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The Cognitive Animal

Empirical and Theoretical Perspectives on Animal Cognition

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OA Funding Provided By:

The open access edition of this book was made possible by generous funding from Arcadia—a charitable fund of Lisbet Rausing and Peter Baldwin.

The title-level DOI for this work is:

[doi:10.7551/mitpress/1885.001.0001](https://doi.org/10.7551/mitpress/1885.001.0001)

Adrian Treves and Diego Pizzagalli

To survive and protect their offspring, animals must detect threats before they suffer damage. This requires efficient information gathering, as well as rapid information processing. Studies of nonhuman primate behavior reveal that individuals direct frequent and time-consuming vigilance (information gathering by visual search of the environment beyond the immediate vicinity) toward members of the same species (conspecifics), particularly with increasing risk of aggressive competition. In addition, interactions with unfamiliar conspecifics are generally aversive.

In a complementary fashion, electrophysiological and neuroimaging research on the human brain provides independent lines of evidence that socially relevant stimuli are processed quickly (<200 ms) and by a phylogenetically ancient brain region. Hence, we propose that the primate brain is adapted to rapid and sensitive processing of information about conspecifics, which derives from vigilance directed to the dynamic interactions of associates. We use this link to illustrate the potential for fruitful collaboration between neuroscientists and ethologists, and to suggest improvements in current practices in both fields.

Interaction of Ethology and Neuroscience

Cognitive ethology has the potential to unite two heretofore separate biological disciplines: neuroscience (the study of brain–behavior relationships) and ethology (the study of animal behavior). Despite separate histories and different investigative methods, neuroscience and ethology often address related and complementary topics. Neuroscientists' concentration on brain function has advanced our understanding of the proximate mechanisms underlying behavior. Ethologists' comparative, functional approaches have elucidated ultimate, evolutionary explanations for behavior. Anyone interested in sensory-processing and information-gathering behavior would gain

from understanding the brain functions of their subjects. Likewise, anyone unraveling the secrets of the brain should understand the evolutionary history and past environmental pressures that shaped the cognition and behavior of their subjects. Cognitive ethology can advance both disciplines because it places information on how brain and behavior interact in an evolutionary context that explains why they do so.

In this essay we illustrate how brain research can inform ethology and how in turn the study of animal behavior can inform neuroscience. We happened on this collaboration by chance, unaware of the similarity of our research questions. Our intuition tells us that many fruitful collaborations between neuroscientists and ethologists never occur because terminologies, techniques, and theories appear mutually unintelligible. This essay was designed to facilitate collaboration, using vigilance behavior to illustrate the utility of close communication between neuroscientists and ethologists. Our interdisciplinary approach, which could be useful in other domains of neuroscience and ethology, also suggests a modification of existing methods in both disciplines. Our focus is on the visual gathering and processing of social information related to members of the same species. Although many group-living species may show similar patterns of brain–behavior interactions involving several sensory channels, we concentrate here on visual cues used by primates.

Ethology Can Inform Neuroscience

Social neuroscientists often present stimuli to elicit changes in their subjects' brain activity. For humans, these stimuli are often images of the faces of strangers. In these studies, the null hypothesis is that strangers' faces are neutral stimuli, with pleasing or aversive properties being generated by different facial expressions. This may create a problem if strangers are inherently

aversive. Today, seeing a stranger's face is commonplace for humans, yet our brains are the products of millions of years of evolution under different circumstances. For our ancestors, encounters with strangers were probably rare, owing to low population densities and territorial defense against outsiders, and they were possibly accompanied by strong emotions (e.g., anxiety, hostility, sexual interest). Hence, ethologists would caution neuroscientists to consider the evolutionary history of their subjects, particularly if they study phylogenetically older brain regions. Ethologists can clarify the socioecological relevance of candidate stimuli, based on their understanding of ancestral environments and selective pressures.

Neuroscience Can Inform Ethology

Ethologists study both the evolutionary origins of behavior and its consequences for current fitness. For example, variation in vigilance is considered to have fitness consequences when it correlates with risk or reduces the time allocated to other important activities. Consequently, ethologists have long assumed that individuals with low rates of vigilance perceive less risk, all else being equal. This assumption is invalid if different classes of targets of vigilance (e.g., associates versus escape routes) require glances of different durations irrespective of risk (Treves 2000a). Here neuroscientists can provide crucial information on processing speed for certain classes of target. Indeed, neuroscientists would caution ethologists that inferences about evolutionary origins of behavior—such as vigilance toward conspecifics—can be drawn with more confidence if associated stimuli receive priority in the information-processing flow or if a functionally specialized brain region is identified.

Nonhuman Primate Vigilance

Vigilance is defined differently in ethology than it is in neuroscience, where vigilance refers to

a brain state of receptivity to external stimuli directly associated with alertness. By contrast, ethologists studying a wide range of taxa usually define vigilance as looking up from foraging or simply as visual search of the environment beyond the immediate vicinity. As such, vigilance can be studied by observing an animal's eyes and its direction of gaze. Researchers have focused on measures of rate of vigilance in relation to variation in the risk of predation or environmental context (Elgar 1989). Unlike most other animals in the vigilance literature, primates also reveal the targets of their vigilance (Treves 2000a).

In the wild, nonhuman primates spend their waking hours in two forms of visual activity: inspection of close targets (e.g., nearby foods, grooming partners) and vigilance directed at more distant targets (e.g., travel routes). Among primates, a large proportion of vigilance is directed at associates within groups (Treves 2000a). This reflects in part the fact that competition with associates over resources and mates is frequent and may sometimes result in death (Dittus 1980; Treves 2000b). Indeed, vigilance increases with the intensity of competition from associates. In interspecific comparisons, species that live in more excitable, competitive groups monitor associates more frequently and for longer periods than do species that form calm, cohesive groups (Caine and Marra 1988; Treves 1999). Within species, female enemies in the same group receive more visual attention than do female allies (Watts 1998), and subordinates direct more glances to associates than do dominants (Keverne et al. 1978; Alberts 1994). When infants are born or begin to wander from their mother's reach, within-group vigilance increases significantly (Maestripietri 1993; Treves 1999, 2000a). In primates, therefore, the varied competitive and aggressive threats generated within groups of familiar conspecifics favor vigilance.

Nevertheless, threats posed by *unfamiliar* conspecifics are more likely to result in harm than those arising within groups (Bernstein 1969; Bernstein et al. 1974; Goodall 1986; Treves 1998,

2000b). Although responses to close encounters with unfamiliar conspecifics vary with sex and context, they are generally dangerous and stressful for all parties (Alberts et al. 1992). Accordingly, a higher risk of encountering unfamiliar conspecifics triggers increases in vigilance (Rose and Fedigan 1995; Steenbeck et al. 1999). In sum, for wild primates, unfamiliar conspecifics present many threats and few attractions. It is in light of this information that we should reconsider the use of strangers' faces as neutral stimuli in neuroscience, especially if phylogenetically older brain regions are involved.

Based on nonhuman primate vigilance toward conspecifics and responses to strangers, we propose that natural selection has favored individuals that are sensitive to rapid change in the social environment and those that interact cautiously with strangers. Modern humans are of course different from wild nonhuman primates. In many cultures, we are socialized and habituated to strangers from an early age. Culture and learning may override our evolutionary history. Yet, infants predictably go through a phase of aversion to strangers (Mangelsdorf 1992). If the human brain retains pathways that evolved millions of years ago, phylogenetically older brain regions may still produce aversive responses to strangers' faces, while more recently evolved regions may secondarily modulate aversion to strangers through social and cultural experience. We suggest therefore that experiments that present strangers' faces as stimuli should be expected to elicit a negative response at the outset.

Neuroscience and the Study of Social Perception

Social perception refers to the processing of information about conspecifics and the social environment. In humans, it can be studied by measuring electrical and physiological activation of the brain in response to stimuli. Typically, faces and direction of gaze are employed as stimuli because they convey considerable information about conspecifics' emotional and motivational

state as well as the focus of their attention (Tomassello et al. 1999; Allison et al. 2000; Langton et al. 2000). Noninvasive electrophysiological studies have millisecond time resolution, allowing researchers to unravel the temporal dynamics and sequences of brain processes. However, they do not provide fine-grained spatial information about the brain regions involved. For this, neuroimaging techniques with their spatial resolution in the millimeter range can map brain regions involved in social perception, without, however, furnishing fine-grained temporal information. When information from the two techniques is combined, a more comprehensive view of human brain functions emerges.

The vigilance behavior of nonhuman primates suggests that information about the social environment has consequences for fitness; hence we would expect social perception to be rapid, sensitive, and dependent on functionally specialized brain regions. This idea is supported by pioneering work in nonhuman primates using invasive, single-unit recordings (Brothers et al. 1990; Perrett et al. 1992). In the next two sections we summarize studies of human social perception that extend this nonhuman work with independent lines of evidence demonstrating the involvement of (1) a preattentive response and (2) a phylogenetically ancient brain region in processing conspecific stimuli.

Human Electrophysiological Studies

Brain electrical activity can be monitored noninvasively by attaching electrodes to the scalp (electroencephalogram). Typically, differences in electrical potential are recorded from multiple scalp sites and sampled several hundred times per second. Changes in functional brain state, whether endogenous or induced by a task, can be measured. For instance, brain electrical activity (event-related potentials, ERPs) can be related directly to the presentation of a stimulus after background activity (noise) is eliminated.

Recently, ERPs have been used to study the time course of brain responses to a variety of

socially relevant stimuli. For instance, strangers' faces elicited stronger responses than control stimuli—including heterospecific faces—as early as 170 ms after stimulus onset (for a review see McCarthy 2000). Also, stronger responses were elicited by an averted gaze than a gaze directed to the subject (Puce et al. 2000). Notably, even more subtle characteristics of faces, such as sex (145–185 ms: Mouchetant-Rostaing et al. 2000), likability (80–116 ms: Pizzagalli et al. 1999), expression (160 ms: Streit et al. 1999; 110 ms: Halgren et al. 2000), and attractiveness (170 ms: Halit et al. 2000) have been shown to be processed very rapidly. Thus, mechanisms exist that extract subtle information about conspecifics quickly and automatically (effortlessly and preattentively).

Neuroimaging Studies

Neuroimaging techniques (functional magnetic resonance imaging, fMRI, or positron emission tomography, PET) take advantage of fleeting increases in blood flow to the brain regions activated by a given stimulus. Such changes in regional cerebral blood flow and blood oxygenation can be measured with high spatial resolution to map human brain functions.

Neuroimaging has been employed recently to investigate brain regions underlying the processing of socially relevant information in humans (Davidson and Irwin 1999). Extrapolating from pioneering research in rodents that identified a subcortical (thalamo-amygdalar) pathway involved in rapid processing of fear-related stimuli (LeDoux 1996), several researchers have proposed that automatic and rapid processing of threat-related cues in humans may also be mediated by the amygdala¹ (Öhman 1993; LeDoux 1996; Whalen 1998).

Consistent with this view, human amygdalar activation has been reported during presentation of angry (e.g., Hariri et al. 2000) and fearful (e.g., Morris et al. 1996) faces, even when stimuli were presented below the level of conscious

awareness (Morris et al. 1999; Whalen et al. 1998). In agreement with our proposal that unfamiliar conspecifics may generally be aversive stimuli, amygdalar activation also followed the presentation of unfamiliar faces with neutral expression, whether of the subject's own race (Dubois et al. 1999) or another race (Phelps et al. 2000; Hart et al. 2000). Moreover, human patients with amygdalar lesions judged unfamiliar faces to be more approachable and trustworthy than did controls (Adolphs et al. 1998).

However, subsequent studies suggest that the human amygdala may play a broader role than simply responding to threat-related stimuli. For example, amygdalar activation increased when comparisons were made between biological and random motion (Bonda et al. 1996), direct and averted gaze (Kawashima et al. 1999), and images of friends and those of loved ones (Bartels and Zeki 2000). Clearly, not all of these stimuli conveyed threats, yet the amygdala was implicated. Notably, autistic individuals with deficits in social perception showed amygdalar dysfunction (Baron-Cohen et al. 1999). Collectively, animal and human studies suggest that one function of the amygdala is to process species-specific cues that predict biologically significant outcomes, based on either personal experience or evolved mechanisms (LeDoux 1996; Whalen 1998).

In summary, ERP studies reveal that the human brain performs social perception rapidly (<200 ms) and automatically, while fMRI and PET studies reveal a key role for an ancient brain region, the amygdala, in social perception. Although it is reasonable to infer a link between the two sets of studies, their radically different temporal resolutions preclude a direct connection so far. If a link is found between rapid processing and amygdalar processing of conspecific stimuli, it would represent evidence for a brain mechanism shaped by selective pressures imposed by the social environment. This does not contradict the idea that subcortical responses may prime the phylogenetically more recent cor-

tical regions responsible for a slower, more complete, and richer response to the same stimuli. It is safe to assume that vigilance toward conspecifics involves both cortical and subcortical pathways (Morris et al. 1999; Hariri et al. 2000). Yet the involvement of the amygdala suggests to us that the primate brain contains an evolutionarily conserved pathway specialized to process conspecific stimuli with high priority.

Conclusion

In group-living primates, the social environment has shaped behavior and brain functions to coordinate and streamline the collection and processing of information about conspecifics. Both within-group vigilance and responses to unfamiliar conspecifics reflect selection imposed by allies, enemies, and strangers. Frequent, time-consuming, and sensitive vigilance toward conspecifics reflects the importance and priority of gathering socially relevant information. In turn, the primate brain shows adaptations to processing such socially relevant information, which is reflected by the involvement of a functionally specialized, ancient brain region and rapid extraction of subtle cues from conspecifics. Specifically, we hypothesize that the primate amygdala is adapted to simple, fast processing of socially relevant stimuli gathered by vigilance toward conspecifics—not only threat related but also other salient stimuli such as gaze direction and body movements. This integrated brain–behavior system would maximize fitness in environments where conspecifics hold the key to survival and reproduction.

Implications

If our proposal is correct, it has implications for neuroscientists and ethologists alike. Socially irrelevant stimuli should trigger a slower brain electrical response (using ERP) and less amygdalar activation (using neuroimaging) than so-

cially relevant stimuli of comparable complexity. Primate ethologists should expect conspecific stimuli to have priority over other stimuli when individuals allocate vigilance effort. Moreover, the rapid processing of socially relevant stimuli suggests that glances to associates may be brief but sufficient to extract considerable information; hence the time spent in vigilance should not be equated with the importance of the target, especially during periods of social instability. A global recommendation for both neuroscientists and ethologists is to use paired stimuli (e.g., conspecific vocalizations versus heterospecific calls) carefully selected for their socioecological and evolutionary relevance. In this way, the findings from ethology and neuroscience may become mutually more interesting and intelligible.

Acknowledgments

A. Treves was supported by the Department of Psychology and the Graduate School of the University of Wisconsin—Madison and by a grant to C. T. Snowdon (National Institutes of Health grant MH 35,215). D. Pizzagalli was supported by grants from the Swiss National Research Foundation (81ZH-52864) and Holderbank-Stiftung zur Förderung der wissenschaftlichen Fortbildung. The authors wish to thank R. J. Davidson, W. Irwin, E. Nelson, A. J. Skolnick, and C. T. Snowdon for helpful comments.

Note

1. The amygdala is an almond-shaped brain region located in the depth of the medial temporal lobe. It is believed to be involved in threat processing in birds, mammals, and reptiles (LeDoux 1996).

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