > 0.8$) had approximately three times more serotonin than the most solitariously behaving locusts ($P_{greg} < 0.2$). Furthermore, the amount of serotonin corresponded solely to the degree of gregarization, not the duration of crowding *per se*. A similar relationship was seen in locusts gregarized through the mechanosensory and through the sight + smell pathway.

This strong correlation between the degree of gregarization and serotonin titre in the thoracic ganglia suggested a causal link. To demonstrate causality, we performed the following experiments. First, blocking the action of serotonin prevented behavioural gregarization. Locusts injected with a mixture of two

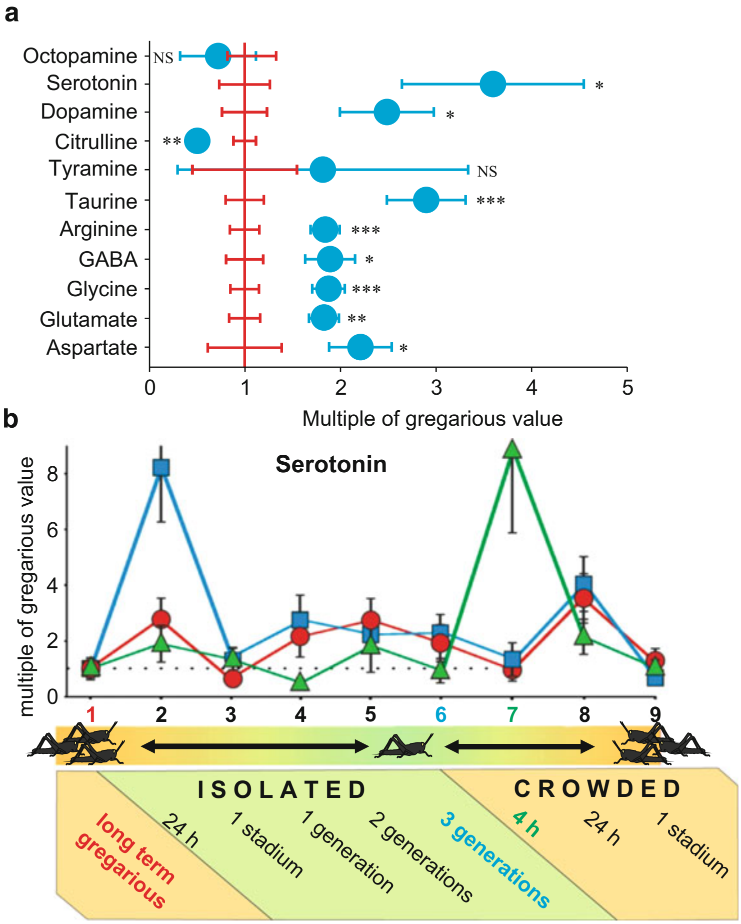

Fig. 5 Changes in brain chemistry accompanying phase change. (**a**) Differences in the amount of 11 neurochemicals in the CNS of adult long-term solitarious (*blue*) and gregarious (*red*) locusts. Amounts are expressed as multiples of the mean gregarious quantity, with error bars representing the SEM. Significances are indicated by *asterisks*: *$P<0.05$; **$P<0.01$; ***$P<0.001$. (**b**) The trajectory of change in the amount of serotonin (5-hydroxytryptamine, 5HT) in different parts of the CNS during the entire phase-change process, starting with the isolation of long-term gregarious on the left for increasing periods before the commencement of crowding of third-generation isolated locusts. Data are mean ± SEM; *green* are the thoracic ganglia; *red* is the central region of the brain and *blue* the optic lobes (Data are from Rogers et al. (2004))

serotonin receptor antagonists failed to gregarize in response to either mechanosensory or sight + smell stimuli, in contrast to saline-injected controls, which gregarized normally (Fig. 6b). Second, we interfered with serotonin synthesis by using α-methyltryptophan (AMTP), a competitive antagonist of tryptophan hydroxylase. AMTP-injected locusts failed to gregarize after having their hind femora stroked for 2 h, in strong contrast to control animals. Third, we showed

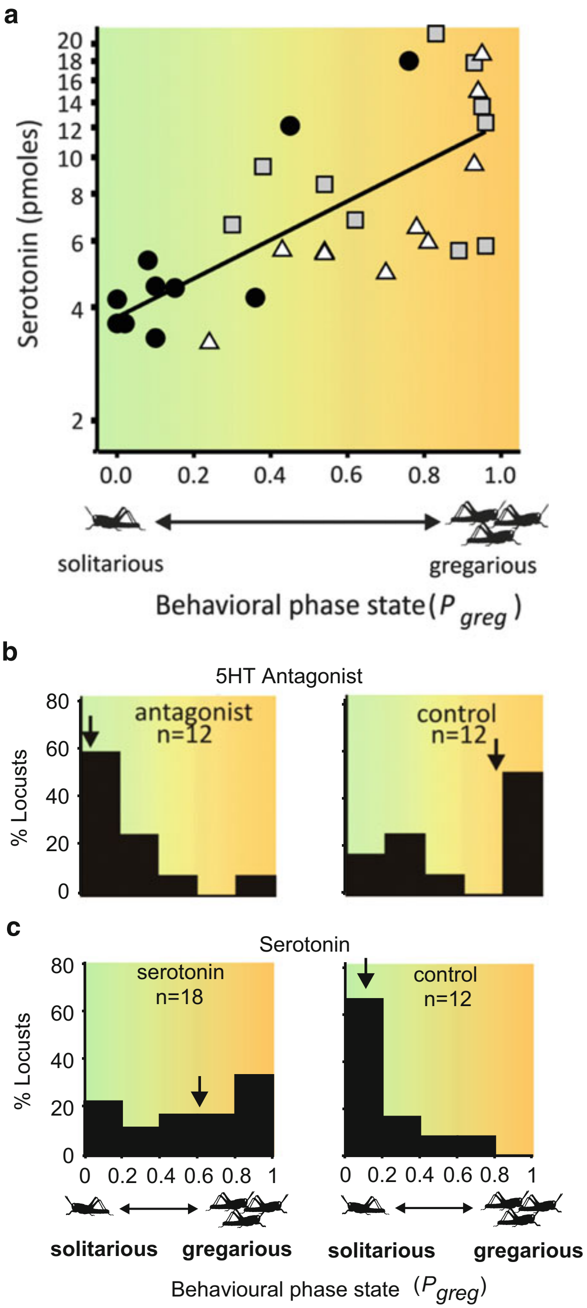

Fig. 6 The key role of serotonin in behavioural gregarization of *Schistocerca gregaria*. (**a**) There was a strong correlation between the extent to which locusts became gregarious after 0 h (*circles*), 1 h (*triangles*) or 2 h (*squares*) crowding and the amount of serotonin expressed in the thoracic CNS. (**b**) Blocking the action of serotonin through the use of 5HT receptor antagonists prevented locusts from becoming gregarious after 2 h of mechanosensory stimulation to a hind femur, whereas locusts treated with a saline control gregarized normally. (**c**) Topically applying serotonin directly to the thoracic ganglia induced a shift towards gregarious behaviour, even though the first time the experimental locusts had ever been exposed to another locust was when they were tested in the arena. Data are histograms of locusts falling into different ranges of P_{greg}, an aggregate measure of solitarious-gregarious behaviour (Data are from Anstey et al. (2009))

that serotonin or serotonin receptor agonists induced behavioural gregarization in the absence of stimuli associated with other locusts. Serotonin in saline or a saline control was topically applied to the exposed thoracic ganglia for 2 h. Serotonin-treated locusts behaved significantly more gregariously in the arena, even though they had never previously been exposed to other locusts; control-treated locusts remained highly solitarious (Fig. 6c). Fourth, locusts injected with a mixture of two serotonin receptor agonists, 1 mM α-methylserotonin and 1 mM 5-carboxamidotryptamine, showed a significant shift toward gregarious behaviour compared to saline-injected controls.

Behavioural Phase Change in the Migratory Locust, Locusta migratoria

The migratory locust represents perhaps an independent evolution of the full phase-change phenotype. The time course and mechanism of phase change show similarities and differences with that of *Schistocerca.* As in *Schistocerca*, the behavioural transitions from solitarious to gregarious and vice versa have different time courses, but in *Locusta* behavioural gregarization is slower than solitarization and is not fully achieved even after 64 h of crowding (Guo et al. 2011). Several olfaction-related genes are strongly regulated and display opposite expression trends in response to changes in population density during both gregarization and solitarization. These include several chemosensory protein (CSP) genes, which code for proteins that are secreted into the lymph of insect chemosensory organs where they are thought to assist in ligand binding (Jacquin-Joly et al. 2001; Ban et al. 2003), but they are also more widely expressed in insect tissue and may have a role in development (Kitabayashi et al. 1998). The other gene of interest is a Takeout (TO) gene, which is also expressed in insect chemosensory organs and has a role in modulating taste sensitivity according to nutritional status (Meunier et al. 2007) and in a circadian manner (Sarov-Blat et al. 2000). The CSP gene LmigCSP3 and the TO gene LmigTO1 in locusts are implicated in the behavioural change between avoidance of and attraction to conspecifics by regulating peripheral odour sensitivity (Guo et al. 2011).

A second and contemporaneous report by the same group (Ma et al. 2011) identified *pale*, *henna* and *vat1*, genes involved in dopamine biosynthesis, synaptic release and cuticular melanisation, as critical targets related to behavioural phase changes. Moreover, injection of dopamine or a dopamine agonist initiated gregarious behaviour as well as serotonin agonists, suggesting that the mechanism mediating the initial shift to gregarious behaviour in *Locusta,* whilst showing some parallels with that to *Schistocerca,* has some differences in the signalling pathway.

Monoamines and Their Role in Social Behaviour

The demonstration that serotonin and dopamine play key roles in the initiation of gregarious behaviour in locusts is consistent with the important roles these monoamine neurotransmitters play in regulating social interaction throughout the animal kingdom. Serotonin, for example, modulates the propensity to engage in intraspecific aggression and establish social status in dominance hierarchies (Miczek et al. 2007; de Boer et al. 2009; Kravitz 2000; Dierick and Greenspan 2006; Yeh et al. 1996; Neumeister et al. 2010). Animals subjected to socially mediated stress often manifest long-term changes in the amount of serotonin in the CNS together with profound changes in perception, cognitive function and behaviour (Fuchs and Flügge 2003), and in humans these are associated with affective disorders such as anxiety and depression (Ansorge et al. 2007).

Dopamine is involved in mediating the brain's response to rewarding situations in both vertebrates and invertebrates (Dayan and Balleine 2002; Perry and Barron 2013) and mediates animals' susceptibility or resilience to social stress (Krishnan et al. 2007; Chaudhury et al. 2013). Dopamine signalling facilitates pair-bond formation in mammals (Young and Wang 2004; Young et al. 2011). In eusocial insects such as bees, alterations in dopamine titre are associated with reproductive dominance (Harris and Woodring 1995; Sasaki et al. 2009) and the changing tasks that workers perform (Schulz and Robinson 1999; Wagener-Hulme et al. 1999; McQuillan et al. 2012).

The Extension and Maintenance of Gregarious Behaviour

Serotonin is essential for the initiation of gregarious behaviour in *Schistocerca gregaria*, but it cannot be responsible for the consolidation and maintenance of the gregarious phase. The initial increase in serotonin that drives gregarization decays to baseline levels within 24 h. Furthermore, locusts that have spent their entire lives in the gregarious phase have half the amount of serotonin in their CNS compared with long-term solitarious locusts. Gregarious behaviour, which leads to the constant presence of reinforcing stimuli from other locusts, maintains the gregarious phenotype but, with time, gregarious behaviour becomes more robust and is retained even after periods of isolation from other locusts. Newly gregarious locusts that have been crowded for just 24 h lose their gregarious behaviour after only 4 h of isolation (Roessingh and Simpson 1994), but locusts that have been gregarious for many generations only start to become behaviourally solitarious after days of isolation. How, then, is the transient spike in serotonin translated into a longer-lasting modification of behaviour and ultimately more extensive phenotypic change?

We investigated the role of two protein kinases in the consolidation of gregarious behaviour (Ott et al. 2012): the *foraging* gene product, a cGMP-dependent protein kinase (PKG) implicated in switching between alternative group-related behaviours in several animal species; and cAMP-dependent protein kinase (PKA), an effector protein with a pre-eminent role in different forms of learning. Injecting the PKA inhibitor KT5720 prior to crowding prevented locusts from becoming gregarious, whereas injecting KT5823, an inhibitor of PKG, did not. Neither drug altered the behaviour of long-term gregarious locusts. RNA interference (RNAi) against *foraging* strongly reduced its expression in the CNS but this did not prevent gregarization upon crowding. By contrast, solitarious locusts with an RNAi-induced reduction in the PKA catalytic subunit C1 expression behaved less gregariously after crowding. Furthermore, RNAi against the PKA regulatory R1 subunit, which inhibits catalytic activity by PKA, promoted more extensive gregarization following a brief period of crowding. These results suggest that PKA, acting in concert with serotonin, which has a highly evolutionarily conserved role in mediating neuronal plasticity under many conditions and in many species (Kandel 2001), has been co-opted into effecting the wide-ranging transformation from solitarious to gregarious behaviour.

In addition to causing rapid but short-term changes in neuronal function through phosphorylation of existing proteins, the PKA effector pathway mediates changes in gene expression (Müller and Carew 1998). Several recent studies have highlighted the extensive differences in gene expression between the solitarious and gregarious phases of both *Schistocerca gregaria* (Badisco et al. 2011a) and *Locusta migratoria* (Kang et al. 2004; Ma et al. 2006; Guo et al. 2011). In a recent study, using microarrays developed from an Expressed Sequence Tag (EST) database of *Schistocerca gregaria* central nervous tissue, 214 differentially expressed genes were detected between long-term solitarious and gregarious locusts, of which only 40 % have a putatively known function (Badisco et al. 2011b). These included genes encoding proteins that are associated with CNS development and modelling, sensory perception, stress response and resistance, and fundamental cellular processes. Genes for heat shock proteins and proteins which confer protection from infection were up-regulated in gregarious locusts, which may allow them to respond to acute physiological challenges. By contrast, the longer-lived solitarious locusts appeared to be more strongly protected from the slowly accumulating effects of ageing by an up-regulation of genes related to anti-oxidant systems, detoxification and anabolic renewal. Gregarious locusts also had a greater abundance of transcripts for proteins involved in sensory processing and in nervous system development and plasticity. An earlier study in *Locusta* identified 532 differentially expressed genes between phases (Kang et al. 2004). These studies probably only provide a flavour of the true scale of differential gene expression that accompanies phase change, and progress continues to be hampered by the lack of a full genome sequence for any species of locust.

Clearly much remains to be done before we have a full conceptual understanding of how social environment, neural circuitry and gene expression interact to produce the profound behavioural transformations associated with phase change in locusts. These analyses hold the promise of providing us with general and profound insights into the interplay between the environment and mechanisms of phenotypic plasticity and, in particular, the neurobiology of social interaction.

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Social Neuroscience and the Study of Animal Communication

Jakob Bro-Jørgensen

> *Nothing in Biology makes sense except in the light of evolution*
> *(Dobzhansky 1973)*

Abstract Research into both the mechanistic and evolutionary basis for animal communication systems is likely to benefit from adopting the interdisciplinary perspective of social neuroscience. Here I primarily concentrate on the enigma surrounding the evolution of multiple signalling systems in animal communication to illustrate the advantages of combining studies of cognitive mechanisms with behavioural ecological approaches.

Introduction

Tinbergen had the insight that questions relating to animal behaviour can basically be divided in two: proximate questions, asking *how* a given behaviour is caused mechanistically, and ultimate questions, asking *why* the behaviour has evolved to function as it does (Tinbergen 1963). Traditionally, neuroscience has played an important part in answering the first type of questions, typically by studying neural pathways within isolated animals in an experimental set-up. The second type of questions has fallen within the realm of behavioural ecology. Whereas Tinbergen's division has been useful in bringing clarity of thought, the proximate and ultimate

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J. Bro-Jørgensen (✉)
Mammalian Behaviour & Evolution Group, Department of Evolution, Ecology & Behaviour,
Institute of Integrative Biology, Faculty of Health and Life Sciences, University of Liverpool,
Leahurst Campus, Neston CH64 7TE, UK
e-mail: bro@liv.ac.uk

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questions are often interlinked, and this is why the integrative approach of social neuroscience may often provide a deeper understanding of animal behaviour by bridging the gap between disciplines. The social neuroscience approach is particularly relevant when it comes to animal communication, which is social by definition. On one hand, if we want to understand the proximate question of *how* the brain processes information from signals, recent studies underscore the benefit of considering the evolutionary function of a signal within its social context (Hasson et al. 2012). For example, to understand patterns in brain activity during speech communication in humans, it has proven useful to adopt a multi-brain framework where brain-to-brain coupling between signaller and receiver is analyzed in relation to whether or not words are socially meaningful (Stephens et al. 2010). On the other hand, understanding *why* a given signalling system has been shaped in a particular way by evolution may often not be possible simply by considering the evolutionary interests of the parties involved without taking into account how the underlying neural processes operate and their inherent constraints (Bro-Jørgensen 2010). In this chapter, I will demonstrate this by focusing mainly on the long-standing puzzle of why animals often use more than one signal to convey a message ('multiple signalling;' Candolin 2003). A particularly interesting scenario is manipulative signalling, where signals have evolved to exploit the way stimuli are processed by the receiver's nervous system. Such sensory exploitation raises interesting questions about the underlying exploitable cognitive mechanisms. However, the deceptive function of signals can only be understood by studying animals in their social context, which I will illustrate by presenting a case study on topi antelopes, *Damaliscus lunatus*.

Multiple Signalling: Social Adaptation Under Neural Constraints

Multiple signals are defined as composite signals that comprise two or more components, each with signal properties (Candolin 2003). They are widespread in the animal kingdom. For example, when the peacock *Pavo cristatus* signals to mates, he uses his train, a morphological trait, but also a 'hoot-dash' display in which he rushes towards the female while giving a characteristic 'hoot' call and lowering the train (Petrie et al. 1991). When signal components are in distinct modalities, as in this example, the multiple signal is referred to as a multimodal signal. Why animals so often use multiple signals to convey a message is intriguing. To the neurophysiologist, it raises questions about neural integration of the stimuli involved, whereas to behavioural ecologist, multiple signals call for an evolutionary explanation: we know that producing and receiving signals are typically associated with costs, and using several costly signals rather than a single one therefore appears maladaptive at first glance. Again, these mechanistic and evolutionary questions are closely linked, and the most fruitful approach will often be to address both at the same time. I will now outline the main evolutionary hypotheses proposed to account for multiple signalling and show how the adaptive value of a multiple signal often only emerges if we consider the constraints on signal production and signal reception, both of which typically rely heavily on neural information processing. Each hypothesis thus makes more or less distinct predictions as to how stimuli are integrated in the receiver's nervous system, where the relationship between signal components can be either one of independence, equivalence, dominance, enhancement, modulation or emergence (Partan and Marler 1999). The way in which stimuli are integrated leads to expectations regarding the cognitive level at which stimulus integration occurs, which in turn have interesting implications for our understanding of the cognitive flexibility of the receiver (Ghazanfar and Schroeder 2006).

Firstly, the multiple messages hypothesis posits that each single signal encodes a distinct aspect of a message (Dawkins and Guilford 1991). For example, in African eland antelopes, *Tragelaphus oryx*, males use a suite of signals to communicate their competitive ability to conspecifics, and several of the signals provide independent information about distinct aspects of fighting ability (Bro-Jørgensen and Dabelsteen 2008). Thus age is indicated by the size of the dewlap which grows through life, the darkness of the male facemask probably conveys information on testosterone levels, and body size is broadcasted by a peculiar loud knee-clicking sound. The multiple messages hypothesis leads to the prediction that the relation between stimuli during primary sensory processing is basically one of independence and that integration only occurs at higher cognitive levels in order to decide the response of the receiver (Partan and Marler 2005). It was indeed widely assumed until more recently that, in mammals, crossmodal stimulus integration was limited to the higher-level processing in the association cortex, the brain area which generates a meaningful representation of the world and allows abstract thought (Ghazanfar and Schroeder 2006). This assumption is now known to be wrong (see below), but still the well-established multisensory responses of higher-order association areas, such as the superior temporal sulcus, the intraparietal sulcus and the frontal lobe (Ghazanfar and Schroeder 2006), agree well with the rather complex evaluation of information postulated by the multiple messages hypothesis.

According to the emergent message hypothesis, single signal components are not informative by themselves and it is only from their combination that the message emerges (Partan and Marler 2005). This can be illustrated by considering the trills of song-birds, which can be analyzed as a multi-component signal. When a male songbird produces a trill, the physiologically demanding feat signals his quality (Podos et al. 2004). However, males experience a trade-off between the rate of the trill and its frequency bandwidth, and limited information is therefore provided by either of these cues on its own. Interestingly, when receivers of both sexes evaluate trills, they take this into account by integrating both trill rate and band width in their assessment of the vocal performance (Ballentine et al. 2004; Illes et al. 2006). In this case, the relationship between stimuli during sensory processing is characterized by emergence. Because the decoding of emergent messages is cognitively demanding for receivers and likely to involve complex stimulus integration, this hypothesis is possibly most applicable to higher vertebrates, such as birds and mammals.

Yet another possibility is that multiple signals are backup signals that all basically encode the same redundant information: the backup signal hypothesis (Hebets and Papaj 2005). The function of the multiple signal in this case is assumed to be overcoming errors that occur during the production of the signal, during transmission of the signal through the environment, or during decoding of the signal in the receiver. Backup signals can also be found in organisms with relatively simple nervous systems. The famous 8-shaped waggle dance of honeybees, *Apis mellifera,* may serve as an example. The dance is used to communicate the location of flowers with nectar to conspecifics; the distance to the flower is conveyed by the duration of the traverse waggle run, whereas the direction is indicated by its angle (von Frisch 1967). However, the angle of each waggle run is associated with a significant degree of error, and receivers have been shown to average the angle indicated by multiple runs (Tanner and Visscher 2008). So each run can essentially be seen as a backup signal, providing mainly redundant information but still improving the overall estimate of the flower's location. In the case of backup signals, the nervous system of the receiver is basically assumed to process single signals as equivalent.

The receiver psychology hypothesis also suggests that signal components are essentially redundant, but here the selective advantage comes from the fact that multiple signals enhance the accuracy and speed of receivers in discrimination and learning tasks (Rowe 1999). For example, cows, *Bos taurus,* will approach both a two-dimensional cow model and a loudspeaker playing back a cow call, but the response to both stimuli combined is more than additive (Soffie and Zayan 1977). We also know that the combination of visual and auditory components accelerates the speed at which the nervous system of domestic fowl learns to discriminate against unpalatable food items (Rowe 2002). In this case, the neural analogue is facilitation, and such relatively simple stimulus integration is more likely to occur during early sensory processing. Increasing evidence indeed shows that sensory convergence between modalities often occurs in the primary sensory cortices. For example, when rhesus macaques, *Macaca mulatta,* listen to vocalizations from conspecifics, neurons in the auditory cortex respond to the combination of auditory and visual components by enhancement as long as the stimuli are separated by less than 0.2 s (Ghazanfar et al. 2005). Such relatively simple neural circuits can select for the use of multiple redundant stimuli by the signaller.

By contrast, a novel suggestion, which is rather more cognitively demanding on the receiver, is that the multiple signals may have evolved due to fluctuating receiver interests in dynamic environments: the dynamic selection hypothesis (Bro-Jørgensen 2010). The idea here is that receivers benefit from evaluating different signals under different social or ecological conditions. For instance, in the monogamous lark bunting, *Calamospiza melanocorys*, a range of signals reflects the quality of males as providers; however, the reliability of each signal depends on the environment, with some signals being superior in benign years and others in harsh years (Chaine and Lyon 2008). Interestingly, females are able to evaluate the multiple signals accordingly, paying more attention to the most informative signals under the given conditions. The adaptive flexibility of receivers in their decoding of signals is thought to maintain the multiple signalling system by inducing fluctuating selection.

Finally, an intriguing idea is that signallers using multiple signals may not serve to convey a message as reliably as possible, but rather to manipulate receivers: the sensory exploitation hypothesis (Hebets and Papaj 2005). Hence signallers may conceal information by exploiting the fact that exposure to multiple stimuli sometimes leads to inhibition rather than enhancement at the neural level in the receiver. In the macaque example, neurons in the auditory cortex in fact respond with suppression rather than by enhancement if multimodal stimuli are separated by more than 0.2 s (Ghazanfar et al. 2005). The potential for multiple signals to cause neuronal suppression was also illustrated by a study on cats, *Felis catus*, in which neurons in the superior colliculus responded differently to the combined presentation of auditory and visual stimuli: some neurons responded by enhancement, others were depressed, and yet others were unaffected (Stein et al. 1995). In line with these findings, there are several examples that interference between multimodal stimuli can hamper information transfer. In male noctuid moths, *Spodoptera littoralis*, exposure to female pheromones inhibits the response of the tympanic nerve to echolocation signals from bats, thereby increasing predation risk (Skals et al. 2005). We still do not have empirical examples where multiple signallers actually benefit from manipulating receivers by causing sensory overload, but to illustrate that signallers may indeed benefit from manipulating receivers by exploiting cognitive constraints, I will close this chapter by presenting a case study of deceptive signalling in African topi antelopes.

Case Study: Social Exploitation of Sensory Constraints – How Male Topi Antelopes Use False Alarms to Secure Matings

In evolutionarily stable signalling systems, both the sender and receiver usually benefit from the information transfer: if a signal is manipulative, the receiver is usually expected to stop responding because of the costs incurred, and the signaller would then no longer benefit from producing the signal. However, this logic does not take into account constraints on neural processing in the receiver. The sensory system of the receiver functions in multiple contexts, and manipulative signals that exploit mechanisms primarily selected to fulfil other functions can therefore be evolutionarily stable, as long as the receiver benefits from reacting in other contexts outweigh the costs incurred by responding to the manipulative signal. Empirical examples of deception have nevertheless remained rare, but the African topi antelopes provide an example where males use tactical signal falsification to deceive sexual partners (Bro-Jørgensen and Pangle 2010).

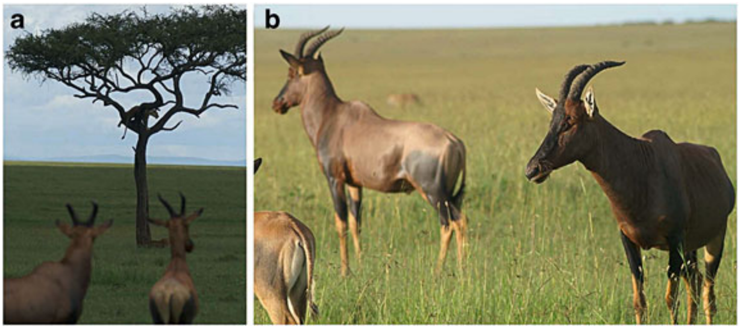

Fig. 1 True and false alarm snorts in topi antelopes. (**a**) A male and a female topi alarm snort upon detecting a lioness, *Panthera leo*. (**b**) A territorial topi male (*at the back*) makes a false alarm snort at his territorial boundary, causing the female (*in front*) to stop and scan for predators

The signal being exploited in this case is the antipredator alarm snort, which the topi usually produces when spotting a stalking predator (Fig. 1a). The topi points its ears and stares directly at the predator at the same time because, by keeping the predator in sight, the topi can prevent it from coming close enough to launch a successful attack. The primary function of the true alarms in topi is probably not to warn conspecifics because solitary topi also alarm snort (Bro-Jørgensen and Pangle 2010); it is rather to signal detection to the predators in order to deter further pursuit.

So what is the function of the false alarm snorts? They are indistinguishable from the true alarms to the human ear, and there is no detectable difference in their acoustic structure (Bro-Jørgensen and Pangle 2010); the only difference is that predators are absent (Fig. 1b). Could the false alarms simply be errors? Contradicting this explanation is the fact that, unlike true alarms which are emitted by both males and females, the false alarms are only ever emitted by territorial males, and only when other topi are around (Bro-Jørgensen and Pangle 2010).

We therefore proposed the 'sensory trap hypothesis,' according to which territorial males exploit the inability of females to discriminate between true and false snorts to make receptive females believe that they are headed towards danger if they leave the male's territory.

Our first line of evidence for this hypothesis came from the fact that territorial males make false snorts practically only when their territory is visited by a female in oestrus and especially around times when she attempts to escape the territory (Bro-Jørgensen and Pangle 2010). Typically, when an oestrous female who is visiting a male territory approaches the territorial boundary, the territory owner moves in front of her and looks in the direction she is heading. He then snorts with his ears pointed forwards and his gaze fixed into the distance, exactly as if a predator had been detected where she intends to go.

To find out how females perceive the false snorts and whether they react in a way that delays their departure from the male's territory, we performed a playback experiment. We found that females indeed responded far more strongly to both true and false alarms than to a control sound, and we did not find any difference in responses to the two alarms (Bro-Jørgensen and Pangle 2010). This finding suggests that females cannot discriminate between true and false alarms. When no predator is detected after a snort, the female will often move away from the alleged location of danger, presumably as a precaution, and this walk-away response brings her back towards the centre of the male's territory under natural conditions, thereby giving the male further mating opportunities at the same time as preventing other males from mating.

In summary, the topi males apparently exploit cognitive constraints that make females unable to distinguish between true and false alarms; females are faced with the option of always responding or always ignoring alarms, whether true or false. The high cost of death can then explain why females keep responding and the sensory trap works.

Concluding Remarks

Because signals only become meaningful in a social context, animal communication presents an exciting new frontier in social neuroscience, a field with the potential to bridge the gap between more conventional neurobiological and behavioural ecological approaches. On one hand, students of the neural basis for communication systems are often likely to benefit from viewing their study organism in a social context and considering the possible signal functions from an evolutionary perspective. On the other, a deeper appreciation of the principles governing how stimuli from social signals are processed at the neural level is likely to advance our understanding of the evolutionary diversity in animal communication systems. Thus often signal evolution can often only be understood as the outcome of social selection if we explicitly also consider the constraints imposed by the function of the nervous system.

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The Group Mind: The Pervasive Influence of Social Identity on Cognition

Jay J. Van Bavel, Leor M. Hackel, and Y. Jenny Xiao

Abstract Humans evolved in social groups and are adapted for group living. In this chapter, we review recent behavioral, physiological, and neuroscience research that provides the psychological and neural architecture for collectively shared representations of the world – the "group mind." We describe how collective identities structure a wide range of human cognitive processes, from rapid evaluation and face memory to mental state attribution and representations of physical distance. This research underscores how psychological and neural processes underlying human cognition are context-dependent, dynamic, and flexibly shaped by motivational states, rather than inevitable, reflexive, and fixed.

The Group Mind

> Man is by nature a social animal; an individual who is unsocial naturally and not accidentally is either beneath our notice or more than human. Society is something that precedes the individual. – Aristotle, *Politics*

The concept of a "group mind" is often used by biologists to describe the collective behavior of hyper-social organisms or by philosophers and sociologists to describe a sense of collective consciousness among humans. A precursor of the concept is found in the entomologist William Morton Wheeler's observation that seemingly independent individuals can cooperate so closely as to become indistinguishable from a single organism (1911). Although the concept of a unified "group mind" has largely been discarded by psychologists and cognitive scientists, there is good reason to believe that group-level concerns have shaped and continue to shape various aspects of human cognition (Brewer 2004; Caporael 1997; Correll and Park 2005; Wilson and Sober 1994). Indeed, decades of research suggest that people

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J.J. Van Bavel (✉) • L.M. Hackel • Y.J. Xiao
Department of Psychology, New York University, New York, NY, USA
e-mail: jay.vanbavel@nyu.edu

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form groups quickly and flexibly and favor in-group members even under rather arbitrary premises, all of which points to the value humans place on social identity and the context-dependent process of identification (Tajfel et al. 1971).

Self-categorization theory explains the emergence of group-level psychological processes in terms of the functioning of the self-concept (Turner et al. 1994). Self-categorization involves the activation of psychological connections between the self and some class of stimuli at the personal (i.e., defining oneself as unique from others) or the collective (i.e., defining oneself in terms of similar characteristics to one's social group) level (Turner et al. 1987). Further, self-categorization is "inherently variable, fluid, and context dependent" (Turner et al. 1994). According to this perspective, reality is always perceived and interpreted through the lens of one's current and socially defined self, which makes all cognition necessarily social (Turner et al. 1994).

Our research capitalizes on the fact that social context can activate different social identities and different aspects of any given social identity to examine the effects of group-level identification on cognition. In this chapter, we review recent behavioral, physiological, and neuroscience research that provides a biological and psychological basis for collectively shared representations of the world – the "group mind." We describe how social identities structure a wide range of human cognitive processes, from rapid evaluation and face memory to mental state attribution and representations of physical distance. Finally, we highlight how psychological and neural processes underlying person perception are context-dependent, dynamic, and shaped by self-representation, rather than inevitable, reflexive, and fixed (Packer and Van Bavel in press; Van Bavel and Cunningham 2011).

To examine the impact of self-categorization on ostensibly automatic components of the person perception network, we took a multi-level approach, variably termed social neuroscience, social cognitive neuroscience, or the social brain sciences (Adolphs 1999; Cacioppo et al. 2000; Ochsner and Lieberman 2001). This approach is based on the assumption that complex social phenomena are best understood by combining social and biological theories and methods (Cunningham and Van Bavel 2009; Van Bavel and Cunningham 2009b). Ultimately, understanding social perception and evaluation across multiple levels of analysis offers the promise of generating more general, process-oriented theories of self and social categorization, developing a functional understanding of the biological systems that underlie social perception and evaluation, and designing interventions for social issues like prejudice and discrimination.

Social Identity and Cognition

Over the past few decades, dual process and continuum models have emerged as the dominant paradigm for understanding human cognition, especially social cognition. In general, these models characterize the unconscious and conscious mind as discrete processes or systems: System 1 is reflexive, automatic, fast, affective, and associative, and System 2 is deliberative, controlled, slow, cognitive, and propositional (e.g., Chaiken and Trope 1999; Kahneman 2003). In the context of social cognition, dual process models assume that people initially perceive targets in terms of their membership in a social category (e.g., age, gender, race), relying on stereotypes about the category to inform their evaluations and judgments. However, people with the motivation and opportunity to suppress their initial, biased impulses can individuate people to avoid applying stereotypes (Brewer 1988; e.g., Devine 1989; Fazio et al. 1995; Fiske and Neuberg 1990; Greenwald and Banaji 1995).

Although these models have motivated considerable research, advances in neuroscience suggest that the human evaluative system is more widely distributed and dynamic than initially assumed by many dual process models (see Cunningham et al. 2007; Freeman and Ambady 2011; Van Bavel et al. 2012b). Instead of construing automatic and controlled processes as dichotomous or independent stages of the perceptual and evaluative processing stream, we argue that dynamic aspects of self-categorization – such as identifying with an arbitrary group – can shape ostensibly automatic aspects of cognition (Van Bavel and Cunningham 2011). Different social identities change how people rapidly and reflexively construe and evaluate stimuli in their environment. When a specific self-categorization becomes salient, one may in turn be more likely to categorize others as friends or foes on the basis of this activated identity. Thus, cognitive and neural processes reflect a combination of bottom-up visual cues (e.g., skin color) and top-down social motives (e.g., group affiliation; see Fig. 1).

Minimal Group Identities Override Racial Biases

To examine the top-down influence of social identity on cognition, we have studied the effect of seemingly trivial social identities on ostensibly automatic racial biases stemming from years of exposure to racial stereotypes (see Van Bavel et al. in press, for a recent review). Specifically, we have conducted several experiments in which we assigned participants to one of two mixed-race arbitary groups (e.g., the Lions or Tigers teams) with an equal number of Black and White males in each group. Participants in these experiments were then given a few minutes to memorize the group membership of these faces before we assessed their attitudes (Van Bavel and Cunningham 2009a), attention (Brosch and Van Bavel 2012), memory (Van Bavel and Cunningham 2012; Van Bavel et al. 2012a), and/or brain activity (Van Bavel et al. 2008, 2011). Assigning people to mixed-race groups allowed us to examine whether arbitrary group membership can override seemingly automatic racial biases in memory and evaluation (Brewer 1988; Devine 1989; Ito and Urland 2005; Taylor et al. 1978).

In a pair of initial experiments, we examined the influence of a shared social identity on ostensibly automatic evaluations (Van Bavel and Cunningham 2009a) and amygdala activity (Van Bavel et al. 2008). To study evaluation, we presented

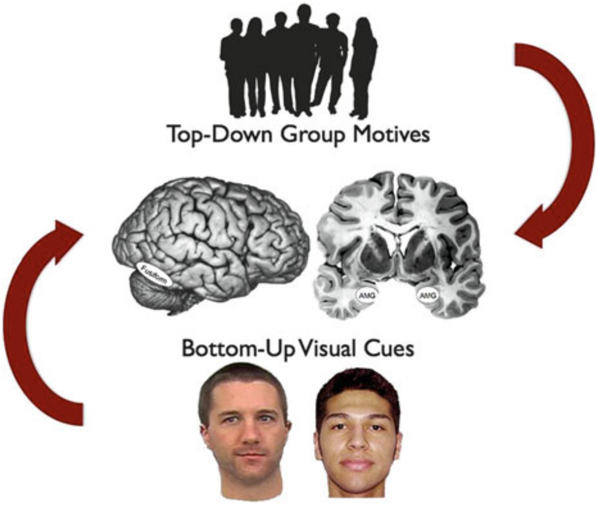

Fig. 1 Neural activity in the context of social cognition is a combination of bottom-up visual cues (e.g., race) and top-down social motives (e.g., group affiliation). AMG, amygdala. The White face was provided courtesy of Dr. Michael J. Tarr, Carnegie Mellon University and the Black face was provided courtesy of Dr. Jennifer Eberhardt, Stanford University

faces of in-group and out-group members for 150 milliseconds in a response-window priming task and examined the effects of these faces on valence judgments of positive and negative words (Cunningham et al. 2001; Draine and Greenwald 1998). This task allowed us to assess very rapid evaluations of faces on the basis of their group membership and race (as well as the interaction between these social categories). As predicted, participants who were assigned to a mixed-race group had positive evaluations of in-group members, regardless of the group members' race. Specifically, we found that group membership increased positivity toward Black in-group members relative to Black out-group members, eliminating the standard pattern of automatic racial bias when evaluating in-group members (Fazio et al. 1995). Thus, participants' evaluations reflected their current self-categorization with a minimal group, even when the in-group and out-group had no history of contact or conflict and when there was an orthogonal, visually salient social category (i.e., race) with strong stereotypic and evaluative associations.

Based on these results, we reasoned that these minimal social identities might also override the racial biases in neural activity observed in previous research (see Amodio and Lieberman 2009; Cunningham and Van Bavel 2009; Kubota et al. 2012 for reviews). Several previous papers on neural responses to race had observed a relationship between the amygdala – a small structure in the temporal lobe – and racial bias. The amygdala has been implicated in a host of social and affective processes (see Macrae and Quadflieg 2010; for a review see Phelps 2006), including fear conditioning (LeDoux 2000), processing negative stimuli (Cunningham et al. 2003; Hariri et al. 2002), and perceiving emotional faces (Whalen et al. 1998). Individual differences in amygdala activity in response to viewing Black compared to White faces are positively correlated with implicit measures of racial bias (Amodio et al. 2003; Cunningham et al. 2004; Phelps et al. 2000). These correlations between differential amygdala activity and implicit racial bias led researchers to interpret differences in amygdala activation in intergroup contexts largely as evidence of implicit negativity toward stigmatized groups (Harris and Fiske 2006; Krendl et al. 2006; Lieberman et al. 2005).

We examined whether amygdala activity would be sensitive to social identity in general, rather than race per se. Previous research suggested that the amygdala is sensitive to motivationally relevant stimuli rather than simply to negative stimuli (Anderson and Phelps 2001; Cunningham et al. 2008; Vuilleumier 2005; Whalen 1998). Therefore, we reasoned that amygdala activity would be greater when viewing in-group members in a minimal group context since in-group members help fulfill a number of important motives (e.g., economic, psychological, and evolutionary). Similar to our other experiments, we randomly assigned White participants to one of two minimal mixed-race groups, had them briefly learn the faces of individuals associated with each group, and then presented them with the same in-group and out-group faces during neuroimaging (Van Bavel et al. 2008). While they were in the scanner, participants categorized each face according to either group membership (Leopard or Tiger) or race (Black or White). As predicted, participants had greater amygdala activity to in-group members than out-group members, regardless of their race (see also Chiao et al. 2008). In-group biases in neural activity were not moderated by target race or categorization task (i.e., categorizing by team or by race), suggesting that these effects did not require explicit attention to group membership. Importantly, in-group biases in amygdala activity occurred within minutes of team assignment, in the absence of explicit group-based rewards or punishments, and independent of pre-existing attitudes, stereotypes, or extensive exposure to the groups. Further, the faces on each team were fully counterbalanced across participants, ensuring that any effects of group membership were due to self-categorization with the in-group and not to the visual properties of different face stimuli (e.g., attractiveness, luminance, symmetry, etc.).

Social Identity and Person Memory

In follow-up research we examined the effects of social identity on the own-race bias (ORB), one of the most robust and widely replicated phenomena in social categorization. According to the ORB, people are better at remembering people from their own race than people from other races because they have more extensive *perceptual expertise* with own-race faces (Malpass and Kravitz 1969). Although the ORB may appear to be a relatively innocuous bias, it can lead an eyewitness in a criminal case to misidentify a suspect from another race, leading to the conviction of an innocent person (Brigham and Ready 2005). Indeed, the majority of false convictions of criminals on death row are based on erroneous cross-race eye-witness misidentification (Scheck et al. 2000). Consistent with this perceptual expertise account, pervious functional magnetic resonance imaging (fMRI) research (Golby et al. 2001; see also Lieberman et al. 2005) reported a correlation between individual differences in the magnitude of ORB and activity in the fusiform face area (FFA), a sub-region of the fusiform gyrus located on the ventral surfaces of the temporal lobe and implicated in face perception (Kanwisher et al. 1997; Sergent et al. 1992) and visual expertise (see Palmeri and Gauthier 2004 for a review). This work suggested that extensive visual experience with own-race faces may have gradually tuned neurons in the FFA to make fine-grained discriminations between exemplars within a stimulus category (Tarr and Gauthier 2000).

We examined whether social identification with a minimal group would lead people to encode in-group members at a subordinate level and out-group members at a superordinate level, despite participants' limited exposure to members of both categories (Bernstein et al. 2007; Levin 1996, 2000; see also discussion of the outgoing homogeneity effect in Ostrom and Sedikides 1992; Sporer 2001). As predicted, we found greater activation within the bi-lateral fusiform gyri for in-group relative to out-group faces (Van Bavel et al. 2008). We replicated this pattern of in-group bias in the FFA (using a functionally localized sub-region of the fusiform gyri that is sensitive to faces) and found that relatively greater activity in the FFA mediated the effects of group membership on recognition memory, a behavioral index of individuation (Van Bavel et al. 2011). Specifically, we found a positive correlation between the FFA differences for in-group versus out-group faces and recognition memory differences for in-group nor out-group faces. Moreover, these effects were not moderated by race (nor was there a main effect of race; see also Hehman et al. 2010; Kinzler et al. 2009; Kurzban et al. 2001; Shriver et al. 2008). Taken together, these findings suggest that in-group members are more likely to be processed as individuals than out-group members, consistent with social cognitive models of person perception (Brewer 1988; Fiske and Neuberg 1990; Hugenberg et al. 2010; Sporer 2001) (Fig. 2).

These results provide evidence that the FFA is sensitive to shifts in self-categorization, responding selectively to face stimuli imbued with psychological significance by virtue of their currently salient group membership and encoding the more motivationally relevant in-group faces at the subordinate level. It is important, however, to note that in-group bias is not inevitable. In follow-up research, we found that superior memory for in-group compared to out-group members was only evident among participants who were highly identified with the in-group (Van Bavel and Cunningham 2012) or had a high need to belong (Van Bavel et al. 2012a). Further, enhanced memory for in-group members was mediated by enhanced attention to in-group members during the learning phase and could be reduced by assigning participants to a role (i.e., spy) that motivated their attention to out-group members (Van Bavel and Cunningham 2012). Thus, our research provides evidence that group membership can shape the *motivational relevance* of categories in a flexible and dynamic fashion even in the absence of long-term experience with the category.

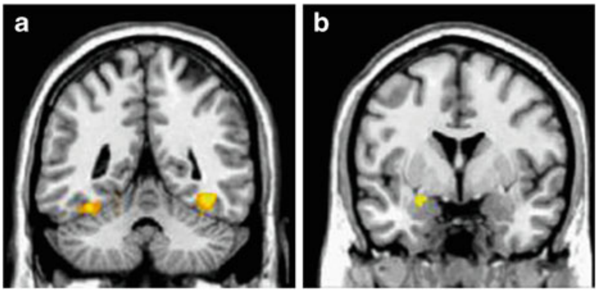

Fig. 2 Participants show greater activation in (**a**) fusiform gyri and (**b**) amygdala when viewing novel in-group members, regardless of race (Adapted from Van Bavel et al. 2008)

Social Identity Alters the Threshold for Mind Perception

The tendency to infer goals, thoughts, and feelings behind the faces of others – termed mind perception – is a reflexive and ubiquitous feature of human social cognition and influences the extent to which people see others as worthy of moral consideration (Gray et al. 2007). Recent work has suggested that people perceive minds behind faces using bottom-up, visual features. In particular, Looser and Wheatley (2010) asked participants to view faces along a spectrum of morphs between human faces and inanimate faces (e.g., dolls) and to indicate whether each face had a mind (see Fig. 3). Results indicated that participants perceived minds categorically past a specific boundary threshold along the morph continuum and that this threshold was biased towards the human end of the spectrum (i.e., people only perceive minds with a high degree of humanness in the face). Other work using electroencephalography suggests that the brain differentiates between human and inanimate faces within a few hundred milliseconds of seeing a face (Wheatley et al. 2011) and that the brain's face perception network encodes the animacy of faces using visual features, allowing people to differentiate between humans and dolls (Looser et al. 2012). Together, this work suggests people are closely attuned to visual cues signifying a mind in a face.

We tested whether group membership could provide a top-down cue shaping the motivational relevance of minds behind faces. We reasoned that in-group members may be seen as more relevant targets for fulfilling social needs (Brewer 1988), and social belonging needs have been connected in past research to anthropomorphism and higher-level attribution of mind to others (Epley et al. 2007). However, in the case of threatening out-groups, it may be advantageous to consider the out-group's mental states and plans rather than to deny them a mind. We therefore hypothesized that collective identification with a group would ordinarily lead people to infer minds more readily for in-group faces but that out-group threat might enhance mind perception toward out-group faces.

In a series of experiments, we had participants view morphs between human and inanimate faces that were ostensibly based on in-group or out-group models across various group contexts (Hackel et al. unpublished manuscript). We asked participants to rate how much each face had a mind, and we examined each subject's Point of Subjective Equality, i.e., the point on the morph spectrum at which faces were

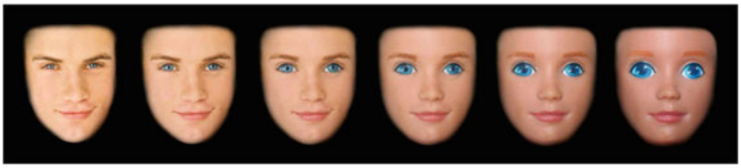

Fig. 3 Participants rated a series of morphs between human and inanimate faces (6 of 11 points along the morph spectrum shown here), letting us examine the threshold (i.e., the tipping point) at which they perceive the faces as having minds (Hackel et al. unpublished manuscript)

equally likely to be seen as having or lacking a mind, which can serve as a measure of threshold or tipping point for perceiving minds along the morph spectrum (Looser and Wheatley 2010). Even in minimal groups, participants had more lenient thresholds for perceiving minds in in-group faces. In other words, they needed less humanness in a face to judge it as having a mind. In further work using real-world groups based on university affiliation, we found that these effects were moderated by individual differences in *collective identification*, i.e., the extent to which people define themselves by and feel invested in the group (Leach et al. 2008). In particular, greater identification with one's group was associated with greater intergroup bias in mind perception. However, we found that perceived out-group threat reversed this effect: Democrats and Republicans, two highly competitive political groups, who saw the other group as a threat to their own had more lenient thresholds for *out*-group mind perception.

These experiments suggest that inferring a mind behind a face depends not only on bottom-up visual cues to humanness, but also on top-down identity motives. More specifically, functionally relevant motivations such as in-group identification and out-group threat can shape mind perception in opposing directions. In follow-up neuroimaging research, we tested whether group membership would differentially impact two dimensions of mind perception: *agency*, which refers to abilities such as thinking and planning, and *experience*, which refers to abilities such as feeling pleasure, pain, or emotion. Specifically, we hypothesized that people might be more ready to perceive experience in in-group members while still seeing agency in out-group members, especially for threatening groups. Indeed, we found that group membership impacted activation in the brain's theory of mind network when participants judged experience, but not agency, in faces (Hackel et al. unpublished manuscript). Altogether, this work suggests that mind perception is a dynamic process: the extent to which we consider others' minds may depend on the intergroup contexts in which we are situated.

Social Identity Shapes Distance Perception

We have also been exploring whether self-categorization with social groups may even shape basic representations of physical reality (Hastorf and Cantril 1954). Decades ago, the "New Look" in perception suggested that values and needs organize people's visual perception of the physical world (Bruner and Goodman 1947). Recent research has demonstrated the influence of motivational factors, including identity-related motives, on perception and representation of physical aspects of stimuli, such as spatial distance (Burris and Branscombe 2005; Proffitt 2006). In a similar vein, we have shown that social identity, identity threat, and degree of collective identification can shape the perception of physical distance (Xiao and Van Bavel 2012).

Specifically, locations signifying a threatening (vs. non-threatening) out-group were perceived as physically closer, particularly among those who strongly identify with their threatened in-group (Xiao and Van Bavel 2012). We tested this effect with various types of social identities, including professional sports team fandom, nationality, and university affiliation. In our experiments, Yankees fans, compared to those not identified with the Yankees, estimated Fenway Park – the stadium of their rival Red Sox – to be physically closer. Highly identified Americans who perceived Mexican immigration to be a threat to America estimated Mexico City to be particularly closer compared to those who did not highly identify with America or did not perceive Mexican immigration to be a threat (see Fig. 4). When we experimentally manipulated threat, highly identified New York University affiliates estimated Columbia University to be closer when Columbia was portrayed as a threat compared to when it was portrayed as of similar status (Xiao and Van Bavel 2012). Although this research has focused on distance *estimations*, it is nevertheless consistent with the notion that social identity may influence perception, and possibly basic sensation (Coppin et al. 2012).

Importantly, estimations of perceptual closeness induced by identity threat are by no means fixed and stable. We subsequently found that perceptual processes are flexibly shaped by other social constructs; perception of a strong intergroup barrier and intergroup forgiveness both eliminated the effects of identity threat on distance estimations. For example, we replicated the relationship between perceived threat from Mexican immigration and closeness in distance perception when Americans perceived the US-Mexico border to be weak. However, when we experimentally manipulated the security of the national border, this relationship was eliminated, suggesting that a strong intergroup barrier served as a psychological buffer against intergroup threat (Xiao et al. unpublished manuscript). Further, manipulating the perceived closeness of a threatening out-group elicits discrimination towards members of this out-group (Xiao et al. unpublished manuscript). In sum, this research suggests that various aspects of social identity and the intergroup context dynamically influence perceptual representations of physical reality and these representations may have important influences on real-world behavior.

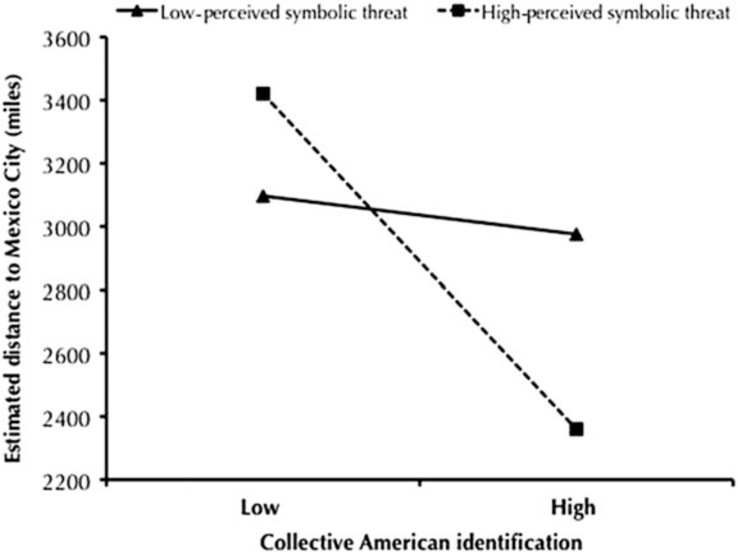

Fig. 4 Mean distance from New York City to Mexico City estimated by participants who reported varying degrees of symbolic threat from Mexican immigrants, as a function of the strength of their collective American identity. Perceived symbolic threat from Mexican immigrants predicted estimated distance to Mexico City for high-identifiers but not for low-identifiers (Xiao and Van Bavel 2012)

Discussion

Our research, using a combination of social, cognitive, and neuroscience techniques, sheds new light on the powerful influences of flexible social identification on cognition. Even rapidly and arbitrarily created social groups, which people have no prior knowledge about or contact with, can override the influences from existing social categories that often carry a great deal of societal and historical baggage, such as racial groups in America. The primary theoretical implication of our work is that social identities can have a profound impact on group members' representations of the social world (Hastorf and Cantril 1954). Although extensive research has investigated the societal and behavioral consequences of forming social groups to alleviate negative intergroup consequences and promote positive intergroup relations (e.g., Sherif and Sherif 1953; Tajfel and Turner 1979), little work has examined the influence of self-categorization on basic cognition. Our research suggests the influence of social identity is far more pervasive and may even penetrate some of the most automatic and basic cognitive processes (Van Bavel and Cunningham 2011).

In our view, one of the most arresting aspects of this research is that very brief exposure to arbitrary intergroup alliances was sufficient to elicit identification with an arbitrary group and make this a more potent social category than race, which is a category marked by years of exposure and associated with relatively stable stereotypes and attitudes. Membership in an arbitrary group was sufficient to increase preferences for in-group members in terms of evaluation (Van Bavel and Cunningham 2009a), memory (Van Bavel and Cunningham 2012; Van Bavel et al. 2012a) and neural activity in the amygdala (Van Bavel et al. 2008) and FFA (Van Bavel et al. 2011). Thus, while visually salient categories like race trigger rapid bottom-up processing due to low-level visual input (e.g., physiognomic features) and stereotypic associations within the first few hundred milliseconds of perceptual processing (Ito and Urland 2003), this does not mean they are automatic or inevitable. As we discuss above, a psychologically salient social identity can exert a top-down influence on these processes and attenuate ostensibly automatic racial biases. These findings introduce the possibility that transient aspects of self-categorization can override visually salient and socially important categories – perhaps before these social categories even begin to influence the perceptual and evaluative system (see also Cunningham et al. 2012).

Although we have acquired extensive evidence that membership in a mixed-race group can override racial bias, we are not suggesting that people in these experiments were genuinely colorblind. It seems likely that race, like any physical or psychological property, may be represented in the brain even when it is silent on a specific mental process or task. Indeed, we have recent evidence that race may be encoded in the visual system, even when it does not produce the standard pattern of racial biases reported above (Kaul et al. 2012; Ratner et al. 2012). Our previous work suggests that the fusiform gyri are sensitive to salient group membership but not race. However, when we re-analyzed the data using Multivariate Pattern Analysis, a technique that can identify distributed representations in the absence of mean-level activation differences between Black and White faces, we found that patterns of neural activity within early visual cortex and a face-sensitive sub-region of the fusiform gyri could decode the race of faces above chance. In other words, *patterns* of activation within the fusiform encode race even when *mean* activation is driven by other motivationally relevant group memberships. Therefore, the human visual system may still *encode* skin color and physiognomic features that allow them to distinguish between Black and White faces, even when other more motivationally salient social categorizations override racial *bias* on specific outcomes.

Our approach offers new perspectives to social psychology and cognitive neuroscience. By bringing a cognitive neuroscience approach to social psychology, we can explore specific cognitive and neural processes that underlie the abstract process of self-categorization and the construct of social identity. Considering the emerging literature in cognitive neuroscience has also encouraged us to re-evaluate the distinction between automatic and controlled processing and suggests that a strict dissociation between these processes is unlikely to be grounded in brain structure or function (Cunningham et al. 2007; Van Bavel et al. 2012b). Our work suggests that salient identities and mindsets brought to bear on a situation determine later supposedly "automatic" reactions. Top-down influences on cognition and emotion need not emerge only after unavoidable automatic responses, controlling these responses through strategies like suppression or reappraisal.

Rather, top-down influences may be able to change which responses become active in the first place through a form of *pre-appraisal*, thus influencing cognitive, evaluative, and affective outcomes.

In addition, by bringing social psychological theories to cognitive neuroscience, our research underscores the flexibility of the person perception network and the power of self-categorization and social identity to shape supposedly "bottom-up" neural processing (Van Bavel et al. 2013). The social cognitive neuroscience perspective highlights the "power of the situation" to influence even basic cognitive processes (Cacioppo et al. 2000; Lieberman 2005; Zaki and Ochsner 2011), suggesting that even basic cognitive processes must be considered within the social identity contexts in which they are situated (Turner et al. 1994).

Conclusion

In his classic book, "The Group Mind" (1921), William McDougall noted that psychology in the nineteenth century had studied the human mind without consideration of the social context. In contrast, he argued that individual psychology could not be understood in the absence of collective social process and that groups have a collective mental life that is not merely the sum of the mental lives of individuals. Our research demonstrates how social groups structure individual cognition across several levels of analysis, providing a cognitive and neural basis for a "group mind." In this way, social identities provide a set of expectations and goals that can elicit a common perceptual and evaluative framework across multiple group members, leading to shared representations and a framework for collective action. In other words, Aristotle was right: humans are highly social animals and our social context shapes our self-representation and, consequently, cognition.

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Development + Social Selection in the Emergence of "Emotionally Modern" Humans

Sarah B. Hrdy

Abstract According to the cooperative breeding hypothesis, apes with the life history attributes of *Homo sapiens* could not have evolved unless alloparents in addition to parents had helped to care for and provision offspring. In this chapter, I explore the psychological implications for infants developing in social contexts where contingent nurture was elicited from multiple providers. I hypothesize that, what was (for an ape) an unusual mode of rearing young, generated novel ape phenotypes subsequently subjected to directional Darwinian selection favoring those infants who were better at monitoring the mental states and intentions of others, motivated to appeal to and please them so as to elicit solicitude. The result was an already socially intelligent ape both emotionally and cognitively preadapted for the evolution of higher levels of cooperation. Relying on the best available proxies we still have for humankind's last common ancestor with other apes, I draw on experimental studies of chimpanzee and modern human infants to test underlying assumptions critical to this mothers-and-others model. Results indicate that rearing by multiple caretakers does indeed generate ape phenotypes in which "other-regarding" potentials are more fully expressed. Preliminary evidence from comparative neuroscience also suggests a mosaic pattern of "fast" as well as "slow" neural development in human infants consistent with the proposition that social selection acted on their ancestors in ways that produced infants that, although utterly dependent, were well equipped to monitor and evaluate others.

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S.B. Hrdy (✉)
University of California, 1 Shields Ave, Davis, CA 95616, USA

Citrona Farms, 21440 County Road 87, Winters, CA 95694, USA
e-mail: sbh@citrona.com

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Introduction: A More Other-Regarding Ape

It was an inspired guess when Charles Darwin proposed that humans evolved in Africa from now-extinct predecessors resembling today's gorillas and chimpanzees (1874). On the basis of fossil and genetic evidence analyzed since then, we now estimate that apes in the line leading to the genus *Homo* split from that leading to gorillas between 10 and 17 million years ago and split from that leading to today's chimpanzees and bonobos between 6 and 11 million years ago (Langergraber et al. 2012). Common descent explains the overlap in genomes as well as such capacities as producing and using tools in multiple ways (Roffman et al. 2012). It also helps explain why developmental profiles of a baby chimpanzee can be evaluated using the same Brazelton Neonatal Behavioral Assessment Scale that pediatricians applied to my own infants.

With each passing year, it becomes harder to draw absolute distinctions between the innate capacities of young humans and those of their ape relations. This blurring of boundaries pertains in almost every cognitive realm except those accomplishments requiring language or the kind of sophisticated teaching along with cumulative culture that language facilitates (Dean et al. 2012; Matsuzawa et al. 2006; Whiten and van Schaik 2007). Even in tasks such as watching and learning from someone else's demonstration or tasks requiring mentalizing about what someone else is likely to know ("theory of mind"), where humans typically test better, considerable overlap exists between the scores of orangutans and chimpanzees and those of two-and-a-half-year-old humans (Herrmann et al. 2007: Fig. 2; see also Dean et al. 2012). In terms of working memory, young chimpanzees can actually outperform human adults. Some specially trained chimpanzees remember ordered symbols briefly flashed onto a computer screen as well as, or better than, humans do (Matsuzawa 2012).

Within minutes of birth, humans are attracted to face-like patterns. By 2 months of age, they recognize their mother's face. But so do other ape newborns. They occasionally gaze into their mother's face (Bard 2005), scan expressions of whoever is holding them, and even seek to engage this caretaker by imitating what they see there – sticking out their own tongues or opening their mouths (Myowa 1996; Myowa-Yamakoshi et al. 2004; Bard 2007). Whether their face-to-face partner is another chimp or a human caretaker, little chimpanzees respond in kind to all sorts of emotionally charged expressions, suggesting that underlying subjective emotions are being shared. However, there are also key differences.

Even though other apes occasionally share food, the possessor is rarely eager to do so (Silk et al. 2005). In the wild, an alpha male chimpanzee may tear off a bit of meat from captured prey to proffer to a strategic ally, but only after persistent solicitation (Watts and Mitani 2000). A mother chimp or bonobo may allow her infant to take food from her mouth, but rarely volunteers it. Bonobos, generally less competitive over food than common chimpanzees (Hare et al. 2007; Hare and Kwetuenda 2010), have been known to open a cage door so another bonobo can

Fig. 1 From an early age, humans will select and proffer an item that they have reason to believe someone else will enjoy, even if it differs from their own preferences (Photo: S. Hrdy)

share a feeding bonanza (Hare 2012), but in no wild ape is voluntary sharing the *routine* part of life that it is in every human society ever studied.

Clearly, socialization plays a role in this, but we are left to explain why the social sharing of food that is universal in human societies is absent from other apes. "Mealtime" simply does not mean the same thing among other apes that it does in humans. In the bonobo case, allomaternal provisioning entails little more than an adult not bothering to object when a youngster removes food from her mouth (Kano 1992). By contrast, among humans, parents and alloparents alike routinely proffer food to children and to each other. Even very young humans spontaneously offer food (Fig. 1), and by 18 months may select just the item they have reason to believe that another will prefer, even if it differs from their own preference (Repacholi and Gopnik 1997).

Such ingratiating impulses go beyond food sharing. More than two centuries ago, in his "Theory of Moral Sentiments" (Smith 1750), Adam Smith spelled out how vitally interested people are in the subjective feelings, underlying motivations, and values with which people judge others. Humans also exhibit powerful desires for others to receive information about their own thoughts and feelings and, moreover, to approve of them. What I focus on here is the recent realization of just how early in development such ingratiating tendencies, combined with mentalizing and questing for intersubjective engagement, emerge, and I ask why they would have been crucial for the survival of entirely dependent (but not quite entirely helpless) immatures?

I concur with comparative psychologists Michael Tomasello and Malinda Carpenter, who propose that such "intersubjective sharing" (defined by them as two humans "experiencing the same thing at the same time and *knowing together that they are doing this*") is the key sociocognitive difference between humans and other apes. As they put it, creating "a shared space of common psychological ground" lays the foundation for a broad range of collaborative activities with shared goals as well as human-style cooperative communication (Tomasello and Carpenter 2007, following Trevarthen 2005).

There is an emotional component to this questing for intersubjective engagement that goes beyond "theory of mind," or being able to attribute mental states or beliefs to others. By 1 year of age, even before human babies talk, they respond with pride to praise and with shame when they sense someone else's disappointment (Darwin

1877; Reddy 2003; Trevarthen 2005). Alone among animals, by age two humans respond to others' assessments by blushing, that peculiarly manifest signal of self-consciousness that led Darwin (1998) to wonder why "the thought that others are thinking about us" could "alter our capillary circulation?" By age four, such coy "aspirations-to-appeal" develop into full-fledged perspective-taking, escalating into outright (not infrequently deceptive) flattery (Fu and Lee 2007), but the underlying concern for what others think emerges even earlier (Reddy 2003). From around the age of three, most humans are motivated to reveal their "inner selves" to someone else, especially when expressing motivations (like behaving generously) that are likely to elicit admiration from others (Leimgruber et al. 2012). The same neural regions activated by anticipation of tasty food (the mesolimbic dopamine system and the ventral tegmental area) light up when people talk about themselves (Tamir and Mitchell 2012).

Rather than viewing language as a unique faculty that evolved so people could coordinate with others in collaborative endeavors, I am convinced that questing for intersubjective engagement had to come first, prompting apes already adept at declarative signaling to become apes capable of producing infinitely recursive symbol-rich vocalizations. As psychiatrist Peter Hobson put it, "Before language, there [had to be] something else . . . that could evolve in tiny steps. . . . That something else was *social engagement with each other*. The links that can join one person's mind with the mind of someone else, especially, to begin with, emotional links" (2004). Trevarthen (2005) makes a similar point when he suggests that the "cooperative awareness" or "secondary intersubjectivity" that permits 1-year-old infants to communicate experiences, feelings, and intentions, provides the foundation on which language is built. Givón (1995) similarly argues that grammar emerged to communicate information in a way that takes into account someone else's knowledge and current state.

If emotional transformations rendering hominins eager to read, influence and appeal to mental and subjective states of others preceded the evolution of uniquely human language, it should not be surprising that human toddlers do not just call out for help, utter commands, or announce what they want. They also express feelings, commenting on what seems to them "good" or "bad." By the time a child can talk, perhaps one third of his or her speech informs others about subjective evaluations, as when, at the age of 27-months, Darwin's son exclaimed, "Oh kind Doddy, kind Doddy" on observing his father give the last piece of gingerbread to the toddler's younger sister (1877). Perhaps especially if accustomed to being surrounded by encouraging and indulgent others (as is typical in many hunter-gatherer societies compared to, say, farming societies; Hewlett and Lamb 2005), youngsters may readily express inner assessments of others.

Indisputably, the evolution of language produced potent downstream consequences in terms of cooperation and cultural transmission (Gergely and Gergely 2011; Tomasello and Carpenter 2007). But what I emphasize here is that the apes who first felt a need for forms of communication that went beyond imperative use of communicative signals were likely to have already been more other-regarding.

They were not only cognitively but also emotionally very different from our last common ancestor with other extant apes.

How to Explain the Origins of Other-Regarding Impulses?

Efforts to explain humankind's planet-populating, world-dominating "success story" emphasize the cognitive and social processes that facilitate acquisition and transmission of cultural information (Tennie et al. 2009; Tomasello 1999; Whiten and van Schaik 2007). Three prerequisites seem especially relevant: closer attention to others, including imitation and observational learning; intentional teaching (including verbal instruction) (Dean et al. 2012); and mutual tolerance and other-regarding, helpful impulses (e.g., Burkart et al. 2009; Whiten and van Schaik 2007). But whence such attributes?

Comparative psychologists have done a brilliant job of demonstrating that human social learners focus more on others' actual actions than do other apes, so that "uniquely human forms of cooperation" can be built up through teaching and transmission of conformity to norms, resulting in a "cultural ratchet" (Tennie et al. 2009 as cited in Dean et al. 2012; Horner and Whiten 2005). It is because our language-using ancestors benefited from new forms of social learning and teaching that, by 100,000 years ago, anatomically modern humans had evolved into fully enculturated ones capable of higher levels of social coordination. However, this sequence begs the question: how did the emotional scaffolding facilitating mutual tolerance, interest in the mental states and thoughts of others, and eagerness to please and share with them, emerge in the hominin line in the first place? Neither does it explain why these hyper-social impulses evolved in humans but not other apes? Why did they appear so early and in both sexes?

It is increasingly apparent that other extant apes possess neural prerequisites to process what someone else does or does not know, to read their intentions, and even to figure out how to help them accomplish specific goals (discussed below). However, ingratiating themselves by running over to help another or spontaneously offering food is not something other apes do. Such behaviors are, however, observed in other primates. Humans have not shared a common ancestor with marmosets and tamarins for over 35 million years, yet these distantly related, tiny-brained little monkeys behave in extraordinarily helpful ways both in the wild (Bales et al. 2002; Garber 1997) and in well-replicated captive experiments (Burkart et al. 2007; Cronin et al. 2010; Hauser et al. 2003; Fig. 2). Striking parallels between humans and this phylogenetically distant subfamily of New World monkeys (who, similar to humans mothers, had to rely on allomaternal care and provisioning to rear surviving young) are listed in Table 1. As discussed elsewhere this convergent evolution cannot be understood without taking cooperative breeding into account (Hrdy 2009; Burkart et al. 2009).

Interestingly, marmosets readily follow others' gazes and eagerly assist them, but they do not appear to take the "mental" perspective of another into account the

Fig. 2 The marmoset (*Calithrix jacchus*) on the left has run over to pull in a tray that will deliver a mealworm to a marmoset on the other side of the cage. This photograph was taken with the assistance of Judith Burkart, illustrating methods she devised to compare levels of spontaneous prosociality across species (Burkart and van Schaik 2012) (Photo: S. Hrdy)

Table 1 Over 35 million years have elapsed since large-brained human foragers last shared a common ancestor with tiny-brained New World monkeys in the subfamily Callitrhichidae (marmosets and tamarins), yet there are remarkable convergences among these otherwise very different cooperative breeders. Parallels include

1. Extensive alloparental care + provisioning
2. Prolonged post-weaning dependence
3. Reliance on hunting + gathering with extractive foraging
4. Adapted to colonizing new habitats
5. Unusually conditional maternal commitment with high rates of abandonment in response to low allomaternal support
6. High levels of foraging cooperation
7. Provisioning by multiple males encouraged by polyandrous mating accompanied by either real chimerism (as in marmosets) or (in human case) fictitious beliefs about it
8. Non-advertised ovulation + mating throughout cycle
9. Weakly developed dominance hierarchies where food concerned
10. Variable group compositions + adults of both sexes move between groups
11. Other-regarding impulses manifested in food-sharing + information-transfer

way humans do (Burkart and Heschl 2007). Other apes are better at doing so, just not as interested in helping. Neither, apart from mutual grooming, do nonhuman apes go out of their way to please others the way marmosets (in their more automatic, "less thoughtful" way) or humans do. In the human case, reward centers in the brain are stimulated just by giving something to someone else (Rilling et al. 2002), but whether such "charitable acts" have comparable effects in any other primate is not yet known. Based purely on behavioral observation, however, other apes do not appear particularly interested in ingratiating behaviors or eager to satisfy another's personal preference. The fact that possessors have to be actively solicited before resources are shared is one more indication that apes do not find it inherently pleasurable to please others, as humans do.

So far, explanations for humankind's peculiarly prosocial impulses have mostly focused on obligate cooperative foraging, especially collaborative hunting and, with it, the need for equitable sharing (Bullinger et al. 2011; Tomasello et al. 2012) or the sort of "parochial altruism" needed for a "band of brothers" to prevail in competition with neighboring bands (Choi and Bowles 2007). Bowles vividly showcases his proposal that "generosity and solidarity towards one's own [group] may have emerged only in combination with hostility towards outsiders" (Bowles 2008a) by asking whether humans "engage in mutual aid *because* evolution is red in tooth and claw" (2008b). Yet both hunting and intergroup conflict are integral to chimpanzee life as well, with *Pan troglodytes* also being meat-loving and probably even more competitive and dominance-striving than humans are, not to mention xenophobic to the point of reflexively attacking outsiders (Wrangham and Peterson 1996). So why didn't their ancestors also spend the past six million years evolving more other-regarding impulses so as to reap manifest benefits of "parochial altruism?" Neither do warfare or hunting models explain why other-regarding impulses characterize both sexes and may indeed even be more expressed in females (de Waal 2013, p. 51); they also do not explain why prosocial impulses emerge so early in development. Surely vulnerable immatures would do better to remain self-servingly focused on staying safe, fed, and growing bigger, as earlier generations of behaviorists assumed that they did (e.g., Watson 1928).

Other-regarding impulses lay the groundwork for cooperative potentials that unquestionably have served humans well, as evidenced by all the enterprises, institutions, factories, and gravity-defying machines that coordination with others facilitate. But Mother Nature (my metaphor for Darwinian natural selection) had no way to foresee such eventual payoffs. It seems circular to argue that humans evolved other-regarding, culture-acquiring attributes in order to become culture-bearing animals. Rather we need to ask under what circumstances an ape would have benefited from better monitoring and responding to the mental states, desires, and needs of others and seeking to appeal to and please them. And why should such impulses emerge so early? Rather than viewing prehuman ancestors as already "exceptional," I prefer to view them as creatures subject to the same evolutionary processes that pertain elsewhere in nature.

These were the challenges that drew my attention to the unusual way that apes in the line leading to the genus *Homo* must have reared their young (Hrdy 1999). While shared care is typical of human foragers and widespread across primates, it is not found among our closest great ape relations and is almost certainly absent among the last common ancestor humans shared with them. Why then, and when, did such extremely un-apelike modes of childcare emerge in the hominin line? And what were the ramifications?

Shared Care, Provisioning Young, and the Evolution of More Generalized Food Sharing

There is an ongoing paradigm shift in how evolutionary anthropologists reconstruct family life among hominins struggling to stay fed and rear offspring in the unpredictably fluctuating climates of Pleistocene Africa. As has long been recognized, all apes are born relatively helpless, maturing slowly through a prolonged infancy followed by a juvenile period and adolescence. Debate persists over just how similar or different these growth stages are in humans and other apes, but indisputably human youngsters remain nutritionally dependent longer. Nonhuman apes tend to be weaned later but thereafter provision themselves, whereas human youngsters continue to need subsidies as late as early adulthood. No one knows how far back in time such dependency extends. But the emergence of *Homo erectus,* with an adult brain more than twice the size of either australopithecines or today's chimpanzees, presumably meant that the diets of immatures, and perhaps their mothers as well, were being subsidized at least by the beginning of the Pleistocene, 1.8 million years ago (O'Connell et al. 2002; Hrdy 2009; Cofran and Desilva 2013).

Based on data from twentieth-century foraging peoples, it takes 10–13 million calories beyond what a growing child provides for himself to grow from birth to age 18, more than a foraging mother could ordinarily provide by herself (Kaplan 1994). Furthermore, shorter inter-birth intervals meant another dependent would be born before older offspring were independent. Even with a father on hand and willing to help, the success rate of a Plio-Pleistocene hunter-scavenger would not have come close to meeting the requirements of a *H. erectus* juvenile needing to be fed several times each day (O'Connell et al. 2002). Alloparental in addition to parental provisioning and processing was essential to ensure that growing children had sufficient palatable foods.

Survival of young required multiple providers. Indeed, fluctuating rainfall and with it unpredictability of food resources (Potts 1996; Wells 2012), specifically in east Africa during the period between 1.8 and 2 million years ago when *Homo erectus* was emerging (Magill et al. 2013), produced the conditions that in other animals are associated with the evolution of cooperative breeding (Jetz and Rubenstein 2011) and with it, more prolonged periods of dependence (Langen 2000; Hrdy 2005). In the early hominin case, opportunistic inputs from multiple scavenger-hunters must have been backed up by more reliable gatherer-processors of plant foods. Other apes exhibit some division of labor (e.g., chimpanzee females fish for termites and crack nuts whereas males do almost all hunting), but the fruits of such gender-specific endeavors are rarely shared, and meat is largely consumed by adult males. So, given notably self-serving, often competitive, apes, how does food sharing get underway?

Across primates, voluntary provisioning is uncommon. Except in humans, it is virtually absent among apes. Shared care is a different matter. Infants are universally attractive to at least some other group members and are protected and even carried by them. Some form of shared infant care is reported for the majority of species in the Primate order (Hrdy 2005, 2009, 2010). Apart from humans and one lesser ape, however (siamang fathers carry older infants; Lappan 2009), hominoid mothers do not permit access to their infants. Nevertheless, so deeply entrenched is responsiveness to infant cues that, even among non-infant-sharing great apes, even normally aloof males may respond to signals of extreme need (e.g., chimp males adopting older orphans; Boesch et al. 2010). Some primate mothers also occasionally allow another female's infant to suckle or to take food. Nevertheless, with the lone exception of humans, extensive alloparental provisioning is confined to the subfamily Callitrichidae (the marmosets and tamarins mentioned above).

Occasionally sharing food with another's infant does not mean that adults share food among themselves; however, provisioning young acts as a gateway to it. Compiling evidence for 68 species of primates, Jaeggi and van Schaik (2011) found that adult-to-adult food sharing is disproportionately likely to evolve in taxonomic groups where adult-to-offspring provisioning is already established. This finding is consistent with the observation that, as with cooperative breeding itself, allomaternal provisioning is more likely to evolve when foods utilized require strength or extractive skills that immatures do not yet possess.

As predicted by Hamilton's Rule, such helping should evolve whenever benefits to the recipient exceed costs to the helper multiplied by degree of relatedness. Thus, even a distantly related group member that had already had his fill of a resource might provide it to immatures unable to access it themselves. Exact costs and benefits vary but, across the natural world in species with biparental and/or alloparental care, in thousands of species of birds as well as quite a few mammals, adults transport food back to a nest, den, or other site where immatures are creched. Social carnivores such as African wild dogs and wolves provide classic examples. Adults return from a kill to the den with predigested meat in their bellies, regurgitating it into the mouths of begging pups waiting there. In the case of the genus *Homo*, adult provisioning of immatures would have set the stage for more generalized food sharing and, in time, cooking as well (Wrangham and Carmody 2010).

By 800,000 years ago, perhaps earlier, routine cooking would release further energy from "pooled" resources (Kramer and Ellison 2010; Reiches et al. 2009) in a self-reinforcing feedback loop, while adult-to-infant transfers facilitated guided transmission of knowledge about appropriate foods and how to obtain them. As it happens, the best documented nonhuman instances of "tutoring" come from species where alloparents take the initiative in providing age-appropriate foods to immatures (e.g., Rapaport 2011; Rapaport and Brown 2008; Thornton and McAuliffe 2006). Going beyond merely tolerating a youngster taking food, or responding to a beggar (e.g., Jaeggi et al. 2008, 2010; Kano 1992; Silk 1978), callitrichid providers proactively deliver food to infants around weaning age (e.g., Burkart et al. 2007). Allomothers also emit special vocalizations signaling novel foods and actively intervene to prevent youngsters from ingesting inappropriate or toxic items (Byrne and Rapaport 2011; Rapaport and Ruiz-Miranda 2002). Such mentoring helps explain why foragers growing up in groups with many helpers may be more adept at harvesting (e.g., Langen and Vehrencamp 1999 for cooperatively breeding magpie jays).

Provisioning of immatures almost certainly preceded the emergence of more generalized adult-to-adult food sharing. This sequence is consistent with accumulating evidence that Pleistocene humans could not have reared young without allomaternal provisioning. Among virtually all Africans still living as hunter-gatherers when first studied, mothers relied on assistance from a fluctuating array of group members of both sexes and various ages, from as young as 10 to over 60 (Blurton Jones et al. 1997; Burkart et al. 2009; Crittenden et al. 2010; Hawkes et al. 1989, 1998; Hewlett and Lamb 2005; Hill and Hurtado 2009; Ivey 2000). According to the cooperative breeding hypothesis, human life histories evolved as by-products of alloparental supplementation of parental provisioning (Hawkes and Paine 2006; Hrdy 1999, 2005; Konner 2010: Chap. 16; Kramer 2009; Newson and Richerson 2013). In particular, inclusive fitness benefits accruing to foragers who remained productive and willing to provision younger kin provide the most plausible explanation to date for why, among humans but no other apes, females go on living for decades after menopause (Hawkes et al. 1998; Kim et al. 2012).

With enhanced buffering of young against food shortage, constraints on slow maturation and post-weaning dependence would be attenuated. Even in the face of fluctuating rainfall and unpredictable resources (Newson and Richerson 2013; Potts 1996) or other challenges, hominins could afford to grow up slowly. They could also accommodate steep learning curves and other challenges from migrating into novel habitats (Hrdy 2005). Meanwhile, stacking of offspring improved the capacity of populations to bounce back after crashes (Hawks et al. 2000; Hawkes and Paine 2006).

Augmentation of energy available to mothers and infants probably also played a role in encephalization (Isler and van Schaik 2012; Navarrete et al. 2011). Isler and Van Schaik (2012) propose that provisioning during periods of rapid brain growth at the end of gestation and during lactation stabilized resource availability. They view this as the "first step" in the threefold increase in brain size characterizing anatomically modern humans. Again, sequence matters. Rather than needing 1,350 cc brains to orchestrate cooperative care, shared nurturing was essential for the evolution of such big brains (Hrdy 1999, 2009).

Changing Our Minds: Psychological Corollaries of Cooperative Breeding

The ongoing paradigm shift within evolutionary anthropology requires a reassessment of early assumptions about the prevalence of exclusive maternal care during humankind's "environment of evolutionary adaptedness" (e.g., Bowlby 1971 [1969]). At the same time, new findings from social neuroscience are Bowlbian attachment theory's central premise regarding the importance of early social experiences (Carter et al. 2005). If infants first develop a sense of self and "internal working models" about their world through responding to others' responses to them, and if as psychiatrist Daniel Siegel puts it, interaction with “the mind of another seems to catalyze the development of self-awareness” (2012), then early social interactions affect both the formation of neural connections and regulation of gene expression. Developmental psychology can now be construed as the study of how children’s minds grow within the context of their relationships with family. Thus, revising our ideas about exactly who constituted “family” in humankind’s environment of evolutionary adaptedness means rethinking neural development. New modes of child rearing mean changing our minds, literally.

As in all primates, maternal nurture was critical for hominin infants’ survival. Frequent breast-feeding along with co-sleeping continued to guarantee this very special relationship. However, as new circumstances made allomaternal as well as maternal care and provisioning increasingly essential, the hominin infant’s own mother ceased to be the sole source of security, warmth, mobility, and nutrition. Neither could infants rely on their mother to obsessively maintain contact with them day and night for the first 6 months of their lives, as is typical of all other extant ape mothers, who thereafter continue to suckle them and remain reliably within eye- or ear-shot for 4 or more years,. Their need for care and feeling secure remained unchanged (Bowlby 1969), but these hominin infants could no longer count on nearly single-minded dedication from a mother who prioritized their well-being above that of all other current and future offspring.

Even prior to conception, all through gestation, lactation, early and late childhood and beyond, this hominin mother’s nutritional status depended on how much social support she had. Her lifetime reproductive success would depend on how strategically she allocated maternal investment between costly, closely spaced offspring. In the hours and days immediately after birth, a postpartum mother’s perception of social support influenced how primed she would be to pick up and hold close the little stranger that had just emerged from her body, and how likely that infant would be to successfully latch onto nipples and, through initiating lactation, promote continued contact and over time the formation of a profoundly close social bond. With the exception of very young or inexperienced first-time mothers or unusually dire circumstances (Hrdy 1999), primate mothers are remarkably undiscriminating, displaying nearly unconditional dedication (e.g., Matsuzawa 2012; Turner et al. 2012). The main exceptions fall among marmosets, tamarins, and humans who, unlike other primates, discriminate on the basis of both infant attributes and availability of allomaternal support. They may abandon, actively reject, or kill specific newborns (Bardi et al. 2001; Culot et al. 2011; Tirado Herrera et al. 2000 for callitrichids; Hrdy 1999 for review of human evidence).

Increased reliance on allomaternal assistance must have been accompanied by both increased maternal sensitivity to cues of social support and selection favoring aptitudes for eliciting it. At the same time, shorter interbirth intervals combined with prolonged juvenile dependence (and perhaps also a greater need for group consensus regarding a specific infant’s viability?) intensified pressure on mothers to evaluate attributes and prospects of each newborn in relation to prospects for older but still dependent siblings, as well as prospects (possibly better?) for any future sibling whose arrival might be delayed or accelerated by the fate of this one. Over generations, a mother's reproductive success and that of close relatives would depend upon how well she negotiated the cost/benefit trade-offs implicit in Hamilton's Rule. Thus was a newly conditional maternal commitment overlain upon the single-minded dedication typical of most primate mothers, helping to explain the curiously prevalent maternal ambivalence in human primates (Hrdy 1999: Chap. 20; Parker 1995).

And what of fathers? As in many primates, paternal commitment would be influenced by both paternity probabilities and alternative mating options. However, among cooperatively breeding hominins, fathers also needed to take into account the availability of alternative nurturers (Meehan 2005). When feasible, hunters preferentially channel meat to their own offspring (Marlowe 2010), but genetic progenitors were not the only hunters bringing back meat to share (Hill and Hurtado 2009; Kaplan et al. 2000; Lee 1979). Furthermore, taking advantage of occasional protein and fat bonanzas was only practical if people could count on more reliably available fruits, tubers, nuts, and other foods gathered by women, to tide them over when hunters returned empty-handed (Lee 1979; Marlowe 2010: Fig. 3.11). As reported by Hawkes et al. (1989) and subsequently confirmed by Marlowe (2010: Fig. 3.11), postreproductive women without infants of their own forage more diligently and bring in more calories than do mothers of childbearing age, with patrilineal as well as matrilineal grandmothers making substantial contributions to child well-being. In some African habitats, children as young as 10 also shared gathered food with younger siblings and more distant kin (Blurton Jones et al. 1997). Just who contributed how much varied so that the fungibility of nurture as well as residential mobility would have been essential for maintaining fits between local conditions and an appropriate mix of providers.

Like other mobile fission-fusion primates (Schreier and Swedell 2012), human hunter-gatherers gravitate away from adversity and toward opportunities, including better access to food, water, and security. Add to such incentives the need for allomaternal assistance and variable impulses among postreproductives to provide it (e.g., Blurton Jones et al. 2005; Scelza 2011). Fortuitously, our last common ancestors with other apes were probably characterized by more flexible transfer patterns than usually assumed. Far from typical, the extreme male-philopatry and xenophobia reported for chimpanzees look more like derived troglodytian outliers than hominoid norms (Koenig and Borries 2012). Even among chimpanzees, females remain in their natal range when the benefits of doing so outweigh the costs of staying (Pusey et al. 1997; Hrdy 1999). Over time, long-distance relationships maintained with kin and "as-if kin" alike would have facilitated flexible group composition among hominin foragers and, with it, more flexible parenting.

Porous social boundaries meant that newcomers with useful services to offer, whether skilled hunters or productive older kinswomen, would have been particularly welcome, while groups with adept hunters or healers (often older men) might be especially attractive (Wiessner 2002b). In this way, flexible group compositions essential for cooperative breeding would have also enhanced exposure to novel artifacts and technologies, not only laying the groundwork for the more formalized exchanges that eventually became hallmarks of hunter-gatherer lives (Wiessner

1977, 2002a) but also for more far-flung kin and as-if kin networks (Wiessner 2002b). Concurrently, psychological corollaries of alloparental provisioning, such as enhanced mutual tolerance and dependence along with the tutoring impulses seen in many cooperative breeders, would have further encouraged social transmission of knowledge (Burkart and van Schaik 2010; Byrne and Rapaport 2011; Rapaport and Ruiz-Miranda 2002).

But what of the implications for infants on the receiving end of all this investment by others? Heightened maternal discrimination would have produced selection pressures on neonates to emerge looking full-term and robust and, after birth, to expeditiously get to the critical task of initiating lactation. Should a mother's commitment falter, infants would do well to catch her attention, vocally reminding her of their vulnerability. Over the course of development, hominin infants and children needed to monitor not only their mother's location and intentions but also those of other potential caretakers. In the process infants, became conditioned by rewards when solicitations succeeded, and disappointed or worse when they misgauged. Such social conditioning affected phenotypic outcomes – what a neuroscientist conceptualizes as the individual's "neural net profile" (Siegel 2012; also see Gopnik 2010).

When availability of allomaternal care is correlated with child survival, as has been repeatedly documented for cooperatively breeding monkeys and, to a lesser extent, for humans (e.g., see Bales et al. 2002 and Garber 1997 for callitrichids; Ivey 2000; Mace and Sear 2005; Sear and Mace 2008, and Lahdenperä et al. 2004 for humans),[1] it can produce directional social selection favoring infant phenotypes that are better at soliciting nurture.

Social Selection Favoring Other-Regarding Aptitudes

Social selection (sensu West-Eberhard 1979, 1983, 2003) entails competition with conspecifics for access to some resource. "Competition" need not imply individuals directly duking it out over a desirable tidbit or location. Consider the conspicuous natal coats typical of many infant-sharing monkeys. Their flamboyance attracts attention from available allomothers while diverting care from other infants born that season (Hrdy and Hrdy 1976). The situation for human babies is different. Right after birth, it is their mothers, not allomothers they need to appeal to. Lacking flamboyant natal coats, human neonates are much fatter than other apes. These fat deposits fuel thermoregulation and stockpile energy for a fast-developing brain (e.g., Matsuzawa 2012), but plumpness may also make neonates appear full-term

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[1] Note that, depending on ecological and customary circumstances (usually having to do with inheritance of property), child survival can also be inversely correlated with the presence of allomothers, including grandmothers (e.g., Voland and Beise 2005; Sear 2008 for the Malawi; Strassmann and Garrard 2011). However, such exceptions have never been reported among band-level hunter-gatherers and thus fall outside of the scope of this chapter.

and robust so as to advertise to their mother that they merit the prolonged investment that will ensue once she allows the baby to suckle, initiating lactation and the ensuing cascade of bonding processes (Hrdy 1999: Chap. 21). Even though no other baby is in sight, this newborn is competing with both older siblings the mother might otherwise continue to invest in and an as-yet-unborn sibling the mother might produce were she to resume cycling sooner. As they mature, babies need to appeal to others as well through monitoring their tastes and intentions – a psychological dimension to Lorenzian *Kindschenschema*. Mothers as well have a stake in making their babies attractive since they too are competing with other mother-offspring dyads for allomaternal assistance (Hrdy 2009).

Conspicuous natal coats presumably attract the attention of predators as well as caretakers, whereas fetal fat deposits built up just prior to birth can impede passage through narrow birth canals. Such costs must be somehow offset. As with Darwin's example of the peacock's tail, otherwise disadvantageous traits continue to be favored if they increase chances of being "chosen" by another (Lyons and Montgomerie 2012; West-Eberhard 2010). This infantile equivalent of "sex appeal" is consistent with the discovery that reward centers in the brains of human alloparents as well as parents are activated merely by looking at cute babies (Glocker et al. 2009; Kringelbach et al. 2008).

In analyzing various contexts where humans benefit from appealing to others, the psychiatrist Randolph Nesse invokes "runaway" social selection to explain why humans so often depart from rational self-interest by remaining loyal to a person or an ideal, by behaving generously when they do not have to, or by otherwise engaging in selfless conduct that exceeds reasonable expectations of return (2007, 2010; see also Flinn and Alexander 2007). People do so, Nesse argues, because selflessly generous or honest behaviors enhance that individual's likelihood of being chosen by an advantageous social partner. Such a partner may in turn benefit from that choice. Such "runaway" social selection only occurs when signal and response are genetically or culturally correlated and both co-evolving. According to Nesse, people's acute sensitivity to embarrassment and the powerful constraining self-consciousness that we call "conscience" (and with it, perhaps, blushing) evolved through social selection as part of the internal monitoring system that helps an individual "behave well" so as to compete with others directly or, more often, indirectly to be chosen by advantageous social partners (see also Boehm 2012).

With such logic in mind, consider how early self-conscious emotions are manifested in our species. I hypothesize that such sensibilities first emerged as corollaries of cooperative breeding in an ape lineage. That is, our ancestors were emotionally pre-adapted for self-consciousness because, in the high-child-mortality environments that presumably prevailed throughout the Plio-Pleistocene, prolonged dependence on an array of caretakers with highly contingent levels of commitment generated novel selection pressures such that, over generations, dependents neurologically disposed to be more "other-regarding" were better cared for. Darwinian social selection would have favored those who grew up more interested in the thoughts, feelings, and needs of others, an emotionally quite distinctive kind of ape, prepared to recognize what expressions, vocalizations, or behaviors would appeal to specific others.

Primate Preadaptations for Cooperative Breeding

Old World monkeys and apes navigate complex, emotionally mediated relationships. They remember whom they grew up around (and thus are probably related to) and who is currently dominant over whom, or likely to soon be so. They recognize special competencies and track reciprocal interactions over time so as to differentiate between useful versus unreliable, potentially harmful, associates (Cheney and Seyfarth 2007; Mitani 2006; Schino and Aureli 2009). If death of a high-ranking relative disrupts an advantageous relationship, primates opportunistically seek substitutes, related or not (Seyfarth and Cheney 2012).

Internalized systems for emotionally based “bookkeeping” similar to that found in cercopithecine primates (Schino and Aureli 2009) and modern humans (Hrdy 1999) surely characterized early hominins as well. Combined with the neurophysiological scaffolding for registering the whereabouts and current condition of tiny individuals outside themselves that is universally present in mammals (Carter et al. 2005), such aptitudes helped mothers decide whether or not to allow allomaternal access to vulnerable newborns. Although all primate infants are attractive to at least some would-be allomothers, voluntary shared care only occurs when mothers feels sufficiently confident of their infants’ safe return. I suspect this is why shared care is only observed in primates where allomothers seeking to hold an infant could be trusted, as in the case of close matrilineal kin or probable progenitors (Hrdy 2009, 2010).

Primate infants are known to be universally attractive to some others, particularly pre-reproductive females and, under some circumstances, adult males. Less attention has been paid to females nearing the end of their reproductive careers. Among langur monkeys, selfless impulses increase as reproductive value declines, e.g., as old female langurs opt out of competition for food yet risk mortal injury defending younger relatives against infanticidal males (Hrdy and Hrdy 1976). Yet this obvious preadaptation for cooperative breeding did not lead to longer post-menopausal life spans in other primates, as Hawkes hypothesizes it did in humans. Without food sharing, opportunities for post-reproductives to enhance the fitness of kin would have been more sporadic than chronic (Hrdy 1999, 2009).

Meanwhile, over millions of years, as maternal horizons expanded to include caring relationships with others besides their own infants, so did cortical capacities for mediating between complex social experiences, long-term bonds, and emotions (Carter et al. 2005). Given this legacy, it is unsurprising that social experiences early in life continue to shape both brain development and subsequent social relationships across primates, and especially in humans (reviewed in Siegel 2012). How can we test the proposition that pre-human apes who relied on multiple caretakers would develop different cognitive and emotional aptitudes than apes reared exclusively by their mothers?

Virtual and Real “Tests” of Assumptions Integral to the Mothers-Plus-Others Model

None of us has a machine to go back in time to observe how hominin infants responded to mothers and allomothers. What we do have are (1) observations from collateral, extant lines of great apes (mostly *Pan troglodytes*) that allow us to study how infant apes respond to different caretaking regimens and (2) new findings from neuroscience that enable us to compare brain development in chimpanzees and humans.

Elsewhere (Hrdy 2009), I reviewed such limited evidence as I could then find that infants with several attachment figures grow up better able to integrate multiple mental perspectives (e.g., Van IJzendoorn et al. 1992). Allomaternal support, whether from a grandmother in the same household or just transient visits by as-if supportive kin, accelerates or enhances social awareness and an infant’s sense of security, both for infants born to young, inexperienced, or unmarried mothers who might otherwise be at risk of insecure attachment (Spieker and Bensley 1994; Olds et al. 2007; Hrdy 2009) and to infants among Aka foragers securely attached to their own mothers plus four to six familiar, trusted others (Meehan and Hawks, submitted for publication). Such findings are consistent with my assumption that shared care and provisioning among already highly social, clever, tool-using and also bipedal apes produce phenotypes increasingly attuned to others. Then assume also that, in each generation, infants a little better at reading the mental states of others and motivated to appeal to them would be better cared for and better fed. Over evolutionary time, immatures would be subjected to directional social selection favoring other-regarding aptitudes (Fig. 3). Although scarcely conclusive, indirect evidence from comparative infant development and comparative neuroscience helps us evaluate the plausibility of these underlying assumptions and also helps to generate new predictions or tests. Let’s begin.

Does Allomaternal Involvement in Rearing Chimpanzees Affect Resulting Phenotypes? And if so, How?

As Bowlby noted long ago, all higher primates are born with innate capacities for emotional engagement and become attached to their most reliable caretaker, usually the mother. Chimpanzee infants cling tightly to this caretaker and calm when held close by her (Bard 2012). At night, infant chimpanzees held by their mothers cry even less than co-sleeping human infants do (Matsuzawa 2012). By 1 month of age,

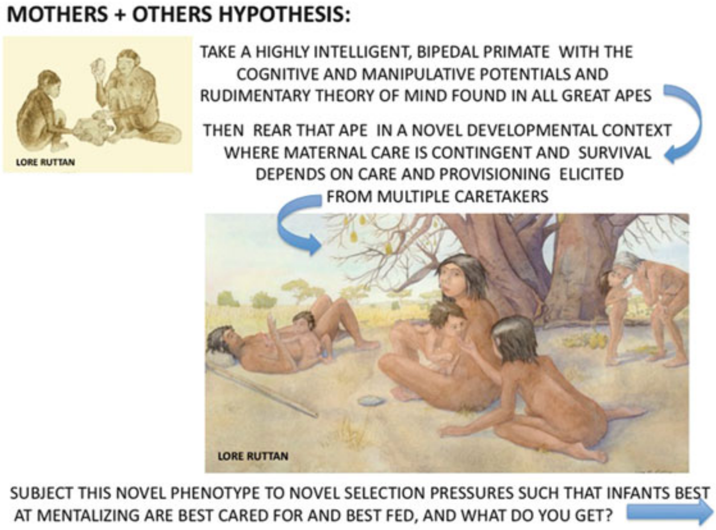

Fig. 3 The mothers-plus-others hypothesis assumes cooperative breeding emerged early, perhaps with *Homo erectus* in the early Pleistocene, and attempts to explain the initial emergence of “emotionally modern” humans through development’s role in the production of selectable variation, as in this graphically presented thought experiment (Art by L. M. Ruttan)

both human and chimpanzee infants recognize and preferentially respond to their mother’s face. Human infants, however, continue to distinguish between their mother’s face and the faces of other individuals long after the stage when infant chimpanzees cease to do so. By the age of 2 months or so, infant chimpanzees no longer discriminate between an image of their own mother’s face and that of a composite digitally generated by averaging chimp faces (Tomonaga et al. 2004).

The frequency of mutual gazing between chimpanzee infants and their mothers is inversely correlated with how much physical contact they have. Between birth and 2 months, as the chimpanzee mother cradles her infant less, the incidence of mutual gazing rises (Bard 2005). Experimental psychologists and cross-cultural anthropologists report a similarly inverse correlation for humans. A Western baby held by his or her mother looks into her face less than does a baby securely propped up on a couch nearby (Lavelli and Fogel 2002). Meanwhile, across traditional societies, babies in societies characterized by more direct tactile contact between infants and mothers exhibit less mutual eye gazing than do babies who are off their mothers more (Keller 2007; see also Bard 2012).

Like chimpanzee infants, human infants out of direct contact with their mothers (but still in non-anxiety-provoking situations) feel a need to “stay in touch without touch,” monitoring their mothers’ expressions more and frequently “checking back” (cf. Falk 2004a, b). Being off the mother alters phenotypic behavior, increasing how often infants attend to faces and the motivations of those nearby. It is also apparent that, at some point in the past, ancestors of human infants must have become more discriminating about the identity of caretakers. Both observations are consistent with a legacy of multiple caretakers and, with it, more conditional maternal commitment.

Little if any pointing or social referencing goes on among wild chimpanzees or among captive-born ones with limited human exposure. However, even though nothing like the eager questing for intersubjective engagement characteristic of humans has been reported, human-reared chimpanzees do communicate intentions to others and even refer someone else to look at something they are interested in (Bard 2012; Leavens et al. 1996; Menzel 1999).

Clearly, rearing conditions, including extent of allomaternal experience (albeit with allomothers of a different species), alter ape phenotypes. Chimpanzees reared in human families (some being trained to use sign language) prove better than their wild counterparts at communicating likes and dislikes through gestures, following with their eyes what someone else is pointing to, and even pointing themselves at what they want. Human-reared chimpanzees are also better at reading human intentions and emotional states and are more inclined to coordinate activities with others (e.g., Fouts and Mills 1997; James Marsh’s 2011 documentary “Project Nim”). Life stories of human-reared chimpanzees are problematic and raise serious ethical as well as scientific questions. However, we are beginning to have more thoughtful, carefully controlled and also hopefully more humane case studies confirming that chimpanzees possess the basic neurological equipment to register someone else’s goals. Exposure to helpful human caretakers really does seem to enhance an ape’s capacity to understand what another needs. In innovative recent experiments, Yamamoto and colleagues (2012) demonstrated that some chimpanzees (all had experienced relationships with trusted human caretakers in addition to their own mothers) could correctly identify the intended goal of another chimpanzee in an adjacent cage and sought to help with the task.

Five of these mother-reared, experimenter-trusting, human-socialized chimpanzees were caged beside five other chimpanzees that were either close kin or as-if kin. In one set of experiments, a window in the partition separating the cages permitted the tool provider to see which tool (from an array of seven) was needed to access a sweet juice reward. In a second set of experiments, the provider was prevented from seeing what the other chimp was trying to do. With vision obscured, tool selection was random. However, when the provider could see what the other chimp was trying to do, he almost always selected the correct tool (a brush or a straw), qualifying the assistance as “targeted help” that takes into account the intentions of the recipient. Such findings are consistent with characterizations of chimpanzees and bonobos as possessing capacities for rudimentary empathy and concern for others, as has long been advocated by de Waal (for updates see de Waal 2006, 2012; de Waal and Ferrari 2012; Warneken et al. 2007).

Of Yamamoto’s five subjects, a chimp named Ayumu stood out as the most other-regarding. Like the other chimpanzees in the experiment, Ayumu was cared for by his own mother (Ai) and, together with his mother, was repeatedly exposed to the same trusted tester. The chimps in these studies are usually described as having a “strong bond” with these testers (e.g., Hayashi and Matsuzawa 2003). However, in Ayumu’s case, allomaternal exposure went beyond that. Right from birth, Ayumu had interacted face-to-face with a particularly responsive experimenter in the person of Tetsoro Matsuzawa, who had spent years patiently interacting with Ai, cultivating her confidence. When Ayumu was born, Matsuzawa became the first scientist ever voluntarily granted access to a newborn by a mother chimpanzee. As a consequence, Ayumu was reared as few chimpanzees ever have been. Was it a coincidence then that, when paired with his own mother in the experimental condition, where the tool provider was prevented from seeing what the other chimp needed, Ayumu was the only one of the five subjects motivated to clamber up the wall and peek over the barrier before handing his mother exactly the tool she needed?

It is not yet clear whether Ayumu was just innately more resourceful or curious, or whether prolonged and intimate exposure to a human allomother conditioned him to be more interested in what someone else might need. From the wild, there are even fewer reports of helping behaviors (e.g., Snare 2012). Nevertheless, even if such capacities usually remain latent, I think we can say that other apes, certainly chimpanzees, possess the basic neural wiring for targeted helping under some conditions. From the wild, the best-documented exceptions where chimpanzees appear to cooperate involve monkey hunting by adult males at Taï Forest. As they pursue their prey, one may post himself below a tree where dinner is likely to descend. Depending on the actual intention behind this mutually beneficial act (whether self-serving, other-regarding, or both), it might count as targeted helping (see Boesch and Boesch-Achermann 1990; Boesch et al. 2006; Tomasello et al. 2012). Nevertheless, compared with humans, wild chimpanzees simply do not engage in targeted helping or cooperation nearly as much or as readily as humans do. The question here is whether rearing by multiple responsive caretakers enhances the requisite perspective-taking?

The closest thing to the relevant experiment we have derives from a long-running project that Kim Bard and coworkers set up while seeking ways to improve psychological well-being in captive-born chimpanzees. To this end, Bard monitored outcomes for chimpanzees under three rearing conditions. Infants were either reared by their own mothers or, in cases where maternal care proved inadequate (as is all too often the case in captivity), were removed and reared in communal nurseries under one of two conditions: in “standard” communal nurseries where their physical needs were met by a series of human caretakers or else in special “responsive care” communal nurseries. In the responsive care situation, familiar, specially trained human caregivers, essentially allomothers-of-another-species, interacted with and stimulated infants for several extra hours, 5 days a week (Bard 2005, 2012). In what follows I summarize Bard’s findings as if they represented results from a “natural” experiment exploring how “proxies” for humankind’s last common ancestors with other apes might have responded to socioenvironmental conditions requiring shared care.

The responsive care infants who interacted with multiple (albeit human) allomothers engaged in more frequent and more sustained mutual eye gazing than either wild chimpanzees or captive infants cared for exclusively by their mothers

(Bard 2005). By 3 months of age, they also exhibited more frequent social smiles. Tested at 9 months using the Bayley Scale for Infant Development (no language required), chimpanzees receiving extra attention from responsive allomothers exhibited more advanced cognitive development than nursery-reared chimpanzees that had not received extra attention. Bard refers to this "responsivity to social interaction" found in both human and chimpanzee infants during face-to-face gazing as "primary intersubjectivity" (different from Trevarthen's "secondary intersubjectivity").

Under suboptimal captive conditions, emotionally deprived chimpanzee infants exhibit similar behavioral disturbances to those observed among institutionalized human children receiving inadequate personal attention. Such infants are unable to mount any organized response to attachment figures – freezing, for example, instead of running to them for comfort. Bard collaborated with Dutch developmental psychologists who had been comparing attachment styles in children from intact nuclear families versus those reared in understaffed orphanages. Their collaboration (van IJzendoorn et al. 2009) was the first to document "disorganized attachment" in another species of primate. It was also the first "prospective" intervention study to evaluate how care differing in quality and quantity of interactions affects cognitive development and emotional security in nonhuman apes.

For obvious reasons, infant-care regimens were quite different for colony-reared chimpanzees and for children. Twenty-nine infant chimpanzees were placed in standard care after being removed from mothers that were deemed inadequate. They were placed in nurseries with a small group of other infants attended by one of four staff members who provided minimal human contact, feeding them and changing their diapers several times a day. Another 17 received responsive care, spending some 4 h, 5 days a week, with one of five caretakers, all familiar and trained to sensitively engage chimpanzee infants (Van IJzendoorn et al. 2009). When tested at 9 months using various measures, including the first-ever application of Ainsworth's Strange Situation procedure to nonhuman apes, chimpanzee infants reared with standard care exhibited attachment disorders similar to those in institutionalized human children. However, infants from the responsive care program tended to be emotionally more secure and also tested significantly better on cognitive development than standard care chimpanzees.

Even though none of these captive infants was reared under species-typical conditions, those exposed to multiple responsive others developed to be more other-regarding than their exclusively mother-reared counterparts. Clearly, interpersonal experiences in the months after birth had a profound impact on resulting phenotypes. Presumably, infant apes in Bard's responsive care condition were expressing cognitive and emotional capacities that otherwise remained latent among chimpanzees in continuous one-on-one contact with their mothers in natural settings. Nevertheless, other-regarding does not mean the same thing in a year-old chimpanzee as in a human.

Among the more striking differences is the relative eagerness with which an infant that is accustomed to responsive care seeks to share experiences with someone else by calling their attention to some object in a triadic interaction.

By 9 months of age, a human infant will hold out an object to a caretaker while eagerly monitoring their reaction to it (Tomasello 1999), as if inquiring, "What do you think of this? And, what should *my* response be?" By that age, however, young chimpanzees (even though interested earlier) are losing interest in that game (Tomonaga et al. 2004). It is not that infant chimpanzees never exhibit such joint attention. Outside the lab, young chimps have been observed interacting with other chimpanzees, cueing off one another's responses to an object. The differences seem to lie in frequency and enthusiasm for mutual engagement during shared attention or, as Kim Bard puts it (personal communication, 2012), the amount of "positive affect" surrounding joint attention.

Like Tomasello (1999), researchers at the Primate Research Institute in Kyoto considered "object-showing" and "object-giving" indicative of "referential communication in a triadic relationship." They specifically set out to learn whether a "nine month revolution" comparable to that in humans occurs in chimpanzees. Given similarities in terms of mutual gazing, smiling, and so on, up until that point, it seems odd that apes endowed with mirror neurons and capable of monitoring and imitating the expressions of others would not develop the same level of interest in sharing another's experience of an outside object that 9-month-old humans do. But they do not. Neither do they develop it later on (Tomonaga et al. 2004; Tomonaga 2006; see also Matsuzawa 2007).

Humans' interest in what others think about something else starts to emerge before language. Six to nine months of age is also roughly the time humans start noting the sounds others use to identify specific things and first learn to recognize common nouns (Bergelson and Swingley 2012). By age 5–7 months, humans also first emit recognizable strings of phonemes. This convergence prompts us to ask if the human infant's enthusiasm for triadic interaction might be due to the need to get ready to acquire language? Or did language evolve among our ancestors because early hominin infants were already interested in monitoring the mental states of others, already prone to babble?

I agree with anthropologist Dean Falk and others (Falk 2004a, b; Locke and Bogin 2006) that babbling probably first emerged as a by-product of infants seeking to attract attention. We differ, however, in our reconstructions of the conditions under which babies did so. In line with this proposed "attention-getting" function, pygmy marmosets begin emitting similarly nonsensical but highly appealing vocal streams at just the age when infants in this cooperatively breeding species need to attract allomaternal attentions (cf. Elowson et al. 1998). As in marmosets, human "babbling" coincides with the developmental stage when interactions with allomothers begins to be most relevant. (Hrdy 2009). In humans this is about 6 months, when the milk teeth come in, infants are fed premasticated or soft foods via kiss-feeding, and, among the Aka at least, there was a marked increase in "attachment behaviors" with allomothers. Thus I hypothesize that the babbling that eventually provided practice for language first emerged as a solution to a challenge other apes rarely confronted: the need to stay in touch without touch. Elicitation of attention and even, occasionally, tasty rewards would have provided contingent reinforcement (the most powerful kind) for continued elaboration and refinement of vocalizations (Goldstein et al. 2003).

Beyond maintaining contact and learning, through such conditioning, how best to appeal to others, infants relying on multiple caretakers would also benefit from being able to assess intentions. In this respect, humans are notably precocious. When Yale University cognitive psychologists showed 6-month-old babies cartoons of a red ball struggling to roll up a hill, either helped by a yellow triangle nudging the ball upwards or hindered by a blue square shoving it back down, babies subsequently looked longer and were more likely to reach out to the helpful symbol (Hamlin et al. 2007). As early as 3 months and certainly by 6 – still before language -infants preferred looking at the helpful character (Hamlin et al. 2010, 2011). They were discerning who is potentially helpful? Who is not?

By 8 months of age, not only are babies making fairly sophisticated social judgments, they are beginning to assign “reputations.” By two, toddlers preferentially provide treats to third parties who behaved positively toward someone else who behaved prosocially, withholding treats from obstructive individuals (Hamlin et al. 2011). By ages three to five, children’s own experience of being shared with influences their decisions about how much to share with another depending on that individual’s past contributions or “merit” (Kanngiesser and Warneken 2012).

In other words, as Henry Wellman and colleagues put it, “social cognition develops in infancy, revolving around understanding of human agents as intentional goal-directed beings and this understanding develops into preschool understanding of persons as mental beings” (2008, p. 622). Those attending to intentional behavior early in development (at 14 months) also test better at theory of mind tasks when they are preschoolers. Furthermore, as reported earlier, infants with more older siblings and caretakers manifest theory of mind at younger ages (Perner et al. 1994; Ruffman et al. 1998).

Adult chimpanzees can also assess competence and, in laboratory tests, they prefer reliable partners (Melis et al. 2006) and also respond more positively to “cooperative” versus obstructive others (Hamann et al. 2011). However, to my knowledge, no one has tested infant chimpanzees or bonobos using the sort of experimental protocols Hamlin et al. used. Thus we do not yet know at what *age* or under what circumstances chimpanzees develop these assessment capacities. Do chimpanzees register the social reputations of others as early as human infants do? And do they do so in the wild or only when socialized in human settings? Neither do we know if social selection operated on earlier humans so as to enhance such discriminative capacities. However, preliminary evidence coming out of the Primate Research Institute in Japan suggests that the neural capacity to make such judgments may indeed develop earlier in humans than it did in our last common ancestor with other apes.

Was There Selection for Early Development of Other-regarding Capacities in Hominin Infants? Evidence from Comparative Neuroscience

No mammal takes longer than humans to grow up, a leisurely pace apparent in brain development as well as eruption of the deciduous (or "milk") teeth and molars. Whereas the larger part of adult-like myelination in chimpanzees occurs before birth, in humans neocortical myelination takes place later, throughout childhood. Indeed, neocortical maturation in humans is extraordinarily prolonged, with synaptic pruning in the prefrontal cortex still ongoing into the 30s (Miller et al. 2012). These are early days in the comparative study of anthropoid brain development, an area that is certainly not my field of expertise. Yet it strikes me as noteworthy that, given this general pattern of prolonged development, the parts of the brain devoted to interpersonal judgments develop earlier in humans than in chimpanzees.

This finding derives from a single study still awaiting replication. Using magnetic resonance imaging, Sakai et al. (2010, 2011) compared trajectories of development for prefrontal white matter in 28 human children between the ages of 1 month and 10.5 years; three mother-reared chimpanzees between 6 months and 6 years; and 37 rhesus macaques between 10 months and 5.3 years. Not surprisingly, absolute brain sizes were larger in humans than chimpanzees and much larger than those of macaques. Yet unlike monkeys, both human and nonhuman apes exhibited delayed maturation of the prefrontal cortex, the brain region mediating working memory, motivation, temporal awareness, decision making, self-awareness and, in humans at least, language (Sakai et al. 2010). The right prefrontal cortex also seems peculiarly implicated in inequity aversion and in how subjects respond to "fair" versus "unfair" offers in experimental ultimatum games. When functioning of their right prefrontal cortex was temporarily disrupted, people tended to respond in a self-serving way regardless of whether the offer made them was equitable or extremely inequitable (Knoch et al. 2006). Presumably this brain region also played a role when infants in Hamlin et al.'s experiments (described above) distinguished "helpful" from "obstructive" cartoon characters.

In the case of unusually clever and Machiavellian, tool-using apes – be they human or chimpanzee – extension of formative periods could presumably be correlated with neuronal plasticity and enhanced mental flexibility owing to extra opportunities for exploration early in life (e.g., Gopnik 2012). According to this view, prolonged neural plasticity allows for learning through both trial-and-error and observation. Anthropologists have long assumed that such extended periods of neuronal plasticity were essential for the evolution of characteristically human higher cognitive functions (e.g., Montagu 1955). Indeed, a need for flexibility is sometimes assumed to be one reason that human brains are so immature at birth and, in this respect, "secondarily altricial" (e.g., Portmann 1962). Similar logic presumably informs the idea that "brain connection development, particularly in the prefrontal portion, may have been under intense selection pressure to remain immature, producing a brain that is more susceptible to acquiring chimpanzee- and human-specific social and technical skills based on early postnatal experience" (Sakai et al. 2011, p. 5).

However, Sakai and colleagues also noticed something else. When controlled for absolute size, white matter development in the frontal cortex developed more rapidly in human than in chimpanzee brains even though (and quite paradoxically) Montagu's logic would lead one to expect an even greater need for flexibility in humans since they grow up absorbing far more cumulative culture than do chimpanzees.

The rapid trajectory of growth in the human prefrontal cortex begins around the second half of the first year of life, coinciding with the increased interactions with allomothers mentioned above, then continues and levels off around age three (Sakai et al. 2011: Fig. 3). This faster rate of prefrontal cortical development contrasts with development in other neural systems, for example, those controlling physical coordination and mobility. In contrast to antelopes and other ungulates with highly precocial infants that off and running within minutes of birth, all apes enter the world dependent on someone else for locomotion. Humans are born most helpless of all, as reflected by the label "exterogestate fetuses". With even less muscle tone or coordination than a newborn chimpanzee, human neonates also do not have the option of catching hold of their mother's body hair. Unless held up by their mother, the only way a human neonate could reach her nipples would be to inch along caterpillar-like, but only if she was horizontal.

By 3–5 months of age, chimpanzee infants grasp and mouth objects more competently than human babies can. Even nursery-reared chimpanzees out-perform little humans in this respect. Chimpanzees presumably also develop chewing capacities earlier, since deciduous dentition erupts at least a year earlier in chimpanzees than in children (by 1.12 years compared with 2.33 years, even though they will be weaned later. Yet by 1 year of age, chimpanzees still do not perform as well as human infants do when pointing out objects, turn-taking, or completing puzzles (e.g., Bard 2012). This is so even though humans and chimpanzees seem equivalently precocious in terms of manipulating objects, exhibiting great competence in object-object combinations and inserting a stick into a hole by 1 year of age.

In terms of overall motor maturation, nonhuman ape infants develop faster than their human counterparts. This difference is apparent to anyone who has watched infant chimpanzees or bonobos crawl, climb, scamper or swing circles around humans of comparable ages. In predator-free, captive environments where less-restrictive chimpanzee mothers allow baby chimpanzees to more fully demonstrate innate abilities, youngsters crawl by 4 months and walk bipedally by 9. By contrast, human babies are only beginning to crawl then and do not walk until the end of the first year. In realms having to do with assessing and discriminating between others, however, these different rates of development are reversed. The white matter in the human prefrontal cortex, the part of the brain that mediates working memory, motivation, temporal awareness, self-awareness, decision making, and eventually language, develops faster in humans than it does in chimpanzees.[2] The brains of human infants, it appears, are only selectively altricial. In respect to assessing others and distinguishing intentions, human infants appear surprisingly precocious. Why?

Apes in the line leading to *Homo sapiens* were walking bipedally by four million years ago, so perhaps the brain-body coordination needed for walking required earlier development in the prefrontal cortex. However, it takes many months before the irregular stepping motions of a baby to become anything like balanced upright walking. Recent analyses reveal that the neural components at work this early are little different from those in other mammals. What distinguishes human bipedality are extra components emerging later in the course of development (Dominici et al. 2011; Grilner 2011), perhaps only emerging "as needed" when needed.

This speculation brings me to the hypothesis I favor: that being able to make interpersonal assessments emerges early because such capacities helped hominin infants more judiciously and effectively elicit maternal and allomaternal care. If such aptitudes began to develop earlier in hominins than physical coordination or other, arguably valuable, abilities, it was because precociality in this realm was advantageous. This hypothesis is not mutually exclusive with more conventional, "head start" explanations by which infants begin early to build the neural scaffolding and infrastructure for later cognitive development (Leigh 2004, cited in Falk et al. 2012) or begin to accumulate experiences acquired through observation, social trial and error, or play that will eventually be useful for negotiating the social and technical complexities of a successful human life (Gopnik 2012).

Glossing over various counter-arguments involving metabolic costs inherent in building neural connections as well as the many specialized capacities that do not develop until needed (and which might even be disadvantageous if they emerged too early) and simply taking the "early start" logic at face value, rapid development of prefrontal connections during infancy might facilitate complex social interactions, providing opportunities for such interactions to continue shaping neuronal connectivity as experience-dependent knowledge and skills build up over time (as in Sakai et al. 2011; see also Luby et al. 2012). An early start might build needed scaffolding essential for language acquisition or other social competencies that evolved later for reasons outside of my scope here. What I want to emphasize here is the sequence. Neither "early start" explanations nor commonly held views about the need for prolonged childhoods in order for humans to fill unusually large, anatomically modern 1,350-cc brains with "social capital" needed for a successful life (Kaplan et al. 2000) are mutually exclusive with the proposal that infants with multiple providers took longer to grow up. All three may have played roles in shaping modern humans. What I am hypothesizing here though is that alloparental

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[2] Sakaii's sample size was small, but it is tantalizing that Ayuma, the chimpanzee co-reared by his mother and human others, was also the chimpanzee exhibiting both unusually well developed capacities for perspective-taking in targeted help experiments (described above) and the fastest trajectory of prefrontal white-matter development of the three chimpanzees scanned (Sakai et al. 2011: Fig. 2).

care, food sharing and, with it, youngsters beginning to take longer to grow up characterized our ancestors prior to the emergence of anatomically modern humans.

Rather than long childhoods evolving to accommodate the growth of big brains, prolonged dependence emerged as a corollary of cooperative breeding. However, with alloparental care came more rapid postnatal development of the frontal cortex and areas of the brain that helps infants monitor and assess commitment levels and intentions of others as well as adjust their facial expressions, vocalizations, hand movements, etc., in ways that engaged and appealed to them. These little apes were already emotionally more similar to modern humans. Shared provisioning permitted the evolution of anatomically modern brains in response to selection pressures favoring them, while "emotional modernity" preadapted these apes to eventually evolve (through processes and feedback loops described elsewhere by Boehm, Flinn and Alexander, Bowles, Tomasello and many others) such behaviorally modern human capacities as language, cumulative culture, or consciences peculiarly attuned to the evaluation of others.

My working assumption is that duration of childhood in *Homo erectus* by 1.8 million years ago fell someplace in between the prolonged childhoods typical of modern humans and the much shorter ones typical of both the genus *Pan* and their anatomically similar australopithecine cousins. There are fascinating hints in the fossil record that larger babies (e.g., DeSilva 2011) and more rapid postnatal expansion of the prefrontal cortex (e.g., Falk et al. 2012; Tague 2012) might go back in the hominin lineage even further than I conservatively postulated in "Mothers and Others" (Hrdy 2009). Either way, it seems unlikely that mothers would have been selected to produce such costly, slow-maturing young without reasonable prospects of assistance. The big question relevant to the evolution of childhood – just when hominins began to be characterized by prolonged nutritional dependence and longer post-reproductive life spans – continues to be debated (summarized by Voland et al. 2005: Table 1.1).

Evolving "Emotionally Modern" Underpinnings for Cooperation: Recap and Conclusions

As a branch of tool-using, bipedal apes equipped with "Machiavellian" social intelligence moved into savanna-woodland habitats and became subject to the ecosystem variability characterizing east Africa from 2 to 1.8 million years ago, selection favored both a more varied diet (including more meat) and a wider array of provisioners. Indeed, cooperative breeding is especially likely to evolve with unpredictable rainfall and, with it, abrupt swings in food availability. With mothers increasingly dependent on allomaternal support, food delivered to immatures produced situations where more generalized food sharing could also get underway. Such sharing increased the chances of survival in famine times while allowing for shorter intervals between births when conditions improved, allowing at least some populations to bounce back after crashes.

Cooperative breeding brought about life historical and psychological changes in all parties concerned, including mothers, fathers, alloparents and, especially, immatures, upon whom selection impacted most immediately and heavily. I hypothesize that, to survive, infants had to become connoisseurs both of mothers and of others. This transformation was mediated via development's role in the production of selectable variation (West-Eberhard 2003). Over generations, immatures buffered from acquiring and processing all their own food could afford to delay the costly production of adult bodies, dentition and brains. However, the need to solicit care required speeding up and refining the development of other capacities important for perspective-taking, understanding how to appeal to others and assess their intentions, which are critical preadaptations for the role reputations would increasingly play in human social organization.

In the absence of direct evidence, I attempted to "test" the underlying assumptions of this mothers-plus-others model by reviewing evidence for how the best available proxies we have for humankind's last common ancestor with other apes (chimpanzees and modern human infants) respond to different rearing conditions. Findings from these "as if" experiments reveal that infants spending time off mothers and those interacting with, and responsively attended by, multiple caretakers develop cognitively and emotionally in the predicted directions. They pay more attention to faces and expressions of potential caretakers, strive to attract their attention and to appeal to them, attend better to their communicative cues and goals and are more likely to engage in targeted helping. Differences in neural development in humans compared to chimpanzees may also be consistent with the mosaic pattern of brain development hypothesized here.

I am not proposing that humans are cooperative because their ancestors were "cooperative breeders." Rather, I believe that these more other-regarding – and, in this sense, emotionally more modern – apes were preadapted for the subsequent evolution of increasingly coordinated social enterprises. At the same time, food sharing would have magnified opportunities for already highly social apes to repeatedly interact with the same individuals over time and benefit from exchanges, providing fertile ground for selection to specifically favor cooperative responses (e.g., Axelrod and Hamilton 1981; Fehr and Fischbacher 2003; Rand et al. 2012).

With no foresight on Mother Nature's part, the same sort of selection pressures that favored cooperative breeding in many other highly social species struggling to rear altricial young in the face of difficult-to-extract and unpredictable resources led to alloparental care and provisioning and, with them, longer childhoods and life spans in our own species. There is no need to invoke "exceptional" processes to account for improved perspective-taking and other-regarding impulses that initially emerged as predictable corollaries of cooperative breeding, albeit corollaries that in an already cognitively sophisticated ape would lay the foundations for the eventual evolution of such uniquely human attributes as language, complex social coordination, and elaborate conscience-based moral systems.

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On Faces, Gazes, Votes, and Followers: Evolutionary Psychological and Social Neuroscience Approaches to Leadership

Mark van Vugt

Abstract Leadership is arguably one of the most important themes in the social sciences, permeating all aspects of human social affairs, from the Euro zone crisis to the re-election of the first black president in the US. Parallel findings across the biological and social sciences suggest that there are both commonalities and differences between humans and non-humans in leadership and followership. Here I propose a new theory of leadership inspired by an evolutionary perspective and informed by recent findings in evolutionary biology, social and cognitive psychology, and social cognitive neuroscience. I will identify some of the evolved functions, developmental origins, and proximate mechanisms underlying leadership and followership in humans. In addition, I will suggest which aspects of leadership are unique and which are shared with other animals and offer new ways of studying leadership and followership employing psychological and neuroscience methods.

Introduction

When a honeybee returns to its hive after foraging for nectar, it performs a dance for the other bees. The bee skips around making a figure-of-eight movement, waggling its abdomen as it does so. Recent findings suggest that the dancer is indicating through its moves the location and quality of a foraging site (Riley et al. 2005), which confirms an earlier discovery by the biologist Karl von Frisch. The direction the bee is facing points to the direction of the food source relative to the sun; the

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M. van Vugt (✉)
Department of Social and Organizational Psychology, VU University Amsterdam, Amsterdam, The Netherlands

Institute for Cognitive and Evolutionary Anthropology, University of Oxford, Oxford, UK

Centre for the Study of Group Processes, University of Kent, Kent, UK
e-mail: m.van.vugt@vu.nl

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duration of the waggle dance represents how far the source lies and its quality. The dancer bee is, in fact, acting as a leader by scouting out food resources for the hive. The best dancers recruit the most followers and this interaction produces a very efficient group performance. The waggle dance of the honeybee is one of many forms of leadership and followership that have been observed in non-human animals, from the migration patterns of birds to foraging activities of fish and peacekeeping and warfare among chimpanzees (King et al. 2009; Van Vugt and Ahuja 2010).

In humans leadership is common, too, and it helps group members to coordinate their actions. When four individuals play a coordination game (the weak-link game) in which they each have to pick a number between 1 and 10, and they get a higher pay-off if they coordinate on higher numbers; their individual pay-offs are suboptimal if they make their individual choices simultaneously. Yet by having one individual move first – leadership by example – and announcing his choice to the others in the group, the team members coordinate on a higher number, and as a consequence, their pay-offs increase (Cartwright et al. 2013). This result is intriguing because the actions almost exactly correspond to the outcomes of models and simulations designed to explore coordination in animal groups (Couzin et al. 2005). It suggests that similar coordination mechanisms are found across species and highlights the importance of leadership and followership, where one or a few individuals initiate an action by moving first and the rest follow.

In his influential, award-winning book, "Leadership," the political scientist James McGregor Burns wrote: "Leadership is one of the most observed and least understood phenomena on earth" (Burns 1978, p. 2). There is little argument about the first part of the statement. Human history is littered with examples of individuals who take charge of a group and lead it – often against the odds – to safety, victory, and prosperity. Military leaders like Alexander the Great, Nelson, and Patton, political leaders like Roosevelt, Nasser, and Mandela, revolutionaries like Mao, Ghandi, and Rosa Luxembourg, business leaders like Ford, Gates, and Branson, and religious leaders like Jesus, Mohammed and Buddha all fit this description. Anthropologists have found evidence of leadership everywhere they looked. Their conclusion is that there are no known human societies without some form of leadership, whereby individuals coordinate the activities of a group although they are not usually institutionalized leaders (Brown 1991). Social psychological research reveals that a leader-follower structure emerges spontaneously when individuals come together to perform a particular task, even when groups set out to be leaderless (Van Vugt 2006). Whenever a group of people comes together, a leader-follower relationship naturally develops. In our laboratory, we have found that leadership develops in around 25 s when individuals are put together in a group to solve a particular task (Gillet et al. 2010).

The psychological literature on leadership is overwhelming. There are more than 1,500,000 hits in Google Scholar on the combined search terms "leadership" and "psychology." Yet most studies in psychology tend to focus on finding proximate explanations for leadership (e.g., "Who emerges as leader when group members are in conflict"). This literature tends to ignore questions about the evolutionary roots and functions of leadership or about the consistencies and inconsistencies between leadership in humans and nonhumans. Biological scientists have had an enduring interest in leadership as well, but there is a dearth of empirical data on the subject in this field. Only recently was the first review article on leadership in animals published in Current Biology (King et al. 2009). The evolutionary biologist E. O. Wilson (1975) summarized his discipline's perspective on leadership some decades ago: "When zoologists speak of leadership, they usually mean the simple act of leading other group members during movement from one place to another" (p. 311). Although group movement is indeed a classic coordination problem for which leadership could have evolved (King et al. 2009), there may be additional evolved functions of leadership.

The biological and psychological literatures on leadership have much in common, and an integrated evolutionary perspective offers a much needed scientific basis for advancing leadership theory and research across the behavioral sciences. Evolutionary leadership theory (Van Vugt and Ahuja 2010) offers such an integrative framework. Utilizing Tinbergen's four questions framework, I first argue why leadership emerged in various species – the ultimate evolutionary function – noting similarities and differences between leadership in humans and nonhumans. Then I address the comparative aspects of leadership, examining who emerges as leaders in animal groups and how they lead. Third, I address the developmental origins of leadership, where I will present new data on gaze following and mimicry as manifestations of leadership and followership. Fourth, I present a time line for the phylogenetic development of leadership, from simple coordination movements between brainless organisms to the complex leadership structures that characterize modern human societies. This review concludes with a list of recent empirical findings from biology, anthropology, psychology and social neuroscience that shows the generativity of adopting an integrative evolutionary approach to leadership.

Leadership and the Need to Coordinate

According to evolutionary leadership theory (Van Vugt and Ahuja 2010), the critical adaptive problem that gave rise to the emergence of leadership and followership across various species is the need for coordination. In species where individuals are better off acting and moving together, leader-follower patterns are likely to emerge (Girardeau and Beauchamp 1999; Van Vugt et al. 2008). A concise review of leadership in nonhumans shows instances of leadership across diverse taxa such as insects, fish, birds, and mammals. Leadership is not only restricted to challenges involving group movement but also to coordinated hunting, group defense against predators, teaching and learning, and peacekeeping (King et al. 2009).

That leadership is the inevitable outcome of strategic interactions between actors can be demonstrated with a simple coordination game with the following constraints (Van Vugt 2006; Van Vugt and Kurzban 2007): (1) organisms must do things to stay alive, and (2) they must do these things with one or more conspecifics. Imagine Jamie and Pat – two humans but they could be members of any social species – who must coordinate on the same waterhole to relieve their thirst (Fig. 1). Suppose they could go to waterhole A or B and will get the same pay-off if they coordinate on the same hole yet they are indifferent as to which hole they coordinate on. If one individual moves first, this leaves the other no option but to follow. Further, if one assumes that for some reason Jamie is always thirstier first, then he will automatically emerge as the leader. More generally, any trait – physical, psychological or behavioral – that increases the likelihood of one of them moving first will make them emerge as the leader more often. This two-player game can be easily generalized to a multiple player game where one or a few knowledgeable or motivated individuals can coordinate a much larger group (Dyer et al. 2009). Turning a simultaneous game into a sequential game paves the way for the emergence of leadership (Van Vugt 2006).

What happens if we introduce conflict among the players? Conflict is rife among members of many group-living species. Jamie prefers Waterhole A over B but the reverse is true for Pat. This is now a “Leader” or “Battle of the Sexes” game (Van Vugt 2006; King et al. 2009), and coordination is more difficult to achieve because whatever hole they coordinate on they will end up with unequal pay-offs. Here there is suddenly an incentive to be the leader (Van Vugt and Kurzban 2007). Greater payoff differences will make it harder for individuals to achieve coordination (Fig. 2).

The sequential version of the game is akin to an ultimatum game. In an ultimatum game, one individual is the proposer and the other is the receiver. The proposer has, say, 10 Euro that he can divide between himself and another player. If the other player accepts the offer, both get what was proposed; yet, if the other player refuses the offer, nobody gets anything. Thus, depending upon whether his offer is accepted, the proposer either emerges as leader or else his attempt to lead fails. Experiments with humans suggest that offers below 40 % are often rejected (Solnick and Schweitzer 1999).

In comparing leadership in humans and nonhumans, one striking difference is that leadership in humans fulfills a number of additional functions beyond organizing group movement. One of these is maintaining group cohesion. In human evolutionary history, as groups get larger and more socially complex, it would have been important to find mechanisms to keep groups together, and leadership (supported by language) might have played a role in this (Dunbar 1993). Anthropologists find that the social lives of hunter-gatherers involve constant conflict, so there is a niche for individuals to step up as peacebrokers or peacekeepers (Boehm 1999). To demonstrate the power of “coercive” leadership, we had groups of four players each play a public-good game over several rounds in different group compositions (O’Gorman et al. 2009; cf. Van Vugt and De Cremer 1999). In each round, one individual was designated as the solitary punisher and he or she could spend his/her earnings to punish others in the group (each unit of punishment subtracted the earnings of others by three units).

Fig. 1 The coordination game. Payoffs are for Pat and Jamie, respectively. Hole A and B constitute alternative game strategies (underpinned by genes); game equilibria are indicated with *asterisks*

		Pat	
		Hole A	Hole B
Jamie	Hole A	1, 1*	0, 0
	Hole B	0, 0	1, 1*

Fig. 2 The leader (battle of sexes) game. Payoffs are for Pat and Jamie, respectively. Hole A and B constitute alternative game strategies (underpinned by genes); game equilibria are indicated with *asterisks*

		Pat	
		Hole A	Hole B
Jamie	Hole A	9, 1*	0, 0
	Hole B	0, 0	1, 9*

The main finding was that this one-punisher condition stabilized cooperation in groups whereas, in groups without punishment, cooperation declined over time. Furthermore, the single-punisher condition was as effective as the all-punisher conditions in the frequently cited Fehr and Gächter experiment (2002). Finally, we compared conditions in which the solitary punisher emerged from the group (endogenous condition) or was randomly picked by the experiment (exogenous condition), but there was no difference between the endogenous or exogenous leaders in terms of punishment or their impact on group cooperation. Across all conditions, the leaders did worse in terms of their earnings than the non-leaders. There are some parallels in the execution of this leadership role between humans and other great apes. For instance, chimpanzees, bonobos, and gorillas all practice peacekeeping and, therefore, I believe that it was almost surely a feature of early human societies as well (Boehm 1999; De Waal 1989).

Another particular niche for human leadership is maintaining relationships with other groups. At various stages of human evolution, there would have been intense competition among groups for scarce reproductive resources such as food, waterholes, and mates (Boehm 1999). Sometimes this competition might have resulted in the formation of alliances with other groups; at other times it may have produced severe intergroup conflict (Chagnon 1997; Van Vugt et al. 2007). Leadership may play a role in warfare and peace-brokering (Van Vugt and Spisak 2008). In traditional societies such as some Native American tribes, different chiefs emerge in war or peacetime and these are different individuals. War leaders tend to be physically stronger, younger, and of a lower class, whereas peace leaders are less formidable, older and of a higher class (Johnson and Earle 2000). This finding is supported by research showing that, when voters elect political leaders during wartime, they prefer a more masculine-looking leader over a more feminine-looking leader whereas the reverse is found during peacetime (Spisak et al. 2012).

In addition, there may be planning and allocation problems in human groups that may require some form of coordination through leadership. For instance, among hunter-gatherers, when a large animal is being killed, how is the meat being shared among the band members? Again, some form of leadership may be useful here where one individual has been assigned to divide the meat.

A final niche for the emergence of leadership in humans is in situations where some individuals in the group are informed and others are uninformed. There is a coordination challenge here, whereby informed individuals take the lead and teach uninformed individuals relevant knowledge and skills. Teaching as a form of leadership has been observed in various other species, such as the social insects. We have already discussed the scout leaders among the honeybees. Teaching has also been observed in ants, where an informed individual teaches an uninformed individual the location of a food resource (Franks and Richardson 2006).

In sum, different coordination challenges may have opened up opportunities for some individuals to emerge as leaders and for others to follow in animal groups. A basic coordination challenge, with deep evolutionary roots, involves movement of individuals in flocks, shoals, swarms or crowds. In humans and perhaps other species, there are additional functions of leaders as peacekeepers, war leaders, diplomats, managers, and teachers.

Leadership Emergence

The coordination game shows that individuals are more likely to emerge as leaders if they have a particular physiology, personality or position in the group that increases their propensity to be a first mover and attract followers. A previously published review of the animal literature (King et al. 2009) suggests that there are at least four behavioral traits that are consistently associated with leadership emergence across species: (1) motivation, (2) personality, (3) experience, and (4) dominance.

First, more motivated individuals are more likely to become leaders. A mathematical model shows that, when two individual coordinate their actions, the one with the lower energy resources will spontaneously emerge as the leader (Rands et al. 2003). Real-world data support this. To the extent that fish are more food-deprived, they are more likely to take the front position in a shoal where they have greater influence on group movement. In addition, among several species such as zebra, lemur and gibbon, the females are found to assume coordinate-group actions when they are in their reproductive phase and hence require more food. Interestingly, more autonomous individuals are also more likely to be leaders, as they have a higher tolerance for allowing distance between themselves and their conspecifics and thus have a lower motivation to coordinate their actions with others. This finding could explain why, in humans, leadership is correlated with autonomy, independence, and internal locus of control (Judge and Bono 2000; Van Vugt 2006).

Differences in personality also underlie leadership and followership across species. Correlations between leadership and specific personality attributes are well documented in humans (Judge and Bono 2000) and to a lesser extent in nonhumans (King et al. 2009). Biologists have traditionally conceived of personality differences as noisy variations in traits that are "adaptive on average." Yet it is now generally agreed that personality differences may be the result of frequency-dependent selection forces, where alternative strategies are viable because they may exploit some ecological or social niche (Nettle 2006). Recent studies had pairs of stickleback fish coordinating their actions to get food. The researchers showed that personality differences between the fish were crucial to achieve coordination. Bold fish emerged as leaders and shy fish emerged as followers, and this difference was enhanced by social feedback (Harcourt et al. 2009). A meta-analysis of the personality literature in humans also reveals that extraversion, which equates to boldness, is most consistently related to leadership emergence (Judge and Bono 2000). Such a correlation across species raises the intriguing question of whether personality differences are maintained through frequency-dependent selection or even group selection to improve social coordination (Wilson et al. 2008).

A third trait that is consistently linked to leadership emergence across species is knowledge or experience. Older females guide herd movement presumably because they possess knowledge of far away waterholes during drought (Foley et al. 2008). In bottle-nose dolphins, more experienced individuals emerge as leaders in foraging expeditions, and having consistent, knowledgeable leaders improves foraging efficiency in groups (Lewis et al. 2013). In humans, individuals with unique, task-relevant expertise also assume leadership roles more often. Research has shown that, after just a few minutes, they can identify the individuals with expertise in a group and these experts achieve greater status and influence (Van Vugt 2006). A final unpublished study from our research group shows that individuals are more likely to vote for older-looking leaders when groups rely on traditional knowledge to solve problems and younger leaders when groups need to find new solutions (Spisak et al. 2012).

Finally, individuals can emerge as leaders because they occupy a dominant position in their group and can sometimes afford to do things by themselves without having to follow anyone. This "byproduct dominance" hypothesis (Van Vugt 2006) is supported by research on wolves and gorill, where the dominant individual sometimes takes on particular leadership roles. One should realize that dominant individuals lead not because they are dominant per se but because they can operate more autonomously given their superior body size, alliances, or access to resources. Specifically, high-ranked individuals are in a better position to elicit followership since they hold a particularly strong influence over the behaviors of group members. Research on baboons confirms that alpha males consistently lead groups to specific food sources despite the followers doing a lot worse than the leader in getting a meal (King and Cowlishaw 2009). Correlations between leadership and dominance are also present in humans, although in humans dominance tends to manifest itself socially (Van Vugt 2006).

Leadership emergence across the animal kingdom has been found to be associated with at least four different traits: motivation, personality, experience, and dominance. Similar patterns have been obtained in humans. Yet the main differences are that in humans leadership is more flexible and, depending upon conditions, anyone can take the lead if he can bring some benefit to the group. In humans, leaders emerge because they possess traits that signal their ability to help the group further their goals (prestige; Henrich and Gil-White 2001).

Styles of Leadership

A further question is how do leaders lead in animal groups. Leadership can be weak, situational, and accidental, such as when dominant individuals emerge as leaders because they simply can afford to be on their own. Leader-follower patterns can also emerge through relatively spontaneous self-organizing processes, where individuals follow a simple coordination rule such as staying close to one’s neighbor (Couzin et al. 2005). These coordination mechanisms are likely to be found in relatively homogeneous groups like insect swarms, fish shoals, and bird flocks, where there is little conflict of interest between individual actors (King et al. 2009; Van Vugt et al. 2008).

Conversely, leadership can be strong, active and sometimes even coercive. Potential leaders can explicitly signal their intentions to the rest of the group. For instance, in ants, individuals who have learned the route to feeding sites use ‘tandem running’ to lead another ant from the nest to food, with signals between the pair of ants controlling both the speed and course of the run (Franks and Richardson 2006). In honeybees, leading individuals (scouts) recruit followers using ‘dances’ that inform proximate colony members on the location of new nest sites when moving home (Riley et al. 2005). More active forms of leadership are also found in species operating in much smaller social groups. Ravens with information about the location of high-quality food sources lead others through a series of acrobatic display flights. Knowledgeable dolphins use visual displays to influence the behaviors of an entire group. Finally, in non-human primates, leaders use vocal and visual signals to initiate collective movement (De Waal 2006). In addition, leadership decision rules can either be despotic or democratic. In some species, for instance those with a clear dominance hierarchy, followers accept the decision of a specific despotic individual on a regular basis, whereas in others, almost any individual can attract followers. In the case of these more democratic forms of leadership, it can be achieved via a majority vote or when a threshold number of followers agrees with a potential leader proposal (Conradt and Roper 2005).

Contrasting human with non-human leadership styles, we see that human leadership styles are more variable, from weak and passive forms of leadership to active and coercive styles. Signaling mechanisms to attract followers are very well developed in humans. Humans use facial expressions, gazes, gestures, rituals and language to attract followers. Furthermore, human leadership is often formalized, in that individuals occupy roles whereby their primary task is to lead others. Oftentimes these consistent leaders employ coercive tactics to get others to follow, such as a manager in the workplace who can demand that subordinates improve their efficiency. Finally, there is considerable evidence that humans are capable of both democratic and despotic leadership styles. Democratic decision making was evident throughout much of early human evolution, where our ancestors lived in relatively egalitarian hunter-gatherer societies (Boehm 1999; Dunbar 1993), whereas despotic leadership is more evident in the non-human primates as well as in episodes of relatively recent human history (e.g., modern dictatorships). It seems that humans are capable of organizing themselves in any way they want, depending on conditions, and further research is needed to find out which leader structures emerge under which conditions (Van Vugt 2009).

In sum, leadership in animal groups can be accidental, passive and weak or strong, coercive and formalized. It seems that humans are highly plastic in the way they organize leadership in groups, from accidental leaders who find themselves at the head of a group, to more consistent, even institutionalized leaders whose primary task it is to get individuals to follow and punish if they fail. Furthermore, depending on socio-environmental conditions such as time pressures and inter- or intra-group conflicts, human groups can revert to either more despotic or more democratic forms of leadership.

Ontogenetic Development of Leadership

The adaptive benefits of leadership hint at the possibility of the presence of various evolved cognitive and neurobiological mechanisms supporting leadership across animal species. An adaptationist analysis suggests that organisms may have specialized mechanisms for (1) identifying situations as requiring coordination, (2) assessing the costs and benefits of following another individual versus going alone, (3) identifying the trade-offs involved in following different individuals, (4) assessing the goals and intentions of different potential leaders, (5) selecting an appropriate individual to follow, (6) getting them to lead, and (7) staying close to the individual leader while following them (Van Vugt and Kurzban 2007). It is likely that these mechanisms are supported by specific neurological mechanisms, and the more complex and variable the forms of leadership that animals display the more sophisticated this neurological machinery will be.

Human leadership is in many ways the same but in some ways very different from that in other animals. Humans use facial expressions, gazing, gestures, rituals, and language to attract followers. Humans also create social institutions and develop rules and laws to induce followership. What specific neurological mechanisms make this possible? Building on the child developmental research by Mike Tomasello and colleagues (2005), I would like to suggest that one of the things that makes human leadership so different is that humans have the capacity for shared intentionality, meaning *the ability to share psychological states with each other for the purposes of engaging in collaborative action.*

Gaze Following

Shared intentionality sets humans apart from other animals, including the non-human primates. It opens up new ways to lead and follow, thus contributing to the genetic and cultural elaboration of leadership to the extent that human leaders can coordinate the actions of millions of individuals in dispersed fission-fusion societies. One of the primary building blocks for the ontogenetic development of leadership is gaze following. Eye gaze following is a powerful cue in various social species (Zuberbuehler 2008). Monitoring and following the gaze of others can provide useful information about threats and opportunities in the environment of an individual. Developmentally, it is one of the earliest manifestations of leadership and followership, as it is already seen in human babies as early as 3 months old. Other animals follow the eye gaze of conspecifics, too, to know what they are looking at. For instance, chimpanzees follow the gaze to external locations and then they check back to see if there is anything interesting. Human infants go far beyond this capacity, however. A 1-year-old human infant does not just follow the gaze of others but also actively shares attention with others. It has been suggested that humans have so much white around their eyes (compared to other animals) to allow them to coordinate their activities better through gaze following: the cooperative eyes hypothesis.

Research into Leadership and Gaze Following. One of the experimental paradigms used in cognitive neuroscience to track gaze following is the gaze cuing paradigm. Cognitive scientists typically use a gaze cuing task to study the influence of gaze on attention. In such tasks, a central face is presented whose diverted gaze is either directed toward the target stimulus (valid cue) or away from the target stimulus (invalid cue). The results typically show that participants respond faster and with fewer errors to a validly cued target than to an invalidly cued target. This is known as the ‘gaze cuing effect.’ Note that this effect occurs despite the fact that the gaze direction does not actually predict the location of the target stimulus.

The gaze cuing task is ideally suited to test evolutionary hypotheses about leadership and followership. Here we report the results of a gaze cuing experiment that was conducted at the VU University Amsterdam, in collaboration with Garian Ohlsen and Dr. Wieske van Zoest, and published recently in PlOS-One (Ohlsen et al. 2013). The experiment examined if humans are biased to follow the gaze of dominant individuals. Some studies have found that cues associated with social status and dominance influence the gaze cuing effect. A study in primates showed that macaque monkeys follow the gaze of dominant monkeys more than of non-dominant monkeys. Comparable results have been found in human populations. People selectively attend more to individuals rated as high in status, and they especially look at their eye regions. Other research has shown that the gaze cuing effect is stronger when participants look at a face of an individual being described as high in status. Social status in humans may be conveyed through facial features like dominance, trustworthiness or competence.

The aim of the study was to investigate whether certain facial features of dominance would affect gaze cuing. Informed by an evolutionary psychological perspective, the idea is that it might be evolutionary adaptive to follow dominant-looking individuals specifically in times of danger, when dominant individuals may provide protection and safety. We hypothesized that, if we primed individuals with threat cues, they would influence gaze cuing only with dominant-looking but not with non-dominant looking faces. Earlier research already showed that people have a stronger preference to follow dominant-looking (masculine) leaders in war and non-dominant-looking (feminine) leaders in peace (Spisak et al. 2012). Building on this work, we predicted that facial cues of dominance enhanced gaze cuing but only under conditions of emotional threat.

The procedure was as follows. Prior to the gaze cue task, participants were primed with emotional pictures signifying no threat or pictures signifying threat to induce either a safe or dangerous condition, respectively. We used pictures from the International Affective Picture System (IAPS) database: 20 pictures denoted threat (e.g., pictures of road accidents, combat situations, physical attacks) and 20 denoted no threat (e.g., pictures of smiling babies, couples holding hands). This gaze cuing task was similar to the one employed in many previous studies. Participants were instructed to focus their attention on the centrally presented fixation point that was visible for 500 ms. After the fixation cue, depending on condition, a non-dominant-looking female face or a dominant-looking male face appeared with a straight-ahead gaze for 1,000 ms. This face was subsequently replaced with exactly the same face with a gaze directed either to the left, right or straight ahead (control condition, no change). The peripherally located target (‘L’ or ‘T’) appeared 200 or 800 ms (SOA) after the presentation of the second face, and its location was unrelated to the gaze direction of the face stimulus. Figure 1 provides an example of the trial sequence and a picture of the dominant-looking male and non-dominant-looking female faces used as gaze cues. The first results were that the dominant male face was indeed rated as more masculine and dominant than the female face and that, in the threat condition, participants felt more negative than in the no-threat condition. Furthermore, the gaze cuing results showed that the gaze cue effect was significantly larger for the dominant male face than the non-dominant female face, yet only in the threat condition and at short viewing times. In the threat condition, the non-dominant female face no longer elicited a gaze cuing effect. The main results are plotted in Fig. 3. This research thus suggests that there is a highly automatic bias to follow dominant-looking faces, especially in times of danger and crisis. This finding has implications for our thinking about the ontogenetic development of leadership in humans.

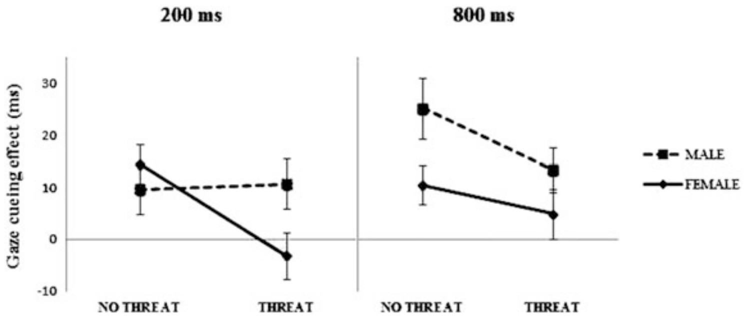

Fig. 3 Gaze cueing effect is absent for female faces when participants are primed with threat pictures (<200 milliseconds; Ohlsen et al. 2013)

Pointing and Gesturing

A second building block for the development of leadership in humans is the capacity for gesturing and pointing. Human infants gesture to communicate, for example, by pointing. These gestures depend fundamentally on shared intentionality because they involve both a shared understanding and cooperative intention. For instance, if children play a hiding-finding game and one child points to a bucket, the other infant will likely infer that he is pointing to inform her of the location of the hidden object. When children are 9 months of age, they already begin to direct others' attention to objects by gesturing. When they are 1-year-old, they point to inform others of things they do not know – in effect sharing information with them – even when there is no benefit to themselves. Leadership through gesturing is rare among other animals. For instance, chimpanzees and other great apes do not generally point, even though they sometimes point to things they want humans to fetch for them. Because they lack shared intentionality, when they observe a pointing gesture they do not understand its underlying cooperative intention. Another highly social species that understands human pointing are dogs, which have co-evolved with humans for the past 30,000 years. Research on canines suggests that the ability to understand human pointing is an instinct and does not require any training (Hare and Tomasello 2005).

Teaching and Instructed Learning

The third cognitive building block underlying the development of leadership in humans, which sets them apart from other species, is teaching. Human infants more readily imitate the actions of adults, and they sometimes do this with the apparent motivation to coordinate their actions with adults. In addition, human adults quite often teach youngsters things by demonstrating what they should do, which the youngsters then respond to by imitating. Interestingly, when adults instruct their children in this way, infants copy the particular actions the adults used and they do so more often than when adults do not actively teach. Human infants also sometimes reverse roles, where they redirect the actions back to the demonstrator.

This form of leadership through teaching is unheard of in non-human animals. For instance, chimpanzees do not engage in imitative learning and adults do not demonstrate things for youngsters. What seems to be lacking is a collaborative mindset whereby the adult builds up an active collaborative relationship with the infant. Of course, active goal-directed social learning through instructed teaching opens up new opportunities for leading and following in humans.

Research into Leadership and Mimicry. One of the neurological mechanisms underlying leadership through teaching is behavioral mimicry. Mimicry is the automatic imitation of the manner in which another person expresses him/herself (Chartrand and Bargh 1999). This includes motor activities such as gestures and postures, vocal signals such as pitch and volume, facial expressions, and language use. Behavioral mimicry is a human universal; it occurs spontaneously, from a very young age, and has been observed in various social species, suggesting that it has important adaptive benefits for group-living species. It has been hypothesized that, through mimicry, humans learn new skills and strategies that are important for their survival and reproductive success (Henrich and Gil-White 2001).

Our present research, conducted with Wouter Wolf and Dr. Claire Ashton-James at the VU University, has examined the role of behavioral mimicry in the effectiveness of leaders to attract followership. Based on the leadership literature, we distinguished between two sources of influence: dominance and prestige. Dominance is based on the ability of an individual to threaten and harm. It is a classic form of influence in species with dominance hierarchies such as non-human primates. Prestige is influence of an individual that is based on his ability to help followers achieve their goals. Competence, expertise, experience and prosociality are aspects of prestige that may give individuals leadership status in humans.

In one study, we showed student participants a clip of one of their professors. First they pre-rated their professor on various aspects of prestige ("Students respect and admire him/her") and dominance ("He/she often tries to get his/her own way regardless of what students may want"). Next, they watched a 3-min video of their professor responding to interview questions. The video was presented without sound because it might influence perceptions of the professor's prestige and dominance. During the pre-recorded interview, the professor enacted a variety of gestures (face touching, head scratching, hair touching, nose wiping). Participants' mimicry of these gestures was recorded by the video camera and was later coded by three research assistants who were blind to any of the participant answers that categorized the video based on either the absence or the presence of mimicry in the video. As predicted, we found that students mimicked their professor more to the extent that they perceived him/her to be a prestige-based leader.

In the next study, we wanted to see if mimicry as a form of followership was strategically motivated or not. We conducted an experiment in which we trained a confederate to be either dominant (e.g., directive) or prestigious (e.g., knowledgeable) while they were leading an individual during a problem-solving task.

In addition, in one condition participants received five Euros for their participation in this study, whereas in the other condition they were told that the leader would decide how much they would get for their participation in the study. We then looked at the extent to which the participant mimicked the leader. As in the previous study, we found that participants mimicked a leader who exhibited prestige more than a leader who exhibited dominance. However, when they could gain financially from affiliation with the leader, they mimicked the dominant leader to the same extent as the prestigious leader.

From these two studies, we conclude that the mimicry of prestige-based leaders is relatively unconditional, whereas the mimicry of dominance-based leaders is more strategic. Also, the mimicry paradigm offers a novel way of studying the implicit influence of leaders on followership, thus offering a great way of testing evolutionary hypotheses about leadership and followership.

Enforcing Social Norms

A fourth and final phase in the development of leadership in humans is its role in promoting cooperation and enforcing social norms. Teaching can channel social learning in ways that benefit individuals and groups but, if there is conflict of interests, then – as we have seen in chimpanzees – collaboration breaks down. An additional function of leadership in humans is to achieve not just coordination but also cooperation by solving the free rider problem. Specific individual leaders may be willing to bear the costs of punishment in return for access to status, resources or reproduction. Our research shows that high levels of cooperation can be achieved with just a single designated punisher (O'Gorman et al. 2009). This capacity is also seen in some non-human species where dominant individuals play a role in enforcing cooperation but they do this entirely to benefit themselves. Yet having a sense of shared intentionality allows leaders to enforce cooperative norms through coercion and punishment because it benefits the group rather than themselves. In support of this finding, a recent study showed that individuals who altruistically punished received greater status in their group and were more likely to be seen as leaders (Barclay 2006).

A Short (Speculative) Evolutionary History of Leadership

The previous information allows us to speculate on the evolutionary history of leadership in humans (King et al. 2009; Van Vugt and Ahuja 2010). As shown, human leaders not only initiate coordination but they also motivate, inspire, plan, organize, direct, monitor, punish, and maintain social cohesion. They may lead democratically and despotically, may lead from the front and from the back, and may lead small groups and groups involving millions of people. How did this all come about? Although there are clearly aspects of leadership that we share with many other organisms, the expansion of the human brain and (not coincidentally) the size of human groups have led to a unique evolutionary history of leadership (Dunbar 1993). I suggest the following evolutionary transitions. First, leadership emerged in animal groups as a mechanism to solve simple coordination problems such as group movement. Second, leadership was enacted primarily by (socially) dominant individuals in species with dominance hierarchies, such as the non-human primates. Third, dominance was attenuated in egalitarian hunter-gatherer societies so that leadership could be enacted by prestigious individuals with a specific personality, knowledge or motivation to foster cooperation in group activities such as hunting, warfare and peacekeeping. Fourth, living in highly cooperative groups selected for the development of sophisticated cognitive mechanisms (e.g., theory of mind, shared intentionality, language) that increased the scale and scope of leadership dramatically. Fifth and finally, interactions in large, complex fission-fusion societies paved the way for the cultural evolution of the formalized (and sometimes hereditary) leadership structures with designated leaders and followers that we see in modern-day organizations such as nations, states and companies.

An Integrative Agenda on Leadership Research in Biology, Psychology, and Neuroscience

Let me conclude with a list of exciting research findings on leadership from evolution-inspired research programs, using a diverse range of methodologies from mathematical models to primate studies, and from archival data to social neuroscience experiments. Although not one of these findings tells a definitive story about the evolution of leadership and followership, together they all point to the possibility of specialized neurological and cognitive mechanisms in both humans and non-humans for solving coordination problems through leadership. These data thus support many different hypotheses from evolutionary leadership theory (Van Vugt and Ahuja 2010).

1. Mathematical models show that, in groups in which information is distributed among many individuals, democratic leadership works better than despotic leadership (Conradt and Roper 2005).
2. A social psychological experiment shows that individuals with high testosterone levels perform better on intellectual tasks when assigned to high-status (leadership) positions, whereas low testosterone individuals perform better on a cognitive tasks in a low-status position (Josephs et al. 2006).
3. An fMRI experiment shows that when a receiver gets an unfair offer from the allocator (leader) in an ultimatum game, it elicits brain activity in areas related to emotion (anterior insula), suggesting that emotions play a role in deciding whether to follow a leader (Sanfey 2007).

4. Archival data from chiefdoms, kingdoms and empires show that their leaders have greater reproductive success than ordinary individuals, suggesting selection for dominance (Betzig 1986).
5. Swarming experiments with humans show that, with just a few informed individuals, large groups can coordinate their activities efficiently (Dyer et al. 2009).
6. Experiments with capuchin monkeys show that they respond negatively to unfair outcome allocations from (human) experimenters, suggesting an early evolutionary origin of injustice aversion in interacting with leaders (Brosnan et al. 2009).
7. Observations from hunter-gatherer societies suggest that they have a host of different leveling mechanisms to keep leaders in check, varying from gossip and ridicule to exclusion and assassination (Boehm 1999).
8. Survey findings show that men in top management positions in Western societies have more sexual liaisons than men in lower-ranked functions in the organization (Perusse 1993).
9. When men and women watch someone who behaves unfairly in an ultimatum game being punished, there is activation in the reward regions of the brain, yet only for men, and this is accompanied by feelings of revenge (Singer et al. 2006).
10. Individuals with leadership roles in organizations have reduced levels of cortisol (the stress hormone), suggesting that high-status positions yield personal health benefits (Sherman et al. 2012).

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Using Awake Animal Imaging to Understand Neural Circuits of Emotion: Studies Ranging from Maternal Care to Aggression

Craig F. Ferris

Abstract Non-invasive, functional magnetic resonance imaging in awake animals gives new insight into the organization of neural circuits involved in behavior associated with intense emotional reactions. The rewarding aspects of breast feeding or the aversive threatening feelings when confronted with a live predator are just two examples of the types of provocation paradigms that can be staged in the magnet during an imaging session. When combined with the use of 3D segmented, annotated brain atlases and computational analysis, it is possible to reconstruct distributed, integrated neural circuits or "fingerprints" of brain activity that reflect emotional and cognitive states. In many cases these neural circuits are similar to those identified in human brain imaging studies, with homologous neural substrates subserving similar functions. While these imaging data cannot tell us how an animal feels, the patterns of brain activity across a range of positive and negative provocation paradigms always include the limbic cortex, basal ganglia and hippocampus. These areas are involved in the integration and processing of information related to the emotional experience and motivation necessary for approach/avoidance behavior.

Imaging Awake Animals

Awake animal imaging is a relatively new and interesting methodological approach to understanding the neurobiology of emotions. How do we know an animal is content, hungry, afraid, angry, or hurt? While there have been many experimental approaches used to address these questions, the most informative to date have been the traditional experimental and ethological observations of animal behavior. We observe an animal's behavior under well-controlled laboratory conditions or in their

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C.F. Ferris (✉)
Psychology Department, Center for Translational NeuroImaging, Northeastern University, Boston, MA, USA
e-mail: C.Ferris@neu.edu

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natural habitat and draw inferences about their emotional states and the motivation behind their motor activities. Using non-invasive functional magnetic resonance imaging (fMRI) in awake animals, we can start to connect these emotions to patterns of brain activity. Indeed, it is now possible to correlate these emotional "states" with changes in neural activity across the entire brain in seconds. When combined with the use of 3D segmented, annotated brain atlases and computational analysis, it is possible to reconstruct distributed, integrated neural circuits or "fingerprints" of brain activity. These fingerprints can be used to study the neurobiology of integrated neural circuits controlling emotion. In many cases these neural circuits are similar to those identified in human brain imaging studies, with homologous neural substrates subserving similar functions.

My laboratory pioneered the field of awake animal imaging with the first publication in 1998 looking at changes in brain activity in rats in response to foot shock (Lahti et al. 1998). Since then we have published numerous studies using fMRI in awake animals. These studies include a variety of behavioral and neurological models ranging from sexual arousal in monkeys (Ferris et al. 2004), pup suckling in rat dams (Febo et al. 2005; Ferris et al. 2005) generalized absence seizures in rats and monkeys (Tenney et al. 2004a, b), aggressive and sexual motivation in rats (Ferris et al. 2008) and non-genomic effects of stress hormone (Ferris and Stolberg 2010). In this paper, data from fMRI studies are presented that use provocation paradigms associated with robust emotional and behavioral responses. These paradigms include food reward, threat of predation, offensive aggression, pain, and the response to pup suckling.

There are certain limitations and complications to imaging awake animals. First and foremost is the restraint of the head, without which it would be impossible to collect a clean image. Head restraint precludes the study of many behaviors that require a consummatory act, as the immobilization alone may prevent the motor response that defines the behavior. Offensive aggression, as measured by the latency to bite and number of bites toward a conspecific, is a case in point. Similarly, an animal cannot engage in eating or run from, or defend oneself from, a predator. However, internal states of arousal and motivation toward rewarding or aversive stimuli, like hunger, sex, fear, pain and aggressive intent, are fertile areas of investigation.

The design of provocation paradigms to elicit brain activity relevant to an emotion of interest is not trivial. In human studies, the subject is presented with visual images having different levels of negative and positive emotional valence. The changes in brain activity can then be correlated with an emotional experience by asking the subjects to describe their feelings. Obviously this approach is not possible in animal studies. To elicit robust emotional responses in awake animals, we have developed provocation paradigms that involve introducing other animals into the bore of the magnet during an imaging session. We have done this for maternal affiliation (Febo et al. 2005; Ferris et al. 2005), aggressive and sexual motivation (Ferris et al. 2008) and, most recently, conditioned predatory fear (unpublished data; Fig. 3) using a live sable ferret to elicit the innate fear response.

The stresses associated with head restraint, restricted movement in the body tube, noise from the gradient coil and the duration of the imaging session are all concerns when imaging awake animals. To address these problems, protocols have been developed for acclimating animals to the environment of the magnetic resonance (MR) scanner and imaging procedure, leading to a reduction in stress hormones levels and measures of autonomic activity regulated by the sympathetic nervous system (King et al. 2005; Zhang et al. 2000). Acclimation protocols have been used to prepare awake animals for a range of behavioral, neurological and pharmacological imaging studies, many of which I noted above. In all cases, acclimation to the scanning session is achieved by putting subjects through several simulated imaging studies. For example, on each day of acclimation, animals are lightly anesthetized with 2–3 % isoflurane while being secured into the restraint system. When the animal is fully conscious, the restraint system is placed into a black opaque box "mock scanner" for 30–60 min with a tape recording of an MRI pulse sequence to simulate the bore of the magnet and an imaging protocol. Significant declines in respiration, heart rate, motor movements, and plasma corticosterone have been measured when the first and last acclimation periods are compared (King et al. 2005). The reduction in autonomic and somatic measures of arousal and stress improve the signal resolution and quality of the MR images. Critical in acclimation is the finding that unacclimated and acclimated animals show no difference in baseline cerebral blood flow, a key determinant in BOLD functional MRI (King et al. 2005).

Olfaction and Food (Approach)

The innate recognition of, and attraction to, palatable, high caloric food would certainly have survival value and, as such, would be selected for over the course of evolution. Consequently, one would predict the presence of olfactory receptors specific to odorants of highly prized foods, in addition to neural circuits needed for the emotional and cognitive responses necessary to assimilate the valued resource into the life of the animal. It would be hypothesized that an animal's behavioral response to a novel, highly desirable food is "hard wired," independent of learning. Indeed, there is considerable literature on rodents showing an innate fear response characterized by freezing behavior when first exposed to a predator odor (Apfelbach et al. 2005), as discussed below, whereas sexually naive male rodents have an innate olfactory preference for female urine (Hayashi and Kimura 1974; Pfaff and Pfaffmann 1969; Swaney et al. 2007).

Figure 1 shows data from a study exposing male rats to one of four odors – almond (benzaldehyde), citrus (limonene), banana (iso-amylacetate), and rose (methyl-benzoate) – during a scanning session (Kulkarni et al. 2012). Using a 3D segmented, annotated rat atlas and computational analysis, we reconstructed the patterns of brain activity and compared them to one another. As anticipated, all animals showed activation of different components of the primary olfactory system (top panel, Fig. 1). Indeed, almond (benzaldehyde) and all of the odorants used in this study have specific odorant receptors and are part of the “odorant code,” i.e., odorant/receptor interaction, neuronal activity and spatial encoding in the glomeruli (Johnson et al. 2002). However, the effect of almond odor on brain areas outside the olfactory system was unexpected (bottom panel, Fig. 1). Almond odor produced strong activation in the limbic cortex, amygdala and hippocampus. Many of the areas of activation, such as the anterior thalamic nucleus and prefrontal cortex, were key neural nodes in the “Papez circuit” of emotional experience. The “Papez circuit” connects the hypothalamus and hippocampus to the limbic cortex, i.e., prelimbic, orbital, anterior cingulate, and retrosplenial cortices, through the anterior thalamus (Papez 1937). Anterior thalamic nuclei send primary projections to the anterior cingulate, retrosplenial, prefrontal, and orbital cortices and somatosensory cortex. The activation of the hippocampus critical for the spatial learning necessary for finding caches of food buried and hidden in the environment supports this notion of distributed neural networks triggered by novel odors toward high caloric food. What made this finding most interesting was the discovery that these animals had never been exposed to almonds or nuts of any kind, either in their standard laboratory chow or during multiple generations of breeding by commercial vendors. They were “odor naive.” Thus we hypothesized that the almond smell activated an innate, integrated neural circuit that was conserved over evolution and critical for assigning emotional valence to stimuli in the environment.

Fear (Avoidance)

The ability to sense a physical threat in the environment, like a predator, and respond appropriately has clear value to the survival of an animal and is undoubtedly selected for over the course of evolution. Indeed, with the beginning of carnivorous life on this planet, complex prey/predator relationships have evolved that govern the struggle for survival. The behavioral and physiological response to this threat falls under the rubric of predatory fear. There is little argument for an innate neural circuitry governing fear of predation independent of learning: you have to respond correctly the first time, as it may be your last.

It is well documented that exposure to predator odors (e.g., cat, fox, and ferret) evokes an instinctual fear response in rats (Apfelbach 1978; Blanchard et al. 1993; Dielenberg et al. 2001). To this end, we designed a study in which a rat was confronted with a live sable ferret during the scanning session (Fig. 2). In a subsequent study, we took advantage of the fact that fear is easily conditioned, hence the long-term biological and behavior consequences of traumatic events that may give rise to psychiatric disorders like PTSD (Adamec and Shallow 1993; Cohen et al. 2003; Masini et al. 2005; Zoladz et al. 2008). In these studies, the introduction of the ferret came with the administration of a 10 % sucrose solution on the tongue of the rat. After an imaging session, the rats were returned to their home cage and remained undisturbed until their next imaging session 14 days later.

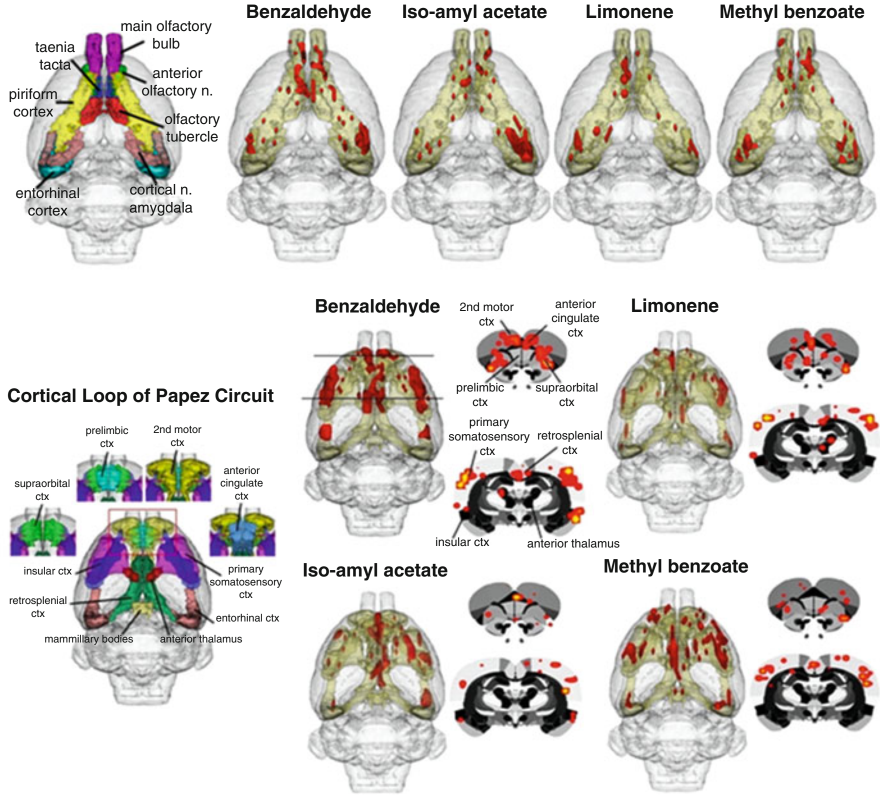


Fig. 1 Almond odor activation of olfactory and limbic areas. Shown in the *upper row* is an increase in activity in the primary olfactory system for each of four different odorants. These 3D volumes of activation are composed of nine subjects each. The image on the far left depicts the subregions of the primary olfactory system. These areas have been coalesced into a single volume as shown in the images for each odorant. Areas in *red* are volumes of positive BOLD activity. The *bottom* images show the increase in activity in the Papez circuit to the smell of almond as compared to the other odorants. The image to the far left depicts the subregions of the Papez circuit. The images to the right of this show both 3D volumes of activation and 2D images of brain activity. The locations of these brain slices are depicted by the *black lines* shown in the 3D benzaldehyde image (Adapted from Kulkarni et al. 2012)

Figure 3 shows data comparing changes in brain activity between rats exposed to a ferret for the first time, to rats exposed to a ferret for the first time together with sucrose on their tongue, and to rats exposed to sucrose alone 2 weeks after their initial fear response. Presentation of the ferret or the ferret with sucrose causes a significant activation of limbic circuitry. We found no significant differences between ferret vs. ferret/sucrose on day 1. However, retrieval of the memory 2 weeks later by the application of sucrose alone in the absence of the ferret elicited a robust increase in brain activity that far exceeded the innate fear response. While the innate fear response to the live predator activated multiple brain sites previously

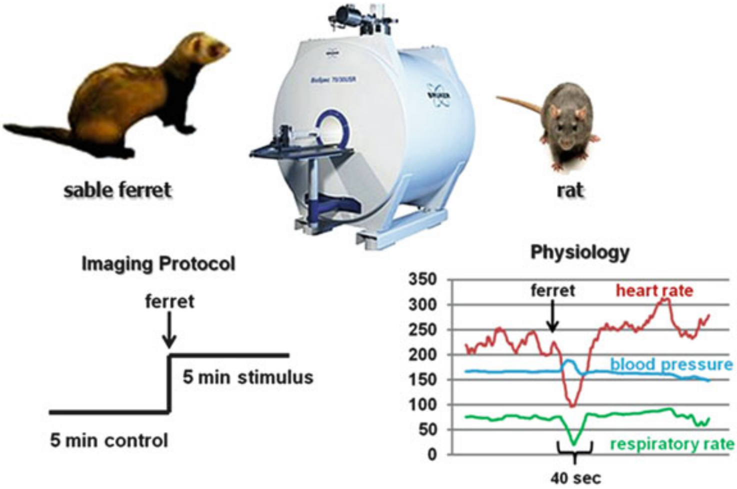


Fig. 2 Experimental protocol for predatory fear. Shown is the 7.0T 20 cm MR scanner used for imaging awake rats. Rats are imaged continuously for 10 min starting with 5 min of control followed by presentation of the ferret. The physiological changes in response to ferret varies widely between animals, but in some cases we observe an acute reduction in heart rate and respiration in the first 40 s followed by a gradual increase in heart rate and respiration over the 5 min stimulation period

identified in various animals studies as part of the fear neural circuit (Blanchard and Blanchard 1972), the conditioned respond had significant representation in circuits of emotional experience, i.e., the Papez circuit and amygdala, and the hippocampal complex for memory.

There is an extensive literature on the neural circuits involved in Pavlovian fear conditioning (for reviews, see Joels and Baram 2009; Sehlmeyer et al. 2009). Of the many brain areas identified, the amygdala would appear to play the most important role (Davis 1997; LeDoux and Gorman 2001). Lesioning the amygdala in rats impairs the autonomic and behavioral (e.g., freezing) responses characteristic of conditioned fear (Blanchard and Blanchard 1972; Hitchcock and Davis 1986). Blocking the basolateral amygdala, a key component of the amygdaloid complex, impairs the acquisition of fear (Helmstetter and Bellgowan 1994; Muller et al. 1997) and the ability to make fear associations (Goosens and Maren 2001; Iwata et al. 1986). Lesioning the amygdala after fear conditioning eliminates the learned fear responses (Anglada-Figueroa and Quirk 2005; Kim and Davis 1993). The prelimbic cortex, which has efferent connections to the basolateral amygdala, is critical for the expression but not acquisition of learned fears (Corcoran and Quirk 2007). In addition, it has been proposed that the prelimbic area integrates inputs from the amygdala, hippocampus and other cortical sites to regulate expression of fear memories (Burgos-Robles et al. 2009). Other areas playing a significant role in fear conditioning are the insular cortex, bed nucleus of the stria terminalis, hippocampus, and anterior cingulate. Those areas showing a significant activation

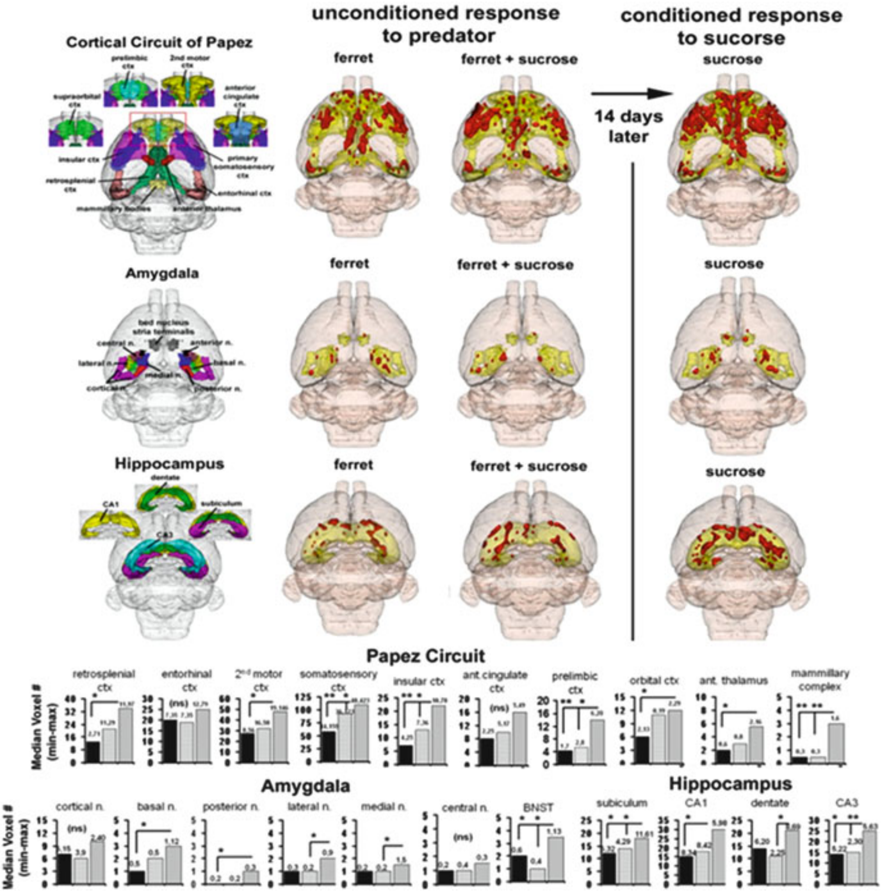


Fig. 3 Imaging conditioned fear. Shown in the far left column are 3D representations of the Papez circuit (limbic cortex involved in emotional experience), along with the amygdala and hippocampus of the rat. Areas in red denote the average significant BOLD activation of nine animals for each condition. The second column from the left shows the pattern of activation for the ferret alone. The third column shows activation when the ferret and sucrose are presented together. The column on the far right shows the activation pattern when the animals are re-exposed to sucrose alone in the magnet 2 weeks later. Note the robust activation pattern. Below are bar graphs showing the volumes of activation in different brain areas for each condition

in the conditioned fear response to a live ferret include the anterior thalamus, mammillary bodies, somatosensory and orbital cortices, prelimbic cortex, retrosplenial cortex (posterior cingulate), amygdala (basolateral amygdala, bed nucleus of the stria terminalis), and hippocampus (subiculum, dentate, CA1, CA3). These fMRI data corroborate c-Fos studies in rats that reported fos protein expression in the mammillary bodies, anterior thalamus and dorsal hippocampus after fear conditioning (Conejo et al. 2007).

Offensive Aggression (Approach)

Aggression is a normal component of mammalian behavior (Huntingford and Turner 1987). For animals there is an adaptive advantage to defending a territory, fighting for limited resources, competing for mates, and protecting young. As noted above, we cannot image the initiation of attacks and bites that characterize offensive aggression but we can image aggressive motivation (Ferris et al. 2008). To trigger aggressive motivation, we presented male rats with their female cage mate plus a novel male intruder in the bore of the magnet during image acquisition. As part of the ethogram of aggression, male rats in the company of their female cage mate will piloerect the fur along the midline back in the presence of a male intruder. This piloerection is unique to offensive aggression, is not seen in other behaviors, and signals an impending attack on the intruder (Blanchard and Blanchard 1977). It can be observed in the magnet and serves as a peripheral autonomic sign of the centrally aroused sensation of aggressive motivation.

As expected, brain areas previously identified as critical in the organization and expression of aggressive behavior were activated, e.g., lateral hypothalamus and medial basal amygdala (Table 1). Unexpected was the intense activation of the forebrain cortex and anterior thalamic nuclei. The putative neural circuit of aggressive motivation identified with fMRI included neural substrates contributing to emotional expression (i.e., cortical and medial amygdala, BNST, lateral hypothalamus), emotional experience (i.e., hippocampus, forebrain cortex, anterior cingulate, retrosplenial cortex) and the anterior thalamic nuclei that bridge the motor and cognitive components of aggressive responding, the cornerstone of the Papez circuit. The significant BOLD signal as a composite of 10 rats showing piloerection to a male intruder during the scanning session is shown in Fig. 4.

In our findings, the cerebrum, particularly the somatosensory, auditory, orbital and retrosplenial cortices, was activated with aggressive motivation. These cortical areas are conspicuously absent from the literature describing the neuroanatomy of aggression in animals and are devoid of direct afferent connections from the lateral hypothalamus. However, they are consonant with an extensive human neuroimaging literature indicating that aggression-inducing stimuli produce activation in frontal cortex sites (Antonucci et al. 2006; Lotze et al. 2007; Nomura and Nomura 2006). This cortical activation is typically interpreted as indicating that the frontal cortex exhibits inhibitory control over a number of strongly motivated behaviors, including both aggression and defense, a suggestion that is supported by the relationships between the prefrontal cortex and subcortical structures involved in these emotional responses (Keay and Bandler 2001) as well as by the effects of frontal cortex lesions (Machado and Bachevalier 2006) and damage (see Raine 2002 for review) on impulsivity and aggression.

Table 1 Putative neural circuit of aggressive motivation

The two left columns report the median (min-max in parentheses) number of voxels activated (volume of activation) in male residents when presented with their female cage mate (mate alone) or their cage mate plus a novel adult male intruder (mate + intruder). Male residents ($n = 10$) were tested for each condition in a counterbalanced design and the data were analyzed using a Wilcoxon Signed-Rank Test. The two columns on the right report the percent change in BOLD signal (mean ± SE) for that brain area for each experimental condition. Those areas that showed a significant increase in the number of activated voxels were screened from a data base of 83 brain areas and comprise the putative neural circuit of aggressive motivation. $p < 0.05^{*}$; $p < 0.01^{**}$ (Adapted from Ferris et al. 2008)

	Volume of activation		% change in BOLD signal	
Brain area	Mate alone	Mate + intruder	Mate alone	Mate + intruder
Retrosplenial cortex	26(10, 61)	$50(26, 99)^{**}$	5.0 ± 0.3	$10.5 \pm 0.5^{*}$
Orbital cortex	9(1, 14)	$19(4, 44)^{*}$	3.0 ± 0.2	4.1 ± 0.2
Auditory cortex	20(4, 61)	$38(23, 51)^{*}$	4.3 ± 0.5	10.1 ± 0.6
Somatosensory cortex	114(16, 266)	$221(141, 392)^{*}$	3.7 ± 0.3	11.9 ± 1.1
Prelimbic cortex	2(0, 11)	$8(2, 25)^{*}$	1.7 ± 0.1	$3.5 \pm 0.2^{*}$
CA1 hippocampus	27(10, 67)	$46(32, 110)^{*}$	3.1 ± 0.2	$5.7 \pm 0.2^{*}$
Dentate gyrus	20(3, 48)	$32(22, 80)^{**}$	2.8 ± 0.2	$5.2 \pm 0.2^{*}$
Cortical n. amygdala	14(5, 29)	$23(14, 52)^{*}$	4.6 ± 0.3	$7.8 \pm 0.3^{*}$
Basal n. amygdala	4(1, 11)	$10(2, 17)^{**}$	3.1 ± 0.2	4.3 ± 0.2
Medial n. amygdala	1(0, 6)	$3(0, 9)^{*}$	2.7 ± 0.2	4.6 ± 0.2
Bed n. stria terminalis	2(0, 5)	$6(2, 16)^{*}$	3.4 ± 0.3	5.1 ± 0.2
Lateral post. n. thalamus	2(0, 9)	$8(2, 11)^{**}$	1.6 ± 0.2	$4.2 \pm 0.2^{*}$
Anterior n. thalamus	3(0, 6)	$6(2, 12)^{**}$	1.4 ± 0.2	$4.9 \pm 0.2^{**}$
Ventral pallidum	5(0, 17)	$11(6, 21)^{*}$	2.2 ± 0.2	4.1 ± 0.2
Lateral hypothalamus	10(3, 26)	$25(6, 54)^{*}$	3.1 ± 0.3	$5.7 \pm 0.2^{*}$
PVN hypothalamus	1(0, 2)	$3(1, 5)^{*}$	2.0 ± 0.1	3.8 ± 0.1

Pain (Avoidance)

Pain represents a complex stimulus that impacts multiple neural circuits in the brain involved in sensory discrimination, perception, motivation and cognition. The neurobiology of pain sensation and processing is highly conserved across the mammalian kingdom. With functional imaging studies, the neurobiology of capsaicin-induced pain in healthy volunteers has extended beyond the primary sensory fiber to include distributed neural circuits in the brain (Baron et al. 1999; Iadarola et al. 1998; Maihofner and Handwerker 2005; Zambreanu et al. 2005). Identifying these neural circuits and how their activity changes over time to injury or a noxious stimulus could reveal how the brain processes and adapts to pain. To this end we used capsaicin, a pharmacologically active agent found in chili peppers, that causes burning and itching when applied topically or intradermally to the skin. Rats were given an intradermal injection of capsaicin into the hindpaw and followed for changes in brain activity.

The positive BOLD signal changes to acute experimental pain are shown in Table 2 and Fig. 5. These data reflect changes in brain activity 3–5 min after

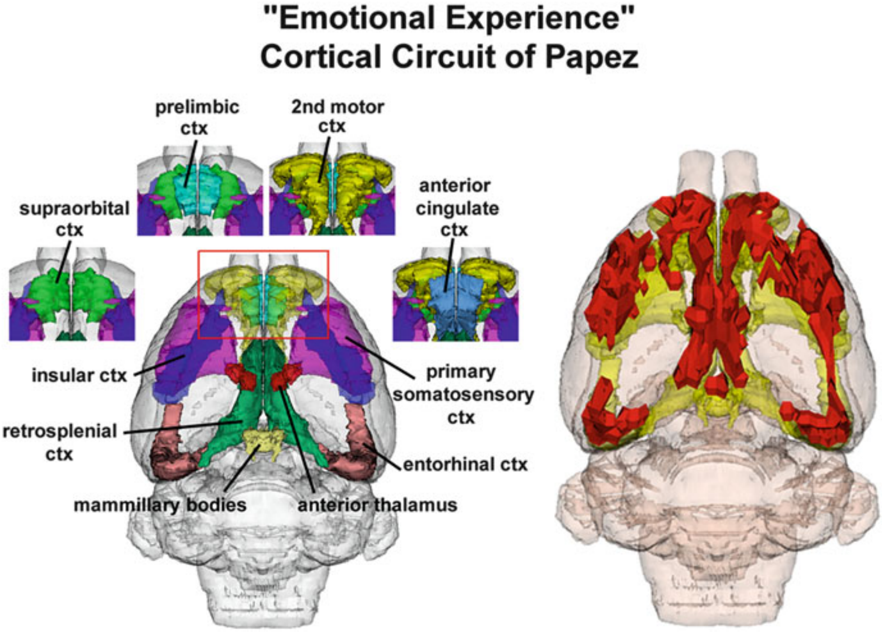
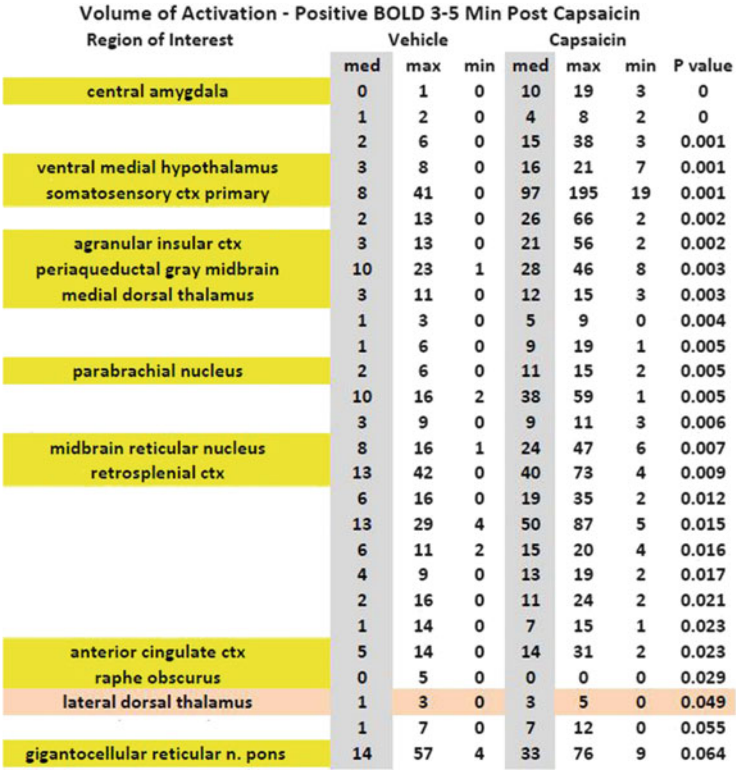


Fig. 4 Aggression motivation and the Papez circuit. The translucent shell of the brain to the left shows the 3D areas comprising the Papez circuit. These areas are coalesced into a single 3D volume (*yellow*) and show the position (*red*) of the average significant BOLD activation ($n = 10$) following presentation of an intruder with the cage mate to elicit aggressive motivation

capsaicin administration. The template used to define the brain areas comprising the putative pain neural circuit of the rat came primarily from the work of Gauriau and Bernard (2002) and from meta-analysis data from various neuroimaging modalities used to study acute pain in humans (Apkarian et al. 2005; Gauriau and Bernard 2002). Using the parabrachial nucleus as a central node, Gauriau and Bernard described its many efferent connections to brainstem, hypothalamus and forebrain areas as the sites comprising the distributed neural circuit of pain. They and others have provided clear anatomical and electrophysiological evidence showing two major pathways of nociceptive fibers emanating from lamina 1 of the dorsal horn of the spinal cord. One pathway projects to the somatosensory cortex through the lateral thalamus (e.g., ventral posterior lateral thalamus) and is involved in sensory discrimination of nociceptive processing. A second, linking the brainstem with the hypothalamus, midline thalamic areas and limbic cortex, is thought to deal with the attentional and motivational aspects of pain. Similar lateral and medial pain systems attending to sensory discrimination and emotion, respectively, have been described in the human imaging literature (Kupers and Kehlet 2006). The areas shown in yellow in Table 2 are brain areas involved in pain perception and processing. One should also note the activation of the basal ganglia, e.g., striatum

Table 2 Capsaicin-induced changes in brain activity
The table below reports the number of positive and negative voxels in a given brain region (volume of activation) in the pain neural circuit in response to vehicle (50 μl of 25 % Captisol/PBS) or capsaicin (50 μg/50 μl). The areas are in rank order for their significance after a multiple comparisons non-parametric Kruskal-Wallis test. Regions of interest shown in yellow comprise part of the putative neural circuit of pain shown in Fig. 5



Volume of Activation - Positive BOLD 3-5 Min Post Capsaicin

Region of Interest	Vehicle			Capsaicin			
	med	max	min	med	max	min	P value
central amygdala	0	1	0	10	19	3	0
	1	2	0	4	8	2	0
	2	6	0	15	38	3	0.001
ventral medial hypothalamus	3	8	0	16	21	7	0.001
somatosensory ctx primary	8	41	0	97	195	19	0.001
	2	13	0	26	66	2	0.002
agranular insular ctx	3	13	0	21	56	2	0.002
periaqueductal gray midbrain	10	23	1	28	46	8	0.003
medial dorsal thalamus	3	11	0	12	15	3	0.003
	1	3	0	5	9	0	0.004
	1	6	0	9	19	1	0.005
parabrachial nucleus	2	6	0	11	15	2	0.005
	10	16	2	38	59	1	0.005
	3	9	0	9	11	3	0.006
midbrain reticular nucleus	8	16	1	24	47	6	0.007
retrosplenial ctx	13	42	0	40	73	4	0.009
	6	16	0	19	35	2	0.012
	13	29	4	50	87	5	0.015
	6	11	2	15	20	4	0.016
	4	9	0	13	19	2	0.017
	2	16	0	11	24	2	0.021
	1	14	0	7	15	1	0.023
anterior cingulate ctx	5	14	0	14	31	2	0.023
raphe obscurus	0	5	0	0	0	0	0.029
lateral dorsal thalamus	1	3	0	3	5	0	0.049
	1	7	0	7	12	0	0.055
gigantocellular reticular n. pons	14	57	4	33	76	9	0.064

and midbrain dopaminergic system, and the different components of the hippocampal system, e.g., CA3, subiculum and dentate gyrus.

Nursing (Approach)

The mother-infant bond is a critical relationship, fostering maternal behavior and enhancing infant survival by providing nutrients and warmth. The initiation and maintenance of maternal behavior in rodents is a complex interaction between the endocrine status of the dam before and after parturition and the continued interaction with and stimulation from pups until weaning (Numan 1994). Hormones combine with the physiology of parturition to foster maternal behavior in first-time mothers. However, from postpartum day 4 through postpartum day 20, the

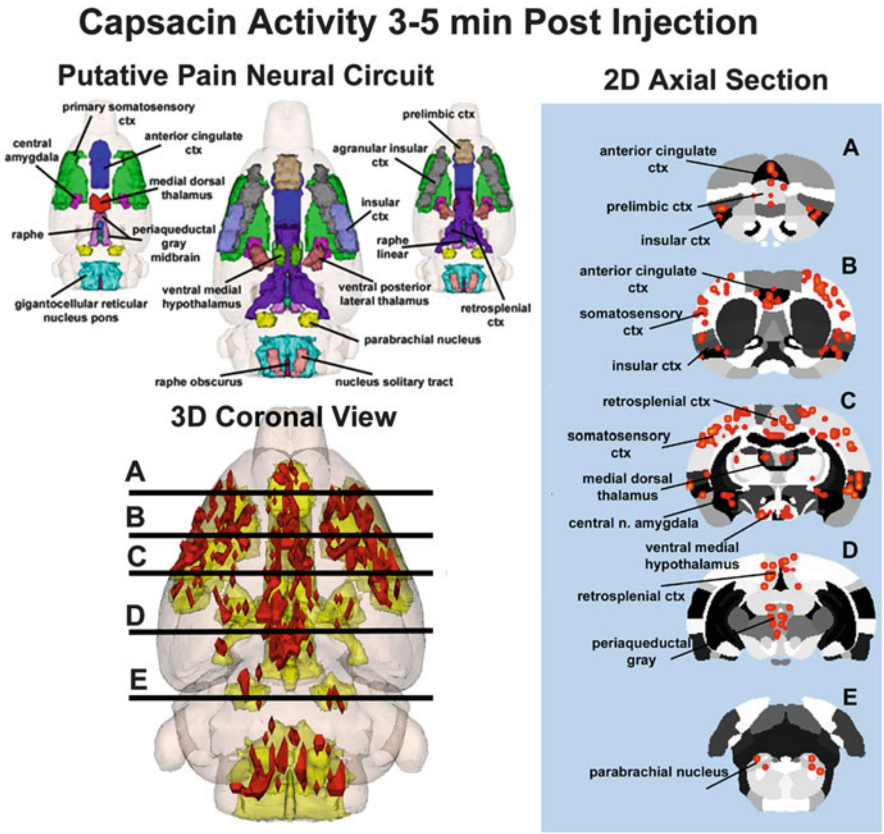


Fig. 5 Activation of the pain neural circuit. The translucent shells of the brain to the left show the 3D areas comprising the pain neural circuit. These areas are coalesced into a single 3D volume (*yellow*) and show the position (*red*) of the average significant BOLD activation (n = 9) for the 3–5 min following capsaicin injection. The localization of BOLD activation is clearly shown on the 2D axial sections of the rat MR atlas to the far right

maintenance of maternal behavior is more strongly influenced by learning and the tactile and odor stimuli coming from the pups.

The study presented here was done to test the “rewarding” nature of nursing (Ferris et al. 2005). While in the home cage and separated by a barrier, dams were kept from having any physical contact with their pups for 3–4 h. Then, during the scanning sessions, we allowed their pups to suckle and imaged the changes in brain activity in the dam with particular attention to the basal ganglia and midbrain dopaminergic system. These data were then compared to two other studies, one comparing virgin females to the presentation of cocaine and another to lactating dams presented with cocaine. A summary of these three studies is shown in Fig. 6. Suckling stimulation in lactating dams and cocaine exposure in virgin females

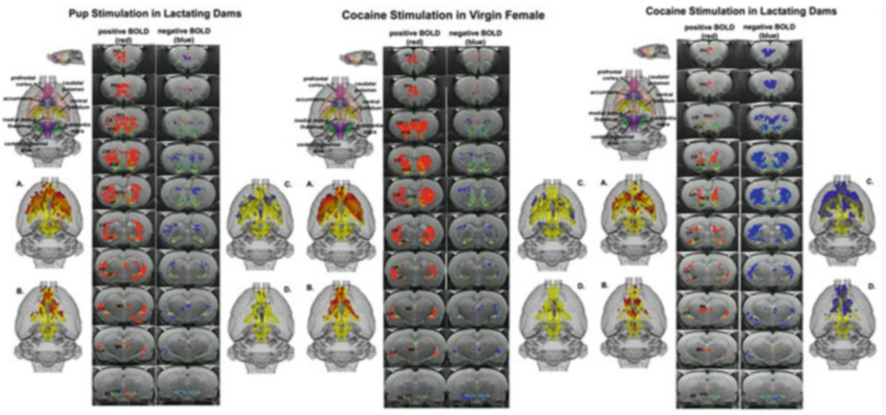


Fig. 6 Pup suckling versus cocaine. Shown in the far left column are 3D maps showing positive (*red*) and negative (*blue*) BOLD signal changes in the basal ganglia in response to pup suckling in lactating dams. Similar 3D maps showing BOLD signal changes in the basal ganglia in virgin females in response to cocaine and lactating dams in response to cocaine are shown in the middle and far right columns, respectively. Between each of these 3D representations are contiguous 2D brain slices showing the location of positive and negative BOLD signal in the basal ganglia for each experimental condition. Note the pronounced negative BOLD in lactating dams in response to cocaine, which is not seen in virgin females given cocaine or lactating dams suckling pups (Adapted from Ferris et al. 2005)

activated the dopamine reward system. In contrast, lactating dams exposed to cocaine instead of pups showed a suppression of brain activity in the reward system.

These data support the notion that pup stimulation is more reinforcing than cocaine, underscoring the importance of pup-seeking over other rewarding stimuli during lactation. This study provided imaging data that corroborated the behavioral literature on dam/pup interactions.

Pups have reinforcing properties that are so salient that they can compete with self-administration of cocaine (Hecht et al. 1999). Over several studies, Fleming and coworkers (1999) characterized the reinforcing nature of pups in maternal behavior, ultimately showing that postpartum dams will bar press for pups in an operant response paradigm (Lee et al. 2000). Activation of the dopaminergic mesocorticolimbic system is critical to the central mechanism contributing to the reinforcing property of pups (Hansen et al. 1993; Lee et al. 1999; Pedersen et al. 1994).

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The Neuroevolution of Empathy and Caring for Others: Why It Matters for Morality

Jean Decety

Abstract Evolutionarily, empathy is central to making adaptive evaluations in social environments, bonding with others, and caring for them. In humans, empathic arousal and feelings of concern for others provide the building blocks for the development of morality. Empathic concern emerges early in life in preverbal infants and requires only a minimal capacity for mindreading and self-awareness. In this chapter, it is proposed that empathy is a capacity shared by humans and other mammals, which is dependent on neural circuits that have evolved in the context of parental care and living in social groups. Empathy-based behaviors have afforded unique survival and reproductive advantages and have co-opted primitive homeostatic processes involved in reward and pain systems in order to facilitate various social attachment processes. Studies in affective and social neuroscience are discussed to document that the same network of regions that are involved in physical pain is also responsive to the perception of pain in others as well as social pain, such as social exclusion, grief, or extreme sadness. The sharing of vicarious negative arousal provides a strong signal that can promote empathic concern and caring for others. To be motivated to help another, one needs to be affectively and empathically aroused and to anticipate the cessation of the mutually experienced personal distress. Finally, drawing on neuroimaging studies with juvenile and adult psychopaths, it is argued that the lack of sensitivity to others' suffering contributes to a callous disregard for the welfare of others and increases vulnerability to amoral conduct.

J. Decety (✉)
Department of Psychology and Department of Psychiatry and Behavioral Neuroscience, The University of Chicago, Chicago, IL 60637, USA
e-mail: decety@uchicago.edu

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Introduction

Empathy shapes the landscape of our social and moral lives. It can motivate helping others in distress, it plays an essential role in inhibiting aggression, and it facilitates cooperation between members of a similar species. We often tend to think of empathy as a uniquely human attribute, but it is something that many other animals demonstrate. Despite the fact that the construct of empathy is complex and involves social, emotional, and motivational facets, none of these facets are specific to humans. Empathy emerges early in life in preverbal infants and is deeply rooted in the propensity for feeling and reacting to the emotions of others. Empathy likely evolved because it promoted our ancestors' survival and increased their fitness, which in mammalian species depends on the ability of conspecifics to communicate with each other, sharing information about their emotions and intentions and appropriately responding to their offspring's or relatives' needs. Although organisms can develop a variety of understanding of others, empathy entails more than just understanding or expectation. When individuals, including non-human animals, empathize, they vicariously experience the emotions of others and can be emotionally moved by witnessing another's distress. This not only promotes affective communication but, depending on the social context and inter-individual relationships, may also motivate pro-social behaviors towards other conspecifics (Decety and Sveltova 2012).

The long history of mammalian evolution shaped our brains to recognize and respond with care to signs of suffering and need of others. Social relationships, including those structured around social bonds, can be a source of life's greatest pleasures and deepest pain. The social attachment system was gradually built up from more primitive regulation systems such as those involved in place attachment, thermoregulation, and physical pain (Panksepp 1998). Evidence from a wide range of academic disciplines, including recent work in pharmacological and neuroscience, converges to suggest that social pain and physical pain operate via common neurophysiological mechanisms (similarly for pleasure; the striatum encodes primary rewards such as food or sexual stimuli as well as secondary rewards such as money or social reputation). Because inclusion in social groups has been essential to survival for social mammals, threats to one's social connections are processed as a severe threat to one's safety and bodily integrity (MacDonald and Leary 2005). Evolutionarily, in social animals, physical and social pain (such as separation calls) were both necessary to promote survival and motivate defensive and protective behaviors. In addition, the sensitivity to the emotions of others likely played a critical role in the development of care-based morality in humans.

The notion that physical and social pain operate via common mechanisms supports the principle of neural reuse theories (Anderson 2010), which state that, instead of giving rise to brand new systems, most evolutionary changes involve the differentiation of a current system to produce a new outcome. Neural circuits established for one purpose can be exapted (exploited, recycled, redeployed) without losing their original functions.

This chapter integrates evolutionary theory with social neuroscience studies on empathy to clarify the interactions between the affective processes involved in the experience and perception of physical and social pain and their relationship to moral cognition. The chapter begins by examining how sensitivity to signs of suffering has evolved in the context of parental care in mammalian species. Then it examines the neurobiological mechanisms supporting its operation. Next, the neurodevelopment of empathy is discussed with reference to early signs of the ability to perceive sensitivity and fairness and exhibit concern for others, abilities posited as precursors to a more mature understanding of morality. The neuroimaging studies focusing on the perception of others' physical and social distress are then presented in support of the adaptive function of empathy in social interactions. Finally, the chapter addresses a number of emotion-processing dysfunctions in individuals with psychopathy to further illustrate how the lack of sensitivity to others' suffering can contribute to a callous disregard for the welfare of others and amoral conduct.

The Mechanisms Involved in Empathy and Caring Are Highly Conserved Across Species

As a species, humans are hyper social mammals that depend on other conspecifics for survival and reproduction. The ability to model the emotions of others and react appropriately when interacting within a social group probably confers a number of evolutionarily advantageous skills (e.g., increased ability to communicate and detect distress in group members and use this information to protect them). Furthermore, positive social behaviors, such as caregiving, are essential for both reproduction and survival.

A number of empirical studies with rodents have shown that empathic arousal prompts efforts to alleviate the distress of a conspecific. For instance, rats that had learned to press a lever to obtain food stop doing so if their action was paired with the delivery of an electrical shock to a visible neighboring rat (Church 1959). Rats will press a bar to lower another rat suspended in mid-air, an action that is interpreted as relieving the suspended animal's distress (Rice and Gainer 1962). Recently, a series of studies have documented that rats will intentionally free a cagemate locked in a restrainer even when social reward was prohibited (Ben-Ami Bartal et al. 2011). This latter study also found that, when liberating a cagemate was pitted against a highly palatable food (chocolate chips) contained within a second restrainer, rats opened both restrainers and typically shared the chocolate. Furthermore, studies have also demonstrated that rodents show social modulation of emotional responses and learning. In one such study, pain sensitivity was modulated in mice by the presence of other mice displaying pain behaviors (Langford et al. 2006). Interestingly, this relationship is conditional upon the identity of the target mouse, such that observing pain-behaviors in conspecifics only influences pain behavior when the target mouse is their cagemate. Female mice show more freezing behavior when exposed to the pain of a close relative than when exposed to the pain of a more distant relative, suggesting that it serves an adaptive function (Jeon et al. 2010). To further investigate whether such pain behavior can serve the function of soliciting a primitive form of empathic concern, Langford and her colleagues (2010) used a social approach paradigm to test mice in various dyadic or triadic conditions. Some conditions involved restrained mice that were in pain as a result of intraperitoneal injection of acetic acid and test mice that were free to approach or avoid the restrained mice. Results showed a sex-specific effect whereby female test mice approached a familiar same-sex conspecific in pain more frequently than an unaffected conspecific. Importantly, the frequency of contact by the test mouse was negatively correlated with the pain behavior of the jailed mouse, suggesting that the proximity of a familiar unaffected conspecific had analgesic properties. Moreover, another study demonstrated that socially isolated mice displayed significantly higher levels of mechanical pain sensitivity as well as depressive-like responses following peripheral nerve injury as compared to their pair-housed counterparts, potentially through a mechanism involving the neuropeptide oxytocin (Norman et al. 2010).

Results from these studies can also be interpreted as evidence of not only emotion contagion but also an effect of social support on the experience of pain – a finding consistent with human literature. Indeed, the presence of an individual who provides passive or active support reduces experimental pain in humans (Brown et al. 2003) and attenuates activation in the neural systems supporting emotional and behavioral threat responses (Coan et al. 2006). Similarly, a study with human subjects determined that the presence of others and perceived empathy (defined as participants' knowledge of the extent to which observers felt they understood and shared their pain) modulated subjective and autonomic responses to physical pain, and these influences could be explained by individual variations in pain coping strategies and social attachment (Sambo et al. 2010).

Research has also shown the presence of empathy in non-human primates. Early experiments demonstrated that rhesus monkeys refrained from operating a device to obtain food if it resulted in another monkey receiving an electric shock (Wechkin et al. 1964). Further research showed that there was a stronger response if the macaque was familiar with the shocked conspecific or if the observer had experience of being shocked itself (Masserman et al. 1964). An experiment in which peripheral skin temperature was measured in chimpanzees while they viewed an emotionally laden video demonstrated a decrease in skin temperature, indicative of sympathetic arousal, when they viewed videos of conspecifics injected with needles or videos of the needles themselves, whereas these changes were not observed when the chimpanzees viewed videos of a conspecific chasing the veterinarian (Parr 2001). Thus, when chimpanzees perceive a conspecific exposed to painful stimuli, they show physiological changes similar to those observed in humans. Chimpanzees are known to spontaneously provide contact comfort to recent victims of aggression, a behavior termed consolation. This consolation behavior reduces the recipient's state of arousal, hence likely alleviating distress (Romero et al. 2010).

Therefore, various social species display aspects of empathy (emotion contagion) and empathic concern. Understanding how these processes function in related animals provides an important insight into their role in human social behavior. A research study that examined post-conflict interactions showed that bonobos across age and sex classes spontaneously offered consolation to distressed parties (Clay and de Waal 2013). Moreover, bystanders were significantly more likely to console relatives or closely bonded partners, and the consolation was more likely to be offered by younger bystanders compared to adults. Additionally, mother-reared individuals were significantly more involved in pot-conflict interactions than orphans. This latter finding highlights the role of early attachment in emotional development.

Most mammals, including humans, are motorically immature at birth, and caregiving is necessary to compensate the infant's undeveloped motor and autonomic nervous systems (Porges and Carter 2012). Many of the same neurophysiological and endocrine systems that permit birth, lactation, and parental behavior have been implicated in the giving and receiving of positive experiences (Carter 1998). However, these processes are not limited to mother-infant interactions. Biologically unrelated individuals may express and experience concern for others and caregiving (Hrdy 2008), suggesting that the motivational system that originally developed to promote care for offspring was co-opted to facilitate positive relationships between biologically unrelated group members. For example, in humans, our relationships with spouses, friends, and co-workers are highly valued despite requiring vast amounts of psychological resources to maintain. In fact, perceiving such relationships as threatened engenders profound emotional and physiological stress responses (Norman et al. 2012). Conversely, feeling well-connected with and supported by friends and family provides a strong behavioral and psychological buffer that can actually diminish stress responses and result in improved health (Uchino et al. 1996). This finding provides strong evidence for the repurposing of motivational components of pro-social behaviors such as empathic concern that originally developed to motivate parental care as invaluable tools for the formation and maintenance of strong social bonds between unrelated individuals.

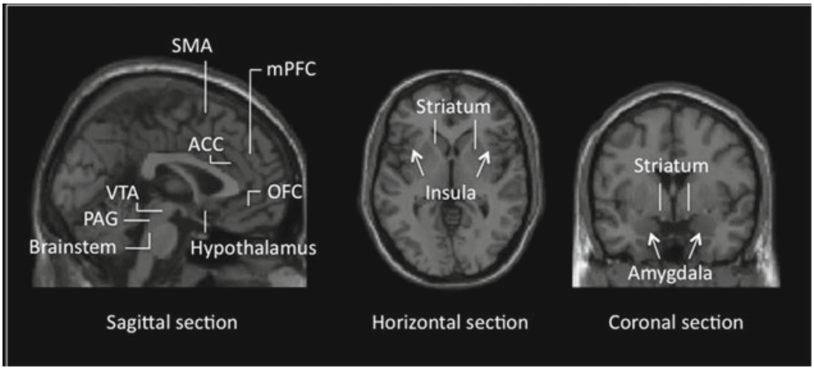
Neurobiological Mechanisms Underpinning Empathy

Animal research demonstrates that the ability to be affected by others' emotional states, integral to maintaining the social relationships important for survival, is organized by basic neural, autonomic, and endocrine systems subserving attachment-related processes, which involve the brainstem, the preoptic area of the thalamus, and paralimbic areas, as well as the autonomic nervous system (Panksepp 1998). These systems underlying attachment appear to exploit the strong, established physical pain system, borrowing aversive signals associated with pain to indicate when relationships are threatened (Eisenberger 2011). Moreover, higher-level cortical structures have been proposed to reflect a system involved in detecting, processing, and reacting to the occurrence of salient events regardless of the sensory modality through which these stimuli are conveyed. Therefore, just as the physical pain system alerts organisms to the presence of a noxious environmental stimulus so too does the social pain system: the experience of social pain alerts an individual to potential threats in his social environment and can induce various coping strategies to attempt to mitigate the threat (e.g., increase motivation to strengthen relationships; MacDonald and Leary 2005).

Converging evidence from animal behavior (Insel and Young 2001), neuroimaging studies in healthy individuals (Lamm et al. 2011), and lesion studies in neurological patients (Shamay-Tsoory 2009) indicates that empathy and caring for others employ a large array of systems neural mechanisms and extend beyond the cortex, including the amygdala, hypothalamus, insula, anterior cingulate cortex (ACC), and orbitofrontal cortex (OFC). They also involve the autonomic nervous system (ANS), hypothalamic-pituitary-adrenal axis (HPA), and endocrine and hormonal systems that regulate bodily states, emotion, and reactivity (Fig. 1).

A growing number of studies implicate a number of neuropeptides in the regulation of sociality, emotion, and the autonomic nervous system. In particular, oxytocin, both a hormone and a neuromodulator, is causally related to caring behavior and stress regulation and has receptors throughout the maternal caregiving circuit (Carter 1998). There is increasing evidence for the role of oxytocin in human social cognition, empathy, and prosocial behavior. Oxytocin administration via nasal spray decreases neurophysiological responses to social stress (Heinrichs et al. 2003). Intranasal administration of oxytocin, compared to placebo, reduces amygdala activation and modulates its coupling with brainstem regions that are involved in automatic fear reactivity (Kirsch et al. 2005). In a double-blind placebo-controlled study, a single dose of oxytocin or placebo was randomly given to male participants 50 min before playing the trust game (Kosfeld et al. 2005). The results showed that investors receiving oxytocin displayed more maximum sharing behavior and had a significantly higher median and higher average transfer of monetary units. When controlling for the possibility that oxytocin just increased risk taking and not trust in particular, a risk game was used; the oxytocin group did not significantly differ from the control group in risk taking. Additionally, a single dose of intranasally administrated oxytocin is sufficient to cause a substantial increase in an individual’s ability to accurately identify affective states on a test relying on the detection of subtle affective facial expressions (Domes et al. 2007). A more nuanced role of oxytocin in social behavior was documented in a study that found that normal variance in baseline social-cognitive competence moderated the effects of oxytocin. In that study, oxytocin improved empathic accuracy only for individuals with lower social-cognitive competence (Bartz et al. 2010).

Genetic variation in the oxytocin receptor (*OXTR*) has been associated with individual differences in the expression of various social behaviors, including empathic concern and social cognition (Park et al. 2010). This was discovered in a study that tested how the rs53576 polymorphism of the oxytocin receptor relates to empathy and stress reactivity (Rodrigues et al. 2009). Compared with individuals homozygous for the G allele of rs53576 (GG), individuals with one or two copies of



Neuroimaging studies have documented that the insula and the anterior cingulate cortex (ACC) are conjointly activated when perceiving or imagining another in physical pain, social distress or extreme sadness. The anterior insula receives projections from the thalamus and from the central nucleus of the amygdala and is reciprocally connected with the secondary somatosensory cortex. This region provides a foundation for the representation of subjective bodily feelings, which substantiates emotional awareness. The ACC can be divided anatomically based on cognitive (dorsal) and emotional (ventral) components. The dorsal part of the ACC is connected to the prefrontal cortex and parietal cortex as well as the motor system, making it a central station for processing top-down and bottom-up stimuli and assigning appropriate control to other areas in the brain. By contrast, the ventral part of the ACC is reciprocally connected with the amygdala, ventral striatum, hypothalamus, and anterior insula and assesses the salience of emotion and motivational information. The orbitofrontal cortex (OFC) is involved in sensory integration, in representing the affective value of reinforcers, and in moral decision-making. In particular, the OFC is thought to regulate planning behavior associated with sensitivity to reward and punishment and is closely connected to the anterior insula and amygdala. The hypothalamus, especially the medial preoptic area, is involved in regulating basic motivational states and is essential for parental behavior and caregiving. This region is heavily interconnected with the ACC and the OFC, as well as the amygdala and periaqueductal gray (PAG). The striatum is the major input station of the basal ganglia and receives massive innervation from the ventral tegmental area (VTA), which is the origin of the mesocorticolimbic dopamine system. This system plays a key role in basic social and motivational mechanisms and has a special function in attachment and parental care.

Fig. 1 Interconnected set of brain regions that facilitate the experience of empathy and care giving labeled on a structural MRI scan the A allele (AG/AA) exhibited lower behavioral and dispositional empathy. Furthermore, AA/AG individuals displayed higher physiological and dispositional stress reactivity than GG individuals, as determined by heart rate response during a startle anticipation task and an affective reactivity scale. Another study reported that individuals with two G alleles of OXTR rs53576 exhibited more sensitive parenting behavior (Bakermans-Kranenburg and van IJzendoorn 2008).

These results concur with animal research suggesting a critical role for oxytocin in prosocial approach behavior and reactivity to social stress. They also demonstrate that the interaction between oxytocin and dopamine enhances reward from social encounters promotes engagement in social interactions (Insel and Young 2001).

Overall, many of the basic components of empathy, such as emotion contagion, empathic concern and caring for others, are deeply rooted in our evolutionary history and their neural and endocrine mechanisms are highly conserved across species (see Box 1 for a critical appraisal of the role of somatosensory resonance in empathy).

One significant difference that must be taken into account in human research is the fact that high-level cognitive abilities such as executive functions, language, and theory of mind, which are largely implemented in the prefrontal cortex, are layered on phylogenetically older social and emotional capacities. These evolutionarily newer aspects of information processing expand the range of behaviors that can be motivated by empathy beyond kin, such as caring for and helping out-group members and even members of a different species (Decety 2011b). Our natural empathy can be “accessed” in reflexive awareness, and over the course of history, humans have enlarged the range of beings whose interests they value as their own. This expanded range contributed to produce meta-level symbolic social structures, like upholding moral principles to all humanity (e.g., human rights, International Criminal Court) that are clear examples of how empathy can be and has been extended beyond the “tribe.”

Box 1: The Contribution of Somatosensory Resonance to Empathy

Sparked by the discovery of sensorimotor neurons (AKA mirror neurons) in the monkey premotor and posterior parietal cortices that discharge both when a particular action is performed (such as grasping) and when the monkey observes the same action performed by another individual, a large number of functional MRI studies have documented shared neural substrates (in fact similar activated voxels) when processing one’s own somatosensory and affective experiences and when one perceives the same states in other individuals. For instance, participants scanned while watching video clips of a leg being touched or having their own leg being touched activated the secondary somatosensory cortex (Keysers et al. 2004). In another study, subjects observed a hand either being touched or not touched by a brush presented

(continued)

Box 1. (continued)

from either an egocentric or an allocentric perspective (Schaefer et al. 2009). Both perspectives of viewing touch were associated with activation of the somatosensory system. The response in regions of the interoceptive sensory system, such as the posterior insula, processing the internal affective feeling states was specifically modulated by the visual perception of other individuals' social or affective cutaneous experiences (Ebisch et al. 2011).

Together, these data support models of embodied simulation, proposing that multimodal cortical areas underlying first-person bodily experiences are also involved with an implicit, bottom-up understanding of the actions and perhaps emotions of other individuals (Decety and Grèzes 2006; Gallese 2003). These findings have also bolstered the theory of shared representations between self and other, relying on similar neural substrates between first-person processing and third-person observation. It is important to note that *shared neural representations* **is not** a synonym for mirror neurons.

However, it is not clear that sensorimotor resonance is the mechanism facilitating emotion contagion or empathic arousal. A growing number of studies do not support such a role. In particular:

- Psychopaths who are characterized by a lack of affective empathy and resonance with the affective experience of another, do not show a deficit in sensorimotor mirroring (Blair 2011; Decety 2011a). For instance, a transcranial magnetic stimulation study demonstrated increased sensorimotor resonance to painful hand-pricking videos in college students scoring high on the psychopathic personality inventory (PPI), an index used to measure psychopathic traits in individuals from the general population, as compared to students who scored low on the PPI (Fecteau et al. 2008). Juvenile psychopaths showed greater sensorimotor resonance as measured by EEG and suppression of the *mu* rhythm when they viewed visual stimuli depicting people being physically injured, despite a lack of affective arousal as measured by event-related potentials (Cheng et al. 2012). Children with aggressive conduct disorder and psychopathic tendencies and incarcerated psychopaths exhibited typical (Marsh et al. 2013) or even stronger activation in the somatosensory cortex than control participants when they watched scenarios depicting people in pain (Decety et al. 2009b, 2013), all of which does not suggest an impairment in somatosensory responses to others' pain.
- Meta-analyses of fMRI studies that compared hemodynamic activations associated with emotional experience and emotion perception show very little overlap between the two, and the overlap is not found in the regions containing mirror neurons, such as the inferior frontal gyrus (Wager et al. 2008).

(continued)

Box 1. (continued)

- Finally, in the context of empathy for pain, fine grain data analyses of fMRI data demonstrate that selective activation in the ACC for felt and seen pain are neither necessarily coincident nor coextensive, even when conjunction-based overlap is observed at the group level (Morrison and Downing 2007). In addition, voxel-wise conjunctions do not necessarily indicate shared representations at the neuronal level. A typical voxel in an fMRI experiment has a resolution of around 3 mm^3, and its signal relates to the activity of thousands of neurons within possibly different neuronal populations.

The Development of Empathy and Its Relationship to Morality

Human babies enter the world ready to attend to social stimuli and engage in social interactions. Newborns look significantly longer at a happy facial expression than a fearful one, indicating that this preference reflects experience acquired over the first few days of life (Farroni et al. 1997). When an infant looks at her mother, she instinctively engages in some forms of prototypical conversations, which facilitates the sharing of basic emotional expressions and affective states (Nadel 2002).

Because of the importance of perceiving other conspecifics in distress to survival and its adaptive value, human infants are biologically predisposed to be sensitive to others' emotional expressions, especially when the expressions are vocalized. Neonates appear to possess a neural mechanism for discriminating vocalizations associated with emotions. For instance, they exhibit a mismatched electroencephalographic response over the right hemisphere in response to emotionally laden syllables (happy or fearful vs. neutral) within the first few days of life (Cheng et al. 2012b). In 3- to 7-day olds, another person's sad vocalizations are associated with a selective increase of neural activity in brain regions involved in processing affective stimuli, such as the OFC and insula (Blasi et al. 2011). These results suggest remarkably early functional specialization for processing negative emotions expressed in the human voice.

Neonates contagiously cry in response to the distress of conspecifics in their proximity (Martin and Clark 1982), a reaction that is heightened in response to another's crying compared to the child's own crying (Dondi et al. 1999). Contagious crying's specificity and characteristics of affect sharing have prompted the hypothesis that it is one of the earliest forms of empathic arousal. Importantly, newborns discriminate between their own (previously recorded) cries and those of another infant. Thus, neonates' contagious crying cannot be explained by lack of differentiation between the distress of self and other. Subcortical pathways connecting the brainstem, superior colliculus, hypothalamus, pulvinar, and amygdala, all of which develop very early in fetal brain development, mediate this affect sharing in neonates (Decety 2010a).

Empathic concern typically emerges during the first year of life and develops in the context of social interactions. While the cognitive components (emotion understanding and perspective taking) gradually increase during the first 3–5 years of life, the affective and motivational components of empathy are in place very early. Infants in their first year begin to show signs of concern for others when they are in distress and are already responding in socially appropriate ways when viewing others in distress or pain (Zahn-Waxler et al. 1992). This emotional motivation requires not only an affective reaction elicited by someone else's emotional state but also a basic attribution of mental states. Importantly, these early signs of empathic concern require only minimal mindreading and perspective-taking capacities. Rather, they merely necessitate the capacity for emotional contagion and the capacity to attribute distress to another. Not only do very young children make pain attributions, but the studies on comforting behavior also demonstrate that they respond to a variety of distress cues, and they direct their comforting behavior in ways that are appropriate to the target's distress. For example, in experimental studies of 1-year olds, crying also elicited comforting behaviors; so did coughing and gagging (Roth-Hanania et al. 2011). Furthermore, in these studies, children often comfort the target in appropriate ways, and actually make pain attribution in conjunction with their comforting behavior and recognize what the target is distressed about. Despite the impressive capacity for prosocial motivation, children under the age of two have severely limited mindreading and perspective-taking abilities. In the early childhood years, prosocial behavior also becomes more selective, directed at friends and relations and not all conspecifics, and is increasingly governed by display rules and social norms (Hay and Cook 2007). Heritable individual differences in empathy and prosocial behavior soon emerge (Knafo and Plomin 2006). Thus, the very high rates of helpfulness observed in nearly all toddlers are likely to decline in favor of more selective displays of helpfulness by particular children to particular people, under particular conditions (Hay 2009).

As infants develop and learn, they are increasingly able to evaluate their social surroundings and even differentiate agents based on their social actions towards each other. Already at 3 months of age, infants preferentially attend to a character who had previously acted in a prosocial (versus anti-social) manner (Hamlin et al. 2010), suggesting a partiality towards those who 'do good things.' By 6 months of age, this visual preference has expanded to behaviors, with participants not only selectively attending to prosocial agents (when paired with anti-social or neutral characters) but also selectively approaching them (Hamlin et al. 2007). Further, by 15 months of age, some infants are able to evaluate the fairness of an agent in a third-party situation. A recent study examining the relationship between a visual violation of expectation task and infants' sharing behaviors found that infants who shared a toy they preferred (over a non-preferred toy or no toy at all) also attended significantly longer to a third-party interaction in which the allocation of resources among conspecifics was unequal (Schmidt and Sommerville 2011). This finding suggests that those infants who behaved altruistically also expanded their prosocial expectations to the interactions of others.

Prosocial behaviors in the form of helping, sharing, and consoling thus emerge shortly after the first year of life. Early signs of helping behavior are reported in the toddler years, with 14- to 18-month-olds fetching objects of desire that appear out of reach of an experimenter (Warneken and Tomasello 2009) and helping to complete household chores (Rheingold 1982). Early other-oriented empathic responding to the distress of another was observed from 8 to 16 months and continued to increase gradually into the second year (Roth-Hanania et al. 2011). Children between the ages of 1 and 2 years exhibit increased comforting behaviors towards individuals in distress (Zahn-Waxler et al. 1992) and may even give up their own favorite objects in an empathetic gesture (Svetlova et al. 2010). Furthermore, toddlers have been found to exhibit more concern towards the victim of a moral transgression than the transgressor, even if the victim did not show any behavioral markers of distress (Vaish et al. 2009). This finding suggests that 18- to 25-month olds are not simply reacting to emotional displays but to the intentions and desires of others. Taken together, children under the age of two already respond in socially appropriate ways when viewing others in distress, and they are able to make social evaluations based on observed behavior.

Neurodevelopmental Changes in Response to Perceived Harm to Others

The importance of emotion and empathy for the development of moral cognition and behavior has long been acknowledged (Blair 1995); however, few studies have been conducted to characterize the neurodevelopment of moral sensitivity in typically developing children. One recent developmental study combined neurophysiological measures, including functional magnetic resonance imaging, eye-tracking, and pupillary response, with behavioral measures to examine affective and moral judgments across age (Decety et al. 2012a). Participants aged between 4 and 37 years viewed scenarios depicting intentional versus accidental actions that caused harm/damage to people and objects. Morally salient scenarios evoked stronger empathic sadness in young participants and were associated with enhanced activity in the amygdala, insula, and temporal poles. While intentional harm was evaluated as equally wrong across all participants, ratings of deserved punishments and malevolent intent gradually differentiated with age. As age increased, participants were more willing to punish an agent who damaged an object less severely than an agent who harmed a person. Furthermore, age-related increase in activity was detected in the ventromedial prefrontal cortex (vmPFC) in response to intentional harm to people, as well as increased functional connectivity between this region and the amygdala. In all participants, irrespective of their age, perceived intentional harm to people (as opposed to accidental harm) was associated with increased activation in brain regions sensitive to the perception, prediction, and interpretation of others' intentions, such as the right posterior superior temporal sulcus (Blakemore et al. 2003), as well as regions processing the affective consequences of these actions, namely the temporal poles, insula, vmPFC/OFC, and amygdala. The more participants reported being upset about harmful actions, the higher the activity in the amygdala. The younger the participants were, the greater their empathic sadness for the victim of harm. Ratings of sadness for the victim correlated with activity in the insula, thalamus, and subgenual prefrontal cortex. This latter region has extensive connections with circuits implicated in emotional behavior and autonomic/neuroendocrine response to stressors, including the amygdala, lateral hypothalamus, and brainstem serotonergic, noradrenergic, and dopaminergic nuclei (Drevets et al. 1997). Damage to this region, especially if it occurs during early childhood, is associated with abnormal autonomic responses to emotional experiences and impaired comprehension of the adverse consequences of pernicious social behaviors (Bechara et al. 1996). In addition, functional connectivity analyses showed that, in early childhood, the brainstem showed greater functional connectivity with OFC/vmPFC, whereas in young adults, the vmPFC increased its connectivity with amygdala and posterior STS. These connectivity data support the primary and initial role of an involvement of regions that play a critical role in emotion processing in moral sensitivity in young children.

Overall, this study shows that the pattern of developmental change in response to the perception of harm is indicative of a gradual shift from the affective and somatovisceral responses in young children to a more cognitive evaluative level associated with executive control of higher-order emotion and moral judgment in older participants.

Neural Response to Perceiving Others in Pain or Distress

Pain facilitates evolved protective social functions, not only warning the person suffering it that something is awry but also providing the understanding that another conspecific is at risk and inducing expressive behaviors that attract the attention of others and motivate prosocial behavior. In support of this, when exposed to their infants' cries (compared to neutral sounds), first-time mothers who were breastfeeding reported higher ratings of sadness and desire to help for their infants' cries than control sounds (Lorberbaum et al. 2002).

Numerous functional neuroimaging studies revealed that, when individuals are presented with stimuli conveying another person's distress and physical pain, reliable activation of a neural network involved in the first-hand experience of pain, including the anterior midcingulate cortex (aMCC), anterior insular cortex (AIC), supplementary motor area (SMA), and periaqueductal gray area (PAG), occurs. Activation in this network has been reported in response to facial expressions of pain, injury of body parts, imagining the pain of others, being socially excluded, or simply observing a signal indicating that someone will receive painful stimulation (see Lamm et al. 2011 for a meta-analysis). The same network of regions, especially the dorsal ACC and anterior insula, are also involved in the experience of social exclusion. Many of the functional MRI studies that examined the neural response to social exclusion have used the cyberball paradigm. Participants in the scanner were led to believe that they were playing the game (tossing a ball between three individuals) with two other people (in fact it is a computer game). Then they played one round of the ball-tossing game in which they were included and a second round in which they were excluded partway through the game (see Eisenberger 2011 for a review). When participants were excluded from the game, increased hemodynamic activity was detected in the ACC and anterior insula, and the more they subjectively felt rejected, the greater the activity in the ACC.

Pharmacological studies with non-human animals and humans also provide evidence that physical and social pain rely on shared neurochemistry by demonstrating that certain drugs have similar effects on both types of pain. For example, opiate drugs, such as morphine and heroin, known primarily for their pain-relieving qualities, have also been shown to reduce behaviors indicative of social pain in animals (Carden et al. 1991; Warnick et al. 2005). In human subjects, it was shown that acetaminophen, a medication commonly used to reduce physical pain, also lessened the pain of social rejection at both neural (significantly less hemodynamic response in the ACC, anterior insula and amygdala to social exclusion) and behavioral levels (deWall et al. 2010).

Activation of the neural circuit involved in the first-hand experience of pain from viewing of others in pain or being in social pain is not specific to the sensory qualities of pain or to nociception. Instead, this response is associated with more general survival mechanisms, such as aversion and withdrawal when exposed to danger and threat (Decety 2010b), and in the context of social pain, acts as a signal that promotes social bonding. The same network of regions is also involved in grief and extreme sadness (see Meerwijk et al. 2013 for a meta-analysis). For example, bereaved participants scanned while viewing pictures of their deceased relatives, compared with pictures of strangers, showed greater activity in the ACC and anterior insula (O'Connor et al. 2008). Viewing human and animal suffering led to large overlapping regions of activation previously implicated in empathic responding to suffering, including the amygdala, ACC, anterior insula, and OFC (Franklin et al. 2013).

Thus various types of unpleasant and socially painful experience, not just the perception of physical pain, activate the same neural network that first evolved to support processing nociceptive information and the control of homeostasis (i.e., the visceral regulation of internal states, such as temperature, thirst, hunger and pain, that are required for the life of an organism).

Importantly, the brain response to signs of pain and distress of others is highly dependent on social relationships, and various social and contextual factors moderate the experience of empathy. Empirical work with both non-human animals (Langford et al. 2010) and humans has shown that empathy can be moderated by how the target person is perceived, including how similar (Batson et al. 1997) or likable that person is to the observer (Kozak et al. 2006) and by group membership (Yabar et al. 2006). This impacts information processing of the different components of empathy such as affective arousal, emotion understanding, and motivation to care (Decety et al. 2009a; Echols and Correll 2012).

For instance, one fMRI study demonstrated that empathic arousal was moderated early during information processing by a priori attitudes toward other people (Decety et al. 2009). In that study, participants were significantly more sensitive to the pain of individuals who had contracted AIDS as the result of a blood transfusion – as evidenced by significantly higher pain and empathy ratings and significantly greater hemodynamic activity in areas associated with pain processing when they viewed videos of facial expression of pain – as compared to individuals who had contracted AIDS as the result of their illicit drug addiction (sharing needles). Another fMRI study found evidence for the modulation of empathic neural responses by racial group membership (Xu et al. 2009). Notably, the neural response in the ACC to perception of others in pain decreased remarkably when participants viewed faces of racial out-group members being pricked by a needle relative to racial in-group members. Furthermore, activity in the pain network was enhanced when people viewed their loved ones in physical pain compared to strangers (Cheng et al. 2010) and was reduced if the person in pain has been unfair in a prior interaction (Singer et al. 2006).

Given the extent to which affective arousal promotes empathic concern and helping behavior, one might expect perceivers to experience reduced concern for out-group victims as well. Recent research provides support for this hypothesis. Soccer fans in one study observed either another fan of their favored team (in-group) or a fan of their rival team (out-group) experiencing painful shocks (Hein et al. 2010). Participants showed increased empathy for in-group over out-group targets, reporting higher pain ratings and showing greater activation in the anterior insula for in-group targets. Participants also reported feeling more empathic concern for in-group targets, and they were more likely to volunteer to help by sharing the pain of in-group than out-group targets. Moreover, the difference in anterior insula activation when viewing in- vs. out-group members in pain predicted group differences in helping behavior. Another neuroimaging study demonstrated that the failures of an in-group member are painful, whereas those of a rival out-group member give pleasure – a feeling that may motivate harming rivals (Cikara et al. 2011).

Individuals' personal context also modulates affective arousal, as demonstrated by two functional neuroimaging studies showing that physicians do not react to the pain of others in the same way as non-physicians do. One study compared the neuro-hemodynamic response in a group of physicians and a group of matched control participants while they viewed short video clips depicting hands and feet being pricked by a needle (painful situations) or being touched by a cotton bud (non-painful situations). The results demonstrated activation of the pain matrix in controls when they attended to the painful situations relative to the non-painful ones. However, when physicians watched painful procedures, a different pattern of activation was observed, with cortical regions underpinning executive function and self-regulation (dlPFC and mPFC) and executive attention (precentral, superior parietal and pSTS/TPJ) activated (Cheng et al. 2007). Unlike in the control group, no signal increase was detected in the pain matrix in the physicians. A second study recorded event-related potentials (ERPs) from physicians and matched controls while they were presented with the same visual stimuli (Decety et al. 2010). The results showed early signal change 110 ms after stimulus presentation, which differentiated between pain and no pain over the frontal cortex, reflecting negative arousal, as well as late P3 over the centro-parietal regions in control participants. In contrast, no such early ERP response was detected in physicians, indicating that affect regulation has very early effects, inhibiting the bottom-up processing of negative arousal from the perception of painful stimuli.

Thus observing another individual in pain induces a visceral negative arousal in the perceiver. This neurological response is modulated, as the evolutionary theory would predict, by our relationship and attachment with others and by various contextual and interpersonal factors. Empathy is in fact a limited resource, and extending it to members of the out-group is possible but effortful.

Lack of Sensitivity to Others in Psychopathy

Psychopathy, a neurodevelopmental personality disorder believed to affect approximately 1 % of the general population, epitomizes the process through which a lack of sensitivity to another's distress or suffering contributes to callous disregard for others (Hare 1999). Individuals with psychopathy demonstrate stunted emotional development and a general lack of empathy exhibited through specific individual traits. Psychopathy has been associated with uncommitted mating behaviors, increased sexual coercion, lack of parental investment and increased sexual promiscuity. Psychopaths are often callous, shallow, and superficial. They do not fear punishment, have difficulty regulating their emotions, and do not experience insight into or empathy for the effect of their behaviors on others.

There is solid evidence that empathy deficits and a lack of regard for others may play a role in aspects of moral judgment, particularly those associated with care-based morality. Adult psychopaths fail to experience distress cues as aversive, regardless of whether that observer is the aggressor or a bystander (Blair 1995), evidenced by work indicating that offenders with high levels of psychopathy show reduced autonomic arousal while viewing a confederate receiving electric shocks (Aniskiewicz 1979). The ability to experience distress as aversive is critical for the development of moral emotions (e.g., guilt and remorse), as distress cues are assumed to activate tendencies to withdraw in any observer who processes them.

These abnormal responses to moral transgressions or to the distress of others are evident as early as in childhood. For example, children with psychopathic tendencies exhibited reduced electrodermal responses to distress cues (e.g., a crying face) and threatening stimuli (e.g., a pointed gun) relative to controls (e.g., Blair 1999). A study using electroencephalography examined this phenomenon by assessing how callous-unemotional traits in juvenile psychopaths were related to empathic arousal deficits (Cheng et al. 2012). In this study, juvenile offenders with high callous-unemotional traits, juvenile offenders with low callous-unemotional traits, and age-matched typically developing adolescents were shown images of people in pain while EEG/ERPs were recorded. Results demonstrated that youth with high callous-unemotional traits exhibited atypical neural dynamics of pain empathy processing in the early stages of affective arousal. This abnormality was exemplified by a lack of the early EPR response (120 ms), which is thought to reflect an automatic aversive reaction to negative stimuli, and was coupled with relative insensitivity to actual pain (as measured with the pressure pain threshold). Nevertheless, their capacity to understand intentionality was not impaired; neither was their sensorimotor resonance. This uncoupling between affective arousal and emotional understanding likely contributes to psychopaths' callous disregard for the rights and feelings of others. Functional MRI studies have reported that adolescents with disruptive psychopathic traits showed reduced activity to increasing perceived pain intensity within structures typically implicated in affective responses to others' pain, including the rostral ACC, insula and amygdala (Marsh et al. 2013). Another study also found reduced neural response to others' physical pain in children with conduct problems in the insula and ACC (Lockwood et al. 2013). Youths with psychopathic traits exhibited reduced amygdala responses to fearful facial expressions (Marsh et al. 2008) and during affective theory of mind tasks (Sebastian et al. 2012).

To identify potential differences in patterns of neural activity in incarcerated psychopaths and incarcerated controls during the perception of empathy-eliciting stimuli depicting other people experiencing pain, one recent fMRI study included 80 incarcerated male participants: 27 classified as high (PCL-R $\geq$ 30), 28 classified as intermediate (PCL-R between 21 and 29), and 25 classified as low (PCL-R $\leq$ 20) in psychopathy using the Psychopathy Check List–Revised (PCL-R; Decety et al. 2013). Psychopaths exhibited significantly less activation in the vmPFC, lateral OFC, and PAG relative to controls but surprisingly showed greater activation in the insula. The major difference in brain response between psychopaths compared to controls during the perception of others in pain was a reduced response in the brainstem and OFC/vmPFC, which was negatively associated with their severity on the PCL-R.

Brain abnormality in a number of neural regions and circuits seems to account for the lack of affective arousal in individuals with psychopathic traits. Structural neuroimaging studies associate psychopathy with a host of morphological brain abnormalities, including reduced volume of the amygdala, reduced gray matter volume in the frontal and temporal cortex, especially in the right posterior superior temporal sulcus, and in the insula, and increased volume of the striatum. Furthermore, psychopaths often exhibit signs of reduced structural integrity of the uncinate fasciculus (Koenigs et al. 2010), which connects parts of the limbic system in the temporal lobe (such as the hippocampus and amygdala) with the OFC, a region necessary for moral decision-making.

Further evidencing abnormalities in moral reasoning in individuals with psychopathy, research indicates that individuals who score high on psychopathy evaluations understand moral norms but generally disregard them. For instance, a study that evaluated incarcerated offenders found no evidence that offenders high in psychopathy – as measured by total psychopathy score – were any worse at distinguishing moral from conventional transgressions than were low-psychopathy offenders (Aharoni et al. 2012). These results are consistent with an fMRI study examining psychopathic responses to pictures depicting morally wrong social actions, unpleasant, but not immoral, social scenes, and neutral social scenes (Harenski et al. 2010). In this research, psychopathic and non-psychopathic criminal offenders rated the severity of the moral violation depicted in each type of stimuli. Both groups rated moral violations significantly higher in moral severity than unpleasant but not immoral scenes, and no differences were observed between groups within any of the image conditions, suggesting equally accurate abilities to distinguish moral violations. Interestingly, brain activation recorded during the evaluation of moral violation pictures did detect differences in processing between psychopaths versus non-psychopaths. Atypical brain activity was detected in several regions involved in moral decision-making, including reduced moral/non-moral picture distinctions in the vmPFC, amygdala, and anterior temporal cortex in psychopaths relative to non-psychopaths. These results indicate that psychopaths use different brain regions when making moral decisions than do non-psychopaths. Importantly, psychopaths have a dysfunction in the vmPFC, a critical region that supports the integration of emotional responses with moral decision-making, which contributes to moral insensitivity and lack of empathic responses. Youths with psychopathic traits showed reduced amygdala responsiveness to legal actions relative to healthy youths and reduced amygdala–OFC connectivity relative to healthy youths during task performance (Marsh et al. 2011).

Together, the available evidence indicates that failures in moral knowledge or reasoning alone do not give rise to antisocial behaviors or callous disregard for others. Rather, these behaviors arise from an inability to combine this reasoning with aversive affective arousal. The atypical processing of negative emotional stimuli, such as perceiving others' suffering, which is an important source for empathic concern, coupled with poor inhibitory control, may account for morally inappropriate behavior in psychopaths. Evidence for such deficiencies is found not only in behavior but also at the neural level of analysis. Dysfunction of the connectivity between the amygdala, insula and vmPFC seems to partially explain low socio-emotional responses to others' distress, though it is important to note that a lack of empathic arousal alone does not explain offensive behaviors. Behavior is motivated by rewards and discouraged by punishments, with the former influencing behavior more effectively than the latter in most individuals. Offending behavior exists and persists because it is rewarding, and these rewards in turn affect the activity of the mesolimbic dopamine system. For example, pathological reward-seeking in individuals with impulsive-antisocial psychopathic traits increases their likelihood of engaging in behaviors that are dangerous to others and themselves (Buckholtz et al. 2010). A functional neuroimaging study of youth with aggressive conduct disorder found increased activation in the striatum and amygdala when adolescents watched people being intentionally hurt by others (Decety et al. 2009).

The extent of amygdala activation to viewing others in pain was positively correlated to the participant's number of aggressive acts and their ratings of daring and sadism scores. This finding suggests that increased activity in the amygdala, particularly when coupled with activation in the striatum, may reflect a general arousing effect of reward (Murray 2007). In keeping with this result, sadists relative to non-sadists showed greater amygdala activation when viewing individuals being physically injured (Harenski et al. 2012). They also rated pain pictures higher on pain severity than non-sadists. Sadists but not non-sadists showed a positive correlation between pain severity ratings and activity in the anterior insula.

Overall, neuroscience research with juvenile and adult psychopaths points out a dysfunction in the response and in the functional connectivity between the amygdala and vmPFC, a circuit that is integral in forming associations between environmental cues and affective states. This lends support to the notion that emotion reactivity plays a central role in empathic concern, moral decision-making, and care-based morality.

Conclusions

Even the most advanced forms of empathy in humans are built on more basic forms and remain connected to core mechanisms associated with affective communication, social attachment, and parental care that are highly conserved across mammalian species. Evolution has tailored the mammalian brain to be sensitive and responsive to the emotional states of others, especially one's offspring, kin, and members of one's social group (Decety et al. 2012b). These empathy-based behaviors have co-opted more primitive homeostatic processes involved in reward and pain systems to facilitate various social attachment processes. Encephalization of pain evaluation transitions the pain experience from being purely a physical phenomenon, in which the body and brain react to physical nociceptive stimuli, to a psychophysiological phenomenon, in which the loss of social contact produces psychological pain (Tucker et al. 2005). The social bonds supported by this nociceptive mechanism, in its most important form, facilitate parental behaviors that ensure the survival of the young. Empathy clearly increases fitness and has a value for survival, insofar as it serves as a mode of communication between members of a family and between members of a social group.

Prosocial behavior emerges early in life and is underpinned by the biological nature of human infants who, in their first year, express signs of concern for the other. Such a concern requires only a minimal capacity for mindreading and self-awareness. Developmental neuroscience research clearly indicates that emotional reactivity and empathic arousal are necessary in the development of moral decision-making and care-based morality. Children with psychopathic tendencies seem to lack empathic arousal. They may cognitively understand the emotional state of others without being moved by their distress. The sharing of vicarious negative arousal provides a strong signal that can promote empathic concern and caring for others. To be motivated to help another, one needs to be affectively, empathically aroused and anticipate the cessation of the mutually experienced personal distress. Without input from the affective system and processing of that input by the OFC, moral behavior is understandably difficult to develop.

One corollary of this evolutionary model is that care giving produces preferences. Kin selection, reciprocal altruism and group selection can be viewed as consequences of the caring motivation. There is plenty of behavioral and neuroscience evidence demonstrating that group-level processes critically moderate the conditions in which empathic understanding and empathic concern are expressed (Echols and Correll 2012). Thus, while empathy plays a fundamental role in the development of morality, by no means is morality reducible to empathy and emotion sensitivity. Our moral sense is the result of laws of nature, forces of culture and contingencies of history.

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The Many Faces of the Emotional Body

Beatrice de Gelder and Ruud Hortensius

Abstract The perception of emotional signals is at the core of the study of the social brain. In this chapter, we discuss research in the field of affective and social neuroscience that specifically uses bodily expressions. Starting with the initial studies mapping the neural substrate of perception of simple bodily expressions, several steps have been taken to grasp the full extent of genuine interactions, from the use of multiple emotional cues, to dynamic social interactions, and recently the use of virtual reality. With increasing complexity of the emotional signals used in neuroscientific research, we can approximate the natural richness of the social and emotional reality.

Introduction

During the past few decades psychologists, and more recently neuroscientist, have tried to capture the reality of emotions. A notion that has repeatedly cropped up in the affective and social neuroscience literature is that of the "social brain." The concept is most often used as an umbrella term covering many of the social skills observed in animals. In a more narrow sense, the concept refers to the neurobiological basis of the ability to engage with conspecifics. A social species is one that spends the better part of its time interacting with others and for whom interaction provides essential benefits. While researchers have tried multiple routes to study the

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B. de Gelder (✉)
Faculty of Social Behavioural Sciences, Tilburg University, Postbus 90153, 5000 LE Tilburg, The Netherlands

Brain and Emotion Laboratory, Maastricht University, Room 3.009, Oxfordlaan 55, 6229 EV Maastricht, The Netherlands
e-mail: b.degelder@maastrichtuniversity.nl

R. Hortensius
Faculty of Social Behavioural Sciences, Tilburg University, Postbus 90153, 5000 LE Tilburg, The Netherlands

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neurobiological basis of emotion, almost all the studies in the literature, including most of our own, take the viewpoint of the passive observer. This has already led to a detailed picture of how the brain of the observer reacts to the sight of a social affective stimulus like a conspecific face, body part, whole body, smell or vocalization and how these neural processes underlie adaptive behavior. This chapter will discuss research that uses bodily expressions from both single and multiple bodies, in a range from prototypical to complex social interactions.

What steps have been taken in the past to gain an understanding of human emotion processing? From the beginning of research on emotion perception, a variety of emotional signals have been used (see Fig. 1). Facial expressions dominated the field for years, the only alternatives being emotional pictures (e.g., International Affective Picture System; Lang et al. 1999) and emotional sounds (e.g., voice or music). In the last decade the field of affective and social neuroscience has started to investigate bodily expressions as an emotional signal (Hadjikhani and de Gelder 2003). We will start this chapter by providing several arguments for why bodies have their place in the study of the social brain. Next, we briefly discuss research that maps the neural substrate of bodily expression perception. In the last few years, the combinations between faces and bodies and between those and contextual information have been used to gain a more accurate picture of emotion perception. As we will discuss, the use of multiple emotional cues provides a valuable starting point to understand the richness of the emotional world. We will end the overview of past research by discussing a new and interesting step that uses social interactions to measure the dynamics of emotion perception. In the remainder of this chapter, we describe a prospect for the future of affective and social neuroscience by providing new ways of investigating the human emotional brain (e.g., the use of virtual reality). Ideally, neuroscientists will leave the comfort of the lab and step into the real world to study real humans having real emotion responses in real interactions. The end result will be a true social and affective neuroscience. While in this chapter we illustrate the evolution of the study of emotion perception in affective and social neuroscience from the perspective of the perception of bodily expressions, we do not mean that research using other methods or emotional signals is not of value. We do not wish to provide an all-encompassing review; we will merely illustrate the flow of research over the last two decades.

Why Bodies?

It is surprising that although Darwin (1872/2002) and James and Lange (1922), forefathers of modern emotion science, wrote on this topic, whole body expression have since largely been ignored. In recent times, the importance of these expressions has been stressed by Frijda (1986) and Tomkins (1995) in their discussion of the interplay between emotion and action. But until recently, these theoretical ideas and early studies by Ekman and colleagues (1965; 1967) and Dittmann et al. (1965) on face and body affect communication did not prompt empirical investigations and

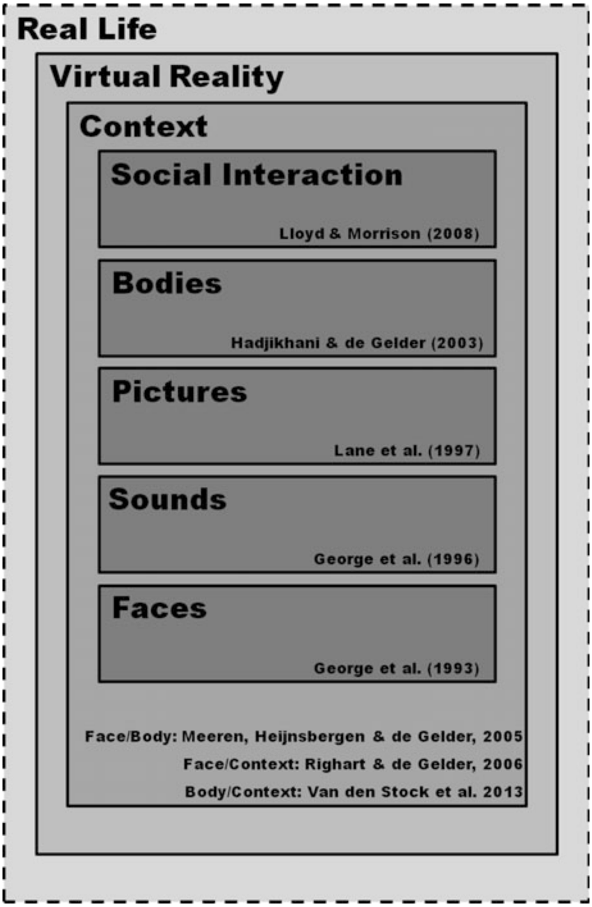

Fig. 1 The use of emotional signals as building blocks of the natural richness of the social and emotional reality Note, only the first published article per emotional signal in the study of emotion perception using imaging techniques (e.g., PET, fMRI) are listed since the emergence of modern social and affective neuroscience

emotion research has used facial expressions as the primary emotional signal to study. Previously, we gave a number of reasons why the field of affective and social neuroscience should integrate bodily expressions in the study of social behavior (de Gelder 2009). Here, we briefly summarize several relevant ones.

In everyday interaction, people not only rely on both facial and bodily communication. Similar to facial expressions, bodily expressions are easily recognized (e.g., Atkinson et al. 2004; de Gelder and Van den Stock 2011) and, as one might observe in an elevator or during a conversation, people imitate each other's posture. Indeed, emotional mimicry can also be observed when bodies are used as stimuli rather than just faces (Magnée et al. 2007). Furthermore, similar to the face action coding system developed by Ekman and collaborators (FACS; Ekman and Friesen 1978), it is possible to build a body action coding system (BACS; Huis in 't Veld et al., submitted for publication) that allows measurement of the muscle groups involved in whole body expressions.

Bodily expressions allow the communication of emotions over a wider spectrum than facial expressions. The possibility of signaling to an observer over a larger distance highlights the possible differences between emotional signals in communicative roles and behavioral outcome. Emotion is closely linked to action (e.g., Frijda 1986) and, while the processing of another individual's facial expressions can lead to an automatic inference of the person's mental state (Baron-Cohen et al. 1997), bodily expressions show the action component of emotion by biasing attention towards the action of the person or group. Thus, an understanding of how bodily expressions are interpreted allows a more direct understanding of the importance of emotions as adaptive actions.

While the study of the perception of bodily expressions in isolation is valuable, combining facial and bodily expressions will provide researchers a unique possibility to study ambiguous perception (e.g., conflicting affective signals) and to test current theories about emotion and face perception. Furthermore, it will permit researchers to disentangle the importance of facial and bodily expressions in communicating a particular emotion (e.g., disgust versus anger). Are some emotional states better transferred by face or body?

The Neurofunctional Basis

Although emotional body postures had not yet been used at the beginning of this century, there were already a few publications available on the brain areas involved in perception of emotionally neutral bodies (e.g., Downing et al. 2001; Grossman and Blake 2002). Two areas have been at the center of research in human fMRI studies (for a review, see Peelen and Downing 2007). Seeing whole human bodies and body parts activates a cortical area near the middle occipital gyrus/middle temporal gyrus, the extrastriate body area. A second area, the fusiform body area, which partially overlaps with the fusiform face area, is also body-selective. While emotion-specific modulation of these areas has been reported (for a review, see de Gelder et al. 2010), the goal of these studies is to identify the brain areas that are specifically dedicated to the representation of bodies as one specific category of visual objects.

From an evolutionary perspective, as noted before, emotions are closely linked to actions. When confronted with an emotional signal in the environment, affect programs will be activated in the individual that produce neurophysiological changes that trigger adaptive behavioral responses (e.g., Darwin 1872/2002; Frijda 1986; Panksepp 1998). Indeed, this is also reflected in the neural substrate. The first fMRI study on the perception of emotional bodily expressions reported the activation of the amygdala and fusiform cortex when subjects observed a fearful whole body expression (Hadjikhani and de Gelder 2003). A follow-up study reported not only activation in areas important for visual and emotional processes but also action representation and motor responses (de Gelder et al. 2004), and this action component was later found to be systematically associated with passive observation of bodily expressions (for a review, see de Gelder 2006; de Gelder et al. 2010). Studies using dynamic images reported similar activation to threatening bodily signals (Grèzes et al. 2007; Pichon et al. 2008, 2009, 2012).

To allow adaptive responses, the processing of threatening bodily expressions needs to be rapid and relatively independent of attention. Indeed, a non-striate, subcortical-based route may play an important role here (Tamietto and de Gelder 2010; Tamietto et al. 2012). First, there is fast detection of and orientation to the bodily expression (superior colliculus and pulvinar). Next, subcortical and cortical connections underlie integration of affective content (superior colliculus, pulvinar, amygdala, and orbitofrontal cortex), followed by adaptive responses (periaqueductal grey, putamen, caudate nucleus, and premotor cortex) (de Gelder et al. 2012). In sum, studies on the neural mechanisms of perception of emotional bodily expressions emphasize more the automatic consequence rather than the cognitive interpretation of the communicated emotion expression.

Perception of Bodily Expressions in Context

While most of the research has focused on emotional signals in isolation, in everyday life no such thing as a headless happy body exists. In recent years, multiple studies have been reported on the combinations of facial and bodily expressions and context. Not only has this approach been valuable to study emotion perception in a more realistic context but also to investigate individual differences in, and the influence of neurological impairments on, emotion perception.

During social interaction, one's attention has to be focused on different cues (e.g., facial or bodily cues). Indeed, not only influences emotional information from bodily expression face memory (Van den Stock and de Gelder 2012), also recognition of facial expressions is modulated by the expression of the body (Aviezer et al. 2008; Kret et al. 2013; Meeren et al. 2005; van den Stock et al. 2007). The perceptual integration of facial and bodily cues, even when not attended to, is rapid *(*Aviezer et al. 2011; Meeren et al. 2005). Interestingly, subjects with basolateral amygdala damage have a deficit in ignoring task-irrelevant bodily threat signals when recognizing facial expressions (de Gelder et al., submitted for publication) and decreased recognition of happy facial expressions when paired with aggressive bodily expressions was observed in imprisoned aggressive male offenders (Kret and de Gelder 2013).

We have outlined several possible mechanisms underlying this body context effect elsewhere (Van den Stock and de Gelder 2012). First, the overlap between facial expressions of surprise and fear illustrate the notion that facial expressions in isolation are ambiguous (de Gelder et al. 2006). Without context, surprise faces can be interpreted as negative or positive in valence, which is reflected in physiological responses (Neta et al. 2009). Bodily expressions provide this context (Aviezer et al. 2012). Second, bodies and faces overlap in terms of the underlying neural network, which might induce competition for neural resources (e.g., Stienen et al., submitted for publication). Lastly, action and information relevant to a behavioral response is better transferred by bodily expressions and, therefore, biases emotion perception.

Similar to previous studies using facial expressions (e.g., de Gelder et al. 2006; Righart and de Gelder 2006; Wieser and Brosch 2012), multiple studies have investigated the effect of emotional context (e.g., a threatening scene) on the recognition and processing of bodily expression (Kret and de Gelder 2010, 2013; Kret et al. 2013; van den Stock et al. 2013). Explicit recognition is influenced by the emotion of the scene (Kret & de Gelder 2010), and the influence of the context is increased in imprisoned aggressive male offenders (Kret and de Gelder 2013). Happy bodily expressions were interpreted by this group as being angry when depicted in an aggressive context. At the neural level, activity in the EBA was increased when an emotionally neutral body was shown in a threatening scene (Van den Stock et al. 2013). The emerging picture is that the effect of context is an early perceptual process, in which the threatening scene biases the perception of bodily expressions and hijacks neural resources (c.f., Sinke et al. 2012).

Social Interactions

In animals, evidence for social abilities is traditionally derived from behavioral observations. In a highly social species, individuals rarely isolate themselves but are constantly involved with each other. Naturalistic observations rarely focus on a single individual but on multiple individuals actively engaged with each other. What we see is small groups or dyads continuously organizing and changing their composition, individuals constantly leaving or joining others, group movements in various directions, and so on. A few recent studies using point-light displays, animations, realistic videos of social interactions or crowds have already put interactions on the agenda and, even if they still involve participants that passively observe others interacting, quite a bit can already be learned from them.

One way to study the neural basis of information transferred in social interaction is the use of whole body point-light displays (Johansson 1973). Using only biological motion, one can distinguish known individuals (Cutting and Kozlowski 1977), gender (Kozlowski and Cutting 1977), action (Dittrich et al. 1996), and emotion (Atkinson et al. 2004; Pollick et al. 2002). Moreover, using only information derived from biological motion, people can easily recognize emotions in a social interaction (Clarke et al. 2005). Minimalistic whole-body point-light displays lead to differential activity for social interactions in brain regions underlying perception of emotion and action (Centelles et al. 2011). While the use of point-light displays in the field of affective and social neuroscience remains infrequent, the possibility of studying the perception-action link with manipulation of motion, spatial and temporal coherence of the used stimuli (e.g., Christensen et al. 2011) provides a unique and intriguing next step.

Another line of research tapping into the dynamics of emotionally interacting people uses fully realistic dynamic stimuli. A study by Lloyd and Morrison (2008) found that the brain codes subtle differences in social interactions (see also, Iacoboni et al. 2004). We have complemented these previous studies by focusing on the effect of attention in the processing of social interaction. Participants implicitly or explicitly observed a social interaction that was threatening or teasing (Sinke et al. 2010). Results showed less deactivation of the amygdala for the threatening compared with the teasing social interaction for both tasks. Moreover, action-related areas, the putamen and premotor area, were activated in both tasks. These results show that, also during complex social interactions, threat can be processed automatically and trigger defensive behavior (cf., Pichon et al. 2012).

Recently, we have started to investigate the neural mechanisms of the perception of a social emotional situation in the context of a group (Hortensius and de Gelder, submitted for publication). Borrowing a phenomenon well studied in social psychology, the bystander effect, we investigated the influence of the group on neural responses to an emergency. The bystander effect refers to the decrease in helping behavior that occurs when one is confronted with an emergency in the presence of other onlookers. It was expected that group influences would already be reflected in neural responses underlying preparation for action (c.f., motor regions). While participants performed an unrelated color-naming task in an fMRI scanner, they observed an emergency with either no, one, two or four bystanders. The results indeed showed a decrease in activity with the increase in group size in the regions that are relevant for action preparation and adaptive behavioral responses (pre- and postcentral gyrus, medial frontal gyrus). This study illustrates how one can investigate the perception of complex everyday situations that lead to emotional reactions in the observer inside the laboratory.

Extending the research perspective from a single individual to that of dyads or small groups is an important next step. Going even further, studies have been performed that investigated crowd perception (Gilbert et al. 2011; McHugh et al. 2010). While this is a first step, it will hopefully provide answers about the neural basis of how emotional reactions (e.g., panic, aggression) are spread within groups and how they guide individual behavior.

Outlook

In the previous sections, we have discussed research on the neural mechanisms of perception of bodily expressions. This research is part of the broad field of social and affective neuroscience. The field is currently thriving and embracing issues as diverse as empathy, decision-making and cultural stereotypes. It is worth noting that research in human social neuroscience is still very much pitched at the individual level. Almost all studies address the social abilities as a set of skills the individual has and that allows him/her to live in a social context with others. But these skills are analyzed as individual attributes. Our current research on bodily perception obviously presents rather a partial view of social perception because it has as its focus the behavior of an observer that is passive and static. The person observed is not influenced by the way his/her actions are perceived by others. On the other hand, the observer does not get any feedback or insight from his/her correct perception; neither does he/she suffers the consequences of misperception. Emotions are relational; they are primarily defined for at least two people interacting rather than for a single subject. Studies focussing on a single individual tend inevitably to look at emotion as an internal process. This passive perspective on social interactions seems one-sided and therefore incomplete.

In contrast, animal studies have traditionally taken the social dimension more literally and have traditionally studied the individual as part of the group and focused on group characteristics. Fortunately, this approach has recently been adopted in human social neuroscience (Konvalinka and Roepstorff 2012; Schilbach et al. 2013). Indeed, two-people neuroscience allows a new vista on the emotional social brain. However, this approach has so far mainly been restricted to action observation and joint action (Sebanz et al. 2006).

Interactions create affective loops, and being involved in these interactions with our bodies is the source of strong affective experiences. Virtual reality provides the field of affective and social neuroscience with a powerful tool to study just that. From body perception (Giannopoulos et al. 2011) to social situations (Pan et al. 2012; Slater et al. 2013), virtual reality allows the study of affective loops under well-controlled conditions and in settings where real life manipulation is not possible, too expensive or unethical. It has successfully been used to study the behavioral and physiological effects of social anxiety on a social interaction (Pan et al. 2012) and it allows the embodiment in an out-group member (Peck et al. 2013), child (Banakou et al. 2013), or even a rat (Normand et al. 2012). Furthermore, virtual reality is well suitable for the study of complex social situations and phenomena. For example, Slater and colleagues (2013) confronted participants with a violent incident involving another individual to investigate the likelihood of helping the victim. Combining virtual reality with new techniques such as motion capture not only gives researchers the possibility of using point-light stimuli in body perception and social interaction research but also provides a tool to systematically vary certain components of a body or social interaction and makes it possible to analyze how kinematics differentiate between emotional scenarios (Barliya et al. 2013; Roether et al. 2008). In sum, the use of new techniques will give the field of affective and social neuroscience valuable and important tools to grasp the full extent of the social world in a well-controlled manner.

Conclusion

Social perception may be an area where the notion of direct perception of intentionality may be studied most successfully. Presently there is still a striking contrast between the view based on available scientific research, which is that of an isolated individual sitting in front of a computer screen and still mostly having his/her reactions measured to still pictures of disembodied faces, and the relentless social communication we are engaged in daily life. In the past, we have used more naturalistic stimuli, e.g., bodily expression, combining facial and bodily expressions, adding contextual information, and social interactions, as a first step to fill this gap. However, the adequate, successful study of social perception predicts, modifies and changes the perceived interacting agent as well as the perceiver. How can we approach the study of genuine interactions? Investigations of this transformative nature of social perception require that we create new concepts and develop the necessary methodological tools. Our perspective is that social interaction abilities are part and parcel of the evolutionary endowment of the species. The consequence of this is that the neuroscience community needs to confront the fact that the brain's natural task is thus not labeling prototypical emotions but registering and responding to the interactive emotional coloring that is part of daily communication. Although this chapter has little to report that is directly related to interactive affective perception in the strictest and most realistic sense, we hope to have made clear that our focus on the body represents a next step towards a novel understanding of active social interaction.

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The Origins of Human Morality: Complex Socio-moral Evaluations by Preverbal Infants

J. Kiley Hamlin

Abstract This chapter reviews a body of recent research suggesting that the capacity to identify and evaluate others based on their prosocial and antisocial acts operates within the first year of life, and is sensitive to many of the same factors that constrain adults' social and moral judgments, including the role of mental states and context in distinguishing good and bad behavior. The work is offered as empirical support for claims that human capacities for social and moral evaluation are rooted in evolved, reliably-developing systems for distinguishing friend from foe, required for the long-term functioning of cooperative systems.

The social world is hugely complex, filled with individuals who differ from each other along seemingly limitless dimensions of physical attributes, intelligence, social status, group membership, personality traits, and preferences, just to name a few. Additionally, individuals are engaged in a great variety of social relationships: two individuals may be friends, business partners, lovers, acquaintances, or strangers. Despite these complexities, human adults seem to have no trouble making nuanced judgments about others, their relationships, and the behaviors that occur therein. We intuitively seem to like some individuals over others; we easily determine who is friends with whom, who is in the popular crowd, who can be trusted and who is better to be avoided. The apparent ease with which human adults evaluate the social world raises the question of exactly how we decide whom we like and whom we dislike: how do we distinguish friend from foe?

Perhaps the most fundamental way to distinguish friends from foes is via an analysis of individuals' behaviors. To the extent that behaviors are inspired by underlying, stable personality traits (with some role for situational constraints; e.g., Heider 1958; Jones and Davis 1965; Kelley 1967: Lieberman et al. 2002), understanding something about an individual's previous actions allows one to predict

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J.K. Hamlin (✉)
UBC Department of Psychology, University of Columbia, Vancouver, Canada
e-mail: kiley.hamlin@psych.ubc.ca

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how that individual will behave in the future. Indeed, human adults appear to be exquisitely, perhaps overly, tuned in to cues that may be relevant to others' enduring personalities and to make rapid, spontaneous trait judgments about others based on extremely minimal behavioral information (e.g., "thin slices;" Ambady and Rosenthal 1992; Ambady et al. 1995). Linking behavior to trait judgments appears to be so automatic in adults that they do so even when they have not intended to form an impression (Uleman et al. 2005; Winter and Uleman 1984) and despite not readily remembering the behavior that led to the impression formation in the first place (Carlston and Skowronski 1994; Todorov and Uleman 2002). Indeed, adults often neglect potentially relevant situational information, pointing to the primacy of inferring traits from behaviors (Gilbert and Malone 1995; Jones and Harris 1967; Ross 1977). Perhaps most extremely, in some cases adults form stable impressions of others even *without* actual behavioral information: someone may be judged as competent or incompetent, aggressive or docile, and trustworthy or untrustworthy in as little as 100 ms of exposure to a still image of his face (Willis and Todorov 2006). These rapid, still-face judgments may seem trivial, but they have been found to predict important real-world outcomes such as election results and sentencing judgments (Ballew and Todorov 2007; Blair et al. 2004; Eberhardt et al. 2006; Todorov et al. 2005). Overall, these results highlight adults' extreme sensitivity to cues that may (or may not) be relevant to social evaluation.

But how do adults come to be so judgmental? One possibility is that adults' pervasive tendencies for social evaluation are the result of a lifetime of explicit and implicit experience in an evaluable, and evaluative, world. Children are engaged in social relationships from birth, in which they can readily observe how behaviors (both their own and those performed by others) influence others and are interpreted by them, as well as how certain patterns of behavior may recur over time. Indeed, psychologists interested in moral development have described how children might come to recognize that certain behaviors are good and others are bad via the myriad ways in which such social and moral rules are reinforced in their daily lives. To illustrate with an example, imagine a young child who possesses the notion that "stealing is wrong." She might have developed this notion via one or several of the following experiences, all of which are presumably fairly common in her everyday life: (1) she feels bad when her own things are stolen, (2) she observes the negative emotional reactions of other children whose things are stolen, (3) she negotiates conflicts with her peers when there are not enough toys to go around, (4) she observes the reactions of her siblings, parents, and teachers when another child steals, (5) she hears specific statements about stealing being bad from older peers, siblings, parents, and teachers, and/or (6) she notices that stealing is relatively rare, especially among the adults around her (see handbook by Killen and Smetana 2006 for extensive review of empirical demonstrations of the effect of these experiences on children's developing knowledge of social and moral rules).

Whatever combination of processes drives development, it is clear that by 4 years of age, if not before, children understand not only what the rules regarding good and bad action *are* but also distinguish between different *kinds* of social rules, such that some things are morally good and bad whereas other things are good and bad due to tradition or convention. Indeed, even very young children reason differently about moral versus conventional rules and rule violations, and they distinguish both moral and conventional rules from personal issues that are not subject to governance by rules at all (e.g., Smetana et al. 1991; Nucci 2001; Nucci and Turiel 1978; Smetana 1981, 2008; Turiel 1983, 1998). This pattern has been shown cross-culturally (Helwig 2006; Wainryb 2005) as well as in autistic populations (e.g., Blair 1995; Leslie et al. 2006), suggesting that these domain distinctions reflect fundamental ways in which social information is organized and processed.

Social Evaluation for Successful Cooperation

Despite the clear effect of learning and development on children's capacity for social and moral evaluation, this need not imply that there are no other factors involved. This chapter borrows its theoretical perspective from evolutionary biology, anthropology, and psychology, whose scholars have posited that the human tendency for social and moral evaluation may have emerged, in part, due to the benefits it conferred on our ancestors living in large groups. Though the exact nature of this process remains controversial, scholars seem to agree that a key factor is humans' tendency to *cooperate*: to come together to fight off enemies, secure food, raise children, etc. (e.g., Axelrod 1984; Axelrod and Hamilton 1981; Cosmides and Tooby 1992; Henrich and Henrich 2007; Hrdy 2009; Trivers 1971). Despite its being an extremely common feature of all known human groups (e.g., Brown 1991), an evolutionary account of the emergence of cooperation is nonetheless a bit of a puzzle: to cooperate one must take costs or risks to oneself in the short term with only the possibility (not the guarantee) of mutual gain in the future. For example, although successfully defeating an enemy might be beneficial for all, engaging in the fights necessary to do so requires that each individual be willing to risk great personal harm. Why would any rational individual engage in such personally risky behavior?

Cooperating Is Beneficial

One solution to this puzzle is that the benefits of being part of a cooperative system are obvious and (under certain circumstances) outweigh the risks. Pursuing outcomes cooperatively increases the efficiency at which everyone's needs are met, such that the relative cost/benefit ratio to achieve the same outcomes is higher for individuals in cooperative groups than for those in non-cooperative groups. As basic needs are met more and more efficiently, given the same environmental conditions, cooperative individuals in cooperative groups can gather more food, raise more children, and generally be better prepared for potential dangers in the environment than can less efficient non-cooperators; as efficiency increases, cooperative groups can sustain more and more individuals. In addition, groups of cooperators can reach new outcomes impossible for non-cooperators to achieve, such as hunting larger and meatier game, keeping many young children safe and fed at the same time, erecting shelters for safety, and dividing labors based on talent. Eventually, forms of cooperation that extend farther through time might emerge, in which the sacrifices an individual takes and the benefits he receives need not occur in close succession. One individual could take a personal cost to help or share with someone currently in need without requiring that the favor be immediately returned if s/he were to trust that the favor will be returned at some point in the future. These extended forms of cooperation allow prototypically "prosocial" or even "altruistic" actions such as helping, sharing, and charitable giving to emerge and spread; each form of cooperation improves the lot of cooperators.

Cooperative Systems Are Fragile

Despite the obvious benefits, cooperation requires more than simply the tendency to cooperate with each other (but see other chapters in this volume for discussion of the mechanisms by which such tendencies may have arisen). Specifically, while *groups* of cooperators may do better than *groups* of non-cooperators, cooperative groups are merely collections of individuals who choose to cooperate and are therefore vulnerable to individuals who reap the benefits of others' cooperative actions but who do not cooperate themselves. These individuals pay minimal costs but receive maximum benefits; such "cheaters" would consistently outperform cooperators who do pay costs and, doing so, would eventually replace cooperators in a population. Given this clear vulnerability to cheating, it is unclear how cooperation and prosociality are maintained.

Solving this problem brings us back to the phenomenon of social evaluation. In particular, scholars have hypothesized not only that individuals are motivated to interact and cooperate with each other but also that they are motivated and able to *evaluate* each other for their cooperatively relevant behaviors and to act on those evaluations. That is, successful cooperators need to identify those who are likely to cooperate faithfully, joining in the work currently and returning favors in the future, and differentiate them from those who are likely to exploit others' work and not return the favors they are lent. Essentially, cooperators must be able to distinguish "friends" from "foes." Doing so, and coupled with evaluative systems that "like" friends and "dislike" foes and influence approach and avoidance behaviors, allows cooperators to keep non-cooperators out of the system, restricting benefits to those who will chip in. In this way, the risks associated with non-cooperators in a population are diminished considerably: non-cooperators are simply left out.

Mechanisms for Distinguishing Friend from Foe

What mechanisms might support identifying friends and foes in the social world? Perhaps the most direct way to determine whether an individual is likely to cooperate with you or not is to gather information about how s/he has treated you in the past: all else being equal, someone who has helped or otherwise cooperated with you before is relatively more likely to do so again, whereas someone who has harmed or otherwise exploited you before is relatively more likely to do so to you again. This first-person form of information gathering is perhaps best captured by the phrase "if you scratch(ed) my back, I'll scratch yours," and is referred to as *direct reciprocity* (Trivers 1971). This strategy is especially beneficial when combined with an initial bias to cooperate with everyone and to shift strategies (from cooperation to non-cooperation and vice versa) only when a current strategy fails (e.g., Nowak and Sigmund 1993).

Direct reciprocity is a relatively good strategy for successfully reaping the benefits of cooperative systems, but it has several limitations. First, as group sizes increase, the likelihood that every individual will have had the occasion to interact with every other individual decreases sharply; there will be more and more cases in which one must choose whether or not to interact with someone without having experienced his or her past behavior. In addition, because a single interaction with an antisocial individual might be extremely costly, it may be dangerous to interact with an unknown other even once. These limitations suggest that direct reciprocity may not be the best mechanism for evaluating social others, especially in large groups. A better mechanism for social evaluation may be to evaluate others via knowledge of their actions toward *third parties*. In such cases, one can gain valuable information about potential interaction partners from a safe distance and at minimal personal risk. This strategy, referred to as *indirect reciprocity* (Nowak and Sigmund 1998), can proceed in two ways. The first is via direct observation: individuals might choose to cooperate only with those whom they have personally observed cooperating with others and/or to avoid anyone observed engaging in uncooperative acts. As with direct reciprocity, this form of indirect reciprocity is limited, however, because the likelihood of acquiring information via observation decreases as group size increases; there may simply be too many individuals to have observed everyone's prior social interactions. In these cases, indirect reciprocity may proceed via *reputation*, in which others' past behaviors (which presumably someone has observed) become socially transmittable knowledge (for example, gossip) that others use to inform their own social evaluations and behaviors (e.g., Nowak and Sigmund 2005).

Several additional complications are associated with indirect reciprocity. First, even in cases in which one observes third party interactions directly, uninvolved observers of social interactions may lack critical contextual information relevant to *why* individuals act in particular ways, leading to inaccurate evaluations. For example, if Person A harms Person B, accurate friend/foe evaluation of A requires knowing about Person A's mental states, for instance whether Person A harmed

Person B intentionally or accidentally. Analyzing mental states hinges upon further contextual information, such as whether A and B are best friends, whether they are fighting over the same girl, or whether their families are allies or have been feuding for generations. As both mental states and relational statuses are essentially unobservable, systems for social evaluation via behavioral observation may not be particularly beneficial without additional mechanisms for identifying mental states, relational status, and group memberships, lest the prosocial/antisocial nature of previous acts not actually predict one's value as a social partner. That is, it would behoove social evaluators to distinguish behaviors that are the result of a particular situation or a specific relationship from those that are predictive of long-term, general behavioral tendencies.

Beyond Social Evaluation: Punishment

Given these difficulties with accurately distinguishing cooperators from non-cooperators, even a finely tuned social evaluation system may occasionally fail. If so, the possibility of being denied access to cooperative benefits may not be sufficiently costly to prevent certain individuals from choosing non-cooperative strategies, and antisocial behaviors may spread. Thankfully, there is a universal and cross-species tendency to *punish* individuals known to have engaged in antisocial acts, providing an additional mechanism for discouraging bad behavior (Boyd and Richerson 1992; Clutton-Brock and Parker 1995; Henrich et al. 2001; Henrich et al. 2006). As punishment places direct costs on antisocial individuals, it serves to make non-cooperation a relatively less-beneficial strategy overall and has been shown to sustain human cooperation (O'Gorman et al. 2009). Indeed, despite its own status as a costly act (it is presumably risky to interact with antisocial others in any way, but especially to attempt to harm or constrain them), punishment is often carried out by individuals who are not personally involved in the situation (who were not directly affected by the act) and who must take a personal cost to themselves to punish wrongdoers (Gintis 2000; Fehr and Fischbacher 2002; Fehr and Rockenbach 2004; Hauert et al. 2007; Henrich et al. 2001; Henrich et al. 2006). Neuroimaging research has demonstrated that costly third-party punishment activates neurological reward systems, suggesting it is individually reinforcing (de Quervain et al. 2004).

Evaluating Punishers?

Yet the tendency for cooperative individuals to punish presents a second-order evaluation problem: as punishment is technically an antisocial act (inasmuch as if acts used to punish were directed toward innocent individuals they would be viewed as negative), performed intentionally, should not punishers be negatively evaluated or even punished themselves? To overcome this problem, humans' social evaluation system must be nuanced enough to excuse, or even support, intentional antisocial acts that are done for justifiable reasons. That is, the system must evaluate the purpose and value of action *in context*. Indeed, despite punishment consisting of locally antisocial behavior, human adults show relatively more trust in individuals who punish, and institutions and political leaders perceived as “tough on crime” are generally supported (Barclay 2006; Bright and Keenan 1995; Gürerk et al. 2006; Mauer 1999).

Social Evaluation in Development?

As reviewed above, theories of the evolution of cooperation require complex systems of social evaluation for distinguishing individuals who are likely to cooperate from those who are not. Thankfully, human adults clearly possess such systems and readily evaluate others in just the ways that are considered necessary to support large-scale cooperation. So the question becomes: are evolutionary theories correct in their assertion that human social and moral systems exist, in part, due to the benefits they conferred on our ancestors? Or are these theories merely “just so” stories, conjured up to “explain” what we already know to be true about humans’ social and moral judgments? Because adults, and even young children, are enveloped within societies whose norms promote these capacities, it is nearly impossible to distinguish the relative role of built-in cognitive mechanisms versus individual experience in their development.

One potentially informative method of studying the origins of humans’ social evaluative abilities is to examine their presence or absence in a population that lacks much of the extensive cultural experience and teaching that is provided to human adults and children: human infants. Of particular theoretical import to this venture are infants in the first year of life, who, despite existing within a complex social world, lack a large amount of the particular experiences and skills that may be considered essential to learning to make these judgments, including developed linguistic abilities, explicit teaching in schools and cultural centers, and various elements of mature executive functioning. In addition, although socialization processes clearly begin at birth (if not before), there is some sense in which parents simply do not consider their very young infants to be capable of social and moral evaluation; thus, various explicit forms of parental inputs to these processes may be limited.

Infants’ Understanding of Social Behavior

While little is known about infants’ *evaluations* of others’ behaviors, research over the last two decades suggests that infants’ analysis of others’ behaviors is quite sophisticated and may be sufficient to support social evaluation. Firstly, infants in the first year of life understand that people's actions are internally driven by underlying mental states. In the first year after birth, infants pay closer attention to the particular goal of an action than they do to its physical structure (Woodward 1998, 1999, 2005), recognize that object goals may signal underlying preferences and epistemic states (e.g., Luo and Baillargeon 2005, 2007; Luo and Johnson 2009), expect agents to pursue rational actions toward their goals (Csibra et al. 1999, 2003; Gergely et al. 1995), and infer the goals of others' actions even if they go unfulfilled (Behne et al. 2005; Brandone and Wellman 2009; Hamlin et al. 2008, 2009). In addition, 10-month-old infants have been shown to restrict their goal interpretations to particular individuals, suggesting that they recognize that different individuals can possess different mental states (e.g., Buresh and Woodward 2007; Henderson and Woodward 2012). Together, these social-cognitive abilities could assist an infant in determining critical aspects of cooperative and non-cooperative behaviors, such as what happened, who did it, and why.

In addition to analyzing the mentalistic structure of agentive action, infants organize actions in terms of their overarching valence, which is critical for distinguishing the wide variety of cooperative actions from non-cooperative actions. For example, 12-month-olds treat physically different actions that share valence (such as helping and caressing versus hindering and hitting) as more similar than physically similar actions that are of opposite valence (such as caressing and hitting versus helping and hindering; Premack and Premack 1997). In addition, by 10–12 months of age, infants appear to use others' dispositional states (which must be inferred from past behavior/experience) to understand their novel, goal-directed actions: they expect that a character that they viewed previously being helped and hindered in its goal should selectively approach (prefer) the individual who helped it (Kuhlmeier et al. 2003; see also Hamlin et al. 2007) and that an actor who previously engaged in a particular kind of action on one object should later select a new object that affords the same kind of action (Song et al. 2005). This tendency to see past behavior as relevant to and predictive of future behavior is fundamental to the current account of the emergence of social evaluation, by which evaluation serves to distinguish friends from foes to inform future social interactions. Although these capacities are presumably not sufficient for demonstrating social evaluation capacities in infancy, they are certainly necessary.

Probing Preverbal Infants' Social Evaluations

How can one examine social evaluations in infancy? While there are presumably countless social actions that provide information as to one's status as cooperative or not, the best information surely comes from cooperative behavior itself: does this individual help those in need or not? In the first exploration of infants' evaluations of individuals who help and harm, infants were shown one of a series of prosocial and antisocial puppet shows, in which a "Protagonist" demonstrated some kind of unfulfilled goal: to climb a steep hill, to open a box, or to retrieve a dropped ball

(Hamlin and Wynn 2011; Hamlin et al. 2007; see also Kuhlmeier et al. 2003). On alternating events, the "Helper" acted to fulfill the Protagonist's goal – for example, pushing the Helper uphill, assisting to open the box, or giving the ball back – while the "Hinderer" acted to block the Protagonist's goal, pushing the Helper downhill, slamming the box closed, or running away with the ball. After being habituated to, or made bored by, these alternating Helper and Hinderer events, infants were given the opportunity to choose between the Helper and Hinderer puppets by an experimenter who was unaware of the previous behavior of each puppet (possible because the shape/color of the Helper and Hinderer varied across subjects).

Infants' choice behaviors suggested that they distinguished the Helpers from the Hinderers in each scenario; they consistently preferred the Helpers. Specifically, a significant proportion of infants who saw the Protagonist fail to get up a hill chose the puppet who pushed the Protagonist to the top over the one who pushed him to the bottom; infants who saw the Protagonist fail to open a box chose the puppet who helped get the box open over the one who slammed the box shut; and infants who saw the Protagonist request its ball back chose the puppet who gave the ball back over the puppet who ran off with it. Notably, infants showed these preferences from around the time that they developed the ability to reach for objects at all, from 4.5 to 6.5 months of age (Hamlin and Wynn 2011; Hamlin et al. 2007); the rate of preferring Helpers to Hinderers was high (around 80 %) and strikingly consistent across the three scenarios. Additional studies utilizing the hill scenario suggested that, by 6 months of age, infants' social preferences reflected both positively evaluating Helpers (choosing Helpers over neutral puppets) and negatively evaluating Hinderers (choosing neutral puppets over Hinderers; Hamlin et al. 2007).

Infants under 4 months of age do not consistently make visually guided reaches toward objects (see McDonnell 1975, for a summary of the development of infants' visually guided reaching); thus, younger infants' evaluations of Helpers and Hinderers were examined utilizing a "preferential looking" procedure, which measured infants' relative attention to Helpers versus Hinderers during a 30 s period in which the puppets were held side-by-side in front of infants' faces. Using this slightly different method, 3-month-olds showed similar preferences to both the hill and ball scenarios; this pattern was evident in both the number of seconds that infants looked toward Helpers versus Hinderers and in the overall number of infants who "preferred," or looked longer toward, Helpers (Hamlin and Wynn 2011; Hamlin et al. 2010). In contrast to older infants, who demonstrated both positive evaluation of Helpers and negative evaluation of Hinderers, 3-month-olds tested via preferential looking demonstrated only negative evaluation of Hinderers: they looked longer to Helpers than to Hinderers and longer to neutral puppets than to Hinderers, but they did not differentially attend to Helpers versus neutral puppets (Hamlin et al. 2010).

What Inferences Constrain Infants' Preferences?

Infants' preferences for Helpers over Hinderers suggest that they possess some kind of evaluation system; yet, from these initial studies, exactly what motivates infants' choices remains unclear. Put another way, these initial studies did little to demonstrate *how* infants go about distinguishing helpful from unhelpful actors: what is it about these individuals' actions that infants evaluate? In the following section, I will review a variety of findings suggesting that infants' choices for helpful over unhelpful puppets are strikingly consistent with adults' social evaluations, including sensitivity to the social status of the parties involved, their intentions, and their epistemic states. In addition, they appear to incorporate contextual nuance, including the past behaviors of the targets of Helping and Hindering. Overall, infants' choices suggest that they possess a sophisticated friend/foe detection mechanism, one that is consistent with theorizing about the role of social and moral evaluation in the evolution of cooperation.

Must Protagonists Be Social Beings?

Adults' notions of helping and hindering assume several characteristics about the recipients of helpful and harmful behaviors. For example, adults' evaluations incorporate more than just the physical characteristics of helpful and harmful behaviors: kicking a person is a fundamentally different act than kicking a soccer ball. To examine whether infants' evaluations also include considerations of the social status of those who receive Helping and Hindering, in each of the studies described above additional groups of infants were shown non-social versions of the helping and hindering events, in which puppets directed their actions toward an inanimate object rather than an animate Protagonist. For example, in the hill study, puppets pushed an eye-less, motion-less shape from the bottom of a hill to the top or from the top of a hill to the bottom; infants subsequently chose between the Pusher-Upper and Pusher-Downer. In the box study, one puppet opened a box that a "mechanical claw" had been acting upon, whereas the other puppet slammed the box closed (see Woodward 1998; Hamlin et al. 2009; Meltzoff 1995 for examples of the use of mechanical claws in studies of infant social cognition); infants chose between the Opener and the Closer puppets. In the ball study, one puppet rolled the ball back to a claw and another puppet took the ball and ran offstage; infants chose between the Giver and the Taker. We reasoned that if infants were evaluating the physical actions performed or the end results achieved in the social versions of Helping and Hindering, they should also prefer the Pusher-Uppers, the Box-Openers, and the Ball-Givers in these non-social scenarios. On the other hand, if infants' evaluations required that helpful and unhelpful behaviors be directed toward a social being, they should not prefer Pusher-Uppers, Openers, or

Givers. This is exactly what we found: infants did not distinguish characters in any non-social condition (Hamlin and Wynn 2011; Hamlin et al. 2007, 2010).

Must Protagonists Have a Goal?

An additional constraint on adults' notions of helping and hindering is that those who are helped and hindered should actually have a goal, desiring that a particular outcome occur. For instance, if someone were to guide an elderly woman across a busy street, but this woman had no desire or intention to cross the street, then the "escorting across the street" actions would not render this individual praiseworthy. Although there are certainly exceptions (for instance, someone may be unaware that they need help), in the great majority of cases helping and hindering acts require that their recipients have a clearly identifiable goal.

We discovered, accidentally, that infants' evaluations also require the Protagonist to have a clearly identifiable goal during the pilot testing of our very first attempt to examine infants' social evaluations in the fall of 2005. Specifically, the first group of subjects who were tested with the hill scenario saw a red circular Protagonist with "googly" eyes, made of the popular craft store-design plastic eyes in which a black "iris" floats freely in a white transparent circle. We showed several 10-month-old infants Helping and Hindering events with this googly-eyed Protagonist, and they failed to distinguish the Helper from the Hinderer during the choice phase. As this finding occurred during initial piloting, we reassessed the stimuli and realized that, due to gravity, the Protagonist's eyes were actually pointing *away* from his goal at the top of the hill for the majority of each event. We reasoned that, because eye-gaze is an important cue for identifying others' goals (e.g., Hood et al. 1998), the Protagonist's goal might have been uninterpretable as a result of this goal-inconsistent gaze information. Indeed, we subsequently glued the eyes in place, and 14 of the following 16 subjects chose the Helper (Hamlin et al. 2007).

More recently I have examined whether a Protagonist must have a clear goal for infants to more systematically prefer Helpers to Hinderers in the hill scenario. This study was largely the result of a recent report by Scarf and colleagues (2012) that convincingly suggested that infants' preferences in the hill paradigm resulted from physical aspects of the stimuli rather than social evaluation. In their studies using an adapted hill paradigm, they demonstrated that infants consistently preferred characters that were associated with the Protagonist producing "bouncing" actions, whether or not helping preceded the bouncing. Infants chose characters associated with bouncing regardless of the prosocial or antisocial nature of the preceding act, suggesting that infants in our original hill study preferred the Helper simply because it was associated with bouncing rather than because it was prosocial. In our response (Hamlin et al. 2012), we noted that this interpretation was confounded with the fact that the Protagonist in Scarf and colleagues' study had unfixed googly eyes, which may have lead infants to fail to identify a goal and to choose based on physical cues instead. I have now run four studies to confirm this interpretation of

Scarf and colleagues' results. First, I replicated infants' preference for Helpers over Hinderers using the original stimuli (which included bouncing) as well as with new stimuli containing no bouncing or other physical differences between how the Protagonist "reacts" following Helping and Hindering acts. In two additional conditions, the Protagonist's eyes were unfixed: in the first unfixed-eye condition, there were additional cues to goal-directedness in the Protagonist's acts, such as appearing to struggle toward the top of the hill; in the second unfixed-eye condition, these cues were absent. Infants in both conditions failed to distinguish the Helper from the Hinderer (Hamlin, under review). These results suggest that infants' social evaluations are sensitive to whether the individual being "helped" actually has a goal in the first place and provide additional evidence that physical cues – in this case, bouncing – are not solely responsible for infants' social preferences.

Must the Helper and the Hinderer Succeed at Helping and Hindering? Intention Versus Outcome

A fundamental aspect of adults' social and moral evaluations is that they incorporate what individuals *meant* to do, whether or not they successfully carried out their intentions (e.g., Baird and Moses 2001; Cushman 2008; Killen and Smetana 2008; Malle 1999; Mikhail 2007; Young et al. 2007). Indeed, the notion that behaviors are driven by mental states that persist through time provides the motivation for engaging in social evaluation in the first place: we must determine how others might behave in the future. Though outcome is often the most salient aspect of a valenced social action, the existence of failed attempts, accidents, and other situationally driven outcomes suggests that intention may be a better predictor than outcome of whether someone is truly a friend or a foe. Although studies using explicit verbal methods have consistently demonstrated that young children focus on outcome, and privilege it over intention, when making social and moral evaluations (e.g., Baird and Astington 2004; Chandler et al. 2001; Costanzo et al. 1973; Cushman et al. 2013; Farnill 1974; Hebble 1971; Imamoglu 1975; Killen et al. 2011; Leon 1980; Piaget 1932; Zelazo et al. 1996), it is possible that age-related changes on verbal tasks are confounded with age-related change in other domains. Indeed, in previous studies it has been demonstrated that infants in the first year of life can infer unfulfilled (and thus unseen) goals from agents' goal-directed acts (e.g., Brandone and Wellman 2009; Hamlin et al. 2008, 2009). In addition, infants tend to become less distressed during sharing interactions in which they are not given a toy if their interaction partner is willing, but unable, to share with them rather than unwilling to share at all, suggesting the intention of a partner is included in infants' assessments of their *own* social interactions (e.g., Behne et al. 2005; Marsh et al. 2010). Finally, a recent study demonstrated that toddlers failed to distinguish individuals who had formerly been willing and able, versus willing but unable, to give a toy to them, suggesting that toddlers do not necessarily evaluate their interaction partners based on outcome, even if there is nothing else to go on (e.g., Dunfield and Kuhlmeier 2010).

Do infants similarly incorporate, and even privilege, intentional information into their evaluations of those who Help and Hinder third parties? A recent study examined whether infants evaluate others based on the intentions that drive their helpful and unhelpful acts, even if those intentions go unfulfilled (Hamlin 2013). In this study, box Helper and Hinderer events were manipulated such that, in some conditions, Helpers and Hinderers *successfully* carried out their intentions to help and hinder the Protagonist open the box (as in previous studies; Hamlin and Wynn 2011) whereas in other conditions, Helpers and Hinderers *failed* to Help and Hinder the Protagonist. Thus, during *Successful* events, the intentions of the Helper and Hinderer matched what the Protagonist achieved whereas in *Failed* events, the intentions of the Helper and Hinderer opposed the Protagonist's outcome. To illustrate, when the Failed Helper tried to help the Protagonist open the box (a positive intention), he was unable to help, and the Protagonist failed to achieve his goal (a negative outcome). When the Failed Hinderer tried to prevent the Protagonist from opening the box (a negative intention), he was unable to hinder, and the Protagonist successfully opened the box on his own, achieving his goal (a positive outcome). Various combinations of Successful and Failed characters were shown to both 8- and 5-month-olds in pairs, in five different conditions over three experiments. Infants subsequently chose between the puppets as in previous studies.

In Experiment 1, infants were shown pairs of Failed and Successful characters who intended either to help or to hinder the Protagonist, such that in each condition the outcome that the Protagonist experienced was identical. Specifically, infants in the "positive outcome" condition chose between a Successful Helper and a Failed Hinderer, whereas infants in the "negative outcome" condition chose between a Failed Helper and a Successful Hinderer. Despite outcomes being equated in each condition, 8-month-olds' choices suggested that they distinguished characters based on intention: they chose Successful Helpers over Failed Hinderers, and Failed Helpers over Successful Hinderers. Five-month-olds, in contrast, failed to distinguish puppets based on intention in either condition in Experiment 1.

Eight-month-olds' preference for characters with positive intentions in Experiment 1 could reflect an ability to evaluate others based on intention, but there was a clear alternative explanation for these results. Specifically, 8-month-olds may have evaluated *only* the Successful puppet in each condition, and subsequently approached the Successful Helper and avoided the Successful Hinderer during choice, without necessarily evaluating the characters with unfulfilled intentions at all. To examine this possibility, infants in Experiment 2 chose between characters who each failed to achieve their goals: a Failed Helper and a Failed Hinderer. In this comparison, the valence of the Helper's and Hinderer's intentions was pitted against that of the Protagonist's outcome, such that infants could systematically choose based on *either* intention-valence *or* outcome-valence, but not both. Consistent with the possibility that infants in Experiment 1 distinguished puppets based on intention-valence, 8-month-olds in Experiment 2 preferred the Failed Helper to the Failed Hinderer; that is, infants preferred the puppet that intended to help the Protagonist as opposed to the puppet that was associated with the Protagonist achieving his goal. Consistent with 5-month-olds' choices in Experiment 1, 5-month-olds in Experiment 2 chose equally between the Failed Helper and Failed Hinderer. Together, while 8-month-olds preferred puppets with positive intentions in Experiments 1 and 2, 5-month-olds showed no evidence of distinguishing puppets in any condition involving failed attempts to help or hinder, whether it was based on intention (Experiments 1 and 2) or on outcome (Experiment 2).

Experiment 3 examined whether 8- and/or 5-month-olds might distinguish puppets based on outcome-valence if it is the only dimension available; that is, if each puppet in the pair has the same positive or negative intention regarding the Protagonist's goal. In the "positive intention" condition, infants chose between a Successful Helper and a Failed Helper: both puppets tried to help, but the Protagonist only achieved his goal during Successful Helper events. In the "negative intention" condition, infants chose between a Successful Hinderer and a Failed Hinderer: both puppets tried to hinder, but the Protagonist only managed to achieve his goal during Failed Hinderer events. Despite the clear outcome differences in each condition, neither 8- nor 5-month-olds distinguished puppets in either one. In an additional control condition, 8-month-olds did not prefer puppets that performed similar physical behaviors to Failed Helpers and Failed Hinderers, such as engaging in coordinated action with the Protagonist or slamming the box lid. This study supports the hypothesis that infants evaluated Failed Helpers and Hinderers based on intention to be helpful or unhelpful, rather than on some physical characteristic of their behaviors. Together with Experiments 1 and 2, these choice patterns suggest that, by 8 months of age, infants *do* incorporate intention into their social evaluations of those who try but fail to help and hinder someone's goal, but they *do not* incorporate outcome. Whether 8-month-olds would use outcome to distinguish puppets in other helping and hindering scenarios (for example, involving accidents; see Le and Hamlin 2013), as well as the exact nature of 5-month-olds' failure to distinguish puppets in any condition, is open for future investigation.

The Role of Knowledge and Preference in Infants' Social Evaluations

The research summarized thus far has demonstrated fairly sophisticated social evaluations in the first year of life. In particular, by 8 months of age, infants' social preferences seem to be based on what an individual intends for another individual rather than on what actually occurs. And yet in each of the previous studies, the helpful/unhelpful nature of an action has been directly observable in the action's physical characteristics: trying to help someone open a box (successfully or not) simply *looks* very different than trying to prevent someone from opening a box (successfully or not). Although a physical distinction between good and bad acts is a common aspect of social behaviors, and though control conditions for each study have ruled out that it is not *only* physical cues that support infants' differential evaluation, it is nonetheless not always the case that helpful and unhelpful behaviors are physically distinct. Sophisticated systems of social evaluation, then, require the ability to view exactly the same action as good in one context, bad in others, and totally neutral in others.

To illustrate, consider the act of giving. While giving is often considered positive, it really depends *what* it is that is being given: does the recipient like the object? Dislike it? Is it harmful? Is it useful? For example, the act of giving a controversial food, such as Brussels sprouts, is ambiguous. Some people like Brussels sprouts but others do not. Clearly, intentionally giving Brussels sprouts to someone who enjoys them is nice, but (assuming the recipient is capable of making his or her own dietary choices) intentionally giving Brussels sprouts to someone who hates them is mean. Critically, the niceness/meanness of a giver does not necessarily rest on whether the recipient likes or dislikes what is being given; rather, what is important is whether the giver *knows* about the recipient's preference when formulating her action plan. In particular, if a giver does know a recipient's preference, then she is nice for giving preferred items and mean for giving dispreferred items. But if a giver does not know a recipient's preference, then the evaluation becomes more difficult: the action is probably not informative of whether the giver is a friend or a foe.

In a recent study (Hamlin et al. 2013b), we examined whether infants incorporate knowledge and preference states into their social evaluations. In each of three conditions, infants chose between two puppets that lifted up doors that were blocking two toys, a flower and a duck. Each Lifter raised a door blocking one of the toys in alternation, and the Protagonist subsequently grasped the toy that sat beyond the lifted door. Critically, prior to lifting events, infants were shown three different types of familiarization events, depending on their assigned condition. In the Preference-Knowledge condition, infants were shown the Protagonist choosing the same object (say the duck; this was counterbalanced across infants) over the other object (the flower) repeatedly and over changes in toy location, implying that the Protagonist preferred the duck to the flower. While the Protagonist made these "choices," the two Lifters sat onstage, pointed toward the actions, implying that they could "see" what was going on and giving them "knowledge" of the Protagonist's preference. In the Preference-Ignorance condition, infants were shown the same duck-over-flower choices by the Protagonist but the Lifters were off-stage during these choice behaviors and so did not know the Protagonist's preference. Finally, in the NoPreference-Knowledge condition, the Protagonist simply chose the only object available on each event (that is, the Protagonist always chose the duck but the flower was absent) while the Lifters looked on. Later, the flower appeared onstage, but infants had no reason to infer that the Protagonist had a preference for the duck over the flower, as the flower had not previously been available. In addition, because the Lifters had observed these same duck-grasps in the absence of the flower, infants could infer that the Lifters were also aware of no preference for ducks versus flower.

The logic of the experimental design was as follows. If infants recognize that only those who *knowingly* facilitate others' *goals* are truly prosocial, they should only prefer the Lifter who gives access to the duck in the Preference-Knowledge condition and not in either the Preference-Ignorance (with no knowledge) or the NoPreference-Knowledge (with no identifiable goal) conditions. If, on the other hand, infants positively evaluate those who facilitate former action sequences, regardless of knowledge or goals, then they should prefer the puppet that gives access to the duck in every condition, as the Protagonist grasped the duck in each familiarization event. Finally, if infants positively evaluate those who facilitate goals even coincidentally (perhaps because infants positively evaluate anyone who acts in a way that leads to a good outcome), then infants should prefer the puppet that gives access to the duck in both the Preference-Knowledge and the Preference-Ignorance conditions, but not in the NoPreference-Knowledge condition. Once again, if the underlying purpose of social evaluation is to determine who is most likely to cooperate, or be helpful in the future, presumably the only condition in which the Lifters' behavior is truly informative is in the Preference-Knowledge condition, as it was the only situation in which puppets acted with a clear intention to help or to hinder the Protagonist in his goal.

Infants' choices revealed that they only distinguished the Door-Lifters in the Preference-Knowledge condition and chose equally between the Lifters in the other two conditions. That is, infants evaluated those who *knew* they were acting to help or hinder the Protagonist, but they did not evaluate those that *happened to* help or hinder the Protagonist or those that facilitated or blocked the Protagonist's former sequence of action. This pattern of results supports the hypothesis that infants' developing system of social evaluation is sensitive to those cues that predict who will behave prosocially and antisocially in the future, rather than to who causes positive outcomes or facilitates behavioral regularities.

Evaluating Action in Context? Infants' Assessments of Rewarders and Punishers

The studies reviewed thus far have been based on the basic assumptions that individuals who are intentionally prosocial in the present are more likely to be prosocial in the future and that individuals who are intentionally antisocial in the preset are more likely to be antisocial in the future. Yet, as discussed above, there is at least one context in which one's current antisocial behavior need not imply a general tendency to be antisocial: someone who engages in antisocial actions specifically for the purpose of punishing wrongdoers. Without the ability to incorporate this and similar contextual nuances into our evaluations of who is friend and foe, punishers, who take costs to themselves that benefit the cooperative system, might be negatively evaluated and excluded from the system in the future.

We examined whether 5-, 8-, and 19-month-old infants interpret action in context by comparing their preferences for Givers versus Takers in the ball show (as in Hamlin and Wynn 2011) in two distinct contexts: in one, the recipient of Giving and Taking was prosocial (and so could be considered deserving of reward) and, in the other, the recipient of Giving and Taking was antisocial (and so could be considered deserving of punishment). At the start of the study, each infant viewed two box puppet show events in which one individual helped the Protagonist open the box and the other individual prevented the Protagonist from opening the box (as in Hamlin and Wynn 2011). After infants viewed these two box events, they were shown two additional events of the ball scenario (also as in Hamlin and Wynn 2011): one Giving and one Taking. Critically, for half of the infants, the target of the Giving and Taking actions was the Helper from the box show; for the other half, the target of Giving and Taking was the Hinderer from the box show.

We had clear hypotheses regarding the choice behaviors of infants who saw a former Helper targeted in the ball show: in addition to infants' general preference for Givers over Takers, the former Helper deserved reward, which the Giver provided. We were decidedly less confident about what infants who saw a former Hinderer targeted might choose: though infants generally prefer Givers to Takers, the target of Giving and Taking deserved punishment, which the Taker provided. We reasoned that these two factors might compete for infants' favor, perhaps leading them to choose randomly in the Hinderer condition. Intriguingly, this was not what we found. While, as predicted, infants at 5, 8, and 19 months all chose the Giver over the Taker when a former Helper asked for his ball back, both 8- and 19-month-olds significantly chose the Taker over the Giver when the target was the former Hinderer (Hamlin et al. 2011). That is, infants' preferences for prosocial versus antisocial actors reversed completely: the rate of choosing the Taker in the Hinderer condition was just as high as the rate of choosing the Giver in the Helper condition. In contrast to the two older age groups, 5-month-olds showed no evidence of interpreting Giving and Taking in context: regardless of the former behavior of the recipient, they consistently preferred the Giver to the Taker. Together, these results suggest that infants develop the ability to interpret behavior in context (specifically, positively evaluating those who take from those who have hindered others) by 8 months of age but not yet by 5 months.

There are two possibilities for why 5-month-olds failed to show evidence of contextual nuance in the previous study. The first possibility, as just suggested, is that 5-month-olds evaluate prosocial and antisocial actions locally, without incorporating information about a recipient's previous behavior into their judgments. An alternative possibility, however, is that our design was too taxing for the limited memory capacities of such young infants. In particular, whereas previous studies of infants in the first year after birth utilized a "habituation" method, in which infants are shown events repeatedly to ensure they have processed them sufficiently, in this study infants were shown each action only a single time, for a total of four events in the whole experiment. Perhaps 5-month-olds always chose the Giver in the ball show not because they always view Giving as good but because they had simply forgotten what the target had done previously. In an attempt to distinguish this possibility, new groups of 5-month-olds were habituated to Helper and Hinderer box events in the first phase of the study before moving on to the Giving and Taking events involving either the former Helper or former Hinderer. To follow the design of the previous studies as closely as possible, infants viewed only one Giver and one Taker event before choice. Consistent with the possibility that 5-month-olds had simply forgotten who did what in the more difficult non-habituation design of the previous study, 5-month-olds who were habituated to box events subsequently preferred the Giver to the Taker when the recipient was the former Helper, and preferred the Taker to the Giver when the recipient was the former Hinderer, at the same rate as 8- and 19-month-olds in the other design (Hamlin, manuscript in preparation).

In addition, at each age, new groups of infants viewed "victim" control events designed to rule out the possibility that they simply preferred puppets that acted in such a way that the valence of the interactions would match across trials. That is, perhaps infants preferred those that took from former Hinderers not because they liked the puppet that was mean to someone who deserved it but because the former Hinderer had been involved in a negative action and the Taker was also involved in a negative action. However, just as adults do not see those who have *been* harmed before as deserving punishment (even though they too have been involved in a negative action), when the target of Giving and Taking had been hindered in the box show infants preferred the Giver to the Taker. Thus, infants' preference for those that Take from former Hinderers does not seem to be due to simply preferring those that match event valence across trials but rather to an ability to perform nuanced social evaluations in which prosocial and antisocial acts are interpreted in context.

Returning to the hypothesis that humans' social evaluation system is guided by a particular need to distinguish friends from foes, there is a clear alternative interpretation of the mechanism driving infants' nuanced social evaluations that does not include notions of reward and punishment. In particular, infants may not consider the former Hinderer to actually *deserve* mistreatment but instead infer that (because someone who harms someone else presumably dislikes him) the Taker shares critical social opinions with them. That is, the mechanism underlying infants' nuanced evaluations may function more as an "enemy of my enemy is my friend" detector rather than as a system supporting punishment in particular. Of course, adults are known to engage in both kinds of social evaluation processes (e.g., Aronson and Cope 1968; Barclay 2006; Heider 1958; Leach and Spears 2009), and both may underlie preferences for those who are antisocial across different contexts. Indeed, a recent study demonstrated that infants also prefer those who direct antisocial behavior toward an individual who simply does not share the infant's own food preference, suggesting that the broader 'enemy of my enemy' process operates in infancy (e.g., Hamlin et al. 2013a). It is up to future study to determine whether these processes ever diverge in infancy, as they often do in adults: adults can like a disliked individual's "enemy" due solely to shared social preferences, without simultaneously considering the disliked individual deserving of punishment.

Summary and Conclusions

Preverbal infants possess a system of social evaluation that is, in some ways, strikingly similar to the one that evolutionary biologists, anthropologists, and psychologists have posited is required for the emergence and persistence of humans' extremely cooperative nature. From 3 months of age, infants distinguish those who help others achieve their unfulfilled goals from those who prevent others from achieving their goals, and they prefer helpful over unhelpful puppets at extremely high rates. As early as 5 months of age, they evaluate action in context, preferring those who harm those who have hindered others, perhaps reflecting a mechanism that allows those who punish wrongdoers to escape negative evaluation and social exclusion. By 8–10 months, infants privilege the mental states that drive prosocial and antisocial acts, including intention and knowledge, and they seem to discount other aspects of behaviors, such as whether a given action led to a good outcome or facilitated a familiar action sequence. Together, infants' evaluations appear to reflect sensitivity to the aspects of prosocial and antisocial behaviors that are most likely to signal future acts: the persistent prosocial and antisocial mental states of the actors themselves. These results support the possibility that some aspects of adults' pervasive tendencies toward social and moral evaluation may be rooted in basic, evolved capacities for distinguishing friend from foe.

To conclude, perhaps it is surprising that a chapter focused solely on the hypothesis that social and moral evaluation evolved to allow individuals to identify who is likely to be cooperative in the future did not include a single study of whether infants actually make predictions about prosocial and antisocial others' future acts. This issue is currently being actively investigated in my lab, and we have found some promising results thus far. Yet, in principle, infants' evaluative system does not require such a predictive capacity to function as hypothesized. Systems supporting critically important abilities (such as avoiding harm) need not produce interpretable, high-level outputs to be beneficial; rather, intuitive outputs may be superior to the extent that they are resistant to various forms of interference. That is, the infants' evaluation system may never compute *why* an individual is appealing or aversive, or what the individual might *actually do* in the future; the benefits gleaned from evaluation can in large part be delivered via a simple urge to approach or avoid an individual *right now*. These simple desires could then serve as inputs into a developing system of mature social and moral evaluation, one that includes action prediction, recall, the ability to reason consciously and report on one's judgments, and even the capacity to change one's initial evaluations should they prove lacking. This maturing system, supported by general improvements in cognitive processing, will incorporate information gleaned entirely from observation and learning processes during development and will incorporate specifics of children's individual cultures with unique sets of social and moral rules. Indeed, what is critically interesting about the current picture of infants' social evaluations is that, despite its extremely simple outputs, the *inputs* over which the system operates appear to be quite complex indeed.

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Can Oxytocin Improve Core Brain and Behavioral Features of Autism Spectrum Disorders in Children?

Ilanit Gordon

Abstract Autism Spectrum Disorders (ASDs) are a group of pervasive developmental conditions characterized in part by atypical development in social-communicative functions. Novel discoveries regarding the impact of the neuropeptide oxytocin (OT) on social behavior and its association with ASD prevalence and phenotypic presentation have generated a great deal of interest into OT's possible role in ASD etiology and excitement about its potential as a therapeutic instrument. And yet, many challenges are faced by translational research efforts for OT in ASD. In this manuscript, some of these challenges are addressed, specifically the complexities of OT's behavioral effects, the yet unknown long-term impact of OT, the undetermined neural mechanism underlying OT's effects, and the non-linear impacts OT has on brain and behavior. In conclusion, guidelines for future translational research efforts are suggested.

Autism Spectrum Disorders: The Case for Oxytocin Involvement

Social-communicative dysfunctions are considered core deficits in individuals with Autism Spectrum Disorders (ASD). While extensive research has been devoted to the development of behavioral interventions for the symptoms of ASD, to date, an understanding of the underlying neural mechanism for social dysfunctions remains elusive. Therefore, effective treatment approaches that target social impairment and its biological basis do not yet exist. A very promising area of investigation has emerged from recent discoveries regarding the neuro-peptide Oxytocin (OT; Gordon et al. 2011; Insel et al. 1999). OT is the most abundant neuropeptide in the hypothalamus, serving multiple specific and integrative functions both in the brain

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I. Gordon (✉)
Yale University, New Haven, USA
e-mail: ilanit.gordon@yale.edu

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and the body (Carter 2003). Mostly known for its function in birth and lactation, OT has also been extensively implicated in a wide range of social processes in animals, including mate selection, parenting, social recognition, and affiliation (Carter 1998; Carter and Keverne 2002; Gordon et al. 2011; Insel 1997; Insel and Young 2001). Until recently, OT research in humans has been restricted due to the inherent limitations on assessing its function in the human central nervous system, its short half-life, the lack of clarity regarding coordination between central and peripheral OT function, and the fact that OT does not readily cross the blood–brain barrier. Studies in recent years have utilized intranasal administration of OT, which presumably allows it to cross the blood–brain barrier and induce a cascade of significant physiological and behavioral effects (Kosfeld et al. 2005). Consequently, intranasal administration of OT has seen an exponential rise in human research (in most studies, a single dose is administered 45 min prior to behavioral assessments of outcome). To date, the majority of experimental investigations have focused on demonstrating a range of positive effects on social functioning in typically developing adults following OT administration, such as increased sociability, trust, social support, empathy, and reduced anxiety (Ditzen et al. 2009; Kosfeld et al. 2005; Meyer-Lindenberg 2008; Shamay-Tsoory 2010).

OT may be involved in the etiology of ASD (Insel et al. 1999; Carter 2007; Green and Hollander 2010; Gurrieri and Neri 2009), and numerous clinical trials utilizing OT administration are already underway as current research is targeting OT as a potential drug for translational medical efforts in disorders characterized by social dysfunction, such as ASD (Meyer-Lindenberg et al. 2011). The most consistent evidence for OT's implication in ASD arises from genetic studies (Campbell et al. 2011; Yamasue 2013). Converging evidence indicates that polymorphism in the OT receptor gene (*OXTR*) may be associated with ASD prevalence and its behavioral symptoms (Egawa et al. 2013; Gregory et al. 2009; Lerer et al. 2008; Liu et al. 2010; Rodrigues et al. 2009; Wermter et al. 2010; Wu et al. 2005).

Some of the most intriguing results stemming from OT studies for ASD are related to the effects OT has on improving the ability of healthy individuals to read the intentions of others (Domes et al. 2007) and gaze more to the eye region during social communication (Guastella et al. 2008). Additionally, promising results have been demonstrated in a few studies that were conducted in individuals with ASD. Following OT administration, there was increased willingness to interact socially and a better evaluation of social reciprocity (Andari et al. 2010), better comprehension of affective speech (Hollander et al. 2007), reduced repetitive behaviors (Hollander et al. 2003), increased understanding of others' mental states (Guastella et al. 2010), and improved social cognition (Bartz and Hollander 2008). Intranasal administration of OT has also been shown to ameliorate some symptoms of social anxiety (helping to increase eye contact and reduce stress reactivity) in patients with Fragile X Syndrome (Hall et al. 2012).

Differential circulating levels of OT have been demonstrated in individuals with ASD compared to typically developing controls (Green et al. 2001; Miller et al. 2013; Modahl et al. 1998). In addition, variations in the *OXTR* gene and the *CD38* gene, (*CD38* is involved in modulating OT release from hypothalamic neurons; Jin et al. 2007) are related to circulating levels of OT as well as core social behaviors when healthy parents interact with their 3- to 6-month-old infants. Parents with certain allelic variations on the *OXTR* and *CD38* genes (Costa et al. 2009; Israel et al. 2008; Munesue et al. 2010) tend to have lower plasma OT concentrations and display a lower frequency of affective touch towards their infants**.** Similarly, the interactions between plasma OT and genetic variation in the *OXTR* and *CD38* genes predicted the durations of social gaze synchrony between parents and infants, a key social behavior that relates to the core deficits in ASD (Feldman et al. 2012). These findings are the first to show associations between central and peripheral markers of the extended OT system in humans and their links with key social behaviors in early infancy**.** Considering the implication of these genetic variations in cases of ASD and the centrality of the social behaviors associated with OT function, the next steps in translational research would be to examine and reach a clearer understanding of the functioning of OT in ASD**.** In this chapter, I will delve into some of the challenges currently faced by research examining the impact of OT on ASD during this translational shift.

Current Challenges for Translational Research into OT and ASD

OT's Impact on Behavior: A Complicated Story

The behavioral effects of a single dose of intranasal OT are multifaceted. When behavioral changes arise following OT administration, they may be best described as nuanced. An underlying characteristic of OT's impact seems to arise from multiple examinations and it points to the fact that meaningful changes to behavior brought on by OT are usually subtle, relatively low-scale in magnitude and most likely complex and interactive.

For instance, in the seminal OT study from 2005, which utilized a single intranasal administration, researchers showed a significant increase in financial entrusting behavior in healthy men. The participants' median transfer of funds to a trustee in this study was 10 monetary units among those given OT compared to 8 units among those given placebo (Kosfeld et al. 2005). In another study, OT was administered to fathers prior to them interacting with their infant (Weisman et al. 2012). After a detailed analysis of the dyadic interaction between father and infant, researchers found that episodes in which the father displayed affectionate touch towards his baby were on average longer under the influence of OT, shifting from approximately 6 to 9 s. On the one hand, these two examples provide extremely meaningful changes in behavior due to OT and, on the other hand, these changes appear to be subtle, requiring sensitive measures to pick up on and a very detailed examination by the researcher.

To further complicate matters, although OT's effects have been frequently described as pro-social (Lukas et al. 2011; Macdonald and Macdonald 2010), some studies have described increases in competition and hostility towards out-group members following OT administration (see review by De Dreu 2012) and a moderation of entrusting behaviors that occurs following certain characterizations of the trustees or under conditions of uncertainty (Declerck et al. 2010).

Finally, and perhaps most relevant to ASD treatment and research, are the results from studies conducted in patient populations. In one of the only studies thus far in which OT was given to youth with ASD, Guastella et al. 2010 reported an improvement of approximately 5 % in accuracy of labeling emotions in a well-validated social mentalization task (Reading the Mind in the Eyes: RMET; Baron-Cohen et al. 1997, 1999, 2001), but strictly for easy items. When this same procedure was performed in adults with ASD, an improvement was detected only for the difficult items of the task (Domes et al. 2007). In both studies, when searching for an effect in all the task items together, there was either a moderate impact of OT administration or none at all. In another study using the RMET, OT increased the speed of response time in healthy participants yet slowed down reaction times in individuals with depression (Pincus et al. 2010). Recently, results of a randomized controlled trial in 19 adults with ASD revealed only modest effects following chronic intranasal OT administration twice a day over a period of 6 weeks and in the absence of any behavioral intervention (Anagnostou et al. 2012). When Guastella was interviewed regarding initial results of an ongoing chronic OT administration study in children with ASD, he was quoted as saying, "Interesting things are coming out of these studies. . .At the same time, we're not seeing a ginormous result that makes us think this is a cure for autism" (Miller 2013).

Combined, these findings suggest that OT administration indeed induces significant observable and socially relevant effects and yet its impact needs to be carefully assessed using sensitive measures that take into account not only individual differences but also context (Bartz et al. 2011). In moving forward towards devising more effective treatment strategies for social dysfunction that include OT, we should also consider the possibility that OT's impact may be highly influenced by feedback and learning opportunities that are inherent in certain circumstances or intervention settings but not in others.

Long-Term Developmental Consequences

Most of the effects of OT described in humans occurred following a single administration of intranasal OT in adults, thus bringing forth burning questions regarding the possible long-term behavioral impacts of either a single or chronic OT treatment, especially when given to a developing child. As ASDs are inherently developmental in nature, researchers, clinicians and parents alike are advocating for early detection and intervention. The pressing need for early assessment and treatment contrasts with the relatively scant data regarding OT function in children and the unknown, long-term effects of OT administration (Miller 2013). This issue is not yet resolved even in animal models, where manipulation and measurement of OT and its consequences are, for obvious reasons, considerably easier compared to humans. For example, when female prairie voles underwent a single injection with one of four possible doses of OT after birth, later in life as adults they displayed different patterns of anxiety-related behaviors, exploration, and partner preferences. These effects were not consistent in direction and not linearly related to the OT dose received neonatally (Bales et al. 2007). In a group of young male voles receiving chronic exposure to OT, there were subsequent impairments in pair bonding and dysfunctional partner preference (Bales et al. 2004).

Despite the numerous clinical trials underway aimed at exploring OT as a potential chronic treatment for ASD, and in the face of a crucial need for bedside solutions, there is concern in the scientific community (Miller 2013). One way to attempt to bridge the gap between basic science and clinical application would be to conduct longitudinal studies of OT function in younger and younger individuals and to follow up on long-term consequences. Another important translational research avenue would be to utilize a mechanistic approach and examine the impact that OT has on brain function in children and adolescents. This approach may boost our understanding of the neural basis of OT's impact during development.

OT's Impact on the Brain: An Initial View into Mechanisms from fMRI Studies

A review of fMRI studies following OT administration in healthy adults highlighted OT's impact on key nodes of the "social brain" (Brothers 1990), either increasing or decreasing activations as well as impacting functional connectivity between these neural regions (see reviews by Bethlehem et al. 2013; Zink and Meyer-Lindenberg 2012). To date, studies have mostly focused on paradigms that assess fear and emotional regulation as well as face processing (Domes et al. 2007, 2010; Gamer et al. 2010; Labuschagne et al. 2011; Kirsch et al. 2005; Petrovic et al. 2008). The brain regions most frequently implicated have been the amygdala and the medial prefrontal cortex (mPFC). The amygdala is well known for its role in responding to fearful stimuli and emotional regulation (Davies 1992; Phelps and LeDoux 2005). The mPFC is known for its broad involvement in social cognition, self-reflection, mentalizing, and theory-of-mind (Lieberman 2007; Mitchell et al. 2005; Saxe and Powell 2006). Other brain regions impacted by OT have been the fusiform gyrus (FG), known for its role in processing faces (Kanwisher and Yovel 2006), and striatal structures, known for their role in reward processing, motivation, and hedonic shifts (Haber and Knutson 2010; Sesack and Grace 2010). Many of these regions also tend to be naturally hypoactive in ASD (Kaiser et al. 2010), and thus a reasonable hypotheses for brain function outcome studies would be that OT may increase functional activation in these “dormant” neurological circuits in ASD.

Neural mechanisms that have been elucidated to involve an impact of OT on attentional processes and social salience via amygdala activations (Domes et al. 2007, 2010; Gamer et al. 2010), as well as an impact of OT on the hedonic value being associated with social stimuli and the motivation to subsequently approach or avoid, possibly modulated by striatal and midbrain structures (Atzil et al. 2012; Groppe et al. 2013). Interactions between amygdala, frontal and striatal activations (Riem et al. 2012; Zink and Meyer-Lindenberg 2012) may point to an interface between social saliency, emotion regulation and social motivational processes, and possibly involving inter-relations between several neuromodulators – namely OT, vasopressin and dopamine (See Gordon et al. 2011 for review).

In a study examining how OT impacts functional brain activity in the aforementioned emotional recognition and mental labeling task (RMET), researchers found that OT increased activation in the superior middle frontal gyrus and insula in a group of depressed patients. In healthy adult controls, OT increased activity in more ventral neural regions (Pincus et al. 2010). The differential impact of OT on the brain was also extended to its behavioral effects: inverse effects of OT were found in reaction times, with controls getting faster and depressed individuals slower to respond (Pincus et al. 2010). This differential effect of OT on brain and behavior in patients versus healthy controls should also be taken into account when transitioning from basic research into a translational clinical phase.

In the first ever OT administration and fMRI study in adults with ASD, researchers found that participants with ASD had reduced activity in the right amygdala, FG, and inferior occipital gyrus compared to healthy controls during a faces and houses matching task. After OT was given to the individuals with ASD, activity in the right amygdala increased when matching facial stimuli. Although ASD participants were not as good at matching faces compared to healthy controls (an effect that is unique to faces and not houses), there was no behavioral impact of OT in task performance (Domes et al. 2013).

These initial findings related to OT’s impact on the brain in patient populations and its associated behavioral effects bring us to another important issue currently faced by OT and ASD researchers: understanding the gaps between non-linear effects of OT on brain and behavior. Some aspects of this gap have to do with the practicalities of conducting behavioral versus brain imaging research. Behavioral and clinical studies usually employ study designs with relatively large sample sizes compared to fMRI studies, thus challenging the different methodologies to create combined study designs powerful enough to exhibit results in multiple modalities: behavioral, neurological and physiological. This is one possible explanation for the modest behavioral results that accompany the quite significant impacts reported in the brain. It is also possible that the behavioral measures usually used in fMRI paradigms are not optimal for eliciting or sensitively detecting differences induced by OT, especially in the highly diverse and phenotypically variable ASD population. Finally, it is possible that OT’s impact on the brain represents a shift in neurological function that requires feedback or a social learning context in order to be displayed behaviorally. In that case, it is crucial to devise treatment studies and interventions that combine OT administration with well-validated behavioral settings that include learning and social feedback.

Taking the Next Steps in Translational OT Research

The next steps in translational research should be to examine the functioning of OT in individuals with ASD, possibly targeting younger age groups compared to what has been done thus far. OT should be examined in relation to variability in social behavior during real social interactions and its relation to intervention outcomes. Experimental goals might include assessment of multiple markers of the social brain circuitry in relation to genetic and peripheral measures of OT and the potential effects of OT administration on the brain, the peripheral functioning of the OT system, and improvement in key social behaviors.

At this point, assessing peripheral functioning of OT, beyond genetic variation and OT administration, is of great importance. The fact that previous work focusing on measuring OT peripherally, either in plasma or saliva, has demonstrated a stability of peripheral OT measures within individuals (Feldman et al. 2010; Gordon et al. 2010) suggests that peripheral OT may serve as a trait-like index of individual variability in social functioning. Further exploration of the genetic and peripheral measures of OT and their interaction as it impacts markers of social functioning (see Feldman et al. 2013 for an example) may prove very useful for ASD diagnosis and treatment.

To conclude, a major innovation in the translational neuroscience of ASD would be to assess the effects of OT administration on brain functioning in younger children with ASD while combining administration with measurement of peripheral and central substrates of the OT system. Perhaps administration should not be chronic but be done prior to several critical intervention sessions. Expanding our view beyond the neurophysiology of OT in ASD, it will become crucial to characterize the short-and long-term impact of OT administration not only on brain function and task-related performance but also on the social behavioral repertoire. It will be essential to examine behavioral outcomes that relate both to naturalistic social interaction and to well-validated treatment outcomes. This type of research may benefit from utilizing sensitive, state-of-the-art behavioral measures that can tap into the complexities of OT's effects, such as the ones derived from microanalysis of behavior (Warner 2002), thus allowing researchers to index dyadic social engagement and interactive synchrony (Feldman 2007). The dyadic interactive context (either with a parent, a sibling, a friend or a clinician) may also provide inherent opportunities for social feedback and learning, so that OT's function in ASD may be best explored and understood.

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Testosterone and Dominance in Humans: Behavioral and Brain Mechanisms

Jack van Honk, Peter A. Bos, and David Terburg

Abstract Most people think that the hormone testosterone especially triggers aggression and antisocial behavior in humans. Mistakenly, the male sex steroid principally underlies each and every aspect of human social behavior but especially social dominance behavior. Testosterone by itself or by way of its metabolite, estradiol, the female sex steroid, is essential in the action of the social peptides oxytocin and vasopressin and regulates the turnover of the social monoamines, dopamine and serotonin. The hormone also has many other actions in the brain; thus the social brain's main chemical, without exaggeration, is testosterone. Here we review a line of findings with placebo-controlled testosterone administration in the field of social neuroscience in which various techniques are used to investigate social dominance and trustworthiness behaviors. These findings give insights into how and by what biobehavioral mechanisms testosterone acts in humans to motivate them to establish and maintain a dominant status.

A Multipurpose Hormone

From prenatal life until death, the male sex steroid testosterone, together with its metabolite, the female sex steroid estradiol, builds and rebuilds the human social brain (Chang and Sanfey 2009; Harle et al. 2010). The brain's plasticity, even in later life, importantly depends on testosterone and estradiol. Furthermore, sex differences in social brain and behavior importantly arise from diverging testosterone levels during developmental periods, and they can even be sex reversed by acutely or chronically changing the levels of circulating testosterone to that of the other sex (van Honk 2009). The acute effects of testosterone occur via a large

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J. van Honk (✉) • P.A. Bos • D. Terburg
Department of Psychology, Utrecht University, Utrecht, The Netherlands

Department of Psychiatry, University of Cape Town, Cape Town, South Africa
e-mail: j.vanhonk@uu.nl

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number of pathways, with the regulating action of testosterone, and its metabolite estradiol, on the gene expression of the peptides vasopressin and oxytocin synthesis playing an important role in the effects of these social peptides on social cognition and behavior (Sanfey et al. 2003). Furthermore, testosterone alters the turnover of the monoamines serotonin and dopamine in specific brain regions, and these monoamines have been implicated in moral decision-making and social-economic behavior (Eisenegger et al. 2010a, b). Crucially, the actions of testosterone on social behavior may depend upon a variety of personal and situational factors, such as genetic predisposition, personality characteristics (Bos et al. 2010), prenatal priming (van Honk et al. 2011a) and social environment (van Honk et al. 2011b).

The Tuiten Method

In this chapter, we will describe a range of studies that use a multiplicity of research strategies and methodologies to investigate the acute effects of testosterone administration on social dominance and trustworthiness behaviors in human females. The main reason for using females is that only in females have the quantity and time course of effects of testosterone been (and can be) objectively quantified. Adriaan Tuiten and co-workers developed a sublingual administration method in our laboratory with which, paired with the non-habitual measure vaginal response amplitude, they were able to define the time course of the effect of testosterone (Tuiten et al. 2000). In the Tuiten method, testosterone levels in females are temporarily raised to male levels by a single sublingual administration of 0.5 mg of testosterone. This administration results in a tenfold increase in total testosterone (in each individual) 15 min after intake, whereafter testosterone levels return to baseline within 90 min. Crucially, however, the behavioral effect of administration peaks 2.5 h after testosterone levels in the blood have returned to baseline; the hormone significantly elevates vaginal pulse amplitude approximately 4 h after administration of the drug (Tuiten et al. 2000). The reliability and generalizability of the 4-h time course has been successfully established in over 20 social and affective neuroscience studies (Bos et al. 2012). Among the first studies in our ongoing research on testosterone and social dominance were those investigating behavioral, psycho-physiological and neural responses to angry facial expressions. Most, but not all (van Honk et al. 1999, 2000) of these studies were done with females. Although perhaps not true of all of the effects of testosterone on social behavior (Montoya et al. 2013; van Honk et al. 2012), the effects of testosterone on dominance behavior strongly generalize between the sexes of many species, including humans, human primates and cattle (Boissy and Bouissou 1994; Bos et al. 2010; Eisenegger et al. 2010b).

Testosterone and Dominance Behavior

This line of research started off with an early observation using correlational methods in which we demonstrated that *male and female* individuals with high levels of salivary testosterone vigilantly attended to angry facial expressions in an emotional Stroop task (van Honk et al. 1999; see Fig. 1). This effect was later replicated and, more fascinatingly, under masked exposure conditions (Wirth and Schultheiss 2007). We explained the effect in the following manner: in primates, the angry facial expression evolved to function as a threat signal in dominance encounters (Öhman 1986). In face-to-face challenges, an enduring angry gaze signals dominance, whereas avoidant responses, i.e., gaze aversion, signals submission (Mazur and Booth 1998). Depending on the social relation between sender and receiver, angry faces may thus be met with dominant or submissive responses, which represent social vigilance or avoidance (van Honk and Schutter 2007b). Accordingly, since high levels of testosterone are associated with social dominance in several species, the vigilant, "enduring gaze" to the angry face is positively related to testosterone levels in males and females (van Honk et al. 1999).

Cardiac Responses to Angry Faces

This interpretation in term of dominance behavior was, however, rather speculative as it was based on verbal reaction times in the emotional Stroop task and actual gaze behaviors were not measured. Moreover, the findings were correlational in nature, and saliva testosterone is not a pure reflection of brain testosterone levels, because testosterone is produced not only by the gonads and adrenals but also as a neurosteroid in the brain (Remage-Healey et al. 2008). In sum, no firm conclusions could be drawn on the basis of these findings. To seek more definite evidence, we administered testosterone and used a physiological measure, the cardiac defense response: an acceleration of heart beat within 5 s after stimulus presentation that signals flight-fight preparation (Öhman 1997). In a placebo-controlled design, young women passively viewed neutral, happy, or angry faces, and we assessed whether testosterone induced cardiac acceleration in response to angry facial expressions specifically (van Honk et al. 2001). As can be seen from Fig. 2, testosterone indeed induced these increases significantly in the angry face condition.

These causal findings using pharmacological psychophysiology strongly support our earlier interpretations (van Honk et al. 1999), and we argued that encouragement of dominance behavior was driven by testosterone. Furthermore, possible neural mechanisms involving steroid-responsive networks in the limbic system centering on the amygdala that regulate social behavior were discussed.

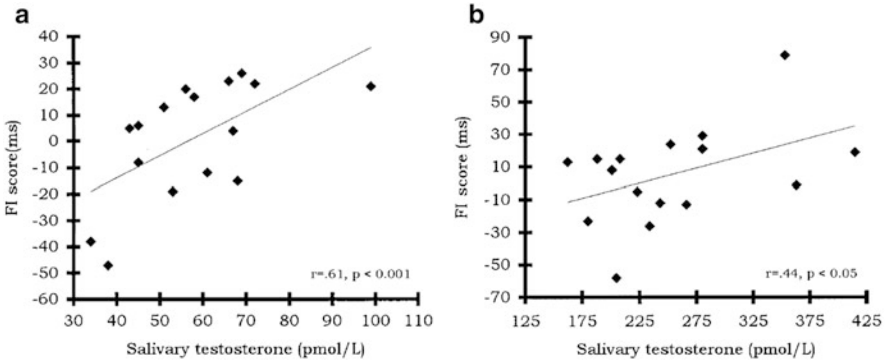


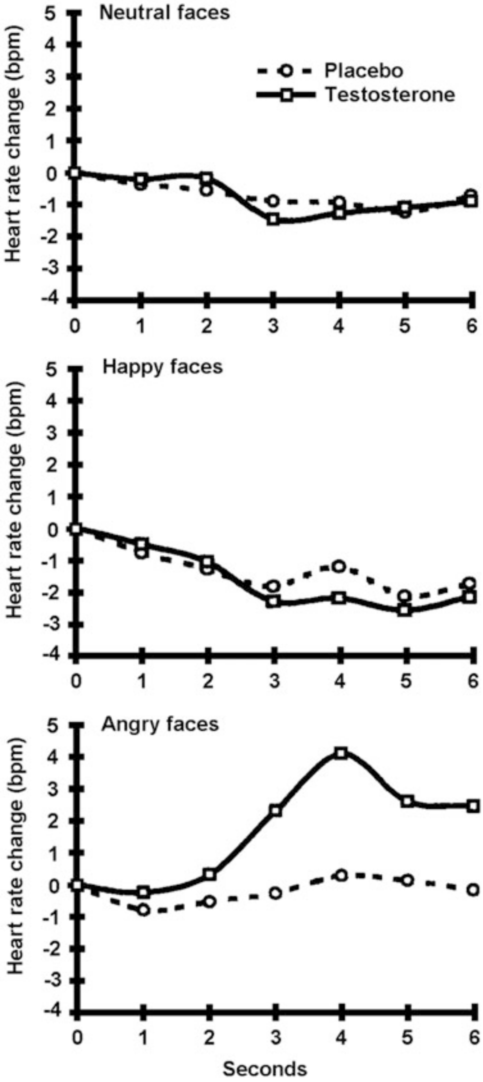
Fig. 1 Scatterplots of testosterone levels versus attentional bias (facilitation-interference (FI) scores for angry facial expressions in females (**a**) and males (**b**))

Neural Responses to Angry Faces

Steroid hormones such as testosterone are thought to act on social motivation particularly by binding to steroid responsive networks in the limbic system (Wood 1996). A hub in these networks is the amygdala, which interacts with the hypothalamus and innervates brainstem centers that control heart rate. Several neuroimaging studies have shown neural activation of the amygdala response to angry faces (e.g., Morris et al. 1999). However, there were no clues as to how, or by what neural mechanisms, testosterone acted in the human brain to influence dominance behaviors. To gather direct insights, we redesigned our cardiac response design for application with neuroimaging. In rodents, testosterone acts upon a subcortical brain circuit, featuring the amygdala, hypothalamus and brainstem, that sub-serves aggressive and dominance behaviors. We therefore expected the amygdala, hypothalamus and brainstem to be instrumental in the behaviorally vigilant responses to angry faces after testosterone administration (van Honk et al. 1999, 2001) and they were used as regions of interest. Female subjects first underwent functional magnetic resonance imaging while passively viewing angry and happy facial expressions and were retested in a second and third session, which was a placebo-controlled testosterone design (Hermans et al. 2008). At baseline there was activation to angry faces (compared to happy faces) in the amygdala, hypothalamus and brainstem (see Fig. 3) but also in the orbitofrontal cortex (OFC), a region importantly implicated in the control of human social aggression (Blair 2004).

Furthermore, the second part of this study showed increased activation of the amygdala, hypothalamus and brainstem in response to angry faces after testosterone administration, compared to placebo. We thus showed that testosterone's actions on the amygdala- hypothalamus-brainstem circuit in rodents translated to humans. Furthermore, there was a small effect after testosterone in the OFC in response to angry faces, which might reflect increased effort for inhibitory control over the

Fig. 2 Mean heart rate changes in beats per minute (bpm) from baseline (1 s pre-stimulus) during 6 s of post-stimulus for neutral, happy and angry faces



strongly increased subcortical activations. Nonetheless, our neuroimaging data were in tune with our earlier findings on testosterone and vigilant responses to facial anger, and they are translational to rodent research.

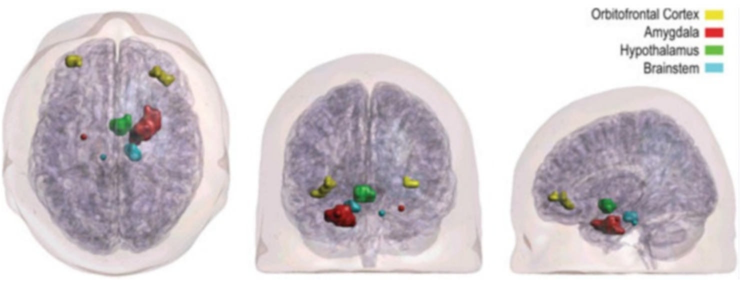


Fig. 3 Three-dimensional rendering of the skin and the brain from a T1-weighted magnetic resonance imaging scan (*top*, *frontal* and *left* views, respectively). Clusters of suprathreshold activity in response to angry versus happy facial expressions during the first session in the main regions of interest are color-coded

Testosterone and the Recognition of Facial Anger

Evidence has been found that aggressive patients have problems with consciously recognizing facial anger, somewhat counterintuitive to our findings above (Best 2002; Blair 2003). Conscious recognition of anger, however, acts at explicit, higher levels of processing, whereas the above data on testosterone and emotional and neural responses to angry facial expressions involve implicit processing levels (Toates 2006). Impairments in the recognition of facial anger could underlie the resistance of socially aggressive individuals to correction, in that, at higher levels of processings facial anger has socially corrective properties (Blair 2003). Accordingly, we tested whether testosterone might impair the explicit recognition of facial anger, notwithstanding the production of vigilant responses to angry faces on implicit processing levels (Hermans et al. 2008; van Honk et al. 1999, 2001).

We administered testosterone and placebo to female volunteers who performed an emotion recognition task using morphed displays to index the effects of testosterone on their sensitivity for consciously recognizing the facial expressions of threat (fear, anger, and disgust) and non-threat (happiness, sadness, and surprise). Results showed that testosterone induced a significant reduction in the conscious recognition of facial threat and that this effect, in separate analyses, could be qualified for angry facial expressions exclusively (van Honk and Schutter 2007a; Fig. 4).

In summary, testosterone augments physiological and affective responses and activates brain structures involved in dominant and aggressive behaviors in response to angry facial expressions (Hermans et al. 2008; van Honk et al. 1999, 2001), but the hormone impairs the conscious recognition of facial anger (Benarroch 2012). How can these seemingly divergent findings be explained? Testosterone has properties that enable the hormone to influence brain processing locally but particularly alter brain communication. Cross-frequency EEG analyses, which provide an index for cortical- subcortical communication, have revealed that testosterone decreases information transfer among subcortical and cortical regions

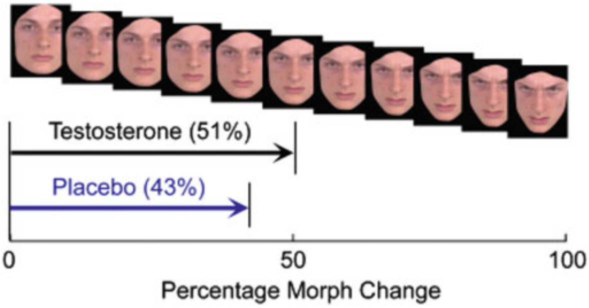


Fig. 4 Example of the morph from neutral expression to full-blown anger. The difference between the amount of morphing needed for the emotion to be recognized in the placebo and testosterone conditions indicates the percentage of recognition sensitivity lost after administration of testosterone

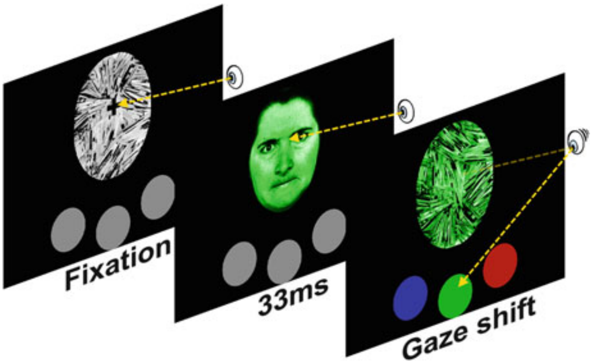
(Schutter and van Honk 2004). Cortical- subcortical communication not only is vital for the top-down control of social behavior (Blair 2004) but also mediates bottom-up transmission of information conveying angry threat value. This threat value is speedily spotted and transmitted by the basolateral amygdala to the orbitofrontal cortex, where higher-level modulation of emotion occurs. Thus a possible neurobiological mechanism for the observed testosterone-induced reduction in the recognition of facial anger is the reduction in cortical-subcortical communication, which blocks information transfer between amygdala and orbitofrontal cortex (van Honk and Schutter 2006).

Testosterone and Interactive Eye Gaze Tracking of Facial Anger

Our line of corresponding findings with testosterone and angry facial expressions discussed above may seem convincing, but they still have a major caveat. In primates, including humans, angry eye-contact is a main factor in the formation of social hierarchies (Mazur and Booth 1998). When this eye contact is established, a staring contest arises until *gaze aversion* of one of the opponents signals submission and prevents an aggressive confrontation. Primates thus importantly establish and maintain high status rank by angrily *outstaring* conspecifics. These actual behaviors had never been measured in research, either by us or by others. Therefore, we developed an interactive eye-tracking task that implicitly indexes genuine gaze aversion in response to (masked) angry faces (see Fig. 5).

With this task we showed that male and female subjects high in self-reported dominance showed an enduring gaze (inhibition of gaze aversion) to these unseen angry faces (Terburg et al. 2011). Furthermore, in another experiment, we showed that, after testosterone administration, young women showed increased reflexive

Fig. 5 Example trial of the eye-tracked gaze aversion task. Participants watch *gray* pictures change color, upon which their gaze is shifted to the dot with the same color. Unknown to the participants, facial expressions are presented during the color transition, which makes the gaze shift an implicit act of gaze aversion



dominance behavior in terms of as significant slowing down in gaze aversion from unseen angry faces (Terburg et al. 2012; Fig. 6). These findings definitively establish that testosterone in humans increases primal dominance display (Terburg and van Honk 2013).

Testosterone and Interpersonal Trust

Trust plays a vital role in the establishment and maintenance of social relations in humans (Kosfeld et al. 2005). However, trustfulness or social naivety might be hazardous, perhaps especially for those high in the social hierarchy. The alpha male or female needs to defend personal status and is responsible for the safety of the group. Given harsh competition and the prevalence of cheaters and deceivers among humans, trust is important, but social vigilance likely is more crucial for the CEO (Sapolsky 2011). The peptide hormone oxytocin increases trust in humans and even appears to make individuals susceptible to betrayal. After administration of oxytocin, male subjects perseverate in giving trust to others despite knowing that these others are untrustworthy (Baumgartner et al. 2008). Since testosterone is associated with social dominance, the hormone may act in an opposite manner to oxytocin and down-regulate interpersonal trust. In a placebo-controlled design using a facial trustworthiness-rating task (Adolphs et al. 1998), we investigated whether testosterone would decrease interpersonal trust (Fig. 7). We showed that testosterone indeed significantly decreased interpersonal trust, particularly in those who (in placebo) gave trust easily, that is, the most socially naïve subjects (Bos et al. 2010).

We argued that testosterone may have increased social vigilance in the socially naïve individuals to better prepare them for competition over status and resources. In sum, testosterone not only seems to down-regulate interpersonal trust but it also does so in an adaptive manner. We furthermore suggested that the mechanism by which testosterone acts on the brain to decrease trust might involve the amygdala (see also Johnson and Breedlove 2010), a topic that was addressed in follow-up research.

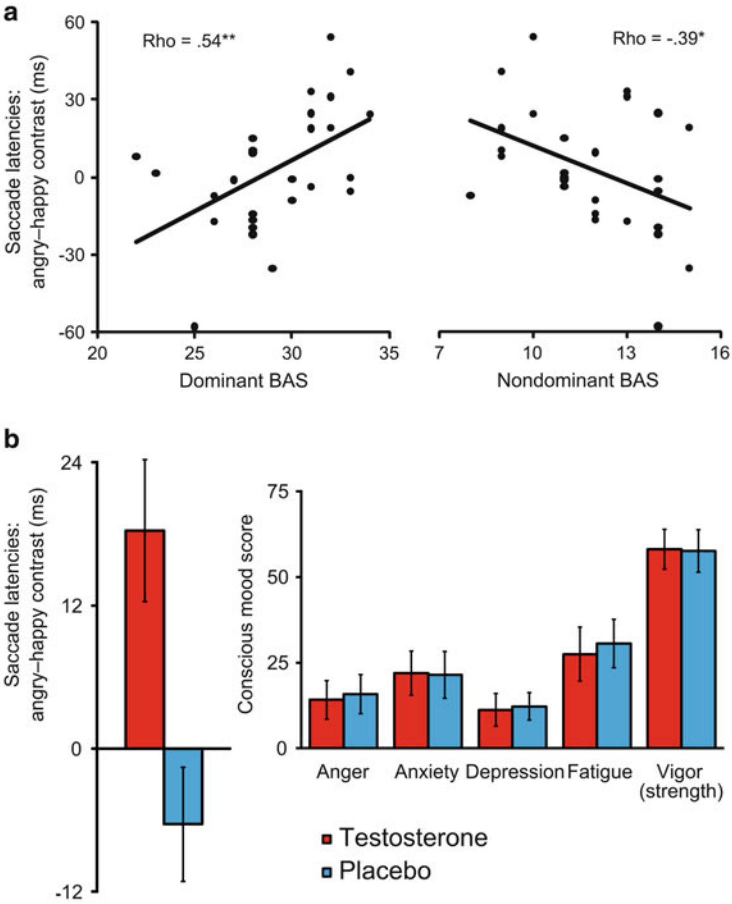


Fig. 6 Evidence from the eye-tracked gaze aversion task (see Fig. 5). (**a**) Correlations of dominant and non-dominant behavioral activation scales (BAS) with the contrast of angry and happy faces. High-contrast scores represent longer saccade latencies for angry trials, i.e., inhibition of submissive gaze aversion. (**b**) Gaze aversion latency from angry versus happy faces, and conscious motivational states. After testosterone administration, gaze aversion from angry faces is slower, whereas conscious motivational states are unaffected. $*p < 0.05$; $**p < 0.01$. Error-bars represent SEM

The Neural Mechanism by Which Testosterone Decreases Interpersonal Trust

Testosterone thus decreases interpersonal trust in humans, and as mentioned above, the hormone has manifold actions in the brain. However, for reductions in interpersonal trust and increased social vigilance, two possible mechanisms come to mind. Testosterone might increase social vigilance by up-regulating vasopressin gene expression in the amygdala, which augments the communication between the

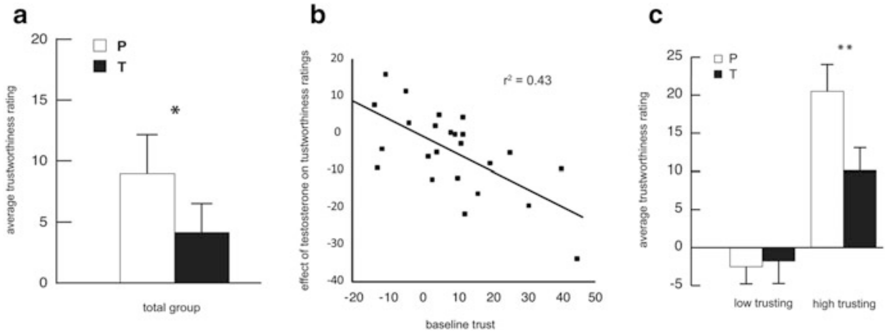


Fig. 7 (**a**) Testosterone induced a significant decrease in interpersonal trust in the total group (n = 24). A repeated-measures ANOVA (testosterone-placebo) showed (F(1,23) = 4.56, *P = 0.044). *White bars* represent placebo (P), *black bars* represent testosterone (T), and error bars represent standard error of the mean (SEM). (**b**) Plot of the baseline trust ratings, correlated against the effect of testosterone on trust judgments. The points on the left side of the graph, representing subjects who displayed low interpersonal trust in baseline measures, are clustered around zero for an effect of testosterone, indicating that their behavior was not affected by hormone treatment. In contrast, in the subjects displaying high interpersonal baseline trust, represented by the points on the right side of the graph, testosterone significantly decreased interpersonal trust. (**c**) Separate repeated-measures ANOVAs for the low- and high-trusting subject groups showed that low-trusting participants were completely unaffected by testosterone administration (F(1,11) = 0.79, NS), whereas high-trusting participants showed a sizeable reduction in the evaluation of facial trustworthiness (F(1,11) = 10.89, **P = 0.007). *White bars* represent placebo (P), *black bars* represent testosterone (T), and error bars represent standard error of the mean (SEM)

amygdala and the brainstem (Johnson and Breedlove 2010; van Honk et al. 2012). On the other hand, testosterone might reduce the functional connectivity between the OFC and the amygdala (van Wingen et al. 2010), possibly by up-regulating dopamine action in the OFC (Aubele and Kritzer 2012). The latter can lead to increased social vigilance because there is reduced top-down control of the OFC over the amygdala (Blasi et al. 2009). To gather critical insights, we used functional magnetic resonance imaging in a testosterone administration study to investigate the neural mechanisms by which testosterone acts on interpersonal trust. We showed that several cortical structures, including the OFC, are involved in the evaluation of facial trustworthiness. Crucially, however, testosterone administration decreased functional connectivity between the amygdala and the OFC during these trustworthiness evaluations and increased amygdala responses to, in particular, the faces that were rated untrustworthy (see Fig. 8).

On the basis of these findings, we suggested that, in conditions of social uncertainty, i.e., when meeting unfamiliar others, testosterone directly decouples the OFC and the amygdala via a dopaminergic mechanism in the OFC. This decoupling of OFC and the amygdala sets the social brain in a vigilance stance and, when signals of untrustworthiness are encountered, there is heightened activation of the amygdala.

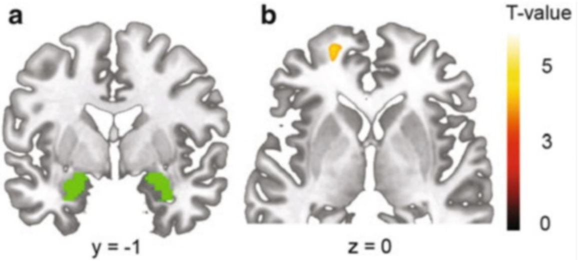


Fig. 8 (**a**) Coronal image of the mask for the bilateral amygdala, which was chosen as a seed region in the connectivity analysis. (**b**) Frontal part of the axial slice of the prefrontal cortex, which shows the region of the OFC in which connectivity to the bilateral amygdala is significantly reduced after testosterone compared to placebo. The t-map, which overlays a T1-weighted canonical image, is thresholded at $P < 0.001$ uncorrected for illustration purposes

A Cross-Species Framework for Testosterone and Dominance

In rodents, social dominance is typically established with short-term outbursts of aggression (Mazur and Booth 1998), and testosterone in these aggressive behaviors likely boosts the motivation to win the competition. However, the effects of testosterone and human dominance behavior often do not travel this primal social aggression pathway (Dabbs and Dabbs 2000; van Honk and Schutter 2007b). Nonetheless, the hormone remains vital in status-seeking behaviors and the formation of social hierarchies (Eisenegger et al. 2011). In this chapter, we reviewed behavioral and brain research that showed that testosterone up-regulates social vigilance in response to status threats, i.e., facial anger, and that, in the brain, this process especially centers on the amygdala, hypothalamus and brainstem (O'Doherty 2003; van Honk and Schutter 2007b). Moreover, we showed that testosterone induces social vigilance in uncertain social conditions, i.e., when meeting unfamiliar others (Bos et al. 2010), with the OFC and the amygdala implicated in the underlying neural process (O'Doherty 2003).

Our research points to two possible neurobiological mechanisms with which the hormone might increase social vigilance to defend status. Firstly, in most human social interactions, threat to status will be relatively low. Under low status threat, testosterone up-regulates dopamine action in the OFC, which functionally decouples the OFC and the amygdala. The subsequent loss of OFC inhibition over the amygdala sets the brain in a safeguarding mode (see Fig. 9). Our findings with testosterone administration and facial trustworthiness research provide an example (O'Doherty 2003). Testosterone, however, also up-regulates gene expression of vasopressin in the amygdala (Bos et al. 2012). This might happen when individuals encounter direct status threats, i.e., facial anger (Hermans et al. 2008), and there will be increased activation in the social alarm pathway to the brainstem (see Fig. 9). By way of this mechanism, which seamlessly translates to the neural

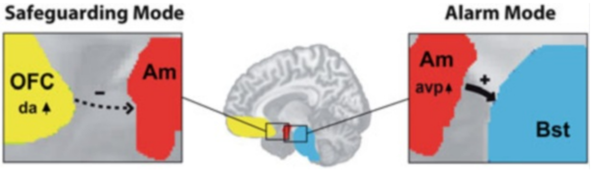


Fig. 9 Actions of testosterone on the brain under increasing status threat. (a) Testosterone's action on the brain during low status threat. Testosterone up-regulates dopamine action in the OFC, which induces decoupling of the OFC and the amygdala. Consequently, there is impaired inhibitory control of the OFC over the amygdala and the brain runs in 'safeguarding mode.' (b) Testosterone's action on the brain during high status threat. In addition to the decoupling of the OFC and amygdala, testosterone, by up-regulating vasopressin gene expression in the amygdala, induces hyper-coupling of the amygdala and the brainstem. Under the hyper-coupling of the amygdala and brainstem, the brain is in 'social alarm mode.' *AM* amygdala, *Bst* brainstem, *da* dopamine, *avp* vasopressin

pathways of dominance and aggression in the rodents' brain, testosterone upholds the individual's readiness to defend status and resources with physical aggression (van Honk et al. 2011b).

In sum, the neurobiological processes by which testosterone acts on the social brain are translational between rodents and humans, but rodents dominate more rigidly with social aggression utilizing the social alarm pathway. The twofold mechanism described above in humans allows for more behavioral variation in social interaction, with the exact mechanism by which the hormone acts on human brain and behavior depending on the social context, i.e., whether there is low or high status threat. Progress in the understanding of these intricate processes is a great challenge for the field of social neuroscience.

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