

V SOCIAL ENTITIES

The final section of this volume deals with the cognitive biology of social entities, broadly conceived as other conspecifics in an organism's environment. Some of the questions investigated are "How are conspecifics attended, perceived, and represented?" and "What cues reveal important aspects in inter-individual exchange (from social cues of intentionality to language)?" This is another cognitive science subject that has been advanced substantially by converging data cutting across the domains of human adult and developmental psychology, comparative psychology, the neurosciences, and primatology and anthropology. The topics of interest range from the understanding of face processing to the complex issues of social referencing, gaze following, and theory of mind, abilities that are foundational for engaging in dynamic social interactions and for establishing a moral sense. And of course social behavior must have had a profound impact on the evolution of more basic cognitive functions, as Jacobs shows in chapter 2.

In chapter 14, Stephen Shepherd and Michael Platt describe research that combines ethological and psychophysical approaches in an attempt to develop a unified, evolutionarily motivated theory of attention, with an emphasis on how social cues, such as the direction of gaze of other individuals, rapidly guide attention in both human and nonhuman primates such as macaques and ring-tailed lemurs. They examine gaze in both natural and laboratory settings. Shepherd and Platt inferred animals' goals by examining where they look naturally rather than where they look in the service of a task artificially imposed by the experimenters. To do so, they used noninvasive, noncumbersome gaze-tracking devices. They found that social entities, rather than physically salient stimuli, were often the focus of attention, and that conspecifics' gaze direction was a powerful determinant of gaze, although factors such as gender, testosterone levels, and task also had an effect. Shepherd and Platt complement their naturalistic eye movement studies with a psychophysical choice task that allows them to examine the value of looking at social entities. Shepherd and Platt also review research (their own and others') showing that looking behavior can drive preferences and social affiliation. They end their chapter with a proposal regarding the neural substrate for social attention; they take a two-systems approach, advocating a ventral cortical system and a subcortical-to-frontal-lobe system. Although

some theorists claim that social attention is a separate module from nonsocial attention, Shepherd and Platt review research inconsistent with a modular interpretation. Much remains to be done in this exciting area of research. This chapter sets the stage, and integrates well with the next chapter, by Mark Johnson.

In chapter 15, Johnson presents an account of the universal role of development in constructing what has come to be known as the “social brain” by comparing two dominant views in developmental cognitive neuroscience: that positing a fully prespecified cortical module and that positing a major role of maturation and epigenetic factors in establishing cortical specialization. Johnson advocates a theoretical position, interactive specialization, that cuts across these two views: he suggests that the interplay of activations of one region and all those connected to it in the implementation of specific behaviors and faculties during development ends up giving organisms the potential for establishing specializations in many cortical regions. Johnson considers the fusiform “face area” as an example of how specialization can arise through development given the interaction of two brain systems: a subcortical system, which predisposes infants to look at or attend to their caregiver’s face, and a cortical system, which acquires information about the objects to which the infants attend. Johnson shows how similar constraints can produce imprinting behavior and neural specialization in chicks, albeit mediated by different neural tissue. Given its focus on attention, modularity, and development, chapter 15 integrates well with many chapters in this book. Notably, cortical development is taken as a successful example of approaching the issue of evolutionary and developmental interactions by means of the careful comparative analysis of neural and cognitive development.

In chapter 16, the last chapter in this section and the last chapter of the book, Sylvain Sirois and Annette Karmiloff-Smith present a critical overview on cognition and its ontogenesis, targeting nativist positions at their deep roots. The authors challenge the idea that cognitive abilities are prespecified in the genetic code and argue instead for an essentially plastic organism with some behavioral biases that allow abilities to emerge through development. The discussion grows into a critique of the canonical (read: modular) interpretation of atypical development (genetic disorders) that is paralleled by a close examination of the neural bases of face processing and how they can be altered in atypical development. Thus, in chapter 16 (as in chapter 15) it is argued that behavioral biases, experience, and neural interactions all play a role in normal and abnormal development. On the view espoused in chapter 16, abnormally developing children cannot be easily classified into types with different spared vs. impaired cognitive abilities. Instead, unique ensembles of impairments can arise because of different experiences during development. Chapter 15 ends with a discussion of the value of computational approaches to development in that they can examine the constructive nature of development and can avoid purely taxonomic approaches.

Thus, the three chapters in this section explore major issues in cognitive science from a comparative evolutionary-developmental approach, and thus provide an excellent coda for the preceding chapters.

14 Neuroethology of Attention in Primates

Stephen V. Shepherd and Michael L. Platt

Mobile animals orient to salient features of their environment. In primates, orienting can be covert or overt; covert orienting of attention appears to have evolved as a flexible mechanism for monitoring potentially important locations or stimuli in the absence of overt orienting. Psychophysical, electrophysiological, and neuroimaging studies conducted in the laboratory have extensively probed attention in both human and nonhuman primates trained to discriminate simple stimuli whose salience or behavioral significance has been arbitrarily assigned, typically through verbal instruction or association with rewards (Posner 1980). Such studies suggest the operation of two distinct systems for orienting attention (James 1890; Jonides 1981; Posner and Cohen 1984)—one fast and involuntary (exogenous) and the other slow and voluntary (endogenous), each one associated with partially distinct neural circuitry (Mangun 1995; Eget and Yantis 1997; Corbetta and Shulman 2002).

In contrast, observational studies conducted in natural settings suggest that social stimuli are intrinsically salient and attract attention (Keverne et al. 1978; Caine and Marra 1988; McNelis and Boatright-Horowitz 1998). Moreover, recent laboratory studies indicate that social cues, such as the direction of gaze of other individuals, access a privileged information channel that rapidly guides attention in both human and nonhuman primates (Friesen and Kingstone 1998; Deaner and Platt 2003). These studies imply that at least some mechanisms of attention have evolved in primates to be sensitive to cues predicting the goals and intentions of other individuals, but the precise identity of these social cues and the specific neural systems by which they are processed remain somewhat obscure. Adding to uncertainty regarding the neural substrates of attention, socially cued attention appears to have unique properties that map poorly onto existing models, which emphasize dichotomous exogenous and endogenous attention systems.

To explore these issues, we have investigated the visual orienting behavior of several different primate species in response to social stimuli in both field and laboratory settings. A complete understanding of visual attention in primates must account not only for gross patterns of visual orienting in natural environments but also for the fine spatiotemporal details of visual 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 recording of visual orienting behavior. Likewise, psychophysical experiments have typically failed to replicate the behavioral contexts in which visual orienting behavior normally operates. Nonetheless, it is our contention that these divisions are not insurmountable and that combining ethological and psychophysical approaches will foster the development of a unified, evolutionarily motivated theory of attention. Here we consider the impact of social contexts on visual attention, outlining some of what has been learned from each tradition. In particular, we describe our own efforts to bridge these approaches, and to sketch a tentative model of primate attention for further study.

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. Nonhuman primates might thus be expected to use vision primarily for locomotion and food acquisition, and perhaps also, like many other mammals, for 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 conspecifics, and likewise devote a large portion of their brains to visual processing; the parallel expansion of the primate brain has been accompanied by a corresponding increase in the flexibility and complexity of primate social groups (Allman 1999). Whereas 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, including coloration, posture, movements, facial expressions, and gaze (de Waal 2003; note also Gilad et al. 2004), as well as affective and referential vocalizations (Cheney and Seyfarth 1990; Seyfarth and Cheney 2003). Researchers have long recognized the importance of studying primate visual attention in the laboratory, but we have all too often neglected the ecological and social role attention plays in natural behavior.

Behavioral Goals Drive Orienting in Natural Settings

The Russian psychologist Alfred Yarbus investigated overt visual orienting behavior in humans (Yarbus 1967) by recording visual fixation patterns during free and instructed

scanning of pictures. Recording conditions were decidedly non-naturalistic: light-reflecting mirrors were suction-cupped to the eyes of volunteers. However, the visual stimuli consisted of photographs and paintings of humans and human artifacts, thus representing a significant enhancement in naturalism over contemporary psychophysical studies of attention. Yarbus's seminal work demonstrated the intrinsic salience of social stimuli as well as the strong influence of behavioral goals on visual orienting. For example, when subjects were shown the painting *An Unexpected Visitor*, fixation patterns focused on the people in the scene but were also heavily influenced by verbal instructions (figure 14.1).

Recently, Land and Hayhoe (2001), using noninvasive video gaze-tracking, have reported similar context-dependence in visual orienting. They report that fixations are almost completely specified by task demands, at least during performance of simple actions such as making a sandwich or preparing tea, and that very few fixations are made to task-irrelevant regions of space. These data suggest that visual fixation priorities not only are shaped by evolutionary pressures but also can serve as an external indicator of shifting internal goals that govern an animal's moment-to-moment behavior (Shepherd and Platt 2008).

Social Orienting Bias in Natural Settings

Observational data support the idea that visual orienting in nonhuman primates is also biased toward social stimuli (Keverne et al. 1978; Caine and Marra 1988; McNelis and Boatright-Horowitz 1998). Furthermore, these biases are not uniform; instead, some social stimuli attract more attention than others. For example, monkeys spend more time looking at pictures of faces gazing toward them than at faces with averted gaze (Keating and Keating 1982) and also look more often toward higher-ranking animals than lower-ranking animals (Keverne et al. 1978; McNelis and Boatright-Horowitz 1998). When viewing images of faces, nonhuman primates look preferentially toward the eyes and mouth (Keating and Keating 1982; Kyes and Candland 1987; Guo et al. 2003). Such data have been limited, however, to observations at distance 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 visual orienting by nonhuman primates in naturalistic social and physical settings. To do this, we recorded gaze behavior in socially housed ringtailed lemurs (*Lemur catta*) freely moving and interacting in large three dimensional environments. We used a lightweight telemetric optical gaze-tracking device (figure 14.2) (Shepherd and Platt 2006) operating at 0.22 degrees \times 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 attempted to infer the goals guiding visual orienting in natural behavioral contexts from the observed patterns of visual behavior (Shepherd and Platt 2008). Ringtailed

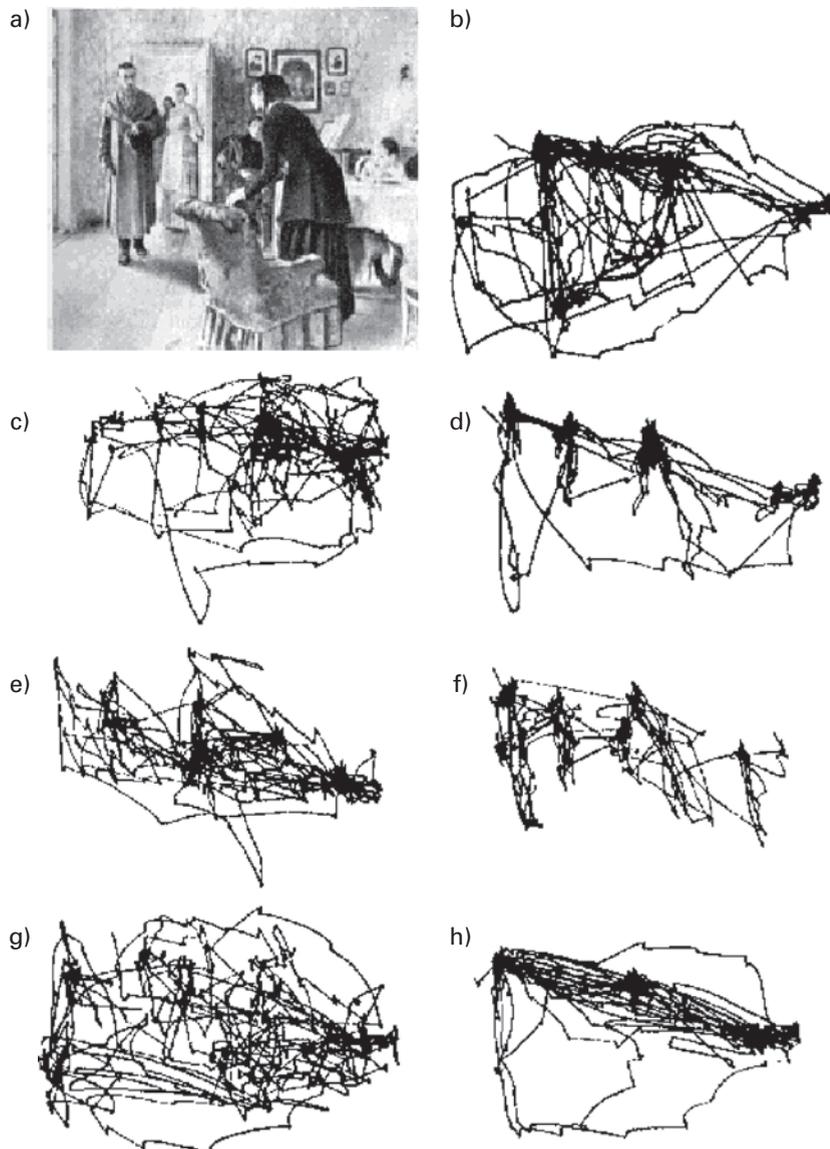


Figure 14.1

Social context and behavioral goals alter fixation patterns during free viewing. Panels b-h show the different gaze patterns of viewers when asked different questions about the illustration, Ilya 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 (1957).

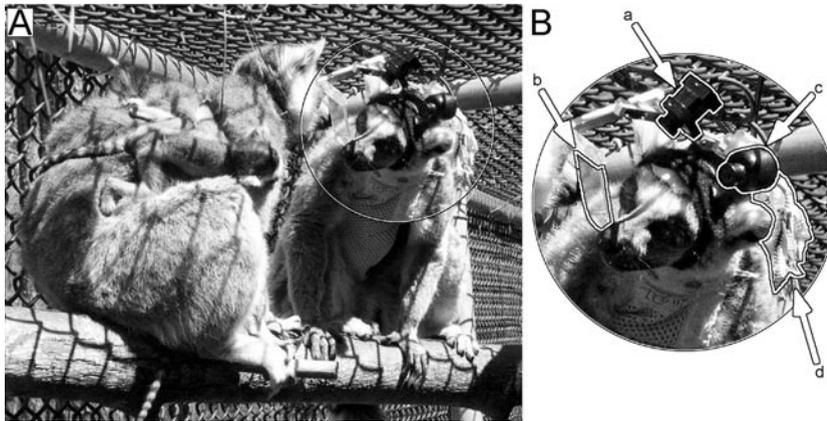


Figure 14.2

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 and Platt (2006).

lemurs, prosimian primates that diverged from the ancestors of “higher” primates some 60 million years ago, were chosen as subjects for their tolerance of handling and their availability at the Duke University Lemur Center. Ringtailed lemur social groups are similar to those of many higher primates, comprising ten to twenty 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 ringtailed lemurs fixated their human handlers, as would be expected, given we had just suited them temporarily into recording equipment. More important, they also fixated their social companions, and did so more often than they fixated small food rewards (figure 14.3a).

Each of these three categories—human handlers, conspecifics, and food rewards—were fixated significantly more often than chance; furthermore, they were fixated significantly more often than high-contrast environmental features (e.g. dark branches in foreground with light-colored ground behind), stimuli we naively expected to attract attention based on their low-level visual salience. Elevating contrast is one of the simplest and most traditional means of driving bottom-up attention, and environmental features were selected partly on the basis of strong visual contrast between them and the local background. These data suggest that animals and food rewards were identified and localized and that this information was used to guide visual orienting during natural behaviors. Social orienting bias was not inflexible, however, and in fact was reversed during periods of active

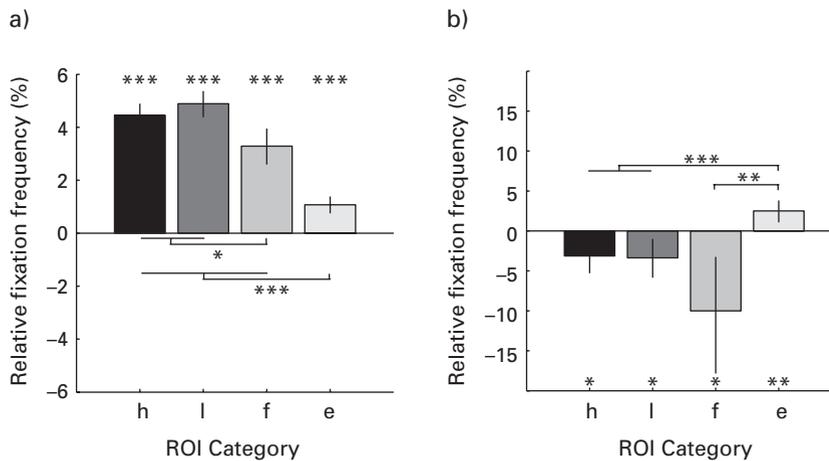


Figure 14.3

Fixation priorities in stationary and moving lemurs. (A) Lemurs fixated humans (h), lemurs (l), food (f), and high-contrast environmental features (e) significantly more than chance expectation; fixated humans and lemurs significantly more than food rewards; and all three significantly more than environmental features. (B) Lemurs fixated environmental features significantly more often when moving than when stationary, seemingly at the cost of fixations toward animals and rewards. After Shepherd and Platt (2008). *** $P < 0.0005$; ** $P < 0.001$; * $P < 0.01$.

locomotion (figure 14.3b). While moving, lemurs instead fixated environmental features that served as potential surfaces across which the lemur could travel toward their subsequent destination. Together with earlier research (Yarbus 1967; Land and Hayhoe 2001), these findings validate the use of quantitative gaze measurements as an externally observable indicator of otherwise unobservable mental states—the specific current behavioral goals of a given animal—and further reveal that the typical behavioral context for a stationary lemur involves not only monitoring environmental threats, such as predators, and rewards, such as food, but also other members of the social group.

Dominance, Sex, and Social Salience

Our ongoing field studies of orienting in ringtailed lemurs support the idea that early primates possessed neural specializations for orienting toward and extracting relevant information from other animals. The sheer variety and complexity of possible stimuli and contexts available in the field, however, has challenged our ability to draw definitive conclusions regarding the specific social stimuli that guide visual orienting during any specific behavior—an endeavor that is ongoing in our laboratory. Moreover, despite the evident similarity between human visual orienting priorities and those we observed in lemurs, the brains, genomes, and social systems of these two species differ dramatically. Finally,

ringtailed lemurs do not serve as a model species for any particular neurological or psychological behavior or disorder, and thus little is known about brain function in these animals.

To deal with 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 actively studied anthropoid primate with relatively well-understood biology, and like humans, they live in large, hierarchical social groups with extensive repertoires of visual, auditory, and tactile behavioral interaction.

Although rhesus monkeys have been widely used to study visual attention, most of these studies have used arbitrary stimuli with little or no intrinsic behavioral relevance. We know, however, that in the wild, monkeys visually monitor one another (Keverne et al. 1978; Caine and Marra 1988; McNelis and Boatright-Horowitz 1998), and in the laboratory, will preferentially seek out visual stimuli with social content (Butler 1954; Sackett 1966). To precisely quantify how rhesus monkeys prioritize specific classes of social stimuli for orienting, we developed a choice task designed to balance fluid rewards against the potential reward value of seeing images 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 photograph of a monkey. By determining the value of differential reward at which monkeys were equally likely to choose the social or control image, we were able to quantify the reward value of different classes of social stimuli (Deaner et al. 2005). 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 (figure 14.4).

The attraction of gaze to high-ranking males is somewhat counterintuitive, 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 looking at social stimuli once foveated—provides a potential explanation for this paradox: potential mating cues evoked prolonged stares, whereas faces 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 Gaze Attraction

Thus, both for freely moving lemurs and for macaques performing attention tasks in the laboratory, visual inspection of conspecifics seems to be an important goal of visual orienting. Ethological studies of primate behavior suggest that this behavioral bias may serve at least two important biological functions. Vision has long been known to play a role in hunting and foraging, affecting both predators, where selection pressures favor narrowed,

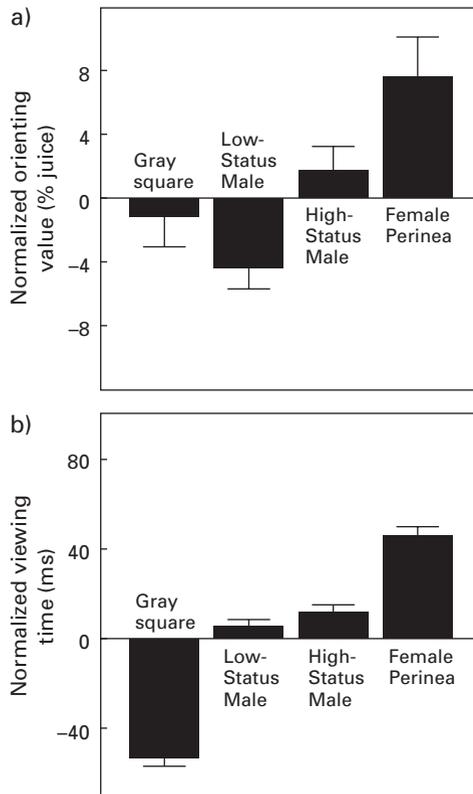


Figure 14.4

Monkeys sacrifice juice to view important social stimuli. (a) 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. Monkeys paid the highest amount of juice to see female perineia and a lower amount to see high-ranking male faces, but required extra juice to look at low-ranking male faces or, to a lesser extent, uniform gray squares. (b) A similar pattern is evident in the amount of time per presentation that monkeys fixated each category of image. This measure differs, however, in that monkeys dwell for similar lengths of time on low- and high-status faces. After Deaner et al. (2005).

binocular fields of view (such as in carnivores) and prey, where selection favors widened, monocular visual fields (such as in ungulates). Primates have largely binocular visual fields, but this does not free them from the need to be vigilant for hungry predators or for hostile competitors. Primate social groups are often characterized by a certain baseline level of aggression, and individuals thus need to spend some of their time surveying conspecifics, both from within and outside the social group, for possible threats. In fact, many primates may have to actively balance centrifugal surveillance (against external predation or rival social groups) and centripetal surveillance (against bullying from within the social group; Caine and Marra 1988).

Centripetal surveillance, however, implies that there is a social group in the first place. From this we infer a second, more subtle role for social attention, first articulated by Chance and Jolly (1970). Cohesion of social groups requires, as a principal element, the coordination of movements so as to regulate spacing between each individual and its cohort. For this reason, Chance and Jolly (1970) suggested that “the social attention of individuals within a cohort . . . must be directed exclusively at the other members of it” and went 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 capture 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-ranking animals.

Although dominance may be structured by the threat of violence and by the need for coalitional defense against such threats (Keverne et al. 1978; Cheney and Seyfarth 1990), status-based saliency seems to be largely prosocial, and in some sense positively valenced, in that it promotes proximity to the group. For example, Chance and Jolly (1970) describe a behavior called “reflected escape” in which a subordinate animal, threatened, runs in a looping arch, first away from the challenger and then back toward the central members of the group—even if these were the same dominant individuals who initiated the threat. These ideas seem to be supported by findings that gaze (Keverne et al. 1978), allegiances, and grooming (Cheney and Seyfarth 1990) are allocated preferentially to dominant individuals of the group, independent of those individuals’ aggressiveness, and also by our finding that macaques sacrifice more juice to view dominant animals than subordinate animals. It currently remains unclear whether the privileged saliency of the social cohort, and particularly the most dominant individuals, is driven by neural systems governing vigilance (such as the amygdala) or those driving pursuit of rewards (such as the ventral striatum).

Our initial assumption was that fixating high-value social targets reflects some sort of intrinsic reward, as suggested by the increased juice premiums paid by monkeys given an opportunity to see these categories of stimuli. However, enhanced saliency may in fact be *driving* reward, rather than deriving from it: several strands of research suggest that the mere act of attending to a stimulus may enhance its desirability. Zajonc first described these effects in 1968 when he found that brief presentation of unfamiliar visual stimuli caused human subjects to subsequently rate those stimuli more aesthetically 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, a finding that confirmed attention could mediate “mere-exposure”-like effects. 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 select it as the most desirable. Together, these findings suggest that differential orienting may drive changes in affective judgments, and furthermore, that these “mere exposure” effects may mediate social cohesion in primates by encouraging approach behavior toward salient targets. 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 most desirable for approach.

A fascinating illustration of this process might be the tendency for both human and nonhuman animals to increase their visual salience during the mating season. Both humans and other animals either maintain sexually selected ornamentation year-round or acquire ornamentation when interest in mating peaks (von Schantz et al. 1999; Haselton et al. 2007). Whether or not these bright, high-contrast ornaments serve to signal reproductive fitness, they may operate by enhancing saliency, and thus the likelihood the ornamented individual will be approached by potential mates.

Socially Cued Attention: Following the Gaze of Another Individual

In 1876, Ralph Waldo Emerson 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” (p. 173). As Emerson intimated, where we look often betrays our interests, intentions, and desires. Thus, 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 conspecifics to infer the location of important stimuli and events, to predict behavior, and perhaps even to interpret social relationships among others (Cheney and Seyfarth 1990). Subtler still, humans (and perhaps other primates, particularly apes; de Waal 2003) use and recognize a number of deictic gestures, varying from discreet (a quick flick of the eyes) to overt (pointing), that signal important perceptions and plans. Furthermore, we use these signals in competitive contexts to read intent and predict action (watching someone’s eyes during chess) and to confound such predictions by others (the “no look pass” of soccer and basketball, in which a player looks toward a different teammate than the one to whom 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. One typical laboratory approach to visual attention asks subjects to stare at a fixation point, which is followed by either a central cue or peripheral stimulus directing attention to a peripheral location (Posner 1980). Studies using this technique have revealed that central cues that validly predict the location of a future peripheral target shift attention in a voluntary (“endogenous” or “top-down”) manner toward the likely location of the

target, whereas abrupt peripheral cues, even when nonpredictive, automatically attract attention (“exogenous”, “reflexive”, “bottom-up” attention). These attention shifts are evidenced by changes in sensory discrimination performance and reaction time, and have distinct time courses (Muller and Rabbitt 1989): exogenous attention operates more quickly and generates a subsequent orienting deficit (“inhibition of return”), whereas endogenous attention is slower and more sustained. Despite the utility of this paradigm, its generality remains limited because of a failure to study orienting by human and nonhuman primates in the natural world.

To explore this issue, Friesen and Kingstone (1998) modified the Posner paradigm to investigate socially cued attention. In their experiments, subjects were instructed to fixate a central point, where a face briefly appeared with eyes cast either rightward or leftward. A split second after face presentation, a target appeared randomly on the right or left of this cue, irrespective of gaze direction in the face. Subjects were faster to respond to targets appearing in the direction of the observed gaze, even for cue-to-target delays as brief as 105 ms (stimulus onset asynchronies, or SOA). Thus, they discovered that viewing a face that has an averted gaze rapidly and reflexively shifts the viewer’s attention in the same direction, even when gaze direction does not predict the eventual location of the target. Subsequent studies reported these effects were both general (viewing a head turned to the side also shifts attention in that direction; Langton and Bruce 1999) and involuntary (social cuing persists even when the target was 80 percent likely to appear in the direction *opposite* viewed gaze; Driver et al. 1999). Attention shifts associated with observed gaze thus appear categorically distinct from both responses to explicit cues (Friesen et al. 2004) and to abstract spatial associations (Galfano et al. 2006).

Results like these supported the argument that humans had evolved a dedicated gaze-following module specialized for rapid and reflexive sharing of attention in social groups (Baron-Cohen 1994; Perrett and Emery 1994). We tested this hypothesis explicitly by measuring visual orienting responses to social gaze cues in monkeys and humans (Deaner and Platt 2003). Surprisingly, we found that both monkeys and humans responded more quickly to an unpredictable target when it appeared where a monkey presented at fixation had been looking. Furthermore, fixation position in both species drifted in the direction of gaze, likely reflecting cumulative microsaccades (Hafed and Clark 2002; Engbert and Kliegl 2003). The magnitude and time course of the gaze-following response was highly similar in the two species (figure 14.5), suggesting shared underlying neural circuitry.

Our results strongly support the conclusion that social gaze following is not unique to humans, and may in fact rely on neural substrates that are widespread among primates and possibly other animals. Though gaze following by nonhuman primates may differ, in both strength and kind, from that evinced by humans (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

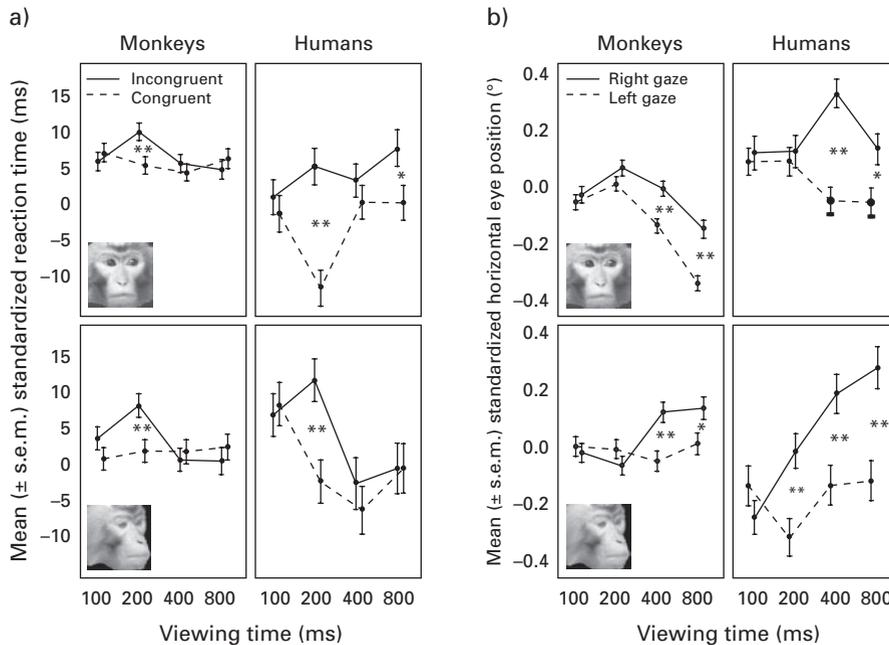


Figure 14.5

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. (a) These attention shifts were evident both by decreases in normalized reaction times to congruent (dashed) vs. incongruent (solid) stimuli and (b) by microsaccades in the direction of observed gaze during cue presentation. After Deaner and Platt (2003). ** $P < 0.001$; * $P < 0.05$.

animals, including apes (Brauer et al. 2005), dogs (Agnetta et al. 2000), monkeys (Tomassello et al. 1998), goats (Kaminski et al. 2005), dolphins (Tschudin et al. 2001), and ravens (Bugnyar et al. 2004), can use gaze cues to find hidden food or retrieve objects (reviewed in Emery 2000; Itakura 2004).

This conclusion is supported by our work tracking visual orienting patterns among freely interacting lemurs. Uniquely among studies of gaze following, we quantitatively and precisely monitored gaze during spontaneous interaction with conspecifics. We found that lemurs tended to orient their eyes in the same direction that observed lemurs oriented their bodies and heads (figures 14.6a, 14.6b).

This gaze alignment, however, could reflect simultaneous orienting to the same salient events in a shared environment rather than active gaze following. In order to explore this question we examined the temporal sequence of gaze alignment when the subject 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,

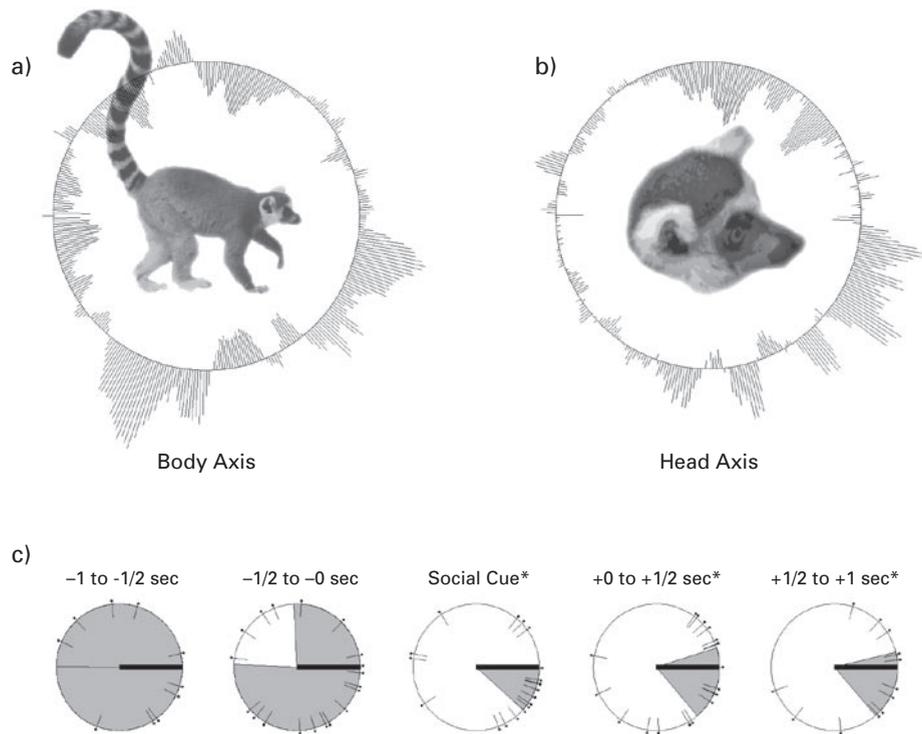


Figure 14.6

Spontaneous gaze-following in lemurs. Lemurs spontaneously follow the gaze direction of their conspecifics in natural interaction. Lemurs not only co-orient with the body (a) and head (b) axes of observed lemurs, but selectively increase gaze alignment with those individuals they have recently attended (c). In panels (a) and (b), outward lines are gaze offsets that are overrepresented with respect to chance, whereas inward lines are gaze offsets that are underrepresented. In panel (c), tick marks occur at mean gaze offsets recorded in half-second periods prior to fixation, in the period during which the lemur is fixated, and for half-second periods after fixation. Shaded regions in panel (c) reflect the dispersion of gaze alignments. Starred intervals are significantly aligned with gaze (χ^2 test $P < 0.05$). After Shepherd and Platt (2008).

gaze alignment increased significantly (figure 14.6c). The temporal sequence of gaze alignment supports the conclusion that lemurs actively follow the gaze of other individuals (Shepherd and Platt 2007). Our results stand in sharp contrast to at least two prior observational studies (Itakura 1996; Anderson and Mitchell 1999) that concluded that prosimian primates cannot follow the gaze of human observers.

Modulation of the Social-Gaze Module

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 social gaze following is a strictly reflexive behavior generated by a dedicated neural module (Driver et al. 1999; Deaner and Platt 2003). Recent studies, however, challenge the notion that gaze cueing is purely reflexive, instead indicating that social context can influence gaze-following behavior in both humans and monkeys. Specifically, several lines of evidence suggest that neural systems contributing to social gaze following are regulated by the social milieu as well as by intrinsic factors, including sex hormones such as testosterone or neuromodulators such as serotonin. In humans, for example, females show much stronger attention shifts in response to gaze cues than do males (figure 14.7; Bayliss et al. 2005; Deaner et al. 2007); moreover, our lab has found that gaze following in females, but not in males, is influenced by the familiarity of the observed face (Deaner et al. 2007).

These observations suggest the possibility that sex hormones may play an important role in regulating social attention. Supporting this idea, the amygdala, orbitofrontal cortex (OFC), and hippocampus form a functional circuit important for associating emotional and social salience with mnemonic and perceptual information (Vuilleumier 2002; Sabbagh 2004; Smith et al. 2006), and actively contribute to 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.

Intriguingly, patients with anxiety disorders show heightened following of a fearful gaze relative to other emotional expressions (Mathews et al. 2003; Hori et al. 2005; Holmes

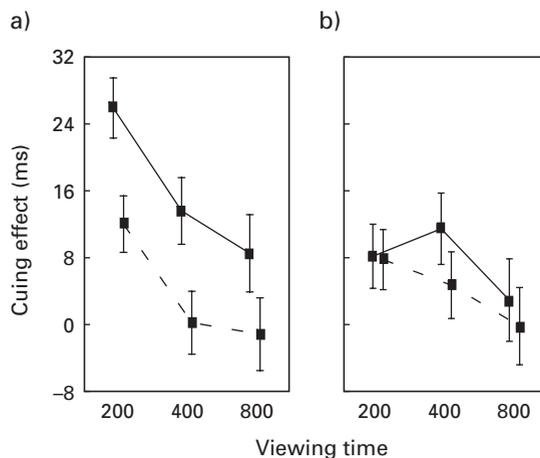


Figure 14.7

Sex differences in gaze following in humans. Human females exhibit stronger gaze following than males, furthermore, discriminate between familiar and unfamiliar individuals when following another's 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 et al. (2007).

et al. 2006; note also Hietanen and Leppanen 2003; Putman et al. 2006). This contextual effect probably reflects the tendency for patients with anxiety to more strongly attend negatively valenced social stimuli, whereas normal subjects dwell less on them (e.g., Bradley et al. 1997; Bar-Haim et al. 2005). These studies imply that focused attention on a social target naturally extends to the objects it attends and the tasks in which it is engaged.

We have found similar evidence that 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 gaze cues from each of four familiar monkeys. Importantly, each animal was designated dominant or subordinate on the basis of the direction and frequency of threat and submission gestures during controlled pairwise 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 (figure 14.8a), while dominant monkeys followed the gaze later, and then only in response to other dominant monkeys' also following it (figure 14.8b).

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 and Ziegler 2002). We interpret these data to indicate that biological factors such as testosterone may influence the strength of gaze-following behavior in macaques, and further that the strength of gaze-following behavior in monkeys is modulated by social context, just as it is in humans.

Together, these results demonstrate that gaze following is deeply integrated into the larger social information-processing stream. That gaze following is an inherent component of face perception is indicated by the fact that heightened attention to faces attracts attention centrifugally 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 such as familiarity and social dominance suggests that it is not 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. This supposition is strengthened by various results showing that fetal testosterone negatively impacts both social attention and social relationships in human juveniles (Knickmeyer and Baron-Cohen 2006). Together these findings strongly support the idea that social attention contributes strongly to natural primate behavior and cognition, and presents a significant addition to the traditional endogenous/exogenous model of attention control.

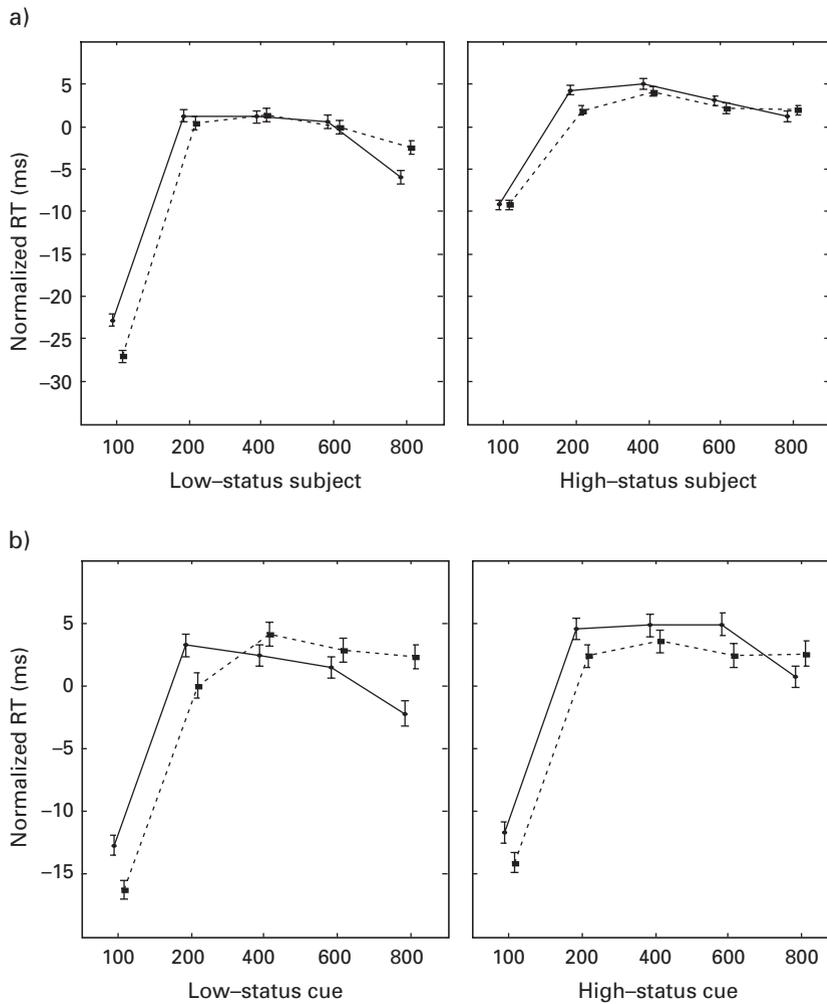


Figure 14.8

Social context influences gaze-following in macaques. (a) Even at the briefest cue durations, subject social status appears to influence gaze-following behavior ($P < 0.005$). 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 such as testosterone on social-processing circuitry in the brain. (b) Cue social status also plays an important role ($P < 0.01$), 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 dashed lines and for incongruent trials are shown in solid lines. After Shepherd et al. (2006).

Social Attention and Autism: From the Lab to the Field

Data from the study of autism and other syndromes that disrupt social behavior suggest a gulf between behavioral responses in the laboratory and spontaneous use of social cues in the real world. Contrasting visual behavior in autistic subjects to that of typically developing children, van der Geest and colleagues (2002) showed that the fixation patterns of the two groups could not be distinguished when they viewed simple cartoons that included human figures. In contrast, Pelphrey and colleagues (2002) found substantial differences between these populations when they were inspecting photographs of faces. Similarly, although researchers have often failed to find dysfunctional gaze following in autism using the Posner attention task (Chawarska et al. 2003; Swettenham et al. 2003; Kylliainen and Hietanen 2004; but see Bayliss et al. 2005; Ristic et al. 2005), autistic individuals show severe disruptions of visuosocial orienting in naturalistic contexts. For example, Klin and colleagues (2002a, 2002b) measured gaze patterns in autistic individuals watching the movie *Who's Afraid of Virginia Woolf*, and found that gaze toward social stimuli was disordered—for example, fixations toward the eye regions were seemingly replaced by fixations toward the mouth—and that socially cued locations were severely neglected, as shown by a marked lack of fixations toward gaze- and gesture-cued regions of space. Furthermore, they found that the degree of abnormality in the fixation pattern of individual autistic subjects was strongly predictive of future social impairment.

Outside the laboratory, even high-functioning autistic individuals unaffected by common symptoms, such as seizures or repetitive movements, are nonetheless challenged in responding to the constant exchange of social cues that structures our daily lives. Temple Grandin (1999), 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 . . . I did not know that eye movements had meaning until I read *Mindblindness* 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.” Autism frequently involves 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, p. 66). It may be that the complement of rewards and reflexes 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 (Raleigh et al. 1991; Edwards

and Kravitz 1997), suggesting that it may also influence socially cued orienting between dominant and subordinate macaques. Together, these findings hint at a role for serotonin in regulating social attention in 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.

Gaze as a Strategic Social Signal

As we have seen, social saliency may play a role not only in guiding attention but also in shaping the physical spacing of social group members and the affective tenor of their social 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—for example, “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 un-crowded orbitals.” Typically developing humans have an intuitive expertise at communicating affect and attentional state, perhaps in part 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 that shapes primate social interactions. We have mentioned the role of eye movements in initiating conflict, but monkeys make far more sophisticated use of gaze. For example, eye contact can signal sexual interest (Dixson 1998), aggression (van Hoof 1967), and solicitation for coalition formation in agonistic interactions against third parties (de Waal 2003). Likewise, humans use eye contact as a key aspect of affiliation, courtship, and intimidation (Argyle and 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 taking turns in conversation (Argyle and Cook 1976).

With the evolution of increased visual and social complexity, 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. Apes are even reported to use deictic gestures (de Waal 2003), though these signals may receive little currency due

to the ubiquity of competitive and paucity of cooperative interactions among nonhuman primates (Hare and Tomasello 2004). The importance of gaze cues for facilitating increased cooperation among human ancestors may even have led to somatic adaptations that increase the saliency and specificity of social attention cues, for example, by enhancing the visibility of gaze through increased contrast of the pupil against the sclera (Kobayashi and Koshima 2001; Tomasello et al. 2006). At the same time, however, the continued relevance of competitive interactions between human ancestors may have led to a compensatory enhancement of covert attention abilities in humans relative to those of non-human primates and, especially, other mammals.

This manipulative role of gaze is perhaps the least understood aspect of visual orienting behavior, and nothing is known about how the demands of signaling bring their influence to bear on the gaze control system of the brain. Following convention, we have approached macaque orienting toward other macaques in terms of intrinsic reward, and orienting to follow gaze in terms of visuosocial reflex. However, it might be more realistic to assume that initial rapid orienting responses depend upon reflexive processes and that slower orienting behaviors and sustained fixations depend upon reward evaluations. For example, all monkeys in our studies initially looked toward other individuals and followed their gaze, but other behavioral contingencies shaped gaze behavior, as well, such as abbreviating risky glances toward higher-ranked individuals (Haude et al. 1976; Deaner et al. 2005), extinguishing gaze following of lower-ranking animals (Shepherd et al. 2006), and prolonging male visual orienting toward female hindquarters (Deaner et al. 2005).

Toward a Neuroethological Model of Attention in Primates

If we were to develop a biologically plausible, ethologically motivated model of primate gaze, 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 realistic ecological and social contexts. For example, Laurent Itti and colleagues, among others, have used visual filters, inspired loosely by the physiology of the primate visual system, to predict human visual attention. Such models can successfully estimate spatial saliency by filtering images through a series of low-level feature maps (Peters et al. 2005; Carmi and Itti 2006). Each map tracks the extent to which a region “pops out” from its surroundings in a particular dimension, such as brightness, orientation, texture, motion, or color, and these maps can be combined to successfully model many aspects of bottom-up attention.

Although 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 this accomplishment 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 such as running water or blowing leaves produce irrelevant image motion. Moreover, whereas 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 and 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 and Mishkin 1982) to quickly identify images containing animals. It is important to note, however, that this model explicitly fails to localize the animals within the images. The processes that link object recognition by the ventral visual processing stream to target localization within the dorsal visual processing stream remain largely unknown, despite the fact that these processes determine how attention 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,” 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.”

This study 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 fMRI studies have identified human 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), and are beginning to identify macaque homologs (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 among those primordial visual cortical areas (for example, V1, V2, V5; see Tootell et al. 2003; Rosa and Tweedale 2005) present in stem primates, and perhaps others mammals (Kendrick et al. 2001).

As revealed through behavioral studies, the gaze-control system must recognize and respond appropriately to biological targets. We speculate that two parallel pathways accomplish this goal (Adolphs 2002; Vuilleumier 2002; see figure 14.9). First, a primitive retino-tectal pathway uses crude biological primitives to quickly identify social targets and their gaze direction (Johnson 2005). Just such a relay of social threat signals, from the retina through the superior colliculus (SC) and pulvinar nucleus of the thalamus to the amygdala, has already been identified in humans (Morris et al. 1999), and neurons in the amygdala are sensitive to gaze direction in a viewed face (Kawashima et al. 1999; Hoffman et al. 2007). The amygdala, in turn, sends this first-pass analysis of social targets toward attention control centers and higher visual areas (Vuilleumier 2002).

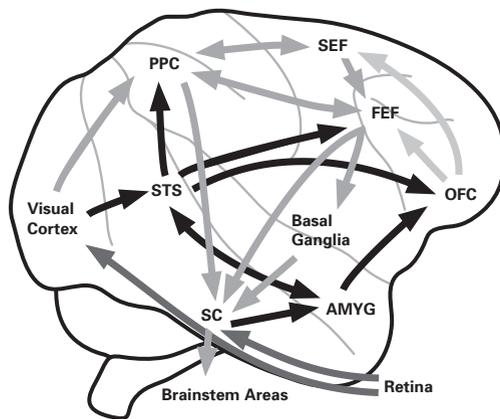


Figure 14.9

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

At longer time scales, information processed in the temporal cortex, in conjunction with contextual signals from the hippocampus and the orbitofrontal cortex (OFC), modulates visual attention via the amygdala (Vuilleumier 2002; Sabbagh 2004; Smith et al. 2006). This pathway may be highly sensitive to biological factors that differentiate circuitry and behavior between the sexes (Goldstein et al. 2001; Bayliss et al. 2005; Deaner et al. 2007) and across psychological conditions (Mathews et al. 2003; Hori et al. 2005; Holmes et al. 2006; Putman et al. 2006), and may, when compromised, contribute to the development of autism (Schultz 2005; though note also Amaral et al. 2003). Ultimately, amygdala-mediated signals pass through the supplementary and frontal eye fields (SEF and FEF), the lateral intraparietal area (LIP), and ultimately to the superior colliculus (SC) as a final common output governing most, if not all, gaze behavior.

Second, and in parallel, a more recently evolved cortical pathway leading from V1 through the ventral pathway to the extrastriate body area (EBA; Downing et al. 2001), the fusiform face area (FFA; Haxby et al. 1994), and the superior temporal sulcus (STS; Allison et al. 2000) identifies biological targets. It remains unclear whether these areas are primarily involved in assessing subordinate-level distinctions between hierarchically classifiable objects; or are more specifically involved in distinguishing the identities and actions of animate objects; or, finally, are areas optimized for visual 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 (Schultz 2005).

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 then ramify to multiple targets in the visual orienting system. How exactly this may occur is an open question, since much of the visuosocial cortex (Tsao et al. 2003) is connected in one or two steps to posterior parietal (7A and LIP; Seltzer and Pandya 1991), frontal (SEF and FEF; Seltzer and Pandya 1989), and subcortical orienting areas (pulvinar nucleus; Romanski et al. 1997; superior colliculus; Fries 1984). Some of this ambiguity arises from the inconsistent localization of socially activated cortical domains in terms of previous architectonic and tracing studies, especially along the STS. For example, although particular areas within the STS (Allison et al. 2000; Tsao et al. 2003; Calder et al. 2007) are preferentially activated by particular visuosocial tasks, distinct subregions of the STS appear to have radically different connectivity (Seltzer and Pandya 1989, 1991). It seems likely that whatever pathways are involved, contextual effects on social orienting are implemented by an even more diverse group of cortical areas involved in memory, emotion, and motivation, including the hippocampus, the amygdala, and the OFC. These regions are differentially regulated by sex hormones and make up part of a network of neural populations activated in many visuosocial tasks.

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. Neuroethological studies of visual attention, by contrast, have revealed a suite of socially motivated and socially cued orienting behaviors that do not divide 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 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, determining 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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