CHAPTER 26

Neuroethology of Attention in Primates

Stephen V. Shepherd and Michael L. Platt

> ***Expert Commission Decides That the Horse Actually Reasons.***
>
> BERLIN, Sept. 13. — The remarkable horse called "Clever Hans" has just been examined by a special commission of experts, in order that a decision might be arrived at whether it is a horse possessed of extraordinary brain power . . .
>
> —From *The London Standard*, in *The New York Times*, October 2, 1904

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The case of "Clever Hans" is perhaps the most famous con job in the history of psychology. Both experts and public were taken in, believing that human-like perceptual and reasoning abilities could be exhibited by a horse trained by Wilhelm van Osten. After 3 years and a great deal of public scrutiny, however, Oskar Pfungst determined that the horse could only answer questions to which the experimenters already knew the answer—in short, the horse did not have these human abilities, and was merely responding to subtle social cues provided by his audience. Thus, the horse's exceptional brainpower was dismissed.

But this is the wrong lesson of this story. After all, the con artist was not Wilhelm van Osten—he was taken in as well—but *his horse*. A better lesson is that the horse, like many animals, is exquisitely capable of learning to recognize subtle cues to the emotions, intentions, expectations, and knowledge not only of his own species, but even humans. These abilities are no less impressive because they are social, rather than abstract. Indeed, humans with selective disruption of social cognition have great difficulty navigating the overwhelmingly complex societies in which we live, and by which we thrive. As Clever Hans demonstrated, the cognitive mechanisms underlying our shared humanity appear to also be shared with many other species. It thus seems likely that advances in the evolution of cognition derive, at least in part, from the need to predict the actions of others. These social cognitive abilities are built on a long genetic and developmental history, but are founded on something so simple and fundamental that we often fail to notice it. To learn how to make sense of another's actions—whether human, monkey, or horse—we have to *attend* to them. In the following pages, we explore this social orienting behavior, describe its apparent adaptive functions, and attempt to understand how orienting decisions are made within the brain.

PSYCHOLOGICAL, ETHOLOGICAL, AND NEUROETHOLOGICAL APPROACHES TO ATTENTION

All mobile animals orient to salient features of their environment. This can occur overtly, by shifting gaze, or covertly, by deploying attention without eye movements. Psychophysical, electrophysiological, and neuroimaging studies conducted in the laboratory have extensively probed orienting in both human and nonhuman primates. Generally, subjects have been trained to discriminate simple stimuli whose salience or

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behavioral significance has been arbitrarily assigned through explicit instruction or association with rewards (e.g., Posner, 1980). Such studies suggest the operation of two distinct systems for orienting attention (James, 1890; Jonides, 1981; Posner & Cohen, 1984), one fast and reflexive (exogenous) and the other slow and voluntary (endogenous), mediated by partially overlapping neural circuits (Corbetta & Shulman, 2002; Egeth & Yantis, 1997; Mangun, 1995).

Outside the laboratory, observational studies in natural settings indicate that social stimuli are intrinsically salient and strongly attract attention (Caine & Marra, 1988; Keverne et al., 1978; McNelis & Boatright-Horowitz, 1998). Moreover, recent laboratory studies have suggested that social cues, such as the direction of gaze in an observed individual, access a privileged information channel capable of directing attention (Deaner & Platt, 2003; Driver et al., 1999; Friesen & Kingstone, 1998). These studies imply that the neural mechanisms that mediate attention have evolved sensitivity to cues predicting the goals and intentions of other individuals—but the precise nature of these social cues, and the specific neural systems by which they are processed, remain obscure. Indeed, current evidence suggests that social attention maps poorly onto existing models of attention, which emphasize dichotomous exogenous and endogenous orienting systems.

The neuroethological approach is an alternative paradigm that works to resolve these issues. We contend that complete understanding of the biology of attention must account not only for gross patterns of orienting in natural environments but also for the fine spatiotemporal details of orienting measured in controlled laboratory settings. These ethological and psychophysical goals are often approached separately, using different animal models and highly divergent techniques, reflecting in part the fact that the demands of naturalistic observation generally preclude precise measurements of orienting. Likewise, psychophysical experiments have typically failed to simulate the behavioral contexts in which orienting behavior normally operates.

Nonetheless, we contend that these divisions are surmountable, and that combining ethological and laboratory approaches will foster the development of a unified evolutionarily motivated theory of attention, which will have broad impact on our understanding of brain systems. For many animals, in particular primates like ourselves, one of the most important variables influencing attentional deployment is the current behavioral state of nearby individuals—the current social context. In the following sections, we consider the impact of social context on attention, outlining some of what has been learned from both laboratory and field studies. In particular, we describe our own efforts to bridge these approaches by studying the neuroethology of social attention in human and nonhuman primates.

EVOLUTION OF VISUAL SPECIALIZATIONS IN PRIMATES

Primates are unusual among mammals in their strong reliance on vision (Allman, 1999). Initially, visual specializations probably evolved in primates to support movement through upper tree branches (Robert Martin's ''fine-branch niche hypothesis,'' Martin, 1990), to facilitate hunting for insects (Matt Cartmill's ''visual predator'' hypothesis, Cartmill, 1972), or both. Primates might thus be expected to use vision primarily for locomotion and food acquisition while retaining common mammalian visual functions such as predator avoidance.

Over the course of primate evolution, however, visual processing appears to have become increasingly specialized for guiding social interaction. Many primates make extensive use of vision to localize, monitor, and interact with other individuals, and likewise devote a large portion of their brains to visual processing. Notably, the expansion of the primate brain has been accompanied by a corresponding increase in the flexibility and complexity of primate social groups (Allman, 1999; Barton & Dunbar, 1997). While prosimian primates rely heavily on olfactory and pheromone-mediated modes of communication, these ancestral sensory modalities have been supplanted in more derived primates by visually mediated signals such as coloration, poise, gesture, facial

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expression, and gaze (de Waal, 2003; note also Gilad et al., 2004), as well as affective and referential vocalizations (Cheney & Seyfarth, 1990; Seyfarth & Cheney, 2003). While scientists have long recognized the importance of studying primate visual attention in the laboratory, we have all too often neglected the role of attention in the natural social ecology.

BEHAVIORAL GOALS DRIVE ORIENTING IN NATURALISTIC SETTINGS

The first studies of naturalistic orienting in primates were conducted in humans by the Russian psychologist Alfred Yarbus in the 1950s and 1960s (Yarbus, 1967). He measured overt visual orienting behavior by recording visual fixation patterns during free and instructed scanning of pictures with light-reflecting mirrors suction-cupped to the eyes. Yarbus demonstrated that social stimuli are intrinsically salient and strongly attract attention. Despite this strong bias, current behavioral goals also regulate visual attention. For example, when shown the painting "An Unexpected Visitor," subjects consistently oriented attention toward the faces of people in the scene (Fig. 26.1). When asked to determine the wealth of the family in the picture, however, subjects shifted their gaze to the clothing worn by the figures in order to extract the information requested by the experimenter.

Recently, Land and Hayhoe (2001) reported similar context dependence using noninvasive video gaze tracking in human subjects. They showed that attention was almost completely determined by task demands during simple actions such as making a sandwich or preparing tea. By contrast, subjects almost never attended to task-irrelevant regions of space. These data suggest that attentional priorities not only are shaped by evolutionary pressures but also can serve as external indicators of the shifting internal goals governing an individual's moment-to-moment behavior (Shepherd & Platt, 2008).

To make sense of natural orienting patterns, then, requires not just the sophisticated understanding of behavioral repertoire and ecological

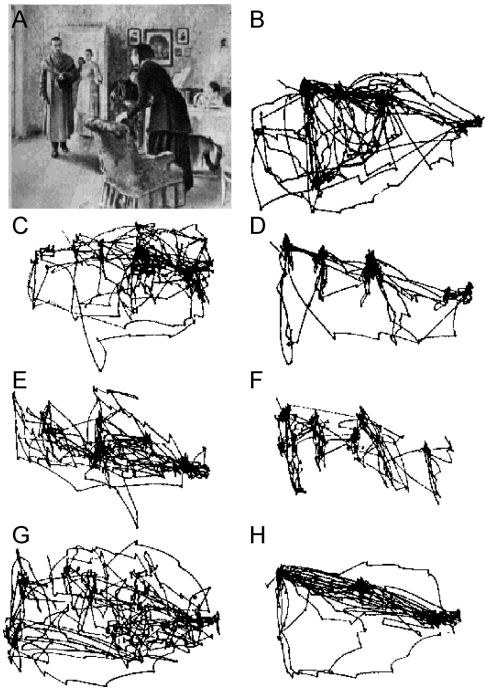


Figure 26.1 Social context and behavioral goals alter fixation patterns during free viewing. Panels 1–7 show the different gaze patterns of viewers when asked different questions about the illustration, Rjepin's "Unexpected Visitor," shown at upper left. Viewers scanned the photographs in very different ways when asked to estimate the family's wealth (**C**), estimate their ages (**D**), memorize the position of people and objects (**G**), or estimate how long the "unexpected visitor" had been away (**H**). After Yarbus, A. (1967). Eye movements during perception of complex objects. In: *Eye movements and vision* (pp. 171–211). New York: Plenum Press. Used with permission.

niche supplied by ethology, but also the rigorous mathematical tool set for understanding decision making provided by behavioral economics. The marriage of the latter fields with electrophysiology and functional imaging has produced an explosive change in our approach to human decisions through the field of neuroeconomics, and neuroethology holds similar promise for extending our mechanistic understanding of behavioral evolution. A central message of both these disciplines, however, has been that neural processes are strongly influenced by social

variables, ranging from the framing effects invoked by word choice in task instructions (De Martino et al., 2006; Tversky & Kahneman, 1981) to the intrinsic reward of watching other individuals (Aharon et al., 2001; Hayden et al., 2007).

SOCIAL ATTENTION IN NATURAL SETTINGS

Observational data support the idea that visual attention in nonhuman primates is also biased toward social stimuli (Caine & Marra, 1988; Keverne et al., 1978; McNelis & Boatright-Horowitz, 1998). Furthermore, these biases are not uniform; some social stimuli attract more attention than others. For example, monkeys spend more time looking at pictures of faces gazing toward them than faces with averted gaze (Keating & Keating, 1982), and look preferentially toward the regions around the eyes and mouth (Guo et al., 2003; Keating & Keating, 1982; Kyes & Candland, 1987). They also look more often toward higher-ranking animals than lower-ranking animals (Keverne et al., 1978; McNelis & Boatright-Horowitz, 1998). Such data have generally been limited, however, to distal observations in natural settings or, in the laboratory, to qualitative analysis of fixation patterns within still photographs.

Given the various limitations of previous studies, one goal of our research has been to quantitatively measure primate visual attention in naturalistic environments and species-typical social groups. To do this, we recorded gaze behavior in socially housed, freely moving ring-tailed lemurs (*Lemur catta*) interacting in large three-dimensional environments. We used a lightweight telemetric optical gaze-tracking device (Fig. 26.2; see Shepherd & Platt, 2006) operating at 0.22 degrees × 33 ms resolution—a degree of precision comparable to eye-tracking methods used in the laboratory. Our approach differed, however, in that we did not provide any task or instruction, but instead inferred the goals guiding visual attention in natural contexts from the observed patterns of typical behavior (Shepherd & Platt, 2008). Ring-tailed lemurs, prosimian primates that diverged from the ancestors of "higher" primates some 60 million

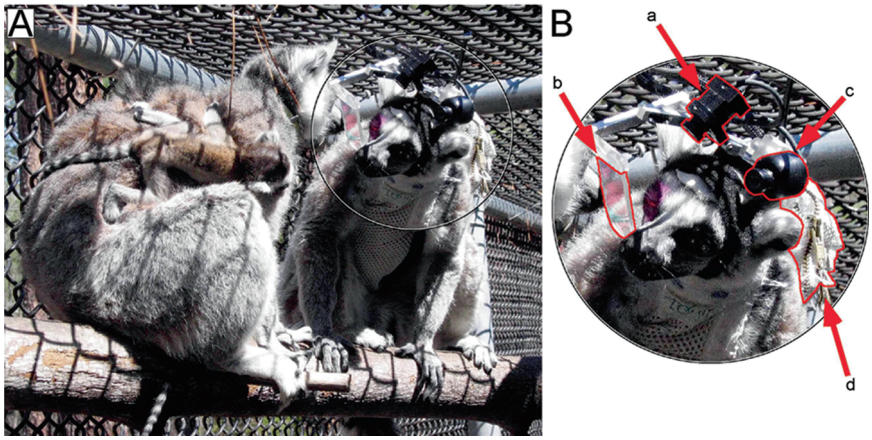


Figure 26.2 Equipment for tracking gaze during the natural behavior of freely moving animals. We tracked gaze during spontaneous and natural interactions with cohabitant conspecifics **(A)** using a telemetric optical gaze-tracking system developed by Iscan, Inc. The system **(B)** was composed of an infrared camera and LED (a) imaging the lemur's right eye through a dichroic mirror (b), an optical camera (c) viewing the scene in front the lemur's head, and a telemetry system housed in a primate vest (d), which broadcast to a remote monitoring station where the subject's recorded gaze direction was analyzed and projected onto locations in the recorded visual scene. After Shepherd, S. V., & Platt, M. L. (2006). Noninvasive telemetric gaze tracking in freely moving socially housed prosimian primates. *Methods, 38,* 185–194. Used with permission.

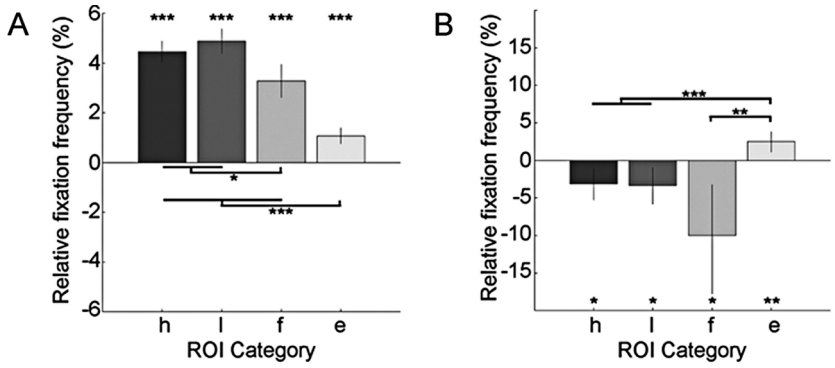


Figure 26.3 Fixation priorities in stationary and moving lemurs. Lemurs fixated humans (h), lemurs (l), food (f), and high-contrast environmental features (e) significantly more than chance expectation, and furthermore fixated humans and lemurs significantly more than food rewards, and all three significantly more than environmental features (**A**). Lemurs fixated environmental features significantly more often when moving than when stationary, seemingly at the cost of fixations toward animals and rewards (**B**). ***, $P < 0.0005$; **, $P < 0.001$; *, $P < 0.01$. After Shepherd, S. V., & Platt, M. L. (2008). Spontaneous social orienting and gaze following in ringtailed lemurs (*Lemur catta*). *Animal Cognition, 11,* 13–20. Used with permission.

years ago, were chosen as subjects based on their tolerance of handling and their availability at the Duke Lemur Center. Ring-tailed lemur social groups are similar to those of many higher primates, comprising 10 to 20 individuals of both sexes organized in well-defined social hierarchies, and communicating through auditory, olfactory, and visual modalities (Jolly, 1966; Sauther et al., 1999).

We found that male ring-tailed lemurs fixated their human handlers—as would be expected given we had just suited them, temporarily, into recording equipment. More important, they fixated their social companions, and did so more often than they fixated small food rewards (Fig. 26.3A). Each of these three a priori categories—human handlers, conspecifics, and food rewards—were fixated significantly more often than chance and significantly more often than high-contrast environmental features, stimuli we expected to attract attention based on low-level visual salience (Carmi & Itti, 2006; Peters et al., 2005). These data suggest that animals, especially conspecifics, and rewards, such as potential food sources, were effectively identified, localized, and attended during natural visual behavior.

These social attention biases were not inflexible, however, and in fact changed during periods of active locomotion (Fig. 26.3B). While moving, lemurs attended to environmental features that served as potential movement substrates along the path toward their destination. At the same time, other visual priorities, such as monitoring other lemurs and foraging, were temporarily but systematically diminished. Together with earlier research (Land & Hayhoe, 2001; Yarbus, 1967), these findings validate the use of quantitative gaze measurements as an externally observable indicator of otherwise unobservable mental states (e.g., the current behavioral goals of an animal) and further reveal that the typical behavioral context for a lemur involves not only monitoring threats, such as predators, and rewards, such as food, but also guiding movement and maintaining observational contact with other members of the social group. AQ2

DOMINANCE, SEX, AND SOCIAL SALIENCE

Our ongoing field studies of orienting in ring-tailed lemurs support the idea that ancestral primates possessed neural specializations for orienting toward and extracting relevant information from other animals (Tomasello et al.,

2005). The diversity of stimuli and complexity of behavioral contexts that typify the field setting, however, has challenged our ability to draw definitive conclusions regarding the specific stimuli that guide visual attention during natural social behavior—an endeavor that is ongoing in our laboratory. Moreover, despite the evident similarity between human visual attention priorities and those observed in lemurs, the genomes, brains, behavioral repertoires, and social systems of our species differ dramatically. Unfortunately, little is known about brain function in lemurs.

To address these limitations, we have conducted parallel investigations of the visual orienting behavior of another primate, whose visual abilities, social structure, environmental niche, and physiology more closely mirror our own. Rhesus macaques (*Macaca mulatta*) are an oft-studied anthropoid primate with relatively well-explored biology, and like humans, they live in large, hierarchical social groups with extensive multisensory behavioral interactions. Although rhesus monkeys have been widely used to study visual attention, most past studies have used arbitrary stimuli with little or no intrinsic behavioral relevance.

We know, however, that in the wild, monkeys visually monitor one another (Caine & Marra, 1988; Keverne et al., 1978; McNelis & Boatright-Horowitz, 1998), and in the laboratory, they preferentially seek out visual stimuli with social content (Butler, 1954; Sackett, 1966). To precisely quantify how rhesus monkeys prioritize attending to specific classes of social stimuli, we developed a choice task designed to balance fluid rewards against the chance to glimpse photos of other monkeys. Specifically, monkeys chose between orienting to either of two targets, one associated with a juice reward and another associated with an alternative juice reward and a picture of a familiar monkey. By determining the differential juice reward at which monkeys were equally likely to choose to view the image, we were able to quantify the reward value of attending to different classes of social stimuli (Deaner et al., 2005).

Using this ''pay-per-view'' paradigm, we found that male monkeys consistently ''overvalued'' seeing potential mating cues (female hindquarters) and faces of dominant males, but ''undervalued'' seeing the faces of low-ranking males (Fig. 26.4). The attraction of attention to high-ranking males is somewhat counterintuitive,

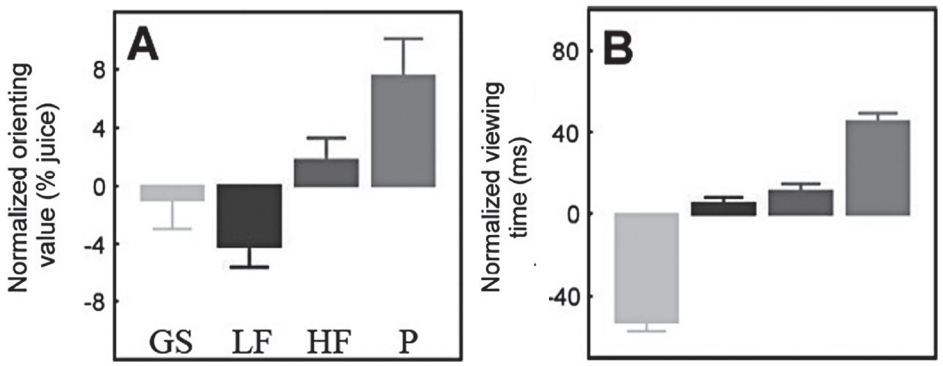


Figure 26.4 Monkeys sacrifice juice to view important social stimuli. When monkeys were offered different juice rewards to fixate two targets, only one of which also yielded an image reward, they chose each option equally when the intrinsic value of viewing an image offset the amount of juice sacrificed (**A**). Monkeys paid the highest amount of juice to see female perinea (P) and a lower amount to see high-ranking male faces (HF), but required extra juice to look at low-ranking male faces (LF) or, to a lesser extent, uniform gray squares (GS). A similar pattern is evident in the amount of time per presentation that monkeys fixated each category of image (**B**). This measure differs, however, in that monkeys dwell for similar lengths of time on low- and high-status faces. After Deaner, R. O., Khera, A. V., & Platt, M. L. (2005). Monkeys pay per view: adaptive valuation of social images by rhesus macaques. *Current Biology, 15,* 543–548. Used with permission.

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since under natural conditions direct staring serves as a threat gesture in many primate species (van Hoof, 1967). Analysis of dwell times—the duration of glances toward particular social stimuli—provides a potential explanation for this paradox: Sexual cues consistently evoked prolonged stares, whereas faces generally evoked fixations of shorter duration. Frequent, furtive glances toward high-ranked males may serve to maximize acquisition of important social information while simultaneously minimizing risk of conflict.

EVOLUTIONARY BIOLOGY OF SOCIAL ATTENTION

Thus, both for freely moving lemurs and for macaques performing tasks in the laboratory, an important goal of visual attention is to maintain observational contact with conspecifics. Ethological studies of primate behavior suggest this behavioral bias may serve at least two complementary biological functions. Vision has long been known to play a role in hunting and foraging, affecting both predators (e.g., carnivores), where selection pressures favor focused binocular fields of view, and prey (e.g., ungulates), where selection favors broad, monocular visual fields (Allman, 1999; Cartmill, 1972). Primates, too, have focused, binocular visual fields (Allman, 1999; Martin, 1990), but this does not free us from the need to be vigilant for predators or hostile competitors. Indeed, primate societies are characterized by certain baseline levels of aggression, and primates must be wary of social threats both external and internal to their own social group. Thus, many primates must actively balance surveillance against external predation or rival social groups with surveillance against aggression from within the social group (e.g., Caine & Marra, 1988). Protection against social threat is a key need driving visual attention.

Centripetal surveillance, however, implies that there is a social group in the first place. From this we infer a second, more subtle role of social attention, first articulated by Chance and Jolly (1970). Cohesion of social groups requires, as a principal element, the coordination of movements to regulate spacing between each individual and its cohort. For this reason, Chance and Jolly (1970: 171) suggested that "The social attention of individuals within a cohort . . . must be directed exclusively at the other members of it," going on to note that "even when they are an integral part of the complete society, the distinct coherence of a cohort. . .may depend on their maintaining a predominant degree of attention toward themselves." Chance and Jolly proposed that the key mechanism of dominance is not the threat of violence from the strongest member of the troop, but rather the ability of these individuals to command the attention of other group members. In short, Chance and Jolly argued that primate societies are bound together by centripetal attention, specifically, in hierarchical societies, by attention toward high-status animals.

Although dominance may be structured by the threat of violence and by the need for coalitional defense against these threats (Cheney & Seyfarth, 1990; Keverne et al., 1978), status-based saliency seems to be positive in valence and largely prosocial, in that it promotes proximity to the group. For example, Chance and Jolly (1970) described a behavior called "reflected escape" in which a subordinate animal, threatened, runs in a looping arc, first away from the challenger and then back toward the central members of the group—even if these same dominant individuals had initiated the threat! These ideas seem to be supported by findings that gaze (Keverne et al., 1978), like allegiance and grooming (Cheney & Seyfarth, 1990), is allocated preferentially to dominant individuals but independently of their aggressiveness, and also by our own finding that macaques sacrifice more juice to view dominant animals than subordinate animals.

Just as prosocial reward may drive attention, however, there is evidence that enhanced salience may itself drive reward. Specifically, the mere act of attending to a stimulus appears to enhance its desirability. Zajonc first described these effects in 1968 when he found that brief presentation of unfamiliar visual stimuli caused people to subsequently rate those stimuli more esthetically pleasing, even when they could not

recall having seen them (Zajonc, 1968, reviewed in Bornstein, 1989). More recently, two studies have generalized this effect from ''mere exposure'' to attentional state. Raymond and colleagues (2003) found that stimuli that were presented, but ignored, accrued negative associations in a variety of task conditions. Shimojo and colleagues (2003) made a complementary discovery, using simple preference judgments. They found that prior to selecting the more attractive of two faces, subjects looked increasingly long and often at the face they subsequently chose. Importantly, when subjects were forced to look at a particular face, they were also more likely to subsequently prefer it. Together, these findings suggest that attention may drive changes in affective judgments. By extension, ''mere exposure'' may mediate social cohesion in primates by encouraging approach toward previously attended members of the social group, even if the attention was initially garnered through such negatively valenced agonistic interactions as direct competition or threat. In this way, social saliency could play a critical role in patterning the spacing behavior of animals in a group, making the most often fixated animals the most desirable for approach.

This complex relationship between attention, approach, and hedonic value suggests that simple approach/avoid, pleasure/pain dichotomies may serve us poorly in studying the neuroscience of attention. Instead, it may be more useful to consider attention in terms of ''motivational salience,'' the predicted marginal behavioral utility of information, and in terms of the specific neural systems through motivational salience that govern behavioral orienting.

It seems reasonable that attention to high-value social targets is promoted by the reward systems of the brain, and this idea is endorsed by ongoing studies in our lab (Klein & Platt, 2008). The motivators that drive attention, however, are not always entirely appetitive; prolonged staring at dominant males, for example, is risky and unlikely to be hedonically pleasing (consequentially, fixation durations are quite short). In the end, it is much harder to answer the question of whether behaviors are mediated by ''pleasure'' or ''fear'' than whether they are mediated by, say, the ventral striatum or amygdala. We tend to estimate the qualities of subjective experiences by analogy: To understand animals whose behavior differs broadly from our own, we may proceed most safely when we can supplement our analogical reasoning with mechanistic, as well as behavioral, data endorsing homology. Cases like this suggest that a neuroethological approach has the potential to clarify both our mechanistic understanding and our theoretical interpretation of adaptive behavior.

ATTENDING TO INTENTIONS

Ralph Waldo Emerson (1876: 118) wrote, ''The eyes of men converse as much as their tongues, with the advantage, [sic] that the ocular dialect needs no dictionary, but is understood all the world over.'' As Emerson intimated, where we look often betrays our deepest interests, intentions, and desires. We use visual orienting not only to localize other individuals but also to interpret their relationships, attitudes, and intentions. Nonhuman primates also appear to use orienting by others to infer the location of important stimuli and events, to predict behavior, and perhaps even to interpret social relationships among others (Cheney & Seyfarth, 1990; Emery, 2000; Tomasello et al., 2005). Subtler still, humans (and perhaps other primates, particularly apes; de Waal, 2003) use and recognize a number of deictic gestures, from a quick flick of the eyes to sustained pointing, which signal important threats and opportunities within our shared environment. Furthermore, we use these signals in competitive contexts to read intent and predict action (watching someone's eyes during chess), and even to confound such predictions by others (the ''no-look pass,'' a feint in which a player looks toward a different teammate than the one to whom he or she intends to pass the ball).

Despite the obvious importance of social cues for guiding attention in natural behavior, this process has remained, until recently, relatively unexplored by psychologists or neurobiologists. A typical laboratory approach to visual attention asks subjects to stare at a fixation point, followed by either a central cue or peripheral stimulus

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directing attention toward a peripheral location, followed by a behavioral measure of attentional deployment at the cued or uncued location (e.g., Posner 1980). Studies using this technique have revealed that central cues that validly predict the location of a future peripheral target cause subjects to shift attention in a voluntary (''endogenous'' or ''top-down'') manner, whereas abrupt peripheral cues, even when they have no predictive value, automatically attract attention (''exogenous,'' ''reflexive,'' ''bottom-up'' attention). These attention shifts are evident in changes in sensory discrimination performance and reaction time, and have distinct time courses: Exogenous attention operates more quickly and generates a subsequent orienting deficit (''inhibition of return''), while endogenous attention is slower and more sustained (Jonides, 1981; Muller & Rabbitt, 1989). Despite the obvious utility of this paradigm for understanding basic aspects of attention, its ethological relevance has long been limited by a failure to apply these laboratory techniques to the kind of social stimuli that pervasively guide orienting by primates in the natural world.

Friesen and Kingstone (1998) addressed this gap by modifying the Posner paradigm to investigate how social cues influence attention. They discovered that viewing a face with averted gaze rapidly and reflexively shifts attention in the same direction, even when gaze direction does not predict the eventual location of the target. In their experiments, human subjects were instructed to fixate a central point, where a face briefly appeared with its eyes cast either rightward or leftward. A split second later, a peripheral target appeared, randomly in the direction of gaze or in the opposite direction. Subjects were faster to respond to targets appearing in the direction of observed gaze, even for cue-to-target delays as brief as 105 ms (termed ''stimulus onset asynchrony,'' or SOA).

Subsequent studies determined that these effects were both general and involuntary—a turned head shifted attention as easily as averted eyes (Langton & Bruce, 1999), and social cuing persisted even when the target was 80% likely to appear in the direction *opposite* viewed gaze (Driver et al., 1999). Attention shifts associated with observed gaze appear to be categorically distinct from attentional responses to explicit cues such as predictive arrows (Friesen et al., 2004) or abstract spatial associations (Galfano et al., 2006), suggesting that social orienting does not neatly fit within classical models of exogenous or endogenous attention. These results appear to support the idea that humans evolved a dedicated gaze-following module specialized for rapid and reflexive sharing of attention in social groups (Baron-Cohen, 1994; Perrett & Emery, 1994).

To test this hypothesis, we contrasted the socially cued orienting responses of rhesus macaques and humans (Deaner & Platt, 2003). Surprisingly, we found that macaques and humans both responded more quickly to an unpredictable target when it appeared where a monkey had just been seen to look. Furthermore, eye position during fixation in both species drifted in the direction of observed gaze, likely reflecting an incompletely suppressed drive to overtly orient in the same direction (Engbert & Kliegl, 2003; Hafed & Clark, 2002). The temporal dynamics with which attention followed observed gaze were highly similar in the two species (Fig. 26.5), suggesting shared neural mechanisms.

Our results strongly support the conclusion that gaze following is not unique to humans, and may, in fact, rely on neural substrates that are widespread among primates and possibly other animals known to follow gaze. Though gaze following by other animals may differ, both in strength and kind, from that evinced by anthropoid primates (Okamoto-Barth et al., 2007; Tomonaga, 2007), it appears that many animals are able to shift attention in response to observed social cues. Consistent with this argument, Tomasello and colleagues, along with a number of other research groups, have amassed a large body of work showing that many animals, including apes (Brauer et al., 2005), dogs (Agnetta et al., 2000), monkeys (Tomasello et al., 1998), goats (Kaminski et al., 2005), dolphins (Tschudin et al., 2001), and ravens (Bugnyar et al., 2004), can use social gaze cues to find hidden food or retrieve objects (reviewed in Emery, 2000, and Itakura, 2004).

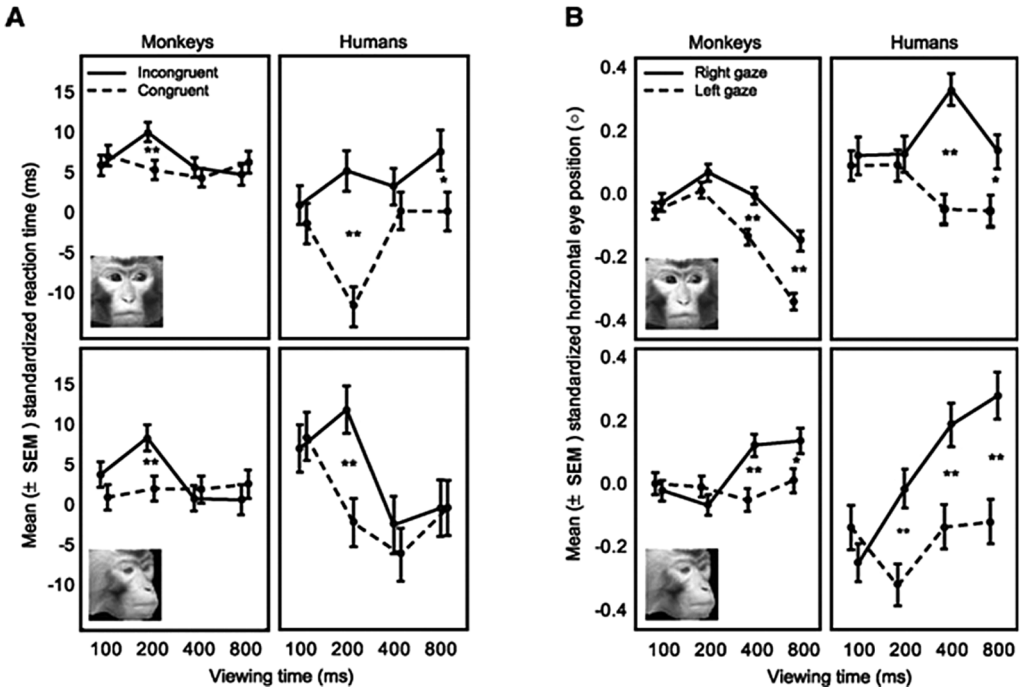


Figure 26.5 Gaze following by monkeys and humans shares psychophysical features. Monkeys and humans show similar magnitude and time course of gaze following in response to nonpredictive monkey gaze cues presented continuously for 100, 200, 400, or 800 ms prior to target presentation. These attention shifts were evident both by decreases in normalized reaction times to congruent (dashed) versus incongruent (solid) stimuli **(A)** and by microsaccades in the direction of observed gaze during cue presentation **(B)**. **, $P < 0.001$; *, $P < 0.05$. After Deaner, R. O., & Platt, M. L. (2003). Reflexive social attention in monkeys and humans. *Current Biology, 13,* 1609–1613. Used with permission.

In most of those studies, human experimenters, rather than conspecifics, provided the social attention stimuli. This technical limitation simultaneously limits the ease with which we can generalize results to naturally occurring social interaction, and poses the fascinating question of how heterospecific and conspecific social perceptions interrelate. As the neural systems mediating predator avoidance, prey capture, and ''pure'' social interaction remain virtually unknown, the many fascinating evolutionary and computational links between them remain almost largely unexplored.

The potential ubiquity of gaze following in primates is supported by our recent studies of visual orienting by freely moving, socially housed lemurs. In those studies, we quantitatively and precisely monitored orienting behavior of two male ring-tail lemurs with an infrared telemetric gaze-tracking device while they spontaneously interacted with other lemurs. We found that lemurs tended to orient their eyes in the same direction that other lemurs oriented their bodies and heads (Fig. 26.6A,B). Such gaze alignment, however, could reflect coincidental orienting to salient events in a shared environment (e.g., a loud sound) rather than active use of social gaze cues. To address this confound, we examined the temporal sequence of gaze alignments around the time the subject lemur oriented to an observed lemur. We found that, prior to fixating the observed lemur, there was no alignment between the two animals' gaze. After fixating the observed lemur, however, gaze alignment increased significantly (Fig. 26.6C). The temporal sequence of gaze alignment supports the conclusion that lemurs actively follow the gaze of other

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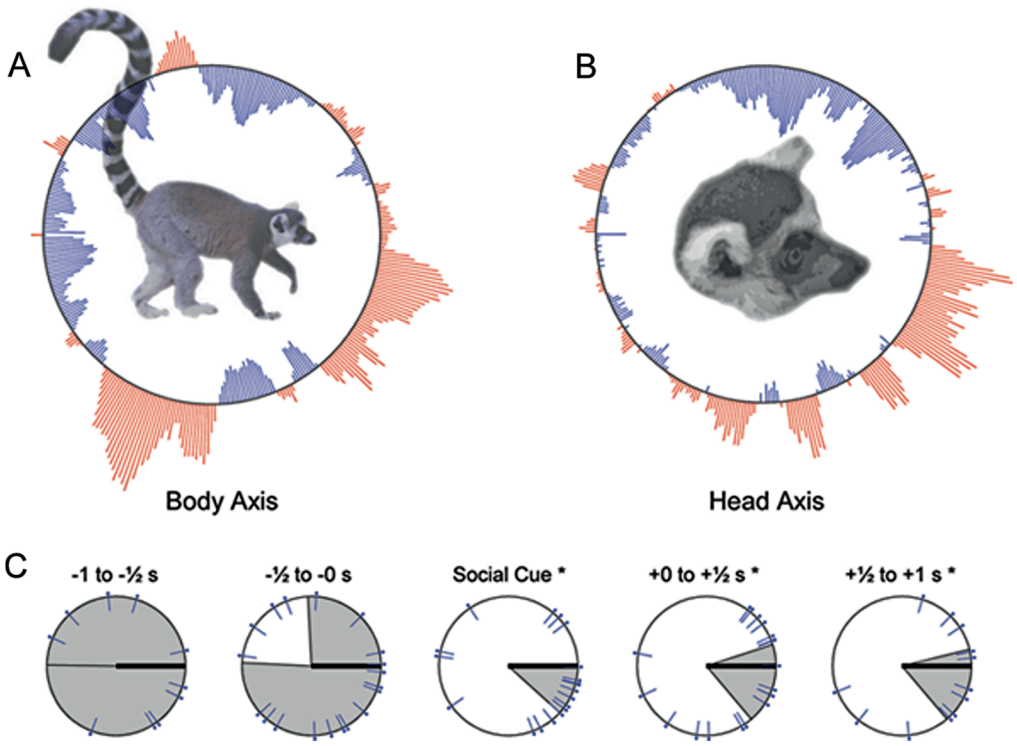


Figure 26.6 Spontaneous gaze following in lemurs. Lemurs spontaneously follow the gaze direction of their conspecifics in natural interaction. Lemurs not only coorient with the body (**A**) and head (**B**) axes of observed lemurs but also selectively increase gaze alignment with those individuals they have recently attended (**C**). In panels A and B, red outward lines are gaze offsets that are overrepresented with respect to chance, while blue inward lines are gaze offsets that are underrepresented. In panel C), tick marks occur at mean gaze offsets recorded in ½-second periods prior to fixation, in the period during which the lemur is fixated, and for ½ second periods after fixation. Shaded regions in panel C reflect the dispersion of gaze alignments. Starred intervals are significantly aligned with gaze (chi^2 test $P < 0.05$). After Shepherd, S. V., & Platt, M. L. (2008). Spontaneous social orienting and gaze following in ringtailed lemurs (*Lemur catta*). *Animal Cognition, 11,* 13–20. Used with permission.

individuals (Shepherd & Platt, 2008). Our results stand in sharp contrast to at least two prior observational studies (Anderson & Mitchell, 1999; Itakura, 1996) that concluded that prosimian primates do not follow the gaze of human observers.

SOCIAL CONTEXT INFLUENCES GAZE FOLLOWING

Because both monkeys and humans shift their attention in response to social gaze cues, even when such cues fail to predict the location of a behavioral goal, it has been argued that gaze following is a strictly reflexive behavior mediated by a dedicated neural module (Deaner & Platt, 2003; Driver et al., 1999). Recent studies, however, challenge the notion that gaze cuing is purely reflexive, and instead indicate that social context can influence gaze-following behavior both in humans and monkeys. Specifically, several lines of evidence suggest that neural systems contributing to gaze following are regulated both by internal factors and online, by social

context. For example, human females respond much more strongly to social gaze cues than do males (Fig. 26.7) (Bayliss et al., 2005; Deaner et al., 2007); moreover, our lab has found that gaze following in females, but not males, is influenced by the familiarity of the observed male cue (Deaner et al., 2007). These observations suggest the possibility that sex hormones may play an important role in regulating social attention. These observations also indicate that gaze-following mechanisms are not strictly reflexive and informationally encapsulated, but instead are sensitive to subtle changes in social variables such as the familiarity of the observed face.

In parallel, we have discovered that both social context and biological factors regulate gaze following in rhesus macaques (Shepherd et al., 2006). Specifically, we probed gaze-following behavior by seven male rhesus macaques in response to four rightward- and four leftward-looking photos of each of four familiar monkeys. Importantly, each animal was designated dominant or subordinate based on the direction and frequency of threat and submission gestures during controlled pair-wise confrontations (see Deaner et al., 2005; Shepherd et al., 2006). We found that subordinate monkeys rapidly and automatically followed the gaze of all other monkeys (Fig. 26.8A), while dominant monkeys followed gaze later, and then only in response to other dominant monkeys (Fig. 26.8B). These differences in gaze-following behavior were weakly correlated with differences in testosterone production (Shepherd et al., 2006), as inferred from measurements of testis volume (Bercovitch & Ziegler, 2002). We interpret these data to indicate that both internal and external factors govern macaque gaze following, comprising both biological variables like testosterone and ecological variables like relative social status.

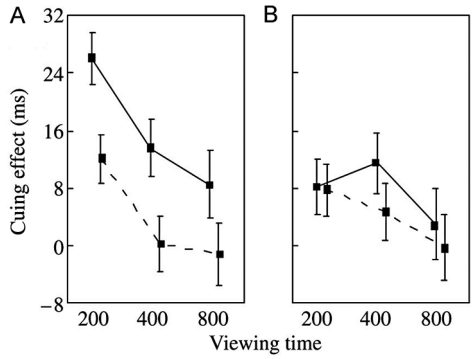


Figure 26.7 Sex differences in gaze following in humans. Human females exhibit stronger gaze following than males, and furthermore discriminate between familiar and unfamiliar individuals when following gaze. Females (solid lines) have greater reaction time savings for gaze-congruent than gaze-incongruent targets when gaze cues were from familiar **(A)** rather than unfamiliar **(B)** individuals (at 200 ms, $P < 0.003$). Males (dashed lines) did not distinguish significantly between these conditions (at 200 ms, $P > 0.4$). After Deaner, R. O., Shepherd, S. V., & Platt, M. L. (2007). Familiarity accentuates gaze cuing in women but not men. *Biology Letters, 3,* 64–67. Used with permission.

One way that familiar or dominant individuals might evoke stronger gaze following is by virtue of their intrinsic salience. Under some conditions, human gaze following appears to be modulated by emotional content in faces. Specifically, patients with anxiety disorders show heightened following of fearful gaze relative to other emotional expressions (Holmes et al., 2006; Hori et al., 2005; Mathews et al., 2003) (note also Hietanen & Leppanen, 2003, and Putman et al., 2006). This interaction probably reflects a tendency for patients with anxiety to more strongly attend to negatively valenced social stimuli, while healthy subjects dwell less on them (e.g., Bar-Haim et al., 2005; Bradley et al., 1997). These studies imply that attention to another individual spreads automatically to other objects with which that individual is engaged.

Together, these results demonstrate that the neural substrates of gaze following are deeply integrated with the larger social information processing stream. That gaze following is an inherent component of face perception is suggested by the fact that heightened attention to faces spreads in the direction of gaze, both in the case of females viewing familiar faces and anxious patients seeing faces with negatively valenced emotional content. At the same time, however, the fact that gaze following is modulated by factors like familiarity

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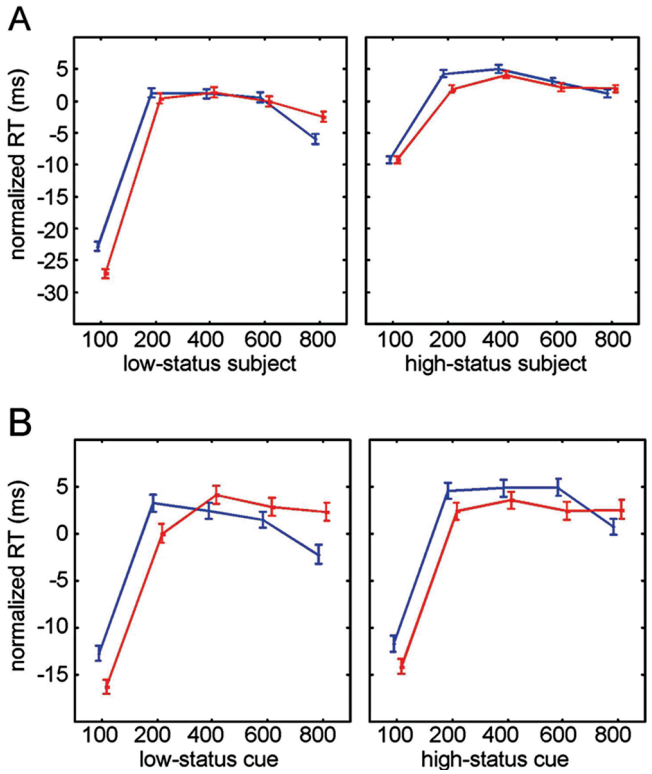


Figure 26.8 Social context influences gaze following in macaques. Even at the briefest cue durations, subject social status appears to influence gaze-following behavior (**A**, $P < 0.005$). Specifically, low social status makes a monkey more likely to follow gaze within 100 ms of seeing the cue, and also more likely to have strong inhibition of return at the latest time point—a temporal profile consistent with a reflexive attention shift, possibly due to increased anxiety or the modulatory effects of sex- and status-linked hormones like testosterone on social processing circuitry in brain. Cue social status also plays an important role (**B,** $P < 0.01$), leading to prolonged attention in the direction of gaze of a high-status cue and inhibited attention in the direction of gaze of a low-status cue, particularly in high-status subjects. Reaction times for congruent trials are shown in red lines and for incongruent trials are shown in blue lines. After Shepherd, S. V., Deaner, R. O, & Platt, M. L. (2006). Social status gates social attention in monkeys. *Current Biology, 16,* R119–120. Used with permission.

and social dominance suggests that it is not mediated by an isolated module sequestered from other aspects of face processing and social knowledge. Finally, sex differences in humans and social rank differences in monkeys both hint at a possible role for sex hormones in shaping social attention systems in the brain. Together these findings strongly support the idea that social attention is a fundamental feature of natural primate behavior and cognition, and provides a fundamental challenge to the traditional endogenous/exogenous model of attentional control.

GAZE AS A STRATEGIC SOCIAL SIGNAL

As described previously, social saliency may play a role not only in guiding attention but also in shaping the physical spacing of group members and the affective tenor of their interactions. It may also serve as a starting point for the development of much more advanced cognitive behaviors. David Perrett and Simon Baron-Cohen have argued that detection of eyes and interpretation of gaze

are foundational to building a theory of mind, by which we intuitively mirror the attentional and perhaps even intentional states of others. We do this so instinctively that we frequently anthropomorphize even alien and impersonal phenomena, perhaps allowing us to understand complex and dynamic patterns by analogy to human behavioral goals (e.g., ''the electrons don't like to be near one another and are instead attracted to the positive core of an atom, causing them to settle sequentially into the centermost uncrowded orbitals''). Typically developing humans have an intuitive expertise at communicating affect and attentional state, in part, perhaps, because they have an intrinsic drive to *learn* to do so: From a young age, typically developing humans take pleasure in successfully directing another's attention toward stimuli that we, too, have perceived (Tomasello et al., 2005).

These considerations naturally lead us to consider overt eye movements as an active signaling mechanism shaping primate social interactions. We have mentioned the role of eye movements in initiating conflict, but primates make far more sophisticated use of gaze. For example, eye contact can signal not only aggression (van Hoof, 1967) but also sexual interest (Dixson, 1998) or solicitation for coalition formation in agonistic interactions versus third parties (de Waal, 2003). Likewise, humans use eye contact as a key aspect of affiliation, courtship (Hrdy & Whitten, 1987), and intimidation (Argyle & Cook, 1976), and also during coordination of attention (''triadic'' or ''joint attention''; Emery, 2000). Moreover, gaze acts to structure both verbal and nonverbal human social interactions. To signal rank relationships, for example, people look preferentially toward the most high-ranking person, and when conversing, gaze is used to emphasize spoken arguments, to conclude statements, to emphasize nonverbal reactions to heard statements, and to coordinate turn-taking in conversation (Argyle & Cook, 1976).

With the evolution of greater visual and social complexity, some primates appear to have evolved ever more sophisticated means of structuring social behavior through gaze. Like humans, many animal species are capable of following gaze. Chimpanzees are even reported to use deictic gestures (de Waal, 2003), though these signals may hold little behavioral currency due to the ubiquity of competitive and paucity of cooperative interactions in these animals (Hare & Tomasello, 2004). The importance of social gaze for facilitating increased cooperation among human ancestors may even have lead to somatic adaptations that increase the saliency and specificity of gaze cues, for example, by enhancing the visibility of gaze through increased contrast of the pupil versus sclera (Kobayashi & Koshima, 2001; Tomasello et al., 2006). At the same time, however, the continued importance of competitive interactions for early human ancestors may have led to a compensatory enhancement of covert attention mechanisms relative to those possessed by most nonhuman primates and, especially, other mammals.

This manipulative role of gaze is perhaps the least understood aspect of visual orienting behavior; virtually nothing is known about how the demands of social signaling bring their influence to bear on the gaze control system of the brain. These considerations challenge the conventional division between ''reflexive'' and ''reward-mediated'' processes in social orienting. Given that current evidence argues against informational encapsulation in social perception and cognition, it seems likely that the fastest orienting processes reflect the need to quickly acquire behaviorally relevant information, and that slower processes reflect more nuanced contextual constraints—whether that information is likely to have predictive value in the present situation, or whether the orienting behavior might expose the subject to risk of agonistic interaction or being ''scooped'' by competitors in pursuit of resources. For example, monkeys in our studies initially looked toward other individuals, generally following their gaze, but at later intervals diverse contextual considerations were brought to bear—abbreviating risky glances toward higher-ranked individuals (Deaner et al., 2005; Haude et al., 1976), extinguishing gaze following of lower-ranking animals (Shepherd et al.,

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2006), and prolonging male fixation on female hindquarters (Deaner et al., 2005). Thus, although much work remains to be done on the neurobiology of orienting responses, it seems clear that neither a strictly reflexive nor a strictly cognitive approach will explain all aspects of social orienting.

SOCIAL ATTENTION AND AUTISM: FROM THE LAB TO THE FIELD

Data from syndromes that disrupt social behavior, notably autism, suggest a gulf between behavioral responses in the laboratory and spontaneous use of social cues in the real world. In a comparison of visual orienting by autistic subjects with that of typically developing children, van der Geest and colleagues (2002) found that the fixation patterns of the two groups could not be distinguished when they viewed simple cartoons including human figures. In contrast, Pelphrey and colleagues (2002) found substantial differences between autistic and typically developing control subjects' inspecting of photographs of real faces. Similarly, although autistic subjects often show normal gaze following in the social variant of the Posner attention task (Chawarska et al., 2003; Kylliainen & Hietanen, 2004; Swettenham et al., 2003; but see Bayliss et al., 2005, and Ristic et al., 2005), they consistently show severe disruptions in social orienting in more natural contexts. When Klin and colleagues (2002a,b) measured gaze behavior in autistic individuals watching the movie *Who's Afraid of Virginia Woolf*, they found that gaze toward social stimuli was disordered—for example, with normal fixations toward the eye regions replaced by fixations toward the mouth. Moreover, socially cued locations were severely neglected, as shown by a marked lack of fixations toward gaze- and gesture-cued regions of space. Furthermore, the authors found that the degree of abnormality in the fixation pattern of individual autistic subjects in this task was strongly predictive of real-life social impairment.

This is hardly surprising. After all, autism is *defined* by a marked "lack of spontaneous seeking to share enjoyment, interests, or achievements with other people," or to reciprocate when these experiences and emotions are shared by others (American Psychological Association, 1994). Outside the laboratory, even high-functioning autistic individuals, unaffected by physical problems such as seizures or repetitive movements, are nonetheless challenged in responding to the constant exchange of social cues that structures human interaction. Temple Grandin, an associate professor of Animal Science at Colorado State University who has autism, reports that she functions in social situations "solely by intellect and visualization skills" (Grandin, 1999, http://www.autism.org/temple/social.html). She says (ibid) "I did not know that eye movements had meaning until I read *Mind Blindness* by Simon Baron-Cohen. I had no idea that people communicated feelings with their eyes. I also did not know that people get all kinds of little emotional signals which transmit feelings. My understanding of this became clearer after I read *Descartes' Error* by Antonio Damasio." It may be that the complement of processes evoked by social stimuli in typically developing individuals is disrupted in autism spectrum disorders, and that without these foundational elements, more sophisticated forms of empathy and social reasoning cannot develop.

It is interesting to note that both autism (Wassink et al., 2007) and social anxiety disorder (Skuse, 2006) have been associated with dysfunction in the serotonin signaling system. Serotonin has likewise been linked to dominance status, affiliative social interaction, and decreases in antagonistic and impulsive social interactions (Edwards & Kravitz, 1997; Raleigh et al., 1991), suggesting that this neuromodulatory system may also contribute to differences in social attention between dominant and subordinate macaques. Together, these findings hint at a role for serotonin in regulating social attention in both human and nonhuman primates. Determining the impact of biological factors, such as serotonin and testosterone, on social attention may point to possible interventions to improve social functions in common psychopathologies like autism.

TOWARD A NEUROETHOLOGY OF ATTENTION IN PRIMATES

If we were to develop a biologically plausible, ethologically motivated model of attention in primates, what features must it have? We feel strongly that the bottom-up component of these models must not only reflect what we know about the primate visual system but must also consider the role vision plays in guiding the behavior of primates in species-typical ecological and social contexts. For example, Laurent Itti and colleagues, among others, have used visual filters, inspired by the physiology of the primate visual system, to predict human visual attention. Such models estimate saliency by filtering images through a series of low-level feature maps (Carmi & Itti, 2006; Peters et al., 2005). Each map tracks the extent to which a region "pops out" from its surroundings along a particular visual dimension, such as brightness, orientation, texture, motion, or color, and these maps can be combined to successfully model many aspects of bottom-up attention.

While these models can accurately identify salient regions of still images and video, they often fail to highlight social stimuli such as faces, or rely heavily on image motion to assign saliency to humans and animals. Without undervaluing either these accomplishments or the importance of motion as a predictor of animacy, we nevertheless note that demands of both sociality and predator avoidance require accurate and fast discrimination of animals, even when those animals are stationary or when dynamic environments (e.g., running water, blowing leaves) produce irrelevant image motion. Moreover, while it is true that identification and tracking of animate objects has proved a challenge for computer vision, these tasks are performed quickly and easily by the primate brain. In laboratory experiments, humans can initiate saccades toward an animal in a novel photograph in as little as 120 ms (Kirchner & Thorpe, 2006), and in unconstrained viewing, animate stimuli and especially other humans are quickly targeted for visual inspection.

Serre and colleagues (2007) partially addressed these issues by developing a model that uses biologically inspired filters based on neurons in the ventral visual processing stream (Ungerleider & Mishkin, 1982) to quickly identify images *containing* animals. It is important to note, however, that this model explicitly fails to *localize* animals within images. The processes that link object recognition by the ventral visual processing stream to target localization within the dorsal stream thus remain largely unknown, despite the fact that it is the dorsal stream that selects parts of the visual field for further processing. In fact, Serre and colleagues note that their model "cannot account for our everyday vision which involves eye movements and top-down effects," (p. 6426) and that an extension of the model requiring "top-down signals from higher to lower areas . . . limit[ing] visual processing to a 'spotlight of attention' centered around the animal target" results in "significant improvement in the classification performance" (p. 6428).

Serre's study thus illustrates the benefits of considering the natural goals of orienting in social contexts, and likewise of considering evidence from functional imaging and neurophysiological recording studies. Recent functional magnetic resonance imaging (fMRI) studies in humans have identified brain areas that are involved in visual analysis of body position and identity (Downing et al., 2001), identification of faces (Haxby et al., 1994), and interpretation of actions and facial expressions (Allison et al., 2000); other studies suggest that homologous areas operate in macaques (Logothetis et al., 1999; Tsao et al., 2003). The general conservation of cortical organization across primate species, together with these recent findings, suggests that visual areas specialized for processing social stimuli may be part of the primordial visual cortex that was present in stem primates (Rosa & Tweedale, 2005; Tootell et al., 2003) and perhaps others mammals as well (Kendrick et al., 2001).

As revealed through behavioral studies, the gaze-control system must recognize and respond appropriately to biological targets. We speculate that parallel pathways accomplish this goal, which can largely be grouped into a subcortical pathway and a cortical pathway (Adolphs, 2002; Vuilleumier, 2002). Ultimately, both pathways must converge upon the three neural tissues,

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which jointly serve as the final common pathway governing orienting in primates: the parietal eye fields (in macaque, located in the lateral intraparietal sulcus, called LIP), the frontal eye fields (FEFs), and the superior colliculus (SC). To effectively govern orienting, these areas must weigh decision variables comprising the expected rewards and risks associated with a given orienting behavior. For example, Platt and Glimcher showed that neurons in LIP are sensitive to target value when visual stimuli are arbitrarily assigned different amounts of juice reward (Platt & Glimcher, 1999), and subsequent studies have confirmed that neuronal activity throughout this network is similarly modulated by orienting value (LIP, see also Sugrue et al., 2004; SC, Ikeda & Hikosaka, 2003; but *not* FEF, Leon & Shadlen, 1999).

Critically, we have recently shown that in the ''pay-per-view'' paradigm discussed previously, neurons in LIP are modulated by the intrinsic social value of orienting to images in much the same way that they are modulated by primary juice rewards (Klein et al., 2008). Specifically, LIP neurons respond most strongly when monkeys evaluate targets associated with the acquisition of information about female reproductive signals and the identity of dominant males, but respond weakly when the same target offers information about subordinate males—despite the fact that monkeys were never explicitly trained to orient toward these stimuli. These observations directly predict the orienting behavior of macaques in the same task. Echoing these findings, a recent fMRI study in humans found stronger activation of parietal cortex when subjects played a game against a dominant opponent compared to an inferior opponent (Zink et al., 2008).

These observations indicate that LIP spontaneously integrates information about target value from multiple sources, in the absence of any explicit training. This, in turn, implies that brain pathways that process social information must ultimately transmit this information to parietal cortex, and likely to other areas involved in orienting behavior as well. This modulation of neural activity by the intrinsic value of acquired visual information seems likely to reflect the native function of LIP, only overridden in tasks where researchers arbitrarily map juice rewards onto specific oculomotor behaviors.

Ultimately, however, the social significance of visual information is probably not computed within the gaze-control network itself. Recent evidence has begun to reveal how social variables, such as dominance status and reproductive state, are processed in primate brains. While social cognition involves broad swaths of brain, we believe it can be simplified into two streams: a streamlined but inflexible subcortical pathway, and a nuanced—and labyrinthine—cortical network.

THE SUBCORTICAL PATHWAY

In this pathway, retinotectal inputs provide coarse visual information in which crude biological primitives can quickly be identified and analyzed, for example, to locate other creatures, detect social signals, and extract gaze direction (Johnson, 2005). The subcortical system appears to by phylogenetically old, shared by all terrestrial vertebrates, and is the major pathway for innate recognition and response to animate targets including predators, prey, and conspecifics (Sewards & Sewards, 2002).

In humans, this system has been suggested to play a crucial role in early visual tracking of faces, and may play a lifelong role in the rapid detection of socially salient or threatening signals, both directly and through interactions with visual cortex and the pulvinar nucleus of the thalamus (Grieve et al., 2000; Johnson, 2005; Sewards & Sewards, 2002). Just such a relay of social threat signals, from retina to SC, pulvinar nucleus, and finally amygdala, has already been identified in humans by neuroimaging (Morris et al., 1999). Furthermore, neurons in the macaque amygdala are sensitive to the expression, gaze, and social dominance of viewed faces (Gothard et al., 2007; Hoffman et al., 2007; Kawashima et al., 1999). The amygdala, in turn, sends this first-pass analysis of social targets toward gaze-control centers and higher visual areas, acting rapidly to strengthen social and threat-related processing (Vuilleumier, 2002).

While a major function of this pathway is indubitably to provide an "early warning" system detecting threats, there is evidence that the amygdala also mediates prosocial behaviors. For example, while eye contact can signal threat, it more generally indicates approach, and often serves to initiate grooming and sexual behavior (Hrdy & Whitten, 1987). Thus, eye contact responses in amygdala may serve to indicate not only threat but also sexual opportunity, and indeed, amygdala is strongly activated by sexual stimuli (Aharon et al., 2001; Hamann et al., 2004).

The amygdala pathway may be highly sensitive to biological factors that mediate sex differences (Bayliss et al., 2005; Deaner et al., 2007; Goldstein et al., 2001; Hamann et al., 2004) as well as psychosocial disorders (Holmes et al., 2006; Hori et al., 2005; Mathews et al., 2003; Putman et al., 2006), and may, when compromised, contribute to the development of autism (Schultz, 2005, though note also Amaral et al., 2003). While amygdala influences the function of a broad swath of cortex, it does not directly interact with the gaze-control network and would instead influence orienting indirectly, through cortical or subcortical intermediaries.

THE CORTICAL NETWORK

In parallel to the subcortical pathway, a slower, more nuanced, and more recently evolved cortical pathway leads from V1 through the ventral visual stream to extrastriate body area (EBA) (Downing et al., 2001), fusiform face area (FFA) (Haxby et al., 1994), and superior temporal sulcus (STS) (Allison et al., 2000). It remains unclear whether these areas assess subordinate-level distinctions between hierarchically classifiable objects or are optimized for processing animate objects or specifically for perception of conspecifics. It seems likely that the development of these areas depends on experience (Gauthier et al., 1999) and may rely upon signals arising in the subcortical pathway for appropriate patterning during development (Johnson, 2005; Schultz, 2005; Sewards & Sewards, 2002). It is known, however, that each of these ventral stream visual areas is strongly activated by social stimuli, extracting posture, identity, and expression, respectively. These areas then transmit output to a broad array of areas in the extended face processing network, interacting with contextual signals from hippocampus, amygdala, and orbitofrontal cortex (OFC) (Ishai et al., 2005; Smith et al., 2006). These socially influenced areas include multiple regions implicated in modulating both attentional allocation and reward processing (Sabbagh, 2004; Vuilleumier, 2002).

It is important to note that both orienting to others and gaze following is regulated by social milieu—as well as by intrinsic factors including sex hormones, such as testosterone, and neuromodulators, such as serotonin. Supporting this idea, amygdala, OFC, and hippocampus form a functional circuit important for associating emotional and social salience with mnemonic and perceptual information (Fig. 26.9) (Sabbagh, 2004; Smith et al., 2006; Vuilleumier, 2002), and are actively involved in the perception of faces (Ishai et al., 2005). Each of these brain structures is sexually dimorphic (Goldstein et al., 2001), suggesting that sexual differentiation in these areas may directly pattern responses to social cues. This supposition is strengthened by various results showing fetal testosterone negatively impacts both social attention and social relationships in human juveniles (Knickmeyer & Baron-Cohen, 2006). Ultimately, signals from these ventral ("what") areas must relay social information to dorsal ("where") orienting and attention control systems. Signals from the higher-order areas of the ventral pathway ramify to multiple targets in the visual orienting system, but exactly how this occurs remains an open question, since much of visuo-social cortex (Tsao et al., 2003) is connected in one or two steps to posterior parietal (7A and LIP; Seltzer & Pandya, 1991), frontal (SEF and FEF; Seltzer & Pandya, 1989), and subcortical orienting areas (pulvinar nucleus; Romanski et al., 1997) and superior colliculus (Fries, 1984).

GAZE FOLLOWING AND THE "MIRROR NETWORK"

One intriguing possibility is that gaze following may be supported by specialized neurons that

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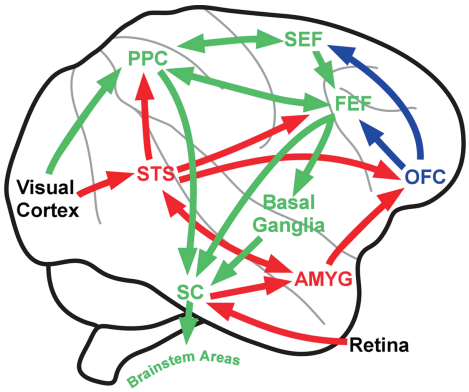


Figure 26.9 Key circuits involved in social attention. Connectivity of social (red), reward (blue), and attention (green) pathways. In addition to the cortical pathway, a fast subcortical pathway connects superior colliculus to amygdala via the thalamus (not shown). Note that several social processing areas lie along superior temporal sulcus, occupying both posterior and anterior temporal lobes, and that functional activity in imaging tasks has not yet been systematically related to past anatomical studies. AMYG, amygdala; FEF, frontal eye fields; OFC, orbitofrontal cortex; PPC, posterior parietal cortex, including 7A and lateral intraparietal sulcus; SEF, supplementary eye fields; STS, superior temporal sulcus regions.

simultaneously map concordant observed/sensory and performed/motor components of this behavior. Similarly specialized "mirror" neurons, first discovered in macaque premotor cortex, respond not just when the subject reaches for an object but also when it observes the experimenter perform a similar movement (di Pellegrino et al., 1992). "Mirroring" responses have been observed in other brain areas (e.g., single units within parietal reach areas; Fogassi et al., 2005), and for other types of movements (e.g., mouth movements; Ferrari et al., 2003). Because mirror neurons appear to signal abstract actions and goals independent of actor, they have been hypothesized to underlie a host of abilities ranging in sophistication from action- and emotion-perception to empathizing, mentalizing, and theory of mind (reviewed in Rizzolatti & Craighero, 2004). Supporting these findings from macaques, imaging studies in humans suggest that homologous brain regions are activated by both the production and observation of specific gestures (Dinstein et al., 2007), and that activations associated with sensory-motor "mirroring" may be widespread in human sensory and motor cortices. To date, however, neither the responses of mirror neurons nor more global sensory-motor mirroring activations observed with fMRI have been directly linked to specific social behaviors in monkeys or humans (Dinstein et al., 2008; but see Prather et al., 2008, for a description of sensory-motor mirroring by neurons in songbirds during social interaction).

Recently, we discovered a population of neurons in macaque LIP that "mirror" the observed gaze of individuals (Shepherd & Platt, submitted), much as neural populations in adjacent areas mirror reaching behavior (Fogassi et al., 2005). LIP neurons respond when monkeys orient attention, either overtly or covertly, to regions of space known as response fields (Colby et al., 1996; Gnadt & Andersen, 1988; Platt & Glimcher, 1998). We found that a subpopulation of LIP neurons responded not only to direct attention toward their response field but also when viewing another monkey that looked in the neuron's preferred direction. Neuronal responses to the observed orienting behavior of another individual occurred despite the fact that there was no visual stimulus in the

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neuron's response field, and that any gaze shift toward the response field would abort the trial without reward. Intriguingly, the time course of social gaze cue signals in LIP strongly paralleled the time course of gaze-following behavior—appearing within a tenth of a second, persisting for several hundred milliseconds, and ultimately fading at the longest intervals tested. These data provide strong support for the idea that some populations of mirror neurons provide an important mechanistic foundation for the abstraction, interpretation, and imitation of behaviors and mental states.

CONCLUSIONS

Laboratory research using arbitrary tasks and stimuli have identified two complementary systems for visual orienting—one fast and reflexive, the other slow and deliberative. Neuroetholo-gical studies of visual attention, by contrast, have revealed a suite of socially motivated and socially cued orienting behaviors that do not cleave neatly along these lines. Specifically, primates and other animals are motivated to look at one another, preferentially orient to high-value social targets such as the faces of dominant males, and follow the orienting movements of others with their own attention. Moreover, these responses are regulated by behavioral context, sex hormones, and serotonin. These observations strongly support the idea that the primate brain is specialized for acquiring behaviorally useful visual information from the social world, and that these adaptations rely on the integration of multiple neural circuits involved in identifying social stimuli and social cues, deter-mining their meaning, and responding appropriately. Despite the commonalities of these systems across primates and even other mammals, the challenge for future neuroethological research is to determine how these mechanisms contribute to adaptive differences in social behavior in different species.

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QUERIES TO BE ANSWERED BY AUTHOR (SEE MANUAL MARKS)

IMPORTANT NOTE: Please mark your corrections and answers to these queries directly onto the proof at the relevant place. Do NOT mark your corrections on this query sheet.

Chapter 26

Q. No.	Pg No.	Query
AQ1	524	Changed ‘‘arrive’’ to "arrived" as meant?
AQ2	528	Misplaced subscript ‘‘2’’ after e.g., as mentioned in the comments is not clear. Please check.
AQ3	542	Please update with year of publication if possible
AQ4	546	Please provide volume and page numbers.
AQ5	548	Please update reference if possible.