

Neuroethology of Social Attention in Primates

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Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
Neurobiology in the Graduate School
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ABSTRACT

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Abstract

To solicit the attention or determine the intentions of another, we use our eyes. While many animals appear to use eyes as an important behavioral cue, for humans, these cues are especially critical. The power of the eyes to attract and direct attention shapes human behavior from an early age and likely serves as a foundation for social skill acquisition, ranging from simple, friendly eye contact to complex, spoken language, even to our almost mystical ability to empathize and “see the world through another’s eyes”. Humans have transformed our environment through our economic alliances and military competitions, and our individual successes and failures depend critically on social skills built on a foundation of shared attention. When these abilities break down, as in autism, pervasive social awkwardness can challenge the close relationship of individuals with their friends, family, and community. Nonetheless, we know almost nothing about the brain mechanisms that have evolved to process social cues and convert them into a rich experience of shared attention. To investigate this process, we explored the ability of primates to follow the attention of other individuals. First, we characterized natural gaze-following behavior using a novel telemetric device in socially-interacting prosimian primates, and later in monkeys responding to gaze cues in the lab. Finally, we examined the neuronal responses to gaze cues in a macaque posterior parietal area implicated in attention control—the lateral intraparietal area, LIP.

Our findings suggest that gaze-following abilities may be widespread in social primates, relying on conserved, homologous brain pathways; and that they may not be informationally-encapsulated reflexes, but rather are densely interwoven with diverse social processes. Indeed, we found gaze cues influenced neurons in LIP, part of the dorsal frontoparietal attention network. Finally, we report that “mirror” neurons in parietal areas may thus play a role not only in representing perceived bodily actions, but also perceived mental states such as observed attention.

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1. Introduction

1.1 *How to See Through Another's Eyes*

George and Martha are arguing again, as George goes to refill their two guests' glasses. Martha has struck a particularly vicious line of attack, recounting how she was foolish to fall in love with him and how his deepest ambitions have all amounted to one gigantic flop. Here's the scene—Martha and her guest, Nick, sit on the couch. Martha is speaking, Nick listening, perhaps occasionally adding a softening remark. George is in the background, bottle in hand—a bottle he'll soon smash—projecting calm as the tension inside him winds toward its imminent snap.

The scene is from *Who's Afraid of Virginia Woolf*, a harrowing movie in which we see two couples explore all the ways human beings can wound one another without ever drawing blood. A hallmark of our humanity is our incredible ability to empathize with others and to flexibly use this knowledge: either to further our mutual ambitions or to frustrate the ambitions of our competitors. Edward Albee's script dwells almost entirely on the way our shared ambitions can turn, tragically, into bitter sniping. But by studying the way our eyes scan these scenes, researchers hoped to achieve an entirely different transmutation: to determine how autistic individuals, who lack social fluency, might learn to more effectively relate to others.

Ami Klin and colleagues tracked the eye movements of autistic individuals and typically-developing controls while they watched short clips of the movie. They found that the visual explorations of the two subject pools were strikingly different: a typically-developing individual might look at the eyes of Martha and Nick as they speak to one another, while regularly—likely nervously—glancing at George, recognizing him as the subject of the conversation, and monitoring for a potentially explosive response. By contrast, a typical individual with autism might fixate locations dominated by low-level visual contrast: looking toward mouths rather than eyes, or tracking the motion of Martha’s bright necklace as she verbally flays her husband (Figure 1).

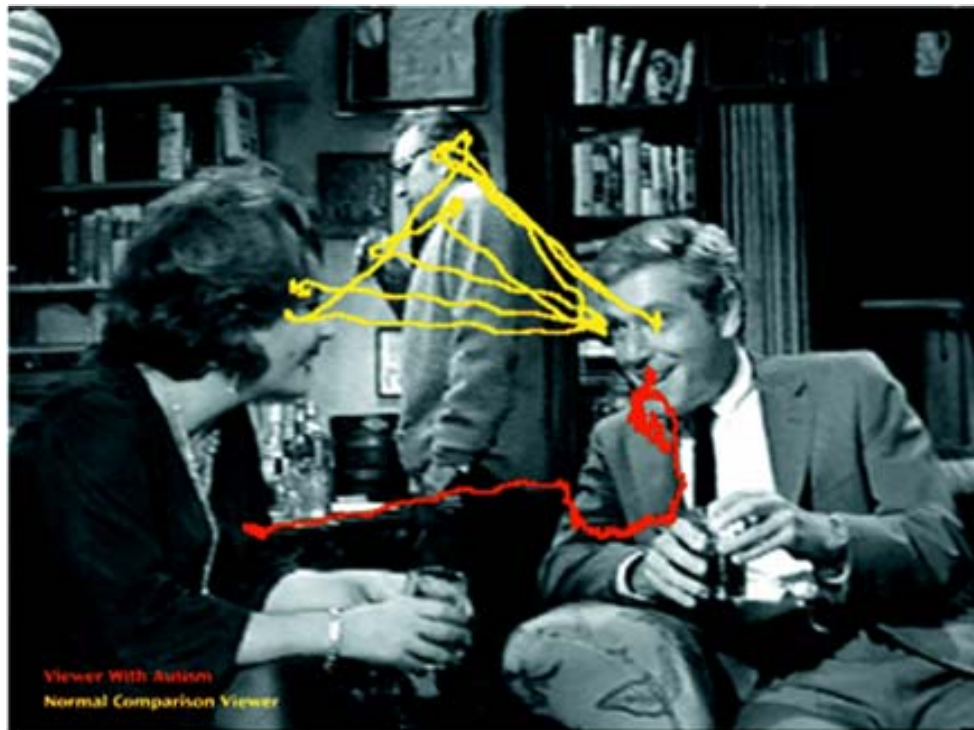


Figure 1: Atypical social orienting in autism.

A healthy subject (yellow), but not an individual with autism (red), orients to socially relevant stimuli, especially toward faces, eyes, and along the line of gaze (Klin et al. 2002a).

In other scenes autistic individuals maintained a striking inattention to social content, failing to visually engage the actors by making eye contact or following pointing gestures. Furthermore, the decrease in social fixations strongly predicted the severity of social dysfunction as assessed by independent measures (Klin et al. 2002b, 2002a). These findings suggest three possible hypotheses: first, autistic individuals may fail to heed social cues because they have not learned how to recognize them; second, autistic individuals do not learn how to read social cues because they do not attend them; third, that autistic individuals neither attend nor become fluent in exchanging social signals because they are unmotivated by social outcomes.

To determine which of these three is most likely, it would be helpful to quantify visual orienting in normal social interactions, and to better understand how these behaviors come about. For example, is orienting behavior innate or learned? Is it cognitive and motivated by predicted rewards, or reflexive, occurring without outcome evaluation? Is it unique to humans, or do other species use similar neural circuits to mediate social behavior? Answering these questions involves not only gaining an understanding of externally-observable behaviors, but also of mechanistic understanding of the evolution and development of social orienting.

In the following pages, I will break off a small part of this problem—the use of another’s gaze as a social orienting cue—and look at it through a number of different lenses, studying orienting both inside and outside of the laboratory, and in both humans and nonhuman primates. While the experiments I describe do not directly address developmental issues, I will attempt to provide adequate background to suggest developmental implications of our findings.

The remainder of this introductory chapter will focus on the following theoretical issues: what are social stimuli, what kinds of adaptive benefits do we gain from attending them, and how does this social saliency interact with other forms of human cognition? In subsequent chapters, I will describe background on gaze-following behavior, as well as experiments in which we’ve probed behavior either in natural interactions or laboratory settings. Finally, I will review what is known about mechanisms of social orienting, and describe our research into how perception of gaze cues influences neurons within the gaze-control system of the macaque brain.

1.2. Vision in Perspective

1.2.1 The invention of attention: the roving eye

The first eye movements were probably used to stabilize the visual world: as animals moved, the world visible to their eyes moved, and this instability limited the

extent to which the world could be resolved. To compensate, the eye evolved the ability to move counter to the movements of the body, and this allowed the world to be stably viewed (Walls 1962). After a time, further adaptations leveraged these eye movements to a new purpose. By shifting position, the movements of the eye could not only stabilize the world, but also select parts of the world to deploy computational resources.

It is unclear whether attention preceded overt eye movements, but it is clear that even in modern humans, the attention system shares many of its resources with the system of eye movement control. Two questions immediately emerge from this. The first, and first-answered in evolution, is “to what should we direct our attention”? The second is “what can we learn from the overt attention of other animals?”

1.2.2 To what should we direct our attention?

Vision has several uses to an animal. The simplest is to distinguish light from dark, and thus regulate orientation and position in the ocean. By placing photoreceptors in an array, a quickly-updating spatial sense arises, where light and dark can be assigned a 2-dimensional position and perhaps also motion and depth. The speed and spatial specificity are useful for dealing with movement, for example one’s own navigation through an obstacle-strewn 3-dimensional environment. But because vision is well suited to processing motion, it is critical primarily for dealing with *other* animate entities. While vision can be used to navigate and forage for vegetation, it is far more useful for tracking the complex movements of other animals. For any animal eking out

an existence as a link in a food chain—and that's most of us—it is critical to be able to track the movements of potential prey and predators. To this, some animals—notably those that moved to land—added another purpose. Having evolved systems of mating that required proximal copulation, these animals not only must search out predators and prey, but conspecifics, as well.

From an early point in the evolution of land animals, then, it seems a high priority for vision was tracking animate objects, and accurately categorizing them in one of four coarse categories: food, mate, threat, or distraction. By no means is vision the solitary sense dedicated to this task, but of all the senses, it is among the best-suited to monitoring animate objects. We therefore expect visual attention to be used in two ways: first, in a goal-directed fashion, to mediate interactions with the environment by monitoring the spatial relationship of the body to proximal objects; second, in a reactive fashion, to identify animate objects in the environment and appropriately categorize them in terms of behavior response: feed on prey; mate with conspecifics; hide, fight or flee from predators; and otherwise ignore dynamic objects until they impinge upon immediate behavioral goals.

1.2.3 What can we learn from the overt attention of others?

Because all seeing animals have the same gross slate of visual priorities—to mediate intentional acts and to attend for relevant animate objects—we can use their overt eye movements as an indicator of their imminent intentions and as a cue toward

the location of animate objects. For most animals, the significance of this information is probably fairly limited. First and foremost, if something is looking at you, you should attend it: best-case scenario, it wants to mate with you; middling, it noticed you might like to eat it; worst, it wants to eat you. To the extent that the animals care about the eye movements of others, their first priority is to detect eye contact.

A subtler kind of information can also be gleaned, but its value is quite limited: Though experimental evidence is lacking, the eye movements of both predators and prey likely predict the pathways they will use for pursuit or escape, respectively. For many animals, this is the extent to which information about gaze direction—other than eye contact—can help them. For animals that live in groups, however, there is more to learn.

Because group-living animals share a basic goal set—eating similar food, avoiding similar predators—the behavioral state of other animals can encode useful information. Reading the intention of other animals can help recognize food sources and group movements, while reading the attention of other animals can speed threat-detection and antipredator behavior (c.f. Giraldeau 1997). For these reasons, it is not unreasonable to suspect that group-living animals have a tendency to ‘mirror’ the behavioral state of other creatures, and that this ability might extend to mirroring the state of attention, as indicated by gaze direction.

For intensely social creatures, such as ourselves and our evolutionary ancestors, the picture becomes much more complicated. Inevitably, primates find that conspecifics can be either allies or antagonists, and are forced to devote computational resources to deciding who is who. It is believed that the earliest primates were modestly social, and the various radiations from this lineage have been marked by several parallel trends: decreasing reliance on olfaction, increasing reliance on vision, increasing use of visual displays, increasing brain size, and increasing social complexity (Allman 1999). Theorists have suggested that these trends are linked: the transition from olfactory to visual communication (Gilad et al. 2004) brought primates the ability to flexibly deploy social signals in a directional way, to specific members of a social group (Allman 1999); meanwhile, the increasing social complexity of primate groups necessitated an expansion of cortex, with a large part of it devoted to decoding social relationships (Barton and Dunbar 1997; Reader and Laland 2002).

For such social creatures, decoding whether another individual should be treated as a threat or an opportunity—e.g. for mating or displacement at a food source—is a complex computation which requires an awareness of historical and present social relationships. Evidence from the field suggests that monkeys have a strong awareness of group membership and a fairly rich representation of relationships and alliances within their group. It is not hard to see how the construction and maintenance of these rich

representations would be aided by an ability to read the attentional state and emotional responses of other monkeys.

1.2.4 Gaze following is a prerequisite for theory of mind

Great uncertainty exists as to whether, and how, the empathic primitives of attention-reading and emotion-reading are combined into a mentalistic account of another individual: that is, whether these abilities combine to form a fully-fledged “theory of mind.” It remains a subject of great debate not only whether nonhuman animals possess this ability, and whether it relies upon processes of simulation or on “folk psychological” rules, but even what observable skills, exactly, a “theory of mind” might produce. In outline, a theory of mind involves mentalistic attributions of beliefs, perceptions, goals, and strategies. This is a deeper and more enigmatic type of representation than mere Skinnerian responses to predictive social signals. Premack (Premack and Woodruff 1978) stressed that theory of mind involves an unlikely leap of faith: to paraphrase Seyfarth and Cheney (Seyfarth and Cheney 2003), it’s called a “theory” because one can never directly observe the mental states that one, nonetheless, believes exist.

For a theory of mind to successfully predict action, it must correctly integrate the external signals of an animal’s internal mental state. Simon Baron-Cohen has echoed Premack’s claim that humans evolved to attribute mental states to others, and hypothesized that doing so involves four hierarchical models: an intentionality detector,

an eye direction detector, a shared attention mechanism, and a theory of mind mechanism (Baron-Cohen 1994). The shared attention mechanism, in Baron-Cohen's view, simultaneously allocates attention both to an actor and the target of its actions; it must be built upon the foundation of pre-existing modules detecting intentionality and eye direction. This shared attention mechanism is, in turn, foundational to theory of mind. Baron-Cohen sees the shared attention mechanism as the source of dysfunction in autism: The lack of shared (also called "joint" or "triadic") attention is believed to have a cascading effect, disrupting the development not just of theory of mind, but also other highly-derived aspects of social competence, such as language.

It remains unclear what processes might transform passive recognition of another's attention into an active convergence of perspectives and goals. It seems likely that some sort of innate process must promote this social coordination, because it seems to arise early in development, before individuals have the skill to contribute to and benefit from collaborative pursuits (Tomasello et al. 2005). Seyfarth and Cheney argue that no extrahominid species—however rich their communicative repertoire—attempts to influence behavior *by means* of mental state (Seyfarth and Cheney 2003). Interestingly, Tomasello and colleagues argue that apes have some ability to make mentalistic attributions, but that these skills are constrained by a paucity of motivation to share the attention, and especially intentions, of others (Tomasello et al. 2005). They further suggest that only humans have evolved this motivation, and that it likely arose due to a

uniquely-hominan excess of cooperative over competitive in-group interactions.

Refining Baron-Cohen's claim, they hold that the absence of this affective predisposition may be the root cause of social dysfunction in autism.

The phylogenetic extent of theory of mind remains controversial. It is not logically necessary that culture require mentalistic representation, because inter-group variation easily arises from any learned pattern of communication. Nonetheless, Frans de Waal argues these features seem to emerge at a common phylogenetic point within primates, namely the ancestral hominid (de Waal 2003). It seems plausible, then, that the ability to share attention, and especially intention, is the key step in the evolution of derived skills as referential language and deictic gesture.

Human theory of mind is almost certainly constructed during development, learned via innately specified interests and biases. As such, the ontogeny of this ability may be as revealing as its phylogeny. Tomasello (Tomasello et al. 2005) describes the ontogeny of human theory of mind as a three-step process. First, infants interacting with adults meet eye contact, alternate active and passive motor roles, and mirror emotions. Around 9-12 months, they begin to play while alternating between eye contact and gaze following, and appear to imitate motor activities and mirror goal states expressed by adults. Finally, starting at 12-15 months, they begin to initiate these collaborative activities, as if motivated to share experiences and goals, and also to use a richer repertoire of communicative signals including deictic gestures and speech. The

development of turn-taking and action coordination, like the drive to share experiences and intentions, appears to be uniquely human. Those apes' activities that appear cooperative, such as hunting and territorial defense, appear to occur through uncoordinated, individual responses to stimuli (Tomasello et al. 2005, but note the de Waal and Boesch commentaries; see also de Waal 2003).

Interestingly, this prosocial outlook among human infants is not universal but structured: early in life, familiar individuals are preferred, especially adults, especially primary caregivers (Tomasello et al. 2005 commentaries, particularly Brownell et al. and Hatano and Takahashi). It is striking that this prioritization of shared attention resembles the allocation of deployed attention by wild primates. Chance hypothesized that social saliency is the glue that binds primate hierarchies, in that the preferential allocation of attention to allies and dominant individuals is a central feature characterizing primate social groups (Chance 1967). Intriguingly, attention and attraction appear to be mutually reinforcing: attended stimuli become more attractive (Bornstein 1989; Raymond et al. 2003; Shimojo et al. 2003) (perhaps mediated by perceptual fluency, see Zajonc 1968; Bornstein 1989), while attractive stimuli sustain attention and unattractive abbreviate it (Compton 2003). Social attention may thus be a major prosocial factor necessary for developing theory of mind.

In summary, I'd like to suggest something like the following might occur: theory of mind is constructed during development from an innate tendency to attend, and to

mirror the attention, of others. This tendency is gated by social saliency, which is highest for caregivers, and is reinforced during development by the fact that successful engagement with parents elicits parental care. This triadic attention makes strong demands on executive function, in that babies must alternate between roles (active/passive) and subjects of attention (social agent/object of mutual regard) while simultaneously holding both in mind. This drives social knowledge that helps older infants to recognize—and mirror—intent, once again as gated by social bonds. This innate bias is again amplified by conditioning during development, in that successful collaboration with allies brings rewards. As knowledge of social collaboration is strengthened, it can be generalized and contingently extended to other, less closely-bonded individuals.

1.3 Specific Aims

The ability to collaborate with others is the foundation of human success, both for our species and as individuals: we thrive only when we can quickly and reliably coordinate with one another. Current evidence suggests that social skills develop through the interaction of innate mechanisms with our social environment, a process that breaks down in developmental disorders such as autism. Social attention appears to play a critical role in the social skill ontogeny, both privileging social stimuli for access to learning mechanisms, and patterning the way those social stimuli are

perceived to interact with their environment. In particular, the ability to recognize, interpret, and follow gaze cues has been proposed as a critical prerequisite for normal social development.

The past three decades have been marked by extensive research into visual perception and the effects of social cues on visual attention. It is only more recently, however, that neuroscience has made a targeted effort to understand perceptual and attentional processing of critically important naturalistic stimuli such as social cues. In particular, it was only recognized a decade ago that observed gaze acts as an obligate cue, shifting human visuospatial attention within tens of milliseconds (Friesen and Kingstone 1998a; Driver et al. 1999b; Langton and Bruce 1999a). Though it was initially suggested that this response might be uniquely human, it now appears that diverse species follow gaze (Emery 2000; Itakura 2004), and in particular, that monkeys follow gaze through similar mechanisms to humans (Deaner and Platt 2003).

Despite the presence of gaze-following behavior in diverse species, and despite its proposed importance to human social development and language acquisition, the pathways integrating social cues with attention remain poorly explored. Social attention fits poorly with past paradigms of attention as dichotomously bottom-up or top-down (Friesen and Kingstone 1998a), and had no known neurobiological substrate. Furthermore, it was likewise unknown whether gaze following was mediated by a classic, informationally-encapsulated cognitive module (Fodor 1983; Baron-Cohen 1994)

or whether, instead, it was responsive to social and behavioral contexts. Finally, a crucial question remained regarding the phylogeny of gaze-following behavior: is primate gaze following unique, or might it share ancestry with gaze following observed in diverse non-primate species?

AIM 1: Determine whether social gaze cues influence prosimian primates under naturalistic conditions.

We addressed the issue of phylogeny first. Past reports suggested that prosimian primates could not follow gaze (Itakura 1996b; Anderson and Mitchell 1999), suggesting that gaze following behavior independently arose in diverse lineages (Itakura 2004). Furthermore, testing methods in captive animals left it uncertain to what extent animals used gaze cues in their natural behavior (Emery 2000; Itakura 2004). To address these issues, we implemented a telemetric gaze-tracking system for measuring social orienting behavior in a freely-moving nonhuman primate. By measuring and analyzing gaze behavior in a colony of ringtailed lemurs (*Lemur catta*) at the Duke Lemur Center, we examined orienting behaviors in interactive social contexts and naturalistic environments. This study marked the first quantitative measurement of ocular orienting by lemurs, the first recording of social attention in lemurs, and the first report that prosimians do, in fact, follow gaze of conspecifics in their natural interactions.

AIM 2: Determine whether social gaze cues in anthropoid primates are reflexive or cognitive.

Based on psychophysical responses to various asocial cues, researchers have classically modeled shifts of attention as mediated through one of two processes, which respectively operate in a bottom-up (“exogenous”, “reflexive”, etc) or top-down (“endogenous”, “voluntary”, etc) fashion (Jonides 1981b; Muller and Rabbitt 1989). In parallel, psychologists have argued that specific cognitive adaptations are generally mediated by specific, informationally-encapsulated systems (Fodor 1983). Because of its speed, automaticity, and proposed evolutionary importance, gaze following was proposed to have a modular mechanism supporting bottom-up attention (Friesen and Kingstone 1998a; Driver et al. 1999b; Langton and Bruce 1999a). However, the behavioral relevance of a gaze cue depends critically on the social context: dominant individuals can displace subordinates at resources, adults may more efficiently explore their environment than children, etc. We explored the psychophysical dynamics of fast gaze following behaviors of both monkeys and humans, specifically investigating differential responses to individuals of different social categories. We found evidence that gaze following is neither informationally-encapsulated nor strictly reflexive, but rather responds to variables such as familiarity and dominance rank. Furthermore, we found evidence for heterogeneity in gaze following strength across subjects, consistent with the possibility that biological factors such as testosterone may suppress gaze following.

AIM 3: Determine whether, and when, gaze-following cues influence posterior parietal orienting areas, specifically macaque LIP.

The lateral intraparietal area (LIP) of the macaque brain plays an important role in both overt and covert shifts of visual attention. Along with the supplemental and frontal eye fields, it comprises the primary cortical control system governing eye movements. Neurons in LIP have well-defined retinotopic response fields, are activated during oculomotor (Gnadt et al. 1991) or attentional deployment (Colby and Goldberg 1999), and predict both instructed and intrinsic rewards from oculomotor behavior (Platt and Glimcher 1999; Klein et al. 2008b). Importantly, LIP is interconnected with areas in the superior temporal sulcus (STS) that process gaze and facial expression (Seltzer and Pandya 1991). LIP was thus a natural cortical route through which the perception of a gaze cue might influence attention. To address this possibility, we recorded extracellular responses of LIP neurons in a socially-cued saccadic reaction time task similar to those used in past behavioral experiments (Posner 1980; Friesen and Kingstone 1998a; Deaner and Platt 2003). We were particularly concerned as to the time course of neuronal and behavioral cue responses, to distinguish whether LIP was mediating or merely reflecting the fastest gaze-following responses. Our findings suggest that neurons in LIP are modulated by gaze cues, and that excitatory modulations have similar time course to cued decreases in saccade onset latency. Furthermore, we note that gaze-excited LIP neurons may represent a novel class of “mirror” neurons, theorized to mediate social perception through simulation of

observed body motor actions. LIP mirror neurons appear particularly novel, because they reflect not just oculomotor activity but sustained attentional state. As such, they may be uniquely useful in mediating cognitive social processes such as joint attention.

2. Background: Observed Gaze

Gaze shifts play a crucial role in the perceptual processes of visual animals: the brain must determine which regions of visual space will most adaptively inform future behavior, stabilize the world across gaze shifts by predicting the retinotopic consequences of saccades, and balance informational salience with the costs and benefits of gaze-related social signals (van Hoof 1967; Argyle and Cook 1976). The relevance of gaze control for cognition is pervasive: common processes govern eye movements and attention shifts (e.g. Sperling and Weichselgartner 1995), and these processes are probably the most basic by which goal-directed computations alter incoming sensory stimuli. It has even been argued (Ballard et al. 1997) that the computations involved in gaze control are so fundamental that they constitute a basic template for, and constraint upon, all other cognitive operations.

But at some level, we already suspected this, didn't we? Cicero noted "*oculus animi index*" — "the eyes are the windows to the soul" — and most of us have tried a variant on the line in one or another adolescent poem. Gaze cues play a large role in regulating human social interactions, indexing social rank and social expectation, and actively regulating turn-taking in conversations [Argyle & Cook, Kleinke]. When we want to know someone's true beliefs or desires, we know to look to their eyes. What do they attend? Then that is where their goals lie.

Typical humans look toward social stimuli. We look toward movement, particularly biological movement, and toward bodies, faces on bodies, eyes within faces, and, especially, eyes making eye contact. Furthermore, we use movement and orientation as a deictic cue—a pointer—directing our attention toward the same regions of space as other individuals. We understand gaze and gesture as occurring in three dimensions, requiring us to localize individuals and consider the perspective available to them, and we understand that individuals are dynamically linked with the objects and regions they orient toward. Finally, this gaze following occurs both quickly and reflexively, in a nuanced and contextually-sensitive fashion; gaze perception interacts with the perception of other social variables in a bidirectional manner.

When confronted with a scene, with no predefined task or instruction, we generally look toward social content: animate objects, especially people, especially faces, and most especially eyes (Yarbus 1967b; Birmingham et al. 2007; Fletcher-Watson et al. 2008a; see also Keating and Keating 1982; Kyes and Candland 1987; Guo et al. 2003 for replication in nonhuman primates). This orienting bias is fast: saccades are preferentially directed toward animals and people as early as 120ms after stimulus presentation (Kirchner and Thorpe 2006; Fletcher-Watson et al. 2008a). The eye region is rich in musculature involved in emotional expression (Ekman 1993; Smith et al. 2005), and fixations toward the eye region may be particularly important in discriminating key affective signals (e.g. see Adolphs et al. 2005). But the *orientation* of observed eyes, and

not merely their surrounding musculature, also influences our visual exploration. Our sensitivity to gaze direction manifests itself in two fundamental ways: first, as sensitivity to being watched, in which we discriminate whether we are being attended by another individual; second, as a sensitivity to deictic gaze, where we discriminate between distal regions which are, or are not, the focus of another individual's attention.

There is overwhelming evidence that the first manner of sensitivity to gaze direction—sensitivity to being watched—is both innate and widespread. The saliency of eye contact is evident soon after parturition: infants prefer full-face to non-face configurations within 72 hours (Macchi Cassia et al. 2001), and prefer direct to averted gaze within 2-5 days (Farroni et al. 2002) and by gestation age 10 months (Batki et al. 2000). Furthermore, this sensitivity is widespread, being shared with diverse vertebrates, reported variously in fish (Coss 1979), primitive primates (Coss 1978), marine mammals (Xitco et al. 2004), lizards (Burger et al. 1992), snakes (Burghardt and Greene 1988), and birds (Ristau 1991).

The second manner of sensitivity to gaze direction—the use of gaze as a deictic cue—remains mysterious. Four questions stand out: Where does it arise in development? How did it evolve? How does it relate to other abilities? And, ultimately, what are the mechanisms?

2.1 Sensitivity to Deictic Gaze in Typical Humans

Typical adults look where other people look. Moreover, the fact that humans use these social cues is common knowledge: publishers have long known to place photographs so that pictured gaze steers people to the intended part of a layout, and ball players have long practiced the head-fake and “no-look” pass. It is only recently, however, that scientists have characterized the psychophysics of this gaze-following response. Since then, a trove of studies has explored the precise nature of these attention shifts.

Early investigations of spatial attention shifts drew a dichotomy between exogenous (reflexive, automatic, bottom-up, stimulus-driven...) and endogenous (intentional, cognitive, conscious, top-down, goal-directed...) attention. These shifts can be characterized both via direct observation, in the case of eye movements, and indirectly, via increased perceptual speed (decreased reaction time, or RT), perceptual sensitivity (perceptual threshold), and target choice. Briefly, exogenous attention is evoked locally by abrupt changes in a region of space; attentional deployment responds quickly, fades quickly, and is replaced with an inhibitory backlash called “inhibition of return” (IOR) (Jonides 1981b; Posner and Cohen 1984; Muller and Rabbitt 1989; Klein 2000). Endogenous attention, in contrast, can be evoked by any useful spatial cue; attentional deployment is slow, sustained, and relies upon the learned predictive value of the cue (Jonides 1981b; Posner and Cohen 1984; Muller and Rabbitt 1989).

Friesen and Kingstone (1998) complicated this picture, showing that the naturalistic cue of observed gaze influenced spatial attention quickly, seemingly reflexively, but at distance. As with earlier studies on nonsocial attention, they based their experiments on the simple Posner cuing paradigm (Posner 1980) in which subjects fixate a central point, see a cue (in this case a centrally-presented schematic face with eyes directed to the left or right), and lastly, responded to a target that appears randomly to the left or right of fixation. They found the face cues sped responses to targets that appeared in the direction of gaze, despite the fact that cues did not predict target location. Moreover, the gaze following effect arose quickly—within 105ms—and was evident regardless of whether subjects were asked to detect, locate, or discriminate between targets.

Since this seminal work, gaze following has been replicated in over a dozen studies (reviewed Frischen and Tipper 2004). From the start, Friesen and Kingstone (1998) explicitly linked the behavior to Baron-Cohen's (1994) suggestion that a unique neural module mediated joint attention. For this reason, the earliest investigations using their paradigm queried whether gaze following was truly an innate, reflexive process.

2.1.1 Reflexivity

Friesen and Kingstone, by showing that observation of nonpredictive eye-gaze shifted attention within 100ms, made a strong case that social attention cues acted in an exogenous fashion. These results were quickly strengthened by Langton and Bruce's

(1999) finding that nonpredictive head-gaze cues evoked a similarly fast shift, and especially by Driver et al's finding (1999) that gaze following was evoked even when photographed gaze cues were—four times out of five—explicitly *counterpredictive*! Subsequent studies would elaborate these findings, consistently finding that socially-cued attention shifts were faster than, and independent of, endogenous shifts. In general, gaze-following effects arose within 100 ms and decayed slowly, with endogenous attention dominating gaze-cued attention after ~600 ms (Friesen and Kingstone 1998a; Driver et al. 1999b; Langton and Bruce 1999a). Gaze cues did not generate IOR at typical cue-to-target intervals (Friesen and Kingstone 1998a; Driver et al. 1999b; Langton and Bruce 1999a; Friesen and Kingstone 2003a, 2003b; Friesen et al. 2004; Friesen et al. 2005). However, IOR was evoked in a study using longer intervals and a slightly modified paradigm (Frischen et al. 2007). Though gaze following has consistently been reported across studies, it is important to note that the effect size is frequently modest, generally much less than a standard deviation.

2.1.2 Modulation by Social Context

Together, these studies suggested that observed gaze quickly shifts attention, even when task-irrelevant, and that this attentional shift is likely mediated by exogenous rather than endogenous orienting systems. In these respects, the data seem strongly consonant with Baron-Cohen's proposal for a modular gaze-following system endemic to humans. Several lines of inquiry suggest that the story is not this simple: gaze

following strength varies across individuals and conditions, suggesting that the mechanisms for gaze following are responsive to a variety of social variables.

Individual differences in gaze following are pronounced. Females show stronger gaze cuing effects than males, particularly at later cue durations; furthermore, these sustained gaze cuing effects correlate inversely with autism quotient, as assessed by questionnaire (Bayliss et al. 2005). Context effects are also evident. While Heitanen and colleagues (Hietanen and Leppanen 2003) failed to find influences of emotion on gaze following, subsequent investigators found that emotions modulated gaze-following responses in subpopulations for whom they were especially salient: for example, two studies have reported enhanced gaze-following of fearful faces by psychologically healthy individuals with high trait-anxiety scores (Mathews et al. 2003; Putman et al. 2006); another found that gaze following was modulated both by cue gender and cue expression, with male gaze more strongly followed than female gaze, and with female gaze followed most strongly when it carried positive affect (Hori et al. 2005).

2.1.3 Uniqueness

While the orientation of the eyes was the first reported type of social orienting cue, it quickly emerged that there were others. Conceptually, body, limb, head, and eye orientation are all cues to the direction of attention and of action, and indeed, the latter have all been shown to quickly influence attention. However, some studies have found

that nonpredictive symbolic cues can also quickly reorient attention. How unique, then, are these social cuing effects?

When humans shift their orientation, their eyes move fastest, followed by their head, followed by their body (e.g. Suzuki et al. 2008). Furthermore, the position of our eyes strongly constrains our attentional focus, much as the posture of our limbs constrain our potential actions. Our head and body orientations, by contrast, make much weaker predictions about where we currently attend and next intend to act. For all of these reasons, we might expect that observed eyes, more than any other bodily signal, most strongly influence our deployments of attention. Friesen and Kingstone (1998) established that humans follow eye gaze, and Langton and Bruce (1999) replicated the effect using photos of individuals with heads oriented up, down, left, or right; gaze following of both cue types is similar in speed and magnitude (Deaner and Platt 2003). Further, snap judgments of gaze direction were confounded when head and eyes were oriented differently (Langton 2000), and similar interference occurred for conflicting head orientation and pointing gestures (Langton and Bruce 2000). An intriguing exception: gaze following responses are *stronger* for incongruent head and body directions, where the lateral rotation of the head relative to the body may suggest temporal specificity (Hietanen 2002).

Gaze cues can be schematic (e.g. Friesen and Kingstone 1998a) or photographic (e.g. Langton and Bruce 1999a), and need not be human, or even all that biologically

plausible: Humans follow not only the gaze of photographed monkeys (Deaner and Platt 2003) but also of cartoons, including eye-endowed gloves and apples (Quadflieg et al. 2004). In a particularly clever study, Ristic and colleagues showed that gaze following was evoked by an ambiguous stimulus only if the stimulus had been perceived as a social being (Ristic and Kingstone 2005): If the stimulus was perceived as a car, no attention shift was evident, but if the stimulus was perceived as eyes under a hat, then subjects followed gaze. Interestingly, subjects prompted to switch their categorization were able to activate, but never to inactivate, gaze following, suggesting that social attribution is privileged and irreversible.

More controversial is whether culturally-ingrained symbolic cues, such as arrows, can also generate fast, gaze-following-like responses. Ricciardelli and colleagues (Ricciardelli et al. 2002, but see also Kuhn and Benson 2007) found that social gaze cues, but not arrows, primed congruent saccades. In two other studies, however, attention reflexively shifted in response to arrows: nonpredictive arrows produced covert attention shifts (Tipples 2002), and these attention shifts were comparable to gaze-following responses (Ristic et al. 2002). Arrows were not reflexively followed when counter-predictive; gaze cues, in contrast, always produced a cuing effect (Friesen et al. 2004). Subsequent studies suggested various subtle differences between social and symbolic cuing, while reaffirming a basic similarity in the size and time-course of attentional response to nonpredictive gaze and arrows (Langdon and Smith 2005; Kuhn

and Benson 2007; Ristic et al. 2007). These findings suggest that symbolic communication using arrows evokes an endogenous response that builds synergistically on intrinsic orienting responses (Ristic and Kingstone 2006). This prompts the intriguing question of whether arrows work, in part, by abstracting deictic social cues. While an appealing idea, the fact that averted eyes, angled noses or snouts, and gesturing hands seems plausibly 'arrow-like' suggests that any low-level biological derivation would be highly abstract, at best.

2.1.4 Perceptual Basis

What perceptual cues are used to interpret social orienting cues? In considering this point it is important to speak both of gaze perception and gaze-following responses, while noting that the same perceptual rules do not necessarily govern both processes. It is entirely possible, in principal, to evoke an attention shift without a corresponding sense of gaze direction, or conversely, to perceive gaze without shifting attention.

Perception of eye gaze direction relies upon locating dark pupils in the lighter background of the sclera, and is impaired when this contrast is reversed (Ricciardelli et al. 2000; Sinha 2000), regardless of whether the background face has also been reversed, or whether the eyes appear in natural or unnatural colors (Ricciardelli et al. 2000). Indeed, gaze-following is increased when scleral area is increased in "wide eyed" cues, and reversed when contrast is reversed in "photo negative" cues (Tipples 2005, though note Ristic et al. 2007). Furthermore, gaze perception was distorted by luminance

changes in a graded fashion (Ando 2002), but contextualized by the immediately surrounding face (Ando 2004), suggesting that local luminance contrasts are used to determine the direction of eye gaze. The positioning of shadows created by the brow in natural lighting conditions may be an important part of this calculation, as inversion of the eyes disrupts gaze perception independently of whether the rest of the head is present and is, or is not, inverted (Jenkins and Langton 2003; Schwaninger et al. 2005). Interestingly, the eye region of humans is uniquely salient, with sharp contrasts between our white sclera and dark pupils (Kobayashi and Kohshima 1997).

Perception of eye direction thus appears to be component-based rather than configural. Gaze processing, however, reflects the integration of perceived eye and head orientation, and these processes are at least partly configural. For example, head profile influences eye gaze perception both in upright and upside-down faces, but nose angle influences gaze perception only for upright faces (Langton et al. 2004). This echoes Langton and Bruce's earlier finding (1999) that gaze-following responses to inverted heads were reduced, but not eliminated, relative to upright. However, the perception of head, face, and eye orientation appear to interact in a complex and dynamic fashion, sometimes reinforcing gaze discrimination when congruent, sometimes reinforcing gaze discrimination when contrasting (Ricciardelli and Driver 2008). This, in turn, echoes Heitanen's finding (2002) that incongruent head and eye direction can sometimes facilitate gaze-following responses to the eyes.

Spatial rotations, like spatial inversions, have also garnered interest. Gaze necessarily relates the internal spatial arrangement of a face with the external spatial arrangement of the environment. This distinction is particularly useful in that gaze-following behavior might include aspects of physical mimicry, driven by head-centered spatial posture, or of deictic signaling, driven by world-centered spatial relationships. Adaptation to perceived eye direction occurs along a left-to-right continuum (Seyama 2006; Seyama and Nagayama 2006) in both reference frames, with 90° rotations revealing adaptation to face posture and 180° dominated by adaptation to gaze direction (Seyama 2006). Jenkins and colleagues, however, reported (Jenkins et al. 2006) that gaze adaptation is neither continuous nor concretely linked to posture: adaptation occurs separately for left- and rightward directions, and occurs even when the face scale and head-vs-eye gaze components are altered. Interestingly, it seems that gaze-following is at least partially head-centered, in that 90° rotations of faces produce slight cuing effects both in the world-centered frame, reflecting external relationships, and in the internal reference frame, as if the faces had been presented upright (Bayliss and Tipper 2006a). This echoes Tipples's finding (2005) that inversion of schematic and photographed eye gaze effects diminishes vertical, but not horizontal, gaze-following behavior.

The accuracy of gaze following responses has received only minimal testing, but in a naturalistic change-detection paradigm, gaze-following responses appeared to have a broad angular distribution (Langton et al. 2006). The results are interesting, in part,

because they contrast with experimental results regarding gaze discrimination.

Detection of direct gaze is strongly sensitive to social context, but is detected as a cone of relatively fixed, 4-9° angular width (Gamer and Hecht 2007). Perception of deictic gaze toward objects is even more precisely tuned, with a standard deviation of only 3° degrees (Bock et al. 2008).

2.1.5 Relevance for Natural Behavior

Humans follow the gaze of other humans: we look where other humans look.

Paired with an ostentive cue such as eye contact, we use caricatured gazing and reaching gestures to explicitly direct attention. The links between short-latency, psychophysically-detected gaze-following responses and naturalistic gaze has only recently been explored. As discussed above, Langton and colleagues have shown (2006) that gaze cues speed responses in a change-blindness task. Similarly, Fletcher-Watson and colleagues found (Fletcher-Watson et al. 2008a) that while the first saccades to a social scene were toward faces, subsequent saccades tended to follow gaze.

Furthermore, just as perception of eye contact patterns interacts with affective judgments (Adams and Kleck 2005; Ganel et al. 2005), deictic gaze has also been recently found to influence affective scene evaluation. Specifically, faces that consistently gaze in a counterpredictive fashion are evaluated as less trustworthy than faces that consistently give useful cues (Bayliss and Tipper 2006b), and similarly, observed facial affect (but *not*

affective value, e.g. attractiveness, Strick et al. 2007) appears to spread toward the object regarded by that face (Bayliss et al. 2007).

Gaze recording in actual human social interactions is difficult, not least of which because humans alter their gaze in response to their awareness of being monitored. However, ongoing efforts to probe gaze behavior in natural interactions has promise for revealing how social scenes are constructed and evaluated, and for linking these processes to fast, psychophysical responses of affect and attention. I describe our efforts to pioneer gaze tracking of naturally-interacting primates in Chapter 4.

2.2 Sensitivity to Deictic Gaze in Nonhuman Species

It is taken for granted that typical human are social, and are motivated to comprehend the experiences of others. It is likewise taken for granted that typical adult humans make mentalistic attributions to others. Because of this, the focus of human gaze-following studies has been to suggest a possible psychological mechanism through which these cognitive skills might arise. In animal research, however, social interest and theory of mind are not taken for granted. Work on psychophysical responses to social stimuli has generally been seen as secondary to larger questions: can animals make mentalistic attributions, can they interpret behavioral cues to other's attention and intentions, and—more recently—under what conditions are they motivated to do so?

It is important to recognize the inherent difficulty of generalizing social attention and intention cues from humans to other species. In humans, these cues are readily interpreted and categorized: heads, and especially eyes, point in the direction of attention; bodies, and especially hands, point in the direction of intention. But the human eyes are, in two respects, rather unusual among vertebrates: they possess small, single, circular, well-defined fovea, and they are pigmented so as to be highly discernable to others (Kobayashi and Kohshima 2001). Human hands are similarly specialized: other species rely on alternate, possibly less salient, effectors.

Generalization of social cues beyond monkeys becomes quite difficult: alternate sensory specializations increase the importance of ear and nose orientation versus more familiar ocular cues, for example; and alternate sense organ layout may make attentional direction difficult to even define—consider the case of the robin, averting its head 90° to point a solitary eye toward a worm. The deictic social cues that apply to other species may not be readily apparent to us, nor ours to them.

Group-living wild animals must coordinate their movements with the other members of their social group; likewise, predatory animals coordinate their movements with the movements of their prey. It would be surprising if these processes occurred without some minimal level of awareness and attention to the intended movements of others. To understand whether animals respond to the psychological states of others, researchers began by investigating whether animals could interpret human gesture and

gaze in order to find food. Later, these efforts diversified to investigate spontaneous responses, conspecific cues, and a growing awareness that tests of cooperative interaction may underestimate the psychological knowledge of species for which competitive interactions are more typical. This review will be necessarily incomplete, but will attempt to trace the major findings regarding attention cues used by other species.

2.2.1 Use of Interspecific Deictic Cues

Anecdotal reports suggest that some species of primate, notably chimpanzees, bonobos, and perhaps capuchins, may spontaneously attempt to direct other's attention through gesture (de Waal 2003); similar observations have been made in social hunters such as wolves (e.g. see Miklosi and Soproni 2006). Perhaps for this reason, the use of gaze and pointing cues were first identified in these species, when tested in laboratory settings (capuchins, Anderson et al. 1996; chimps, Povinelli and Eddy 1996; chimps and an orangutan, but not lower primates, Itakura 1996b). Later studies built upon these results to suggest that anthropoid primates, but not prosimians, spontaneously follow human gaze (macaques but not lemurs, Anderson and Mitchell 1999; marmosets, Burkart and Heschl 2006; all great apes, Brauer et al. 2005). In marmosets and apes, this gaze following behavior was shown to be fairly sophisticated, in that it passed behind barriers and thus required some understanding of the human's point of view (Brauer et al. 2005; Burkart and Heschl 2006). These studies contrast strikingly with the failure of

most primates to use human cues to choose between potential food sources, probably—at least in part—because of the tendency toward competitive rather than cooperative foraging in these animals (c.f. Hare and Tomasello 2004; Miklosi and Soproni 2006).

Intriguingly, use of human deictic cues is also found in some nonhuman species. First, they are evident in a number of domesticated species. Horses may have a limited ability to follow pointing cues to hidden food (Maros et al. 2008). Likewise, goats do not follow human gaze but can use human pointing cues to find food (Kaminski et al. 2005). Comprehension of proximal pointing and touch gestures may piggy-back on essentially nonsocial processes like local enhancement (see Miklosi and Soproni 2006 for a review of pointing comprehension). More impressively, dogs both follow (Soproni et al. 2001; Miklosi et al. 2003) and direct (Miklosi et al. 2000; Miklosi et al. 2003) human gaze, suggesting the capability for shared attention with humans. While socialized wolves also seem to follow human gaze under some circumstances, they do so less readily than dogs (Miklosi et al. 2003, see also Hare et al. 2002), suggesting that domestication has selected for an increased capacity for interspecific shared attention.

Outside of primates and domesticated animals, captive corvids and marine mammals have been shown to respond to deictic signals. Corvids—which include crows, magpies, and jays—are known for their advanced intellectual abilities (reviewed Clayton and Emery 2005), including tool use and, most recently, self-recognition via

mirror (Prior et al. 2008). Ravens have been shown also to follow human gaze cues, and further, to share the primate ability to follow gaze around barriers (Bugnyar et al. 2004).

Finally, dolphins and seals have some ability to follow pointing gestures (Shapiro et al. 2003), and some evidence has arisen that dolphins also have the ability to follow human pointing and head-gaze cues (e.g. Pack and Herman 2004). These results are somewhat curious, because marine mammals normally have limited experience with limb-mediated actions; results from seals are especially surprising because of the limited cooperative behavior in this species. Marine mammals raised in captivity are subjected to extensive training, however, and further research is necessary to determine whether these abilities are typical of animals in the wild.

2.2.2 Use of Conspecific Deictic Cues

While these interspecific abilities are impressive, a larger question is whether animals use social attention cues in their regular interactions with their own species. Surprisingly few studies have addressed this question, likely due to the difficulty of observing subtle gaze shifts at distance and of controlling naturalistic interactions.

It has been informally observed that wild primates sometimes appear to use social cues to guide their attention. Recently, attempts in more controlled studies have found widespread use of conspecific social cues among the species discussed above (chimps, mangabeys, and several species of macaque, Tomasello et al. 1998); domesticated goats, Kaminski et al. 2005; dogs, Hare and Tomasello 1999). Dolphins

posed a particularly fascinating case: while they have not yet been shown to follow gaze, *per se*, they are reported to eavesdrop on, and successfully use, conspecific echolocation pulses (Xitco and Roitblat 1996).

In my work with Michael Platt, we've attempted to develop new techniques to study the use of social attention cues during natural interactions among conspecifics. In Chapter 4, I describe our study of spontaneous gaze following by interacting, naturalistically-housed ringtailed lemurs.

2.2.3 Psychophysics of Gaze Following in Animals

Initial attempts to study conspecific gaze-following in the laboratory had mixed results. While macaques were shown to preferentially orient in the same direction as a videotaped conspecific (Emery et al. 1997), this effect was not replicated in baboons seeing photographs of humans (Fagot and Deruelle 2002). Later experiments affirmed that macaques do follow the gaze of conspecifics, and showed that the attention shifts evoked by observed gaze are similar in magnitude and time-course for both humans and macaques (Deaner and Platt 2003). Furthermore, like humans, macaques are variable in their gaze-following responses: though facial expressions did not strongly modulate gaze following of photographed humans, female macaques follow gaze significantly more than males (Paukner et al. 2007). I describe our research on status contingency in macaque gaze following in Chapter 5.

2.3 Deictic Gaze in Development and Disorder

There is broad theoretical agreement that social cognition is constructed through the interaction of innate mechanisms with developmental experience. To place gaze-following behavior in context, then, it is important to consider when it arises in development—and how this development is altered in social pathology. This is particularly challenging for two reasons. Firstly, most developmental studies are essentially correlative, not causal, despite the appearance of causality implied by temporal sequence. For example, it could be that early gaze following deficit predicts later language deficit, not because the former causes the latter, but because both are disrupted by generalized neural dysfunction. Secondly, it seems likely that natural gaze following behavior involves multiple processes: first, the ability and motivation to attend social stimuli despite potential distractions; second, the release of attentional capture by faces after eye contact is withdrawn; third, a fast reflexive bias to attend in the direction of gaze; fourth, our potential nonsocial bias to follow motion cues; and fifth, any sustained motivation to learn what other individuals look toward. While the development and dysfunction of joint attention were recently subject to an excellent review (Nation and Penny 2008), I concisely summarize major findings and themes here.

2.3.1 Joint attention in typical development

From an early age, humans are sophisticated visual social animals. Human newborns, in many respects underdeveloped compared to other animals, already exhibit

visual preference for faces, particularly those of their mothers, and have a rudimentary attraction to direct gaze (Batki et al. 2000; Macchi Cassia et al. 2001; Farroni et al. 2002). Coordination of attention between individuals is brought about through the use of deictic and ostentive signals: respectively, signals that point toward objects or regions of space; and signals like eye contact or vocalization, which establish the communicative intent of the signaler. It is likely that these abilities are at least partially innate, and human children use both, in a seemingly purposeful manner, from an early age.

Infants make the uniquely human gesture of an index-finger-point from about 2 to 6 months of age, generally in response to interesting objects (reviewed Butterworth 1991); by 12 months, they use directed pointing as a communicative gesture (Liszkowski et al. 2004, see also Brooks and Meltzoff 2002). Pointing is likely perceived before it is produced, and may act to increase the saliency of deictic gaze cues, which are also recognized from an early age. Infants as young as two months have been reported to follow gaze, with a dramatic increase in gaze following between 7 and 11 months of age (Scaife and Bruner 1975); however, we must be cautious in interpreting these data because orienting baselines were not established. Butterworth (1991), reviewing the extant literature, described infants as following general gaze direction at 6 months, but only following precisely (i.e. to the correct object) by 12 months, and only following beyond the infant's point of view ("geometric" gaze following) after 18 months. The detailed time course of these overt behaviors remains controversial: some studies report

gaze following only after 10 months (e.g. Corkum and Moore 1998), and some report the emergence of geometric gaze following as early as 12 months (e.g. Moll and Tomasello 2004). There is some suggestion that gaze cues may influence covert mental processes from a much younger age.

While domain-general associative learning may play a role in the increasing sophistication of gaze following through development, it appears likely that any domain-general mechanism builds off innate social perceptions: for example, infants 8 to 9 months old could be trained to follow predictive gaze to one of two objects, but not to look opposite gaze when gaze was counterpredictive (Corkum and Moore 1998). Nonetheless, there is evidence that infants are sensitive to context when following gaze. Scaife and Bruner (1975), in their pioneering study, had observed informally that rates of gaze following were suppressed by the use of unfamiliar experimenters, rather than parents, as test cues. Since then, infants have been shown to preferentially follow the gaze of individuals who can see (at 10 months, more for open eyes than closed, and at 14 months, more for uncovered than blindfolded, Brooks and Meltzoff 2002, 2005) and who have a history of looking interesting places (at 14 months, Chow et al. 2008).

Two longitudinal studies have examined gaze following and its relation to other social and nonsocial skills. They found that gaze following in 10- to 11-month old infants, and especially vocalization in this context, was predictive of language acquisition assessed approximately 6 months later (Brooks and Meltzoff 2005). Joint

attention was confirmed to predict language acquisition in a subsequent study, but the study found a complex pattern of development (Mundy et al. 2007): no single domain-general or socially-specific module could explain individual differences in developmental trajectory. Initiation and response to joint attention, which predicted language acquisition, nonetheless appeared to each be distinct processes with distinct developmental trajectories. Basic awareness and manipulation of the intentions of others, in contrast, neither predicted language acquisition nor correlated with joint attention behavior.

Psychophysical methods have seen relatively sparse use in infants, for both practical and ethical reasons. Nonetheless, the several experiments performed have been quite useful for deconstructing the processes that contribute to gaze following. In a modified Posner cuing task, the attention of 3- to 7-month-old infants followed eye gaze, but not equivalent tongue movement. In a second experiment, gaze following was detectable by 4 months of age, but was masked by the infants' reluctance to disengage from the central face cue (Hood et al. 1998). In a subsequent study (Farroni et al. 2000), these results were replicated in 4- to 5-month-old infants using longer cue durations (1500ms vs. 1000ms in Hood et al.) and more intrinsically interesting targets (e.g. ducks vs. abstract shapes). In this study, however, gaze following was blocked when averted eyes were preceded directly by closed, and, in fact, reversed when the averted-gaze stimulus was created by moving the face away from the target while holding pupil

position constant. In a follow-up study, however, 4- to 5-month-old infants did not follow eye motion when faces were upside-down, nor when the eyes moved from averted to mutual gaze; demonstrating that a shift from mutual to averted gaze, and not motion *per se*, was the critical variable for gaze following (Farroni et al. 2002). Eye contact thus acts as an ostensive signal: mutual gaze—and especially infant-directed speech—act to increase the likelihood a gaze cue will be followed by a 6.5-month-old infant (Senju and Csibra 2008). Consonant with this, 4-month-old infants appear to process objects more deeply when those objects are inspected by others, even in the absence of overt orienting: when seeing two objects a second time, after first watching an adult gaze toward one while ignoring the other, infants treated the ignored object as more novel (Reid and Striano 2005). In total, these psychophysics suggest an innate gaze following reflex operates both in adults and in the youngest children ever tested. Further, it suggests that in children, as in adults, social factors that modulate the saliency of the face may also modulate the strength of the evoked gaze-following response.

2.3.2 Joint attention in nonhuman development

Few studies have compared human to nonhuman social development. Interspecific gaze following by macaques appears to begin between the 4th and 5th months and steadily increases, with a 'hotspot' of increased gaze following at about one year of age (Tomasello et al. 2001a). At later ages, adults follow gaze more than juveniles and adolescents, and only adults follow eye gaze by itself (Ferrari et al. 2000).

In contrast, chimpanzees did not reliably follow interspecific gaze until the third year—the end of their infancy, as opposed to middle-infancy for macaques (Tomasello et al. 2001a). However, Okamoto and colleagues reported (Okamoto et al. 2002) that a chimpanzee was sensitive to gaze signals at a much younger age, around 9 months, and would follow gaze when it predicted the position of food reward. Like adult macaques, adult chimpanzees can follow eye gaze without head rotation. However, even adult chimpanzees respond more to head- than eye-gaze, whereas human infants preferentially follow the eyes (Tomasello et al. 2006). This is consonant with the idea that the human eye has evolved increased visibility in order to facilitate gaze-following.

2.3.3 Joint attention in dysfunction

Visuosocial behavior is altered in a number of mental illnesses, most notably autism. Healthy humans show attentional bias away from negative stimuli despite the fact that these stimuli pop-out in search tasks (see Compton 2003), but emotion/attention interactions break down in a number of social disorders. Anxious subjects excessively orient toward and fail to disengage from threatening stimuli (see Compton 2003); dysphoric subjects fail to avoid negative face stimuli (Bradley et al. 1997); social phobics hyperscan faces and avoid gaze, particularly for angry faces (Horley et al. 2004). Likewise, schizophrenics are impaired when reading mental states from the eye region (Kington et al. 2000), follow averted gaze more reflexively (Langdon et al. 2006), and are slower when judging mutual gaze (Franck et al. 2002).

Most notable among human social pathologies, however, is autism. Autism is diagnosed, in part, based upon a marked “lack of spontaneous seeking to share enjoyment, interests, or achievements with other people”, or to respond appropriately when these experiences and emotions are shared by others (APA 1994). Furthermore, while there is disagreement as to the root causes of autism—for example, whether weak central coherence explains both social and nonsocial symptoms (Frith and Happe 1994)—there is general consensus that failures of joint attention are among the best predictors of autism in early childhood (see Charman 2003; Klin et al. 2002b).

Some reports have argued that autistic and typically-developing children have similar visual behavior, for example, equivalently exploring social and nonsocial elements of static cartoons (van der Geest et al. 2002). In contrast, Pelphrey and colleagues (Pelphrey et al. 2002) report that autistics adults are less likely to fixate core face areas, particularly eyes, than normal controls; furthermore, they were also impaired at identifying facial emotions, like fear, for which the eye region is discriminative. Similarly, while viewing short movie clips, autistic adolescents fixated eyes half as often as did matched controls, and failed to follow the deictic gestures of characters in the movie (Klin et al. 2002b, 2002a). Using stills, Fletcher-Watson et al failed to replicate decreased fixations toward the eyes, but confirmed that autistic adults made fewer social fixations than typical adults, especially in their first saccades to a scene, and that they failed to follow gaze cues in the photos (Fletcher-Watson et al. 2008b).

Several attempts have been made to investigate gaze-following behavior in autistics using a Posner cuing task, with mixed results. Several reports found that both autistics and typically-developing individuals followed nonpredictive dynamic gaze cues. As toddlers (Chawarska et al. 2003), school-age children (Swettenham et al. 2003; Kylliainen and Hietanen 2004; de Jong et al. 2008), and adults (Vlamings et al. 2005; Rutherford and Krysko 2008), autistics and neurotypicals followed gaze quickly and performed similarly on control tasks. Subtle differences were sometimes recorded: typically-developing toddlers, but not autistic toddlers, were delayed in looking away from faces (Chawarska et al. 2003; Johnson et al. 2005; Vlamings et al. 2005), and autistic children may follow gaze using atypical systems or stimulus features (de Jong et al. 2008). Other studies, however, have found that autistic toddlers (Johnson et al. 2005) and adults (Ristic et al. 2005) fail to reflexively follow gaze. Additionally, Senju and colleagues found that school age children followed gaze cues but not do so, as did typical children, more than arrows; moreover, they were generally slower to respond to targets (Senju et al. 2004); Leekham and colleagues found that while school-age autistics could follow gaze cues, spontaneous use of gaze cues was restricted to the children with mental ages of over four years (Leekham et al. 1998).

In any case, gaze following appears to impact cognition in autistics less than in neurotypicals. Among clinically normal subjects, Bayliss and colleagues found that individuals with a higher autism quotient were equally likely to follow gaze (Bayliss and

Tipper 2005), but less likely to modify social percepts based on gaze following validity (Bayliss and Tipper 2006b). Similarly, while typical subjects prepare to interact with objects they see another individual inspecting or manipulating, autistic subjects do not (Pierno et al. 2006). A challenge in this work has been the likelihood that extensive behavioral training masks the social deficits of adults, and the logical impossibility of testing autistic individuals for developmental delay in the critical window just *prior* to diagnosis. Additionally, it may be the case that gaze following tasks slightly miss the core social deficit in autism: echoing Mundy's finding distinguishing initiation and response to joint attention (Mundy et al. 2007), Bruinsma and colleagues argue that initiation, rather than response, is the most disrupted social skill in autism (Bruinsma et al. 2004).

The etiology of autism remains unknown. Some theorists have proposed that autism may represent an extreme of natural variation across individuals: for example, of gender-linked variation in social sensitivity (e.g. Baron-Cohen 2002). Indeed, on average, women respond more strongly than men to most social cues (Geary 1998), including gaze cues specifically (Bayliss et al. 2005). These arguments suggest that social orienting dysfunctions noted in autism may result from hypermasculinization of key brain areas. Similarly claims have been made about variation in serotonin function, dysfunction of which has been implicated in both autism (Wassink et al. 2007) and social anxiety disorder (Skuse 2006). Obviously, the discovery of biological factors that

exacerbate or ameliorate social function in autism is an important goal. However, given the multifactorial nature of the autism spectrum disorders (Abrahams and Geschwind 2008), it is highly unlikely there exists is any single cause—or simple solution.

3. Neural Mechanisms of Gaze Following

Social behavior involves, at minimum, neural circuitry coordinating sensory perception and behavioral response. While some simple innate, reflexive processes may use shared circuits for both aspects of this task, most social behaviors probably involve separable perceptual releasing mechanisms and behavioral pattern generators. Furthermore, responses to seen social cues may involve additional neural activity which maps to neither visual perception nor behavioral response, *per se*, but rather to intermediate processes. These processes might include covert attention shifts, reassessment of saliency or “informativeness” of regions of interest, and integration with variables such as behavioral goals and social context. Additionally, social behavior may involve representations of other minds—that is, mentalistic attributions, extrapolated through simulation or using intuited principals of “folk psychology”, but ultimately derived from observed physical indicators of attention, emotion, and intention.

A major goal of neuroethology is to parse the contribution of different neural systems to our shared social behavior. Neural circuitry develops at the interaction of genes and environment, and its patterning of our social ecology, in turn, determines whether we will survive and reproduce. The neuroscience of social behavior thus links the gene, the base currency of evolutionary selection, to adaptive fitness of a lineage, the market in which that currency is invested. To understand how social behaviors evolve, we must understand their mechanisms.

I would have liked, in this chapter, to present a simple, linear narrative of mechanisms by which sensory processing gives way to decisions, which in turn pattern our behavioral responses. Unfortunately, no such goal is attainable. Where pathways are discernable, evolutionarily newer paths often operate aside and add nuance to simpler, faster, shorter, older paths. But descent with modification did not just duplicate tissues and pathways, it also cross-linked them. As result, social processes do not progress like a train on a track, passing station to station in an orderly manner. Instead, cognition moves like a river, as much eddied current as steady flow.

A final complexity confounding any simple narrative is the difficulty with which we mechanistically deconstruct cognition: invasive measurement and controlled environments are not compatible with the full, natural expression of social behavior by research subjects. As neuroscientists, we necessarily use a patchwork of techniques to study the social brain without disrupting it. Furthermore, for practical and ethical reasons, we must generally refrain from using precise, invasive techniques to study the most elaborate, flexible and cognitively-demanding social brains—including our own.

So, with these caveats, let us explore the mechanisms of a simple social decision—where to attend—as it is influenced by the visual observation of gaze. The story, loosely, is this: photons excite neurons in the retina. Ions shift, and potentials cascade from the retina to the lateral geniculate and the superior colliculus. They flow on from the lateral geniculate to cortex, and from the superior colliculus to the pulvinar.

They move toward the social processing centers of temporal cortex; and also subcortically, to the amygdala. These signals interact with ongoing activity of the brain, both shaping and shaped by the global state--I am intentionally vague, here, because the dynamic core of cognition remains mysterious. Finally, these signals govern attention through some of combination of at least four inter-related systems: the amygdala, the dorsal and ventral frontoparietal attention systems, and the subcortical attention system.

3.1 Early visual processing

The visual system has often been characterized by dichotomies. There is a cortical and subcortical system, a dorsal and ventral system, and so forth. The earliest division starts right at the eye: the magnocellular stream is coarse, fast, monochrome, and sensitive to motion and subtle contrasts; whereas the evolutionarily-newer parvocellular stream is slow, color sensitive, and higher in resolution (Livingstone and Hubel 1988). These two streams have distinct projections, which can be separately activated in laboratory experiments by filtering out the high spatial frequencies which drive the parvocellular system, or the low spatial frequencies which drive the magnocellular system. Whereas both streams send projections to the lateral geniculate nucleus of the thalamus, and from there to cortex, the direct retinotectal projections from the retina to the superior colliculus lack color-opponency and are essentially magnocellular in character (Schiller and Malpeli 1977). The superior colliculus is the

mammalian homologue of the visual tectum, which performs the majority of visual processing in fish, amphibians, reptiles, and birds (Sewards and Sowards 2002).

Let's pause here to briefly contrast visual processing in primates with the simpler visual processing in fish and amphibians, from which mammals, reptiles, and birds diverged. For the most important and innate responses, these vertebrates have a simple pathway connecting visual detection of animacy with behavioral response. If a frog sees a visual stimulus, signals move from the retina to the visual tectum, where they are processed. If the stimulus is a small, moving spot—a fly, say—then signals propagate from the optic tectum to brainstem motor controls, and the frog attempts to eat it. If the stimulus is a large, looming shape—a hand, say—then different signals flow from the tectum to the brainstem, and the frog attempts to escape. I oversimplify the case, slightly—several other visual nuclei also play a role in visual discrimination and response to animate stimuli—but the take-home message is that these basic responses are innately specified and coordinated by the retinotectal pathway (Sewards and Sowards 2002). This is not to say that these primitive systems have no capacity for learning. They do, but these learned responses are believed to operate through modification of innate sensorimotor mappings (Sewards and Sowards 2002).

We don't know, however, exactly what happens when the stimulus is another frog, and this is a critical case. Perhaps, because these social responses are more subtle (e.g. to attack, vocalize, ignore, retreat, or mate), additional nuclei are activated to shape

behavioral output: these derived mechanisms are relatively more likely to vary across species, and relatively less likely to have mammalian homologues. It is known, however, that at least in some animals, innate recognition of conspecifics is coordinated by the tectum: for example, during bird imprinting (Sewards and Swards 2002).

But what about our central question, that of eye perception? Sensitivity to being looked at is widespread across diverse vertebrates from fish (Coss 1979) to primates (Coss 1978), lizards (Burger et al. 1992) and birds (Ristau 1991). But while most species treat eye contact as a threat, it plays a more nuanced role in primates; similarly, while some nonprimate mammals (Hare and Tomasello 1999; Kaminski et al. 2005) and birds (Bugnyar et al. 2004) are sensitive to deictic gaze, the origins of this sensitivity are unknown. While face processing has received some study in sheep (Kendrick et al. 2001), primates remain the exclusive source of our knowledge about neural responses to perceived eyes.

The bottom line of all of this, is that from the outset, social processes flow through two major channels which can be loosely described as follows: a fast, coarse, innate mechanism, homologous across vertebrates; and a slow-acting, slow-developing, more flexible cortical mechanism which is specific to mammals (Sewards and Swards 2002). To be sure, mature social cognition involves broad swaths of brain, but at a first pass, the primate social brain can be divided into two systems: the streamlined but

relatively inflexible subcortical pathway, and the nuanced—and labyrinthine—cortical network (Adolphs 2002; Vuilleumier 2002a).

3.2 *Visuosocial perception*

From the lateral geniculate nucleus of the thalamus, visual signals are routed to primary visual cortices, and quickly diverge into a dorsal and ventral stream. The dorsal stream receives relatively more magnocellular input and is associated with spatial perception, and is frequently characterized as a “where” (Ungerleider and Mishkin 1982) or “how” (Milner and Goodale 1995) stream facilitating spatial awareness and contributing to interaction with the environment. Conversely, the ventral stream receives relatively greater parvocellular contributions and is generally characterized as a “what” stream (Ungerleider and Mishkin 1982; Milner and Goodale 1995) facilitating in-depth perceptual processing of objects. It is unlikely that social information is neatly segregated into one or the other pathway: to successfully interact with another individual, we must correctly perceive them, localize them, and decouple observation of their movements from visual feedback regarding our own.

3.2.1 Core areas in visuosocial cortex

Functional imaging of humans have identified brain areas that are involved in perception of bodies (Downing et al. 2001), biological motion (Allison et al. 2000), and

faces (Haxby et al. 1994); other studies suggest a similar network of areas operate in macaques (Logothetis et al. 1999; Tsao et al. 2003). These areas appear to arise from preprocessing of biological primitives in the inferior occipital gyrus, and to map along a dorsomedial to ventrolateral axis. Interestingly, this arrangement partially recapitulates the organization of the somatosensory homunculus lying anteriorly in parietal cortex, in which body representations are dorsomedial to face representations. The general conservation of cortical organization across primate species, together with these recent findings, suggest that visual areas specialized for processing social stimuli may have common origins in the primordial visual cortex present in stem primates (Tootell et al. 2003; Rosa and Tweedale 2005) and perhaps others mammals as well (Kendrick et al. 2001).

However, there are some controversies in whether these regions are innately social or whether they expertise areas patterned during development. For example, researchers have debated whether the fusiform face area (FFA) is uniquely activated by faces (Kanwisher et al. 1997) or whether it, instead, is an expert system dedicated to assessing subordinate-level distinctions between any familiar hierarchically-classifiable objects (Gauthier et al. 1999). In particular, it has been suggested that these cortical areas may rely upon subcortical social attention signals for appropriate patterning during development (Sewards and Sewards 2002; Johnson 2005; Johnson et al. 2005), and

further, that disruption of this developmental patterning may be an initial point of divergence in autism (Johnson et al. 2005; Schultz 2005).

For gaze processing, the most relevant perceptual computations appear to take place initially in the biological motion processing areas of the superior temporal sulcus (STS, Allison et al. 2000). Haxby and colleagues (Haxby et al. 2002) have argued that while the patches in inferior occipital gyrus and fusiform gyrus are primarily concerned with static, configural features used to determine facial identity, regions within the STS are optimized instead for dynamic social signals encoded in facial expressions and gaze. In particular, they observe that posterior STS is reciprocally interconnected with posterior parietal attention areas, and that both regions are activated when specifically attending gaze direction (Hoffman and Haxby 2000). By age 10, children show a mature pattern of response to perceived gaze, with activations predominantly in middle temporal gyrus, STS, and inferior parietal lobule (Mosconi et al. 2005).

Macaque visual processing is organized similarly to that of humans (Tootell et al. 2003, c.f. Orban et al. 2004). As in humans, macaques have several socially-selective patches embedded within temporal object-perception areas (Tsao et al. 2003): specifically, in the left fundus of STS, bilaterally in the lower bank of STS (all in caudal area TE), and bilaterally in the anterior middle temporal sulcus (in rostral area TE). Computational deformation of suggests caudal patches may be homologous to human FFA, and rostral patches to human STS, however, functional investigation has been

limited. Though humans recruited face perception areas for interspecific perception, macaques responses were attenuated while viewing humans.

Social processing in macaques has received extensive electrophysiological investigation, though these data do not always line up straightforwardly with reported human imaging results. Dave Perrett, in particular, has studied face selective responses in the temporal lobe of monkeys, finding populations of face-sensitive neurons in the middle of the STS with latencies from 80-160 ms (Perrett et al. 1982). He has further described a variety of neurons in the anterior fundus of the STS that respond selectively to faces with latencies of 100-250ms, making a variety of subordinate-level categorizations of face including facial view, identity and gaze direction (Perrett et al. 1985).

In the anterior STS of the monkey, neurons appear to represent different types of information at different latencies, with representations of shape and species preceding information about identity and expression by 50ms (Sugase et al. 1999). Faces were distinguished (90ms) at earlier latencies than macaque emotion (137ms), individual identity (150ms), and human emotion (180ms). In macaques performing a delayed-match-to-sample task on individual human face stimuli, viewpoint-specific representations of faces arose in anterior STS with latencies of 100-200 ms, and facial identity encoding was evident in anterior inferior temporal gyrus (aITG) at latencies of

100-350 ms; those aITG neurons which predicted task reaction time were last to activate, with latencies ranging from 250 to 350 ms (Eifuku et al. 2004).

Regional specificity within STS is likely of greater theoretical interest than previously imagined. The STS is a large area, cytoarchitectonically divided along both its width and length, with distinct differences in connectivity; while the posterior regions communicate bidirectionally both with posterior parietal areas and frontal areas, while the anterior regions communicate preferentially with frontal and visual areas (Seltzer and Pandya 1989, 1991). Neurons in the middle anterior upper bank of the STS represent gaze direction independently of whether it arises through head or eye posture (Perrett et al. 1992); notably, while neurons in caudal STS respond symmetrically to gaze averted to either the right or left, anterior neurons respond differentially to deictic gaze directions (De Souza et al. 2005). Like macaques, humans processing gaze direction appear to use a number of centers in parietal cortex and along the STS (Wicker et al. 1998). While gaze sensitivity is most robust in the caudal STS (Puce et al. 1998; Hooker et al. 2003), recent studies have suggested that only neuronal activity in the inferior parietal lobule and the anterior STS have specificity for gaze deixis, that is, for particular averted gaze directions (Calder et al. 2007). Furthermore, perception of averted gaze, relative to direct gaze, increases the functional connectivity between the fusiform gyrus and the intraparietal sulcus (George et al. 2001).

Social processing in temporal lobes blends auditory and visual modalities (e.g. Ghazanfar et al. 2005), and likely contributes to generation of modality-independent representation of individual identity. Interestingly, there is some suggestion that vocal processing in other species may be left-lateralized for macaques (Poremba et al. 2004, though see Petkov et al. 2008), just as language is predominantly left-lateralized for humans. Conversely, there seems to be a marked right-hemisphere advantage for visuosocial cortical computations, not only in our own species but possibly in others as well. For example, visuosocial activations in humans are stronger in the right IOG, FFA, STS, and also in a frontal region, the IFG, which we will address later in this chapter (Allison et al. 2000; Haxby et al. 2002; Ishai et al. 2005). Furthermore, similar rightward visuosocial lateralization is hinted at by work in sheep (Peirce et al. 2000), suggesting that this right-hemisphere advantage may be widespread throughout mammals.

The importance of core visuosocial cortices for establishment of joint attention is corroborated by several lesion findings. Gaze-following behavior in a split-brain patient was limited to the left visual field, suggesting a role for right-lateralized cortical processing (Kingstone et al. 2000); a key locus for this lateralized processing is suggested by the selective disruption of gaze discrimination (Akiyama et al. 2006a) and gaze following (Akiyama et al. 2006b) in a patient after a lesion of the right superior temporal gyrus.

Interestingly, these core visuosocial areas are prone to disorder in autism, though the precise nature of these disorders remains the subject of controversy; while temporal cortex generally responds to social stimuli in autism, it does appear to do so in idiosyncratic ways. Identity processing is relatively better in autistics when stimuli are high spatial frequency (e.g. Deruelle et al. 2004), which may be consistent with excessive reliance on local features or, alternately, consistent with relatively increased reliance on cortical over subcortical processing streams. Disruptions are also evident in higher-order social processing: while typically-developing subjects upregulate STS activity upon seeing abnormal gaze behavior, autistic subjects do not (Pelphrey et al. 2005).

3.2.2 The Mirror System

These core social areas are conventionally localized to the ventral stream. Visual observation of social stimuli can also activate the dorsal stream, most intriguingly through “mirror” neurons reported in frontal (F5, di Pellegrino et al. 1992) and parietal (PF, Gallese et al. 2002) areas associated with movement initiation and visual guidance. These neurons fire similarly when actions are performed or observed, and code for narrowly matching visual and motor actions (seeing a grab, making a grab) or for implicitly related visual and motor intentions (seeing food chewed, reaching for food) (reviewed, Rizzolatti and Craighero 2004). Mirror neurons are a minority in their native tissues, but have stoked great theoretical interest. The presence of these neurons in

macaques has caused some confusion, due to the limited imitation abilities of monkeys (Dinstein et al. 2008).

A minimalist account of mirror neurons suggests they are involved in linking visual and somatosensory guidance of action. More suggestively, however, parietal neurons seem well suited to relate the spatial consequences of biological movement, and frontal, to derive the intentions that underlie observed patterns of activity. Supporting these findings from macaques, imaging studies in humans suggest that homologous brain regions are activated by both production and observation of gestures (Dinstein et al. 2007), and sensory-motor “mirroring” may be widespread throughout cortex. Also, recent studies have begun to identify processes in which “mirror” neurons may play a role (e.g. Prather et al. 2008), describing sensory-motor mirroring during bird song).

The mirror / simulation framework has proven especially compelling in the domain of emotional signaling and empathy. Perceiving an emotion triggers a small mirroring response in viewers (Adolphs 2002): seeing a smile, I begin to smile; seeing a frown, I begin to frown. More recently, lesion and neuroimaging data have suggested that the brain regions which interpret internal data and generate appropriate expressions likewise respond to those expressions observed in others (Gallese et al. 2004). It is plausible that mirror activity plays a role in gaze following as well, consistent with a hypothesized general role in perception of actions, intentions and emotions. We address this possibility in Chapter 6.

3.2.3 The Extended Social Perception Network

Visual social observations drive activity through a broad swath of cortex which, though not exclusively social, can be considered part of an extended social perception network. For example, face perception activates a number of areas in frontal and subcortical structures, including the inferior frontal gyrus (IFG), hippocampus, amygdala, and orbitofrontal cortex (OFC) (Ishai et al. 2005). These socially-influenced areas probably integrate contextual information stored in memory and current behavioral goals, and act to modulate both attentional allocation and reward processing (Vuilleumier 2002a; Sabbagh 2004).

It is important to note that both orienting to others and following gaze are regulated by social milieu—as well as by intrinsic factors, potentially including sex hormones such as testosterone, neuromodulators such as serotonin, and neurotransmitters such as vasopressin and oxytocin. Supporting this idea, amygdala, orbitofrontal cortex (OFC) and hippocampus form a functional circuit important for associating emotional and social salience with mnemonic and perceptual information (Vuilleumier 2002a; Sabbagh 2004; Smith et al. 2006). Each of these brain structures is sexually dimorphic (Goldstein et al. 2001), suggesting that sexual differentiation of these areas may be a way through which gender influences 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 and Baron-Cohen 2006).

Several areas that are not reliably activated by passive social stimuli are nonetheless, to be certain, part of social processing in the human brain. Though both behavioral and neural homologies in animals remain unclear, humans extensively use two additional cortical systems to understand other individuals. Specifically, an area at the confluence of the superior temporal sulcus with the temporoparietal junction (TPJ), and a large swatch of cortex on the medial surface of the frontal lobes, loosely divided into the dorsal (dMPFC) and ventral (vMPFC) prefrontal cortex (Saxe 2006; Frith and Frith 2007). TPJ is especially interesting, for our purposes, because it is selectively activated by theory of mind tasks in which an individual must assess the abstract point of view of another person (Saxe 2006; Frith and Frith 2007). Medial prefrontal cortex, by contrast, does not seem to be selectively activated by social judgments, but does appear to play a special role in emotional (vMPFC) and cognitive (dMPFC) empathy and sharing of experience (Saxe 2006; Frith and Frith 2007). Perception of averted gaze has been reported to activate neurons both near the TPJ (Calder et al. 2007) and in the dMPFC (Calder et al. 2002), possibly joined by the left superior frontal gyrus for the specific case of coordinated joint attention (Williams et al. 2005).

One might be tempted to object, at this point, that nearly the entire brain has been implicated in social processing. I would like to suggest that this is probably

accurate: Social experiences are at the core of what it means to be human. Whatever might constitute a “dynamic core” of cognition, there is no question that our social environment plays a large role in our day-to-day thoughts. For many of us, a large part of our active effort—and a large part of our inactive daydreams—revolve around social concerns and goals. Indeed, the medial prefrontal areas most associated with theory of mind and empathy are core constituents of the hypothesized “default mode” brain network—the neural systems that are active when we aren’t explicitly engaged in any particular prespecified task (Fox et al. 2005).

Finally, in addition to the above-described areas, lesion data from one patient suggests that cortex slightly inferior to the IFG may also play a role in joint attention: a patient with tumor damage to frontal areas F7, F11, and F12 could not use central lexical or static gaze cues to direct attention, but exhibited normal exogenous cuing (Vecera and Rizzo 2004). Interestingly, in macaques, frontal areas 11 and 12 interconnect with the polymodal region in the upper bank of the STS, as well with temporal areas TEa and TEm in the rostral lower banks of the STS (Seltzer and Pandya 1989).

Ultimately, signals from social cortex must relay information to behavioral decision areas including orienting and attention control systems. Signals from the higher-order areas of the ventral pathway ramify to multiple targets in the visual attention system, but exactly which is most relevant remains an open question: in monkeys, much of visuosocial cortex 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 including both the pulvinar nucleus of the thalamus (Romanski et al. 1997) and the superior colliculus (Fries 1984).

3.3 The subcortical pathway

As in other vertebrates, retinotectal inputs provide mammals with coarse visual information through which crude visual primitives can quickly be analyzed, for example, to locate other creatures, detect social signals and extract gaze direction. The subcortical system appears to be phylogenetically old, and is the major pathway for innate recognition and response to animate targets including predators, prey, and conspecifics (Sewards and Sewards 2002).

In humans, this system has been suggested to play a crucial role in innate attention to 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 (Sewards and Sewards 2002; Johnson 2005). In theory, collicular contributions to social orienting could be quite quick and reflexive: a homologous structure, the visual tectum, governs both orienting and the bulk of visual processing in most vertebrates (see Sewards and Sewards 2002); and in primates, the superior colliculus acts with cortical areas (including the lateral intraparietal area, LIP, and particularly the frontal eye fields, FEF) as a final common output governing overt

visual attention (Platt et al. 2004). As yet, however, there is little or no evidence suggesting the superior colliculus itself might mediate gaze-following behavior among primates: indeed, in other vertebrates, the tectum alone is often insufficient to correctly specify behavior: appropriate selection of predator and prey responses among frogs requires intact pretectal nuclei, and appropriate parental pursuit behavior during avian imprinting requires intact diencephalic structures (Sewards and Sewards 2002). More plausible, then, is the hypothesis that upstream subcortical nuclei—the pulvinar nucleus of the thalamus and the amygdala—contribute to social attention, and specifically, to primate gaze-following behavior.

3.3.1 The Pulvinar

When juvenile birds imprint upon parental figures, diencephalic structures are thought to provide essential motivation, and telencephalic structures are thought to contribute learning mechanisms necessary for bond specification (Sewards and Sewards 2002). Though its function remains mysterious, the pulvinar nucleus of the thalamus is a multisensory diencephalic structure that serves as the major nexus for subcortical and cortical visual processing. Though it is traditionally conceived as having four subnuclei (inferior, lateral, medial, and oral), these may properly number as many as 10 (Grieve et al. 2000). There is some suggestion that, outside of oral pulvinar, the basic organization maintains a consistent space map, with isometric slabs arcing from ventrolateral to dorsomedial regions: in so passing, the representations of a given spatial region would

first intersect inferior sectors corresponding with retina, superficial SC, and early visual cortex; then lateral sectors corresponding with parietal and temporal lobes; and finally medial sectors corresponding with higher-order sensory and frontal cortices, as well as with intermediate layers of SC (Grieve et al. 2000). Such an organization, along with the presence of parietal-like gain fields (Grieve et al. 2000), suggests that pulvinar acts to transform behaviorally-relevant representations between different spatial reference frames, and in particular, to coordinate spatial attention.

3.3.2 The Amygdala

The ultimate destination of this subcortical pathway is the amygdala (Johnson 2005; Adolphs 2008). The amygdala plays a crucial role in quickly flagging emotionally salient and potentially-threatening stimuli for further processing; stimuli that are so flagged receive both deeper processing in cortex and greater access to memory than stimuli that are not so privileged (Anderson and Phelps 2001; Vuilleumier 2002a; Adolphs 2008). This role may be particularly important during development (Skuse et al. 2003; Johnson 2005), but continues to adulthood and operates even in absence of cortical processing or conscious awareness (Morris et al. 1998; Morris et al. 1999; Vuilleumier 2002a; Jiang and He 2006).

The relay of social threat signals from along the retinotectal pathway through pulvinar to amygdala has been supported both by neuroimaging data (Morris et al. 1999; Jiang and He 2006) and facial emotion discriminations by a blindsight patient

(Pegna et al. 2005). Upon detecting a potential danger, the amygdala upregulates cortical processing to facilitate quick analysis of the threat (Morris et al. 1998; Vuilleumier 2002a). However, while a major function of this pathway is indubitably as an “early warning” system, there is evidence that the amygdala also mediates prosocial behaviors.

Subcortical afferents are joined in the amygdala by cortical afferents, largely from higher-order association area, including the visuosocial regions within temporal lobes (Ghashghaei and Barbas 2002). And just as not all amygdala input is subcortical, not all amygdala processing is dedicated to the detection of danger. In addition to eye contact, neurons in the macaque amygdala have been observed with sensitivity to the expression, gaze direction and social dominance of viewed faces (Kawashima et al. 1999; Gothard et al. 2007; Hoffman et al. 2007). While eye contact can signal threat, it more generally suggests interest or intent to approach, and often serves to initiate grooming and sexual behavior (Hrdy and Whitten 1987); indeed, the amygdala is strongly activated by visual sexual stimuli (Aharon et al. 2001; Hamann et al. 2004). The prosocial role of amygdala again appears to be modulatory: both FFA activity, and functional connectivity between FFA and amygdala, are greater when photographed faces gaze toward the viewer than when they gaze away (George et al. 2001).

The amygdala may play a large role in shaping attention to species-typical social signals, and also to shaping individual differences in social responsiveness.

Amygdalofugal projections ramify broadly across the ventral visual stream, particularly to early visual cortices, and these projections may act to increase the speed and depth of processing in these regions (Amaral et al. 2003a). Importantly, the amygdala is sexually dimorphic (Goldstein et al. 2001; Hamann et al. 2004) and has altered activity in psychosocial dysfunction (Amaral 2002; Anand and Shekhar 2003), perhaps including the autism spectrum disorders (Schultz 2005; Sasson et al. 2007, but see also Amaral et al. 2003b). Furthermore, the caudal orbitofrontal and medial prefrontal cortices, themselves sexually dimorphic (Goldstein et al. 2001), interconnect with approximately the same amygdala zones as receive social afferents from anterior temporal cortices (Ghashghaei and Barbas 2002). This arrangement is consistent with a convergent or modulatory role for OFC outputs onto amygdala-mediated social processing (Sabbagh 2004).

Finally, in addition to this modulatory role, the amygdala may play an explicit role in social orienting, acting to direct gaze toward the eye region of observed faces (Adolphs et al. 2005) and to direct attention in the same direction as perceived gaze (Akiyama et al. 2007). However, because the amygdala projects neither to the SC nor to cortical gaze control centers, any influence on overt orienting must be exerted through indirect pathways such as the pulvinar nucleus.

3.4 Orienting the Brain

In order to affect visual orienting, social interests must be integrated with other attentional priorities and transformed into oculomotor control signals. The superior colliculus serves as a final common output for brain areas contributing to gaze control, however, several cortical brain are strongly linked to the shifts of eye position and spatial attention. Principal among these are the frontal eye fields (FEF), which can direct eye movements independently of the colliculus; the supplemental eye fields (SEF), which feed into FEF; and LIP, which facilitates sensorimotor transformation across eye movements and represents decision variables linked to visual orienting (Platt et al. 2004). Together, these cortical centers make up a dorsal frontoparietal network which mediates both saccades and endogenous attention shifts; it is adjacent to, and operates alongside, a ventral frontoparietal attention network which acts as a circuit-breaker to redirect attention toward exogenously salient events (Corbetta and Shulman 2002). We primarily address the dorsal system, here, but will conclude by briefly exploring a curious feature of the ventral system, as currently described. One caveat is critical: while these areas have clear importance for typical social orienting, they cannot be the sole pathway through which gaze cues operate: in fact, social gaze cues are reported to ameliorate symptoms of neglect in patients for whom these circuits have been compromised (Vuilleumier 2002b).

3.4.1 The dorsal attention system

The dorsal attention system has been relatively well characterized over a long research history—the frontal eye fields, for example, were identified via stimulation well over a century past. Eye movements can also be evoked by stimulation of SC, SEF, and various visual areas within cortex, including LIP (Schiller and Tehovnik 2001); and stimulation too weak to shift overt gaze may nonetheless shift covert attention (posterior parietal, Cutrell and Marrocco 2002; frontal eye fields, Moore and Fallah 2004; and superior colliculus, Muller et al. 2005). The core areas in the gaze control network—SC, FEF, SEF, and LIP—actively coordinate orienting, responding (to varying degrees) to visual stimuli, to sustain attention, to generate saccades; conversely, when any of these regions is inactivated, visual orienting is disrupted (Platt et al. 2004). To the extent that the function of these areas can be considered independently of one another, LIP appears to be more involved in tracking saliency spatial coordinate transforms (Colby and Goldberg 1999; Cohen and Andersen 2002), whereas FEF is more directly involved in programming eye movements (Schall and Thompson 1999) and SEF in preparing future eye movements (Coe et al. 2002); SC, for its part, appears to track both visual stimuli and saccadic responses, but is more closely tethered than cortex to incoming visual stimulation and outgoing saccadic execution (Wurtz et al. 2001). While these descriptions were drawn from macaque electrophysiology, the respective roles of homologous areas have been investigated in human functional imaging, as well (e.g.

Rosen et al. 1999; Mort et al. 2003b; Mayer et al. 2004; see also Koyama et al. 2004 for explicit comparison of macaque and human visuospatial orienting mechanisms).

Of particular interest, for social cuing of attention, LIP appears to estimate the “interestingness” or “informativeness” of regions of space—in short, the expected rewards of orienting to a particular location (c.f. Gold and Shadlen 2001 for formal modeling). 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 and Glimcher 1999). Subsequent studies have extended these findings from highly non-naturalistic juice rewards to the intrinsic visuosocial rewards naturally acquired by eye movements (Klein et al. 2008b). While reward modulations have been replicated in LIP (Sugrue et al. 2004) and observed in SC (Ikeda and Hikosaka 2003), they are absent or reduced in the SEF and FEF (Leon and Shadlen 1999, see also Roesch and Olson 2003), again supporting a special role for LIP in calculating visual saliency. For all of these regions, the lateral intraparietal area is likely to be a key region in translating observed social gaze cues into attentional orienting, and I shall address our work investigating this possibility in the Chapter 6.

3.4.2 The ventral attention system

The ventral frontoparietal attention system is proposed to rapidly and reflexively reorient attention from its original endogenous focus to crucially important external events (Corbetta and Shulman 2002). The mechanism for this, it is proposed, is a

strongly right-lateralized network incorporating the temporoparietal junction (TPJ) and inferior frontal gyrus (IFG). If these regions sound familiar, it may be because I've described them above—in that context, TPJ was described as selectively for theory of mind tasks (Saxe 2006), while IFG was described as part of the extended face perception system (Ishai et al. 2005). Since these conflicting accounts neatly circumscribe our interest in the establishment of joint attention, I shall try to concisely reconcile these accounts below.

Both parietal and frontal cortices have undergone significant reorganization in the time since human and macaque lineages split, and functional homologies are uncertain. While the dorsal frontoparietal network is believed to correspond well between macaques and humans, some ambiguity arises in the relationship of the human inferior parietal lobule and intraparietal sulcus with the macaque areas 7A, LIP, and IPa (Orban et al. 2004). It is quite possible, for example, that humans have more distinct cortical areas in inferior parietal than do macaques; a situation which has been further compounded by the imprecision with which activation boundaries can be described.

The area described in human research as the temporoparietal junction (TPJ) partially overlaps with the several adjacent areas, including the inferior parietal lobule (IPL) and the superior temporal gyrus (STG). In humans, lesions near the right TPJ region are strongly associated with neglect, sometimes including memory as well as spatial deficits (Heilman et al. 1993; Friedrich et al. 1998; Mort et al. 2003a); this

phenomenon is not present in monkeys and may reflect uniquely human adaptations (Husain and Nachev 2007). Furthermore, a right-lateralized network of TPJ, STG and IFG is active in normal, free exploration of visual scenes (Himmelbach et al. 2006), and bilateral activations have been reported in attentional imaging (Rosen et al. 1999; Mort et al. 2003b; Mayer et al. 2004).

However, the precise function of this network remains mysterious. While the left-lateralized network has long been associated with language (Benson 1993), the right-lateralized network appears to govern changes in executive reference frame. For example, it is activated by various forms of novelty, bottom-up saliency and target detection (Corbetta et al. 2000; Downar et al. 2002), results that echo findings from area 7A in monkeys (Constantinidis and Steinmetz 2001b, 2001a); furthermore, TPJ and STG may play a role in shifting between global (right TPJ/STG) and local (left TPJ/STG) processing (Robertson et al. 1988). The TPJ region appears to also be involved in abstracting point-of-view during perspective-taking (Aichhorn et al. 2006; Arzy et al. 2006) and false belief tasks (Saxe and Kanwisher 2003; Saxe and Wexler 2005; Saxe and Powell 2006); moreover, the inferior parietal lobule responds selectively to observed deictic gaze directions (Calder et al. 2007) and has been implicated in a meta-analysis of gaze perception areas (Grosbras et al. 2005). Despite anatomical ambiguities in the region, these attentional and social functions appear to inhabit in the same neural tissue (Mitchell 2008). Finally, while left IFG has associated with temporal and semantic

sequencing, for example in language, right IFG is more strongly associated with response inhibition (Chambers et al. 2007; Chikazoe et al. 2007), suggesting that Corbetta and colleagues' hypothesized "circuit breaker" (Corbetta et al. 2002) may function on an abstract executive, rather than purely visuospatial, level.

3.4.3 Orienting in Response to Gaze Cues

In a series of investigations by Hietanen and colleagues, nonpredictive gaze and arrow cues both shifted attention, but cortical activations in response to gaze cues were much more sparse than to arrows; all reported gaze activations were confined to the occipital lobes (Hietanen et al. 2006). Replicating the experiment using ERP measures, Hietanen and colleagues observed early attentional effects in parietal for arrow, but not gaze, cues (Hietanen et al. 2008). While the authors interpret these findings as dorsal involvement in arrow orienting and ventral involvement in gaze orienting, they could equally well support a subcortical origin for gaze cuing. Furthermore, because gaze cues were quite abstracted, these results may not accurately capture natural gaze-following activity.

Using a different gaze following paradigm, Materna and colleagues (Materna et al. 2008) instructed subjects to either follow the eye color or gaze direction in a dynamic face stimulus. They found that only the cuneus/precuneus border and a region in the posterior medial temporal gyrus distinguished explicit gaze following from grey-level selection, and that the temporal region was located in the vicinity of past-reported gaze

responses in posterior STS. However, reflexive gaze following would be expected to operate even when task irrelevant, making the relevant contrast between gaze shift perception and rest. In this contrast, both variants of the task evoked substantial activity in motion centers, superior occipital areas, the dorsal frontoparietal attention network, and the dorsolateral prefrontal cortex. However, interpretation is here confounded, as well, because all behavioral responses included eye movements known to strongly activate this system.

3.5 Event-Related Responses to Gaze Cues

EEG and MEG provide an alternative means of exploring human gaze processing, in which spatial specificity can be sacrificed in exchange for temporal precision. During face processing, MEG detects two face-specific windows of activity at 100 and 160 ms, with the former likely representing first-pass face processing and the latter corresponding to identification and the EEG-identified N170 (Liu et al. 2002). Gaze contact is associated with a strengthened N170 event-related potential (ERP) associated with occipitotemporal face processing; direct gaze also contrasted with averted gaze in parietal electrodes between 160 and 210 ms latency, and differentially recruited temporoparietal, MPFC and orbitofrontal sources (Conty et al. 2007). Despite increased behavioral report of eye contact, this initial N170 response is not enhanced by adaptation to averted gaze, though adaptation effects could be found in posterior electrodes later, at 270-350 ms latency (Schweinberger et al. 2007).

Deictic gaze cues likewise effect subsequent visual processing. Static gaze cues speed early visual processing in socially-cued regions; enhanced ERPs to congruent targets were detected as early as 100 ms after cue onset—furthermore, the evoked P1 (125 ms) and N1 (180 ms) potentials are particularly enhanced in the right hemisphere (Schuller and Rossion 2004); however, modulatory effects were not observed in the earliest processing window, the C1 onsetting from 50-65 ms, suggesting that gaze cues do not affect the first volley of activity through striate cortex (Schuller and Rossion 2005). Interestingly, eye-contact enhancement of the N170 has been reported in children as young as four months of age (Farroni et al. 2004); at the same age, deictic gaze has been reported to enhance a slow wave of object-evoked activity recorded over frontotemporal cortex (Reid et al. 2004).

Finally, EEG activity can also be used to predict joint attention skills in development. At 14 months, joint attention initiation at 14 and 18 months could be predicted based on 4-6 Hz activity under the left frontal electrode, inactivity under the right central electrode, and high ratio of frontocentral to frontooccipital 4-6 Hz coherence. For these same ages, joint attention responses could be predicted by activity under the left parietal electrode and inactivity under the right parietal electrode (Mundy et al. 2000). This pattern of activity would appear to contrast strongly with adult results, and may suggest that social attention develops through left-lateralized cortices that are

latter taken over by language function, displacing extralinguistic joint attention abilities to the right hemisphere.

3.6 Conclusions

The job of the brain—the way it justifies its metabolic expense—is by mapping sensory stimuli to motor responses so as to increase adaptive fitness. For species, such as our own, in which individual success is predicated on the quality of interactions with conspecifics, brains must efficiently mediate sensorimotor decisions transforming perception of social stimuli into socially-appropriate strategies for action. In humans, a critical step in this process is the attribution to others of internal mental states characterized by sensations, emotions, attentions, desires, and plans. These internal states are hidden, private, but we construct them through careful observation of externally-observable physical cues; indeed, it appears that most of our brain is active in one or another sort of social processing. However, the care with which we observe these social cues does not imply we find the task difficult. We typically do these things reflexively, from an early age, in part by building upon an innate tendency to share in the emotions and attentional focus of others.

Perception of these social attention cues can, in principal, reorganize cognition in any of four ways: by regulating internal information processing, for example via the amygdala; by changing our locus of spatial attention, for example via the pulvinar; by

changing our covert or overt visual orienting behavior, via the superior colliculus and dorsal attention system; or by changing our executive reference frame, via the ventral attention system. In the next chapter, I will describe our work investigating the impact of social gaze perception on the dorsal attention system, specifically the macaque lateral intraparietal area. In particular, I will describe a population of neurons in macaque LIP which appear to “mirror” the observed attentional state of others.

4. Spontaneous social orienting and gaze following in ringtailed lemurs (*Lemur catta*)

4.1 Introduction

Over the last decade, much emphasis has been placed on the ability to recognize and respond to the orienting behavior of others (e.g. Baron-Cohen 1994). Such visual acquisition of social information would seem to depend on an initial bias to attend to others, in particular to the orientation of bodies, heads, and eyes (Langton 2000; Kaminski et al. 2004). Both human and nonhuman primates preferentially gaze toward other individuals, in particular their faces and eyes, under laboratory conditions (Butler 1954; Sackett 1966; Haude and Ray 1974; Deaner et al. 2005). Furthermore, the ability to use social cues such as gaze direction (reviewed Emery 2000; Itakura 2004) has been reported not only in primates, but in species as diverse as dolphins (Tschudin et al. 2001), goats (Kaminski et al. 2005), and ravens (Bugnyar and Heinrich 2006).

One caveat in interpreting such findings is that different measurement techniques and social contexts can themselves influence gaze-following behavior. For example, controlled studies of humans performing artificial “social” tasks report few deficits in gaze following by autistic individuals (Chawarska et al. 2003; Swettenham et al. 2003; but see also Ristic et al. 2005) despite severe disruptions of shared attention outside the laboratory (Roberts and Bruton 1990; APA 1994; Adams and Kleck 2005). Complicating matters further, gaze following in typically-developing humans is

influenced by subject identity (e.g. gender Bayliss et al. 2005; Deaner et al. 2007) and by social context (Deaner et al. 2007). Even the term “gaze following” has been used to indicate a number of different social orienting behaviors (see Emery 2000 for discussion). In this document, we use “gaze following” to indicate an increase in gaze-alignment between the subject and other animals in his field of view, specifically one that follows overt orienting to that animal.

Social context also shapes social attention in nonhuman animals. For example, gaze following in rhesus macaques is influenced by the social status of both the subject and the observed animal (Shepherd et al. 2006), see also Chapter 5). Although several animal species have been reported to use social orienting cues in experimental contexts, such conditions may fail to include important variables that influence deployment of attention under more natural conditions. In particular, most studies of social gaze following in animals have used human experimenters as attention cues—a decidedly non-naturalistic source of social information.

These methodological and contextual considerations suggest that quantifying how gaze is spontaneously deployed during natural social behavior would be crucial for understanding the evolution, development, and neurobiology of gaze following. Yet, where animals look during natural behavior remains virtually unknown (though note Land and Hayhoe 2001 and Carmi and Itti 2006 for work with humans). Here we probe spontaneous social orienting behavior in ringtailed lemurs (*Lemur catta*) during ongoing

behavior in relatively rich physical and social contexts. Ringtailed lemurs form mixed-sex aggregations of 10-20 individuals organized into well-defined social hierarchies, and communicate through auditory, olfactory, and visual modalities (Jolly 1966; Sauther et al. 1999). Previous studies (Itakura 1996b; Anderson and Mitchell 1999) reported that lemurs do not follow human gaze in experimental contexts. Our study differs from these studies, first and foremost, in that we examine responses to animal, rather than human, gaze cues (Tomasello et al. 1998). Additionally, this study is unique in using telemetric infra-red video eye-tracking technology to increase the precision and sensitivity of measurements (Shepherd and Platt 2006, see Appendix) , and in focusing on spontaneous instances of social orienting in order to achieve a species-typical balance of competitive and cooperative motivations (see Hare and Tomasello 2004). In this study, we specifically quantified each lemur's pattern of fixation near lemurs and other potentially salient objects (e.g. food rewards and high-contrast environmental features), and relative to the directions of observed lemurs' head and body axes.

4.2 Results

We first report that ringtailed lemurs showed a bias to fixate near other lemurs. In Figure 2 we show fixations within 10° of humans, lemurs, food rewards, and stationary environmental features relative to chance. Across 76 minutes of data, we found that lemurs consistently biased their gaze toward all measured ROIs—humans

(36739 samples, permutation test, $p < 0.0002$), lemurs (26543 samples, permutation test, $p < 0.0002$), food rewards (11344 samples, permutation test, $p < 0.0002$), and high-contrast environmental features (53735 samples, permutation test, $p < 0.0002$)—but fixations toward animate stimuli were more common than those toward food rewards (versus humans, permutation test, $p = 0.004$; versus lemurs, permutation test, $p < 0.0002$), and both animate stimuli and food rewards were more fixated than static environmental features (versus humans, or lemurs, or food rewards, permutation test, $p < 0.0002$). Lemurs and humans were fixated with equal frequency (permutation test, $p = 0.2034$). Though the saliency of humans in this experiment may have derived from methodological constraints (e.g. capture to manipulate recording equipment and food provisioning to maintain activity levels), the saliency of lemurs likely reflected the intrinsic value of orienting toward these stimuli during natural behavior.

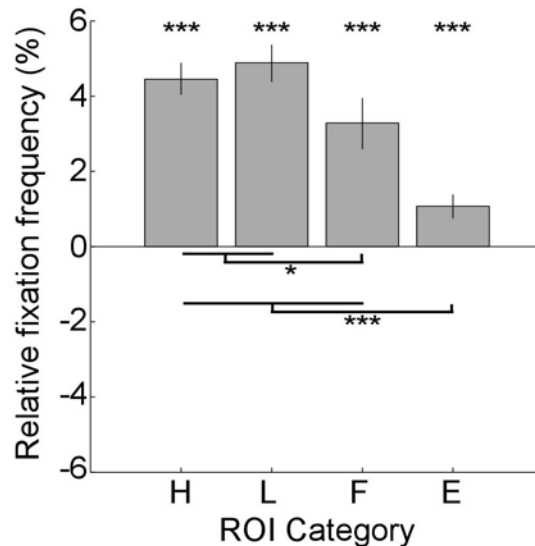


Figure 2: Lemurs are biased to look towards other lemurs.

Gaze bias was computed by examining the portion of observations in which the subject lemur looked within 10° of the nearest member of a category of interest; from these values we subtracted a time-shuffled baseline in which 10,000 bootstrap estimates were calculated from randomly paired gaze and scene coordinates.

Categories include humans (H), lemurs (L), food rewards (F), and environmental features (E). Gaze bias, as plotted here, indicates the amount by which overt visual orienting toward key regions of interest exceeded chance expectation. Bars reflect the 95% confidence interval derived from the time-shuffled bootstrap procedure (see methods). Three stars indicate $p < 0.0005$; two, $p < 0.001$; one, $p < 0.01$.

We next analyzed epochs in which lemurs either were moving between locations or were stationary (Figure 3). During movement epochs, attention to humans (1242 movement and 32620 stationary samples, permutation test, $p = 0.0022$), lemurs (964 and 22726 samples, permutation test, $p = 0.0042$), and especially food rewards (100 and 11160 samples, permutation test, $p = 0.0024$) was reduced, but attention to environmental features (1856 and 42768 samples, permutation test, $p = 0.0006$) was increased (location priority change versus human priority change, permutation test, $p < 0.0002$; versus lemur,

permutation test, $p=0.0002$; versus food, permutation test, $p=0.0004$). These data demonstrate that context strongly influences where lemurs look. When stationary, they tend to monitor food sources, other lemurs, and humans. When moving, however, they ignore these stimuli and gaze along the path of their movement.

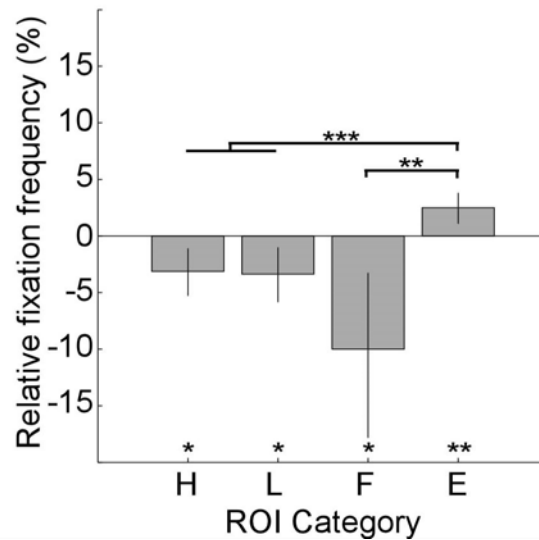


Figure 3: Lemur orienting priorities shift during locomotion.

Attention to humans (H), lemurs (L), and food (F) is reduced, with a concomitant increase in attention to high-contrast environmental features (E) along the path of transit. Gaze bias was calculated as per Figure 2, with positive values indicating categories fixated more often during movement than during rest. Bars reflect the 95% confidence interval derived from the time-shuffled bootstrap procedure (see methods). Three stars indicate $p<0.0005$; two, $p<0.001$; one, $p<0.01$.

Given this strong bias to attend other lemurs, we next investigated whether this attraction may extend in the direction forward from their body and head axes. To test this idea, we examined the distribution of angular offsets between the subject lemur's gaze direction and the observed lemur's gaze direction. It is likely that humans use a

combination of body, head, and eye cues to determine the direction another individual attends (Langton 2000). Since lemurs have relatively low visual acuity (Kay and Kirk 2000), it seems unlikely that they use observed eye direction as the primary social attention signal. Therefore, we tested both the observed body and head axes as indices of observed gaze direction. We observed multiple instances in which both Licinius and Aracus appeared to follow another lemur's orienting behavior. For example, in Figure 4 Aracus aligned gaze with a conspecific. When the observed lemur turned her head, the subject looked toward her and followed her gaze. Across 66 minutes of video, we found that subject lemurs significantly concentrated their gaze (Figure 5) with respect to observed lemurs' head (200975 samples; dispersion decreased 22%, permutation test, $p < 0.0002$; mean offset decreased 0.0232 radians, permutation test, n.s., $p = 0.0626$) and body axes (701714 samples; dispersion decreased 77%, permutation test, $p < 0.0002$; mean offset decreased 0.0609 radians; permutation test, $p < 0.0002$).

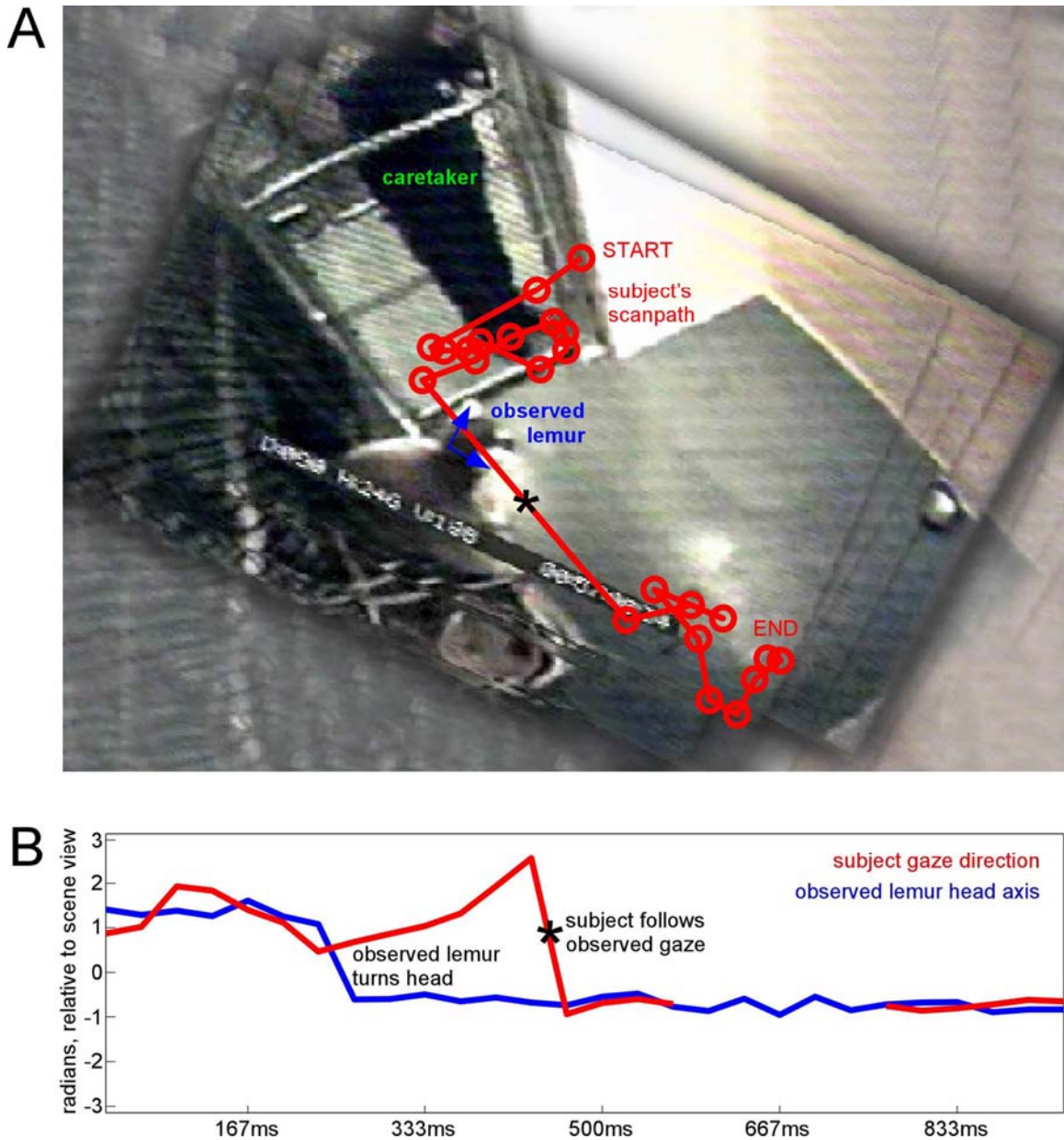


Figure 4: An example of gaze following in ringtailed lemurs.

A. An observed lemur recorded by the head camera across multiple frames, with the scanpath of the subject lemur superimposed in red. In this time period both observed and subject lemurs inspected the feet of a caretaker (“START”), then shifted gaze (starred) toward a proximal location on the floor (“END”). Blue lines represent the initial and final head axis of the observed lemur, here pictured mid gaze-shift. B. Time-course of gaze following. Gaze angle plotted for the observed (blue) and subject

(red) lemurs. The subject lemur traced a similar pattern to the observed lemur, but delayed in time. Furthermore, the subject lemur shifted his gaze to match the observed lemur's heading (starred) only after fixating near to her.

These data suggest that lemurs orient their gaze in the same general direction as other lemurs in their field of view. There are two possible explanations for this gaze alignment. First, both lemurs independently shift their gaze in the direction of an external event. Second, the subject lemur actively follows the gaze of the observed lemur. If the observed gaze alignment reflects shared, but essentially independent, interests in environmental features and events, then gaze alignment should be similar before and after a subject shifts gaze toward an observed lemur. In contrast, if social gaze following is responsible for the observed co-orienting, then relative gaze alignment should increase immediately after a subject looks toward an observed lemur. To address this question, we examined the time course of gaze alignment when the subject lemur shifted gaze to a lemur in view. We found a significant increase in gaze alignment with the observed head axis (1-½ second prior, $\chi^2 p=0.52709$; ½-0 prior second, $p=0.25135$; during fixation event, $p=0.011617$; 0-½ second after, $p=0.011617$; ½-1 second after $\chi^2 p=0.020921$; details in legend of Figure 6), but not body axis, immediately after Licinius or Aracus shifted gaze to an observed lemur (Figure 6). These results demonstrate that lemurs tend to preferentially follow the gaze of individuals toward which they have just looked.

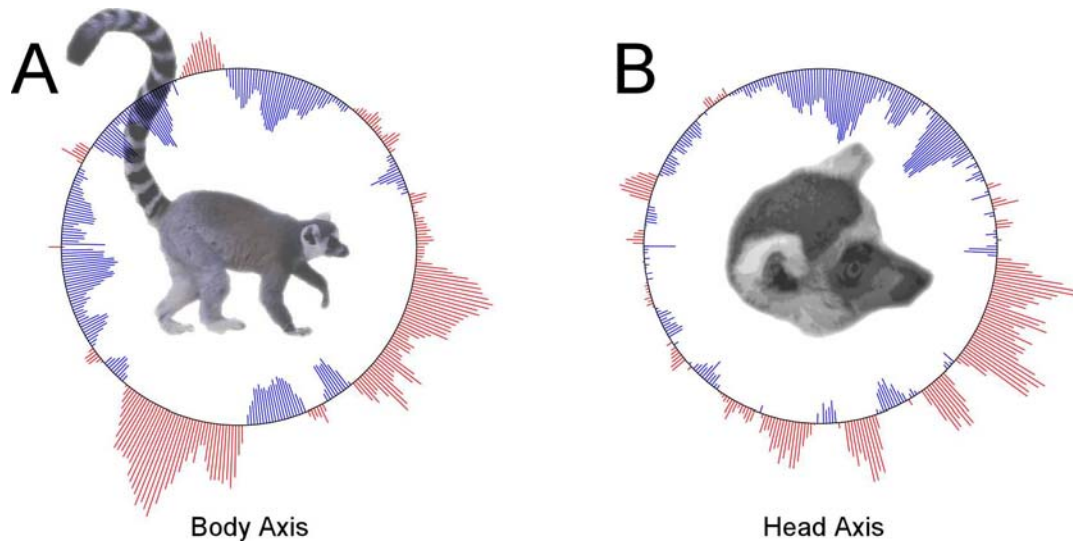


Figure 5: Co-orienting in ringtailed lemurs.

The graphs plot gaze alignment between the subject lemurs and observed lemurs across all video frames. Circular histograms plot the frequency with which a given angular offset was observed between the subject's fixation and the observed lemur's body (A) and head (B) orientation, relative to a time-shuffled baseline. Angular offsets were normalized, through reflection and rotation, so that rightward bars indicate perfect gaze alignment; leftward, perfect gaze avoidance; and upward/downward, approximately skyward/groundward deviations from the observed lemur axis. Each line represents the number of observed instances of a given gaze deviation less the number expected based on a time-shuffled baseline: red, outward-directed lines represent gaze relationships that are more often observed than expected, while blue, inward-directed lines represents gaze relationships that are observed less often than would be expected due to chance. The largest amount by which observations exceeded expectation (i.e. the longest red line) is 0.17% per bin for body axis (A) and 0.14% per bin for head axis (B); there were approximately 57 bins per radian offset.

4.3 Discussion

Contrary to previous reports, our data demonstrate that *Lemur catta* use social cues to orient their attention during social interactions and often follow the gaze of other

lemurs with their own. It has been previously reported that ringtailed lemurs do not follow human gaze (Itakura 1996b; Anderson and Mitchell 1999). Moreover, since prosimian visual acuity is lower than in other primates, it has been suggested that they instead rely nearly exclusively on olfaction (Brothers 1990; Sauther et al. 1999; Kay and Kirk 2000; Gilad et al. 2004). In contrast, our data show that ringtailed lemurs preferentially orient their eyes toward other lemurs and, moreover, that they mirror the attentional state of other lemurs in their social group. Lemurs, like other prosimians, split from the main primate lineage roughly 60 million years ago and retain many ancestral primate traits (Sauther et al. 1999; Yoder and Yang 2004). Our results are thus consistent with the idea that visually-mediated social interactions have played a significant role in primate evolution and support the corollary that mechanisms of visual attention coevolved with social sophistication in primates (Jolly 1966; Barton and Dunbar 1997; Allman 1999; Emery 2000). These results are also compatible with the evolution of gaze following abilities very early in the primate lineage. When considered alongside reports of gaze following in goats (Kaminski et al. 2005), dolphins (Tschudin et al. 2001), and even ravens (Bugnyar et al. 2004), these data suggest either that gaze-following ability is widespread and evolved extraordinarily early, or that gaze-following behavior is strongly adaptive for social group-living animals and that this strong selective pressure promoted convergent evolution in these species.

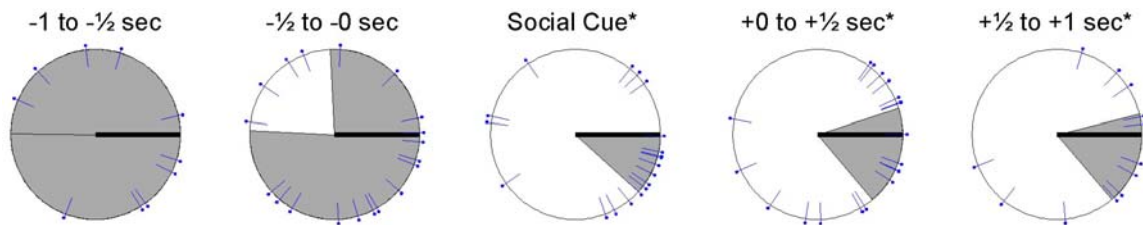


Figure 6: Gaze-alignment dynamics suggest lemurs actively follow gaze.

Successive panels show gaze alignment immediately before, during, and after subjects' gaze passed within 10° distance of the observed lemur (head and body loci only, tail ignored). Blue ticks mark individual observations (not all instances of fixation are represented in a given panel due to transient interruptions of the data stream). Shaded regions represent the mean gaze offset \pm the dispersion of the dataset (gray shading, see (Fisher 1993) for details), normalized so that the largest illustrated dispersion results in a fully-shaded circle. We found a significant increase in gaze alignment with the observed head axis ($1\text{-}\frac{1}{2}$ second prior, 10 cases, dispersion 10.746, chi^2 $p=0.52709$; $\frac{1}{2}\text{-}0$ prior second, 19 cases, dispersion 8.2311, chi^2 $p=0.25135$; during fixation event, 19 cases, dispersion 1.2252, chi^2 $p=0.011617$; $0\text{-}\frac{1}{2}$ second after, 19 cases, dispersion 2.0248, chi^2 $p=0.011617$; $\frac{1}{2}\text{-}1$ second after, 12 cases, dispersion 1.8942, chi^2 $p=0.020921$), but not body axis ($1\text{-}\frac{1}{2}$ second prior, 57 cases, dispersion 96.109, chi^2 $p=0.6911$; $\frac{1}{2}\text{-}0$ prior second, 86 cases, dispersion 6421.4, chi^2 $p=0.82925$; during fixation event, 86 cases, dispersion 34.449, chi^2 $p=0.28089$; $0\text{-}\frac{1}{2}$ second after, 86 cases, dispersion 87.623, chi^2 $p=0.51763$; $\frac{1}{2}\text{-}1$ second after, 63 cases, dispersion 30.18, chi^2 $p=0.25684$), immediately after Licinius or Aracus shifted gaze to an observed lemur. Starred intervals are significantly aligned with gaze (chi^2 test $p<0.05$).

It remains unclear which specific features attract lemur gaze toward other lemurs. Certainly a powerful cue toward animacy is motion. Both lemurs and humans are motile, but environmental features are not. However, it was our impression that humans and lemurs were often fixated despite staying in one place, while moving objects in the background (for example, tree branches swaying in the breeze) were not fixated. Supporting this notion, all fixations toward social targets decreased when the lemur subject was moving. We imagine this decrease reflects a change in visual

priorities driven by proximate behavioral goals, but cannot exclude the possibility that low-level orienting cues (e.g. image movement on the retina) were disrupted by locomotion.

Similar uncertainty exists in which features guided gaze following in this study. For example, while both observed head and body axes predicted gaze, only the head axis predicted gaze better after fixation than before. Two observations may explain this discrepancy. First, body axis was recorded more consistently than head axis across video clips, as demarcation of head axis was more easily disrupted by distance from the subject or small stature (usually in juvenile animals). Lemurs may be less likely to align gaze with juveniles or with lemurs that are very far away. Second, we note that the head and body axes of an animal are often, but not always, aligned—for example, in this data they tended to be well aligned when observed lemurs were moving across the scene, but poorly aligned when observed lemurs were sitting or were approaching the subjects. The discrepancy between head and body alignment suggests that when body and head cues conflict, lemurs preferentially align their gaze with the head.

These results add to the growing body of evidence (Tomasello et al. 1998; Call et al. 2003; Bugnyar et al. 2004) that social attention and gaze following are not exclusive to humans or even apes. Shared attention is thought to underlie theory of mind and language acquisition, and is severely disrupted in human neurological disorders such as autism. Future gaze-tracking studies promise to bridge the gap between field

observation, psychophysics, and neuroscience, and thus may play role in reconciling existing discrepancies (e.g. Klin et al. 2002b; Chawarska et al. 2003; Swettenham et al. 2003; Ristic et al. 2005) between real-world and laboratory descriptions of social attention.

4.4 Methods

We recorded gaze position in two adult male ringtailed lemurs using a wireless infrared optical gaze-tracking system (see Shepherd and Platt 2006 / Appendix for detailed methods). We worked exclusively with males to avoid complications from pregnancy and nursing during training and experimental sessions. System weight was approximately $\frac{1}{4}$ subjects' mass, similar to that experienced by females carrying twins, and did not preclude a normal range of locomotion and social interaction (see Figure 7). Recordings were made during terrestrial and arboreal locomotion, leaps, foraging, and social interaction.

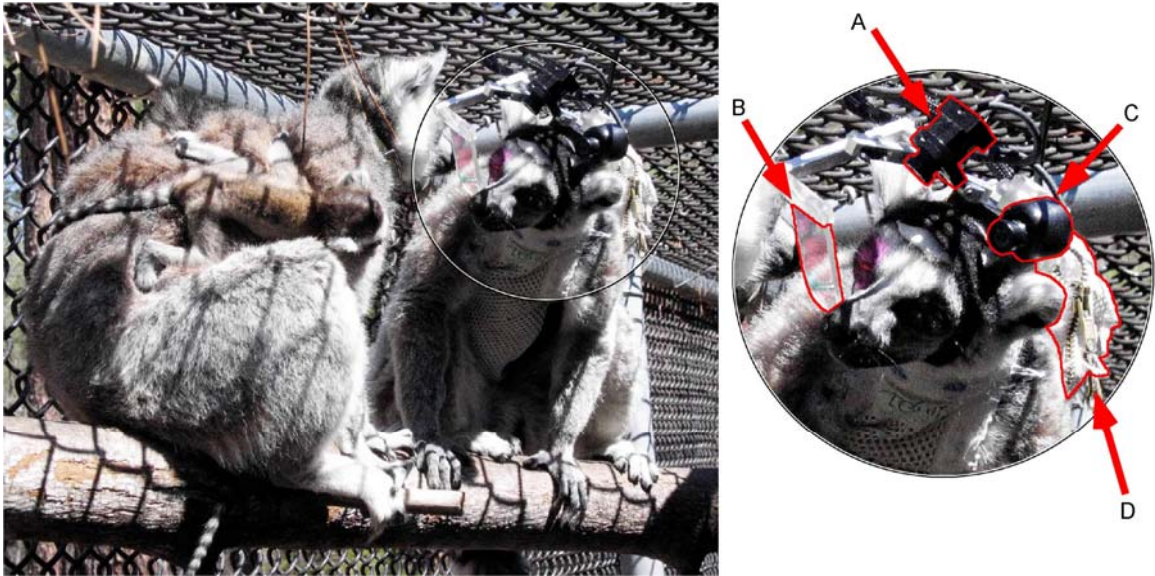


Figure 7: Gaze-tracking set-up.

Gaze-tracking hardware consisted of an infrared LED and camera (A) monitoring the eye by dichroic mirror (B), a head-mounted scene camera (C), and a wireless transmitter housed in a primate backpack (D).

Gaze-tracking was accomplished using a wireless dual-camera system. One camera recorded eye position using infrared light, while the other captured the scene visible forward from the subject's head. A five-point calibration procedure linked recorded eye positions to the corresponding visual stimuli in the scene camera. Signal transmission was vulnerable to several types of distortion or interruption, and while data was collected at 60 Hz, a 200ms smoothing window precluded neat segmentation of gaze data into fixation, pursuit, and saccade. For digital annotation and analysis, data was downsampled to 30 Hz.

Subjects habituated gradually to gaze-tracking after 4-6 weeks of thrice-weekly one-hour sessions. Cohabitant lemurs showed no obvious behavioral changes in

response to the recording equipment. Human experimenters periodically gave the lemurs food during recordings to maintain activity levels. Subjects were studied in their respective home habitats. Lemur “Licinius” was housed in three connecting outdoor rooms (1.4 x 2.0 x 3.4 m each) with branches, potential food sources, platforms, and another lemur (“Maurice”, a brown lemur, *Eulemur fulvus*). Lemur “Aracus” was housed in two indoor (1.8 x 1.6 x 2.4 m each) and one outdoor (3.7 x 3.9 x 2.4 m) connected enclosures; recordings from Aracus were also taken in another outdoor enclosure with similar dimensions and in a large, unroofed, treeless pen (5.6 x 85 m). Aracus shared these areas with up to twelve lemurs: three adult females, four juveniles, four infants, and one older male. The environments occupied by Licinius (one adult male heterospecific lemur companion) and Aracus (3 adult female and up to 1 adult male and 9 juvenile conspecifics) were distinct, and behavior was unconstrained rather than experimentally controlled. As experimental conditions varied substantially, but not systematically, across sessions and subjects, these data were collapsed prior to analysis.

Video data were gathered from five 1-hour recording sessions (2 in Licinius and 3 in Aracus) and digitized at 0.22° x 33ms resolution. One-minute excerpts, chosen for optimal signal strength, were selected for manual coding. These clips were manually coded in a custom-designed Matlab environment (Skriatok Videoscore, www.duke.edu/~svs/skriatok) to note whether the subject was moving or stationary and to extract the frame-by-frame visual coordinates of the subject’s gaze and of four

categories of regions of interest (ROI). Categories of ROI were selected *a priori* based on putative reward value, locomotor relevance, or social relevance: in general, markers were placed at specific positions on all visible humans (H), lemurs (L), food rewards (F), and at a small number of centrally-located, high-contrast environmental features (E). The end result of this coding was a marked video sequence from which we could derive gaze scanpaths, head-centered eye position, and the proximity of gaze to the various categories of ROI. When possible, lemurs were specifically marked at positions including the snout, eyes, body center, and tailbase. Observed head and body orientation were extracted from ROI based on the vector pointing from the tailbase toward the head and from the eyes toward the snout, respectively. See supplemental material for an annotated video sample. In total, 76 minutes of video were coded for analysis: 15 clips with lemur Licinius and 61 clips with lemur Aracus. For co-orienting analyses, 10 clips (all from Aracus) that were found to track gaze onscreen on fewer than half their samples were discarded. We operationalized fixation as any instances in which gaze fell within 10° of an ROI, a distance chosen to accommodate the 4° width of lemur fovea (Pariante 1975) / area centralis (von Rohen and Castenholz 1967) as well as smoothing artifact and drift in gaze calibration.

Because lemurs moved freely through a naturalistic environment, different regions and vectors of interest had different chance likelihood of being a given distance from fixation. For example, if the lemur primarily stayed in a room with three lemurs on

screen but only one food reward, the other lemurs would be more likely to appear close to fixation by simple coincidence. For these reasons we constructed a baseline “chance” distribution using a time-shuffled bootstrap. To do this, we randomly paired gaze and ROI coordinates from different time samples within each clip. These pairings were repeated 200,000 times for linear measures and 100,000 times per animal for angular measures. The distribution of linear and angular statistics generated the “chance” distance and offset expectations predicted by the null hypothesis that the lemur *ignored* these regions or directions of interest when allocating visual attention. This time-shuffling procedure thus allowed us to control for irregularities in gaze-tracker calibration or statistical accidents in the number and distribution of ROI extracted from different clips and sessions.

Bootstrapping procedures were applied as follows: We first calculated the parameter of interest, for example “the portion of time lemurs were within 10° of gaze”. We next repeated this calculation 10,000 times, using an equivalent number of samples, but this time drawing from time-shuffled data instead of raw observations. We accepted as significant any observed parameters that were among the lowest or highest 250 time-shuffled values (two-tailed permutation test, alpha $p=0.05$; see (Hesterberg et al. 2005)). Exact p-values can be calculated by multiplying the number of outliers by $2/10,000$: with 10,000 repetitions, $p<0.0002$ cannot be distinguished from 0. This procedure is easily adapted to assess other parameters, for example “portion of time by which

environmental features were fixated less during rest than locomotion, less the portion of time by which lemurs were fixated less during rest than locomotion.”).

In addition to these bootstrap procedures, we also analyzed the temporal sequence of gaze vectors around fixation events, determining the dispersion (angular variability, see Fisher 1993) of gaze vectors and the shared-hemifield frequency (χ^2 test) before and after subject lemurs aligned their gaze with the observed individuals.

Please see supplemental video S1 (in (Shepherd and Platt 2008)) for a brief sample of annotated data. More sample videos are available at <http://www.duke.edu/~svs/research/lemurgaze>.

5. Social status gates social attention in monkeys

5.1 Introduction

Humans rapidly shift attention in the direction other individuals are looking, following gaze in a manner suggestive of an obligatory social reflex (Friesen and Kingstone 1998b; Driver et al. 1999a; Langton and Bruce 1999b; Hietanen and Leppanen 2003). Monkeys' attention also follows gaze, and the similar magnitude and time-course of gaze-following in rhesus macaques and humans (Deaner and Platt 2003) implicates shared neural mechanisms. Here we show that low-status male rhesus macaques reflexively follow the gaze of all familiar rhesus macaques, but that high-status macaques selectively follow the gaze only of other high-status monkeys. These results suggest that gaze-following in monkeys is composed of reflexive and voluntary components, and that the strength of these mechanisms varies according to social status.

We probed the impact of social status on gaze-following in rhesus macaques performing a simple visual orienting task (Deaner and Platt 2003) (Figure 8a). Each monkey (four high-status, three low-status) fixated a central target which was replaced by an image of a familiar monkey's face looking left or right. After 100, 200, 400, 600, or 800 ms, the face disappeared and a peripheral target appeared randomly left or right; monkeys then shifted gaze to the target to receive a juice reward. Crucially, the face's gaze direction did not predict target location. We demonstrated previously that saccade

reaction times for monkeys and humans were faster on those trials in which observed gaze was congruent with target location; reaction time savings thus served as our operational definition of gaze-following. We hypothesized that monkeys would generally follow gaze, but that the strength and timing of gaze-following would be modulated by social status.

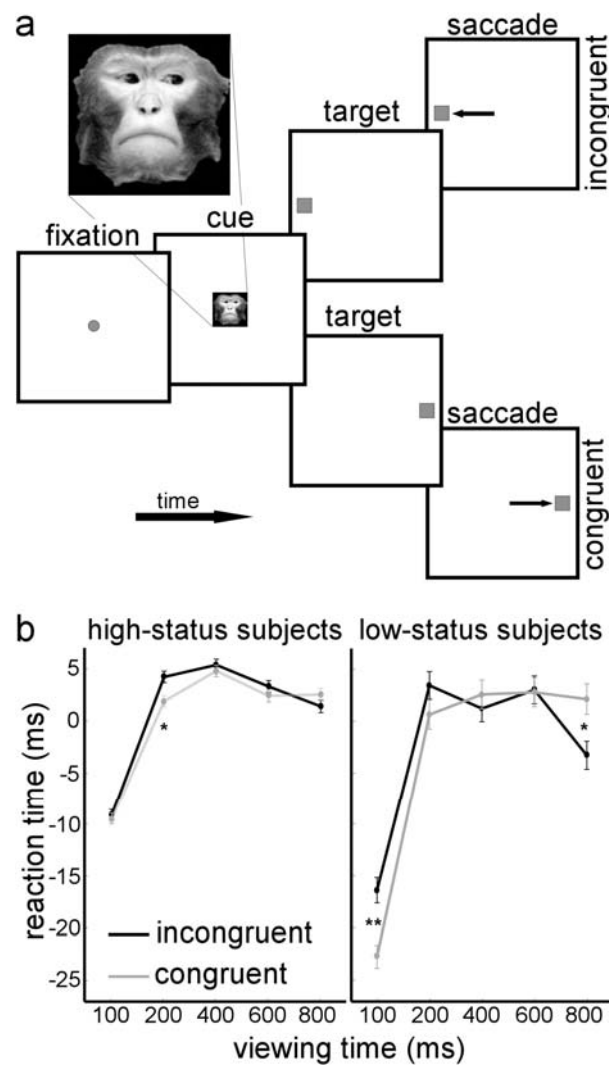


Figure 8: Gaze Following Varies by Status.

(a) **Visual Orienting Task.** The impact of social status on gaze-following was examined by comparing reaction times for saccades made to a peripheral target after viewing an image of a familiar monkey looking left or right. Each monkey first fixated a central yellow square ($\pm 3^\circ$) for 200-500 ms. The yellow square was then extinguished and a monkey face, shown here in inset, was illuminated centrally for a variable duration (100, 200, 400, 600 or 800 ms). If the monkey maintained fixation, the face was extinguished and a peripheral yellow square simultaneously illuminated at one of two fixed positions located symmetrically 10-15° to the left or right. Gaze shifts to the peripheral target within 350 ms were rewarded with a small squirt of juice.

(b) **Gaze-following dynamics vary with social status in male rhesus macaques.** Average (\pm S.E.M.) saccade reaction times plotted as a function of face viewing duration on congruent and incongruent trials, for high-status (left) and low-status (right) subjects. For high-status monkeys, gaze cues evoked significant reaction time savings only at the 200 ms viewing duration. For low-status monkeys, both early reaction time savings and later inhibition of return (IOR) were observed. **post-hoc test $p < 0.00005$; *post-hoc test $p < 0.005$; all other contrasts $p > .05$.

5.2 Results

Overall, monkeys followed gaze at 100 ms (LSD, $p < 0.005$) and 200 ms (LSD, $p < 0.005$) but showed IOR at 800 ms (LSD, $p < 0.01$). More importantly, social status significantly influenced gaze-following (Figure 8b; ANOVA, $p < 0.005$). The three low-status monkeys showed initial gaze-following at 100 ms (LSD, $p < 0.00005$) followed by IOR at 800 ms (LSD, $p < 0.005$). Although reaction times differed significantly amongst individuals (ANOVA, $p < 0.05$), every low-status monkey followed gaze at 100 ms (Mann-Whitney U $p < 0.05$) and tended to show IOR at 800ms. The four high-status monkeys, by contrast, all showed gaze-following at 200 ms (ANOVA, $p < 0.05$; LSD, $p < 0.005$) with no IOR (800 ms, LSD, $p = 0.4$). To control for experience, we repeated the

analyses using only the first 500 correct trials from each monkey and found an identical pattern of results (ANOVA, $p < 0.005$). Rapid gaze-following and IOR in low-status monkeys implies reflexive attention, whereas delayed gaze-following and lack of IOR in high-status monkeys implies voluntary attention (Jonides 1981a; Posner and Cohen 1984; Klein 2000).

We next examined whether the social status of the cuing monkey influenced gaze-following. Across all viewing durations, gaze-following by low-status monkeys was unaffected by cue status (ANOVA, $p = 0.6$); high-status monkeys, by contrast, only followed the gaze of other high-status monkeys (ANOVA, $p < 0.01$; low-status cues, LSD, $p = 0.7$; high-status cues, LSD, $p < 0.005$). This difference may arise from the distinct time course of gaze-following in each group: In fact, across all subjects, late (> 400 ms cue duration) gaze-following was stronger to high- than low-status monkeys (pooled subjects, ANOVA, $p < 0.005$; high-status only, ANOVA, $p < 0.01$; low-status only, ANOVA, $p < 0.05$).

5.3 Discussion

This influence of cue social status complements prior reports (Chance 1967; Keverne et al. 1978; Deaner et al. 2005) that nonhuman primates preferentially attend to high-status individuals and suggests that preferential attention extends in the direction these animals look. The time-course with which the cue's social status influenced gaze-

following is also consistent with the observation that neurons in macaque temporal cortex discriminate identity in a viewpoint-independent manner only after 150 - 400 ms (Sugase et al. 1999; Eifuku et al. 2004).

Our results confirm prior reports that gaze-following in nonhuman primates, as in humans, is composed of reflexive and voluntary components (Tomasello et al. 2001b; Friesen et al. 2004) and, moreover, demonstrate that the strength of these mechanisms varies according to social status. We further speculate that variation in reflexive and voluntary gaze-following among monkeys may share features with variation in social attention in humans. For example, the balance of reflexive and voluntary social attention may be set by neuromodulatory systems (Amaral 2002; Sapolsky 2004) associated with differences in personality or temperament (Clarke and Boinski 1995; Bercovitch and Ziegler 2002). Low social status may correlate with heightened arousal and scanning behavior (Keverne et al. 1978; Caine and Marra 1988; Clarke and Boinski 1995) supporting fast, reflexive gaze-following. High social status, in contrast, may necessitate selective monitoring of only other high-status monkeys (Keverne et al. 1978; Deaner et al. 2005). Though macaque social status does not predict plasma cortisol levels (indexing anxiety), it does predict levels of the male sex hormone testosterone (Sapolsky 2004). Correspondingly, all high-status males in our study had larger testes than all low-status males (Mann-Whitney U, $p < 0.05$), suggesting higher circulating testosterone levels (Bercovitch and Ziegler 2002). Given the recent report that human males follow gaze less

robustly than human females (Bayliss et al. 2005), these data suggest individual variation in androgen-linked masculinization may contribute to differences in the strength of reflexive and voluntary gaze-following in primates.

5.4 Methods

Seven pair-housed male rhesus macaques (*Macaca mulatta*) from our colony at the Duke University Medical Center Vivarium served as subjects; each was assessed as high-status or low-status relative to its cagemate based on unidirectional submissive displays (Deaner et al. 2005). Moreover, pairwise status extended to all other members of the colony (i.e., all low-status monkeys averted gaze from all other high-status monkeys) during controlled confrontation tests (Deaner et al. 2005). All animals were originally reared in naturalistic social groups; cage position and composition for the macaques in our colony remained unchanged for more than three years prior to the initiation of this study. All animal procedures were approved by the Duke University Medical Center Institutional Animal Care and Use Committee and were designed and conducted in compliance with the Public Health Service's Guide for the Care and Use of Animals.

Experiments were run on a Dell Precision 220 Pentium IV computer using custom software (ryklinsoftware.com). Monkeys viewed stimuli on a 24" Sony Trinitron monitor running at a resolution of 1024x768 and refresh rate of 60 Hz. Subjects were

seated with their eyes 45 cm from the center of the monitor. Eye position was monitored using a magnetic search coil surgically implanted beneath the conjunctiva of one eye and sampled at 500 Hz (Fuchs and Robinson 1966; Judge et al. 1980) while head position was maintained with a surgically implanted stainless steel prosthesis (Crist). All surgical procedures were performed aseptically, followed with appropriate analgesics and antibiotics, and in all other ways followed standard protocols described previously (Deaner and Platt 2003).

Monkey faces displayed at fixation were drawn from 32 images of four familiar macaques (two high- and two low-status) looking either left or right. Each monkey and gaze direction was represented with two eye-averted and two head-and-eyes-averted images. Face images were standardized by cropping the head from the background, centering the midpoint of the eye region (eyes-only) or the centermost eye corner (head-and-eyes), and resizing to 115x115 pixels, approximately 5°. All stimuli were presented on a black background. All monkeys, both subjects and cues, were approximately 8 years old at the time they participated in this experiment.

We operationalized gaze-following as a decrease in reaction time for saccades toward targets at the location viewed by the cue image relative to saccades toward targets located opposite the direction of gaze in the cue image. All statistical tests consisted of ANOVA, with post-hoc tests between groups by Fisher's Least Significant Difference (LSD) or by Mann-Whitney U, as noted. Statistical tests were performed as

follows: first we confirmed the presence of time-varying gaze-following across all our macaque subjects, controlling for variation in the number of trials successfully completed by each macaque whenever possible (ANOVA, normalized RT by congruence by cue duration with subject ID as variable of no interest). Significant differences between individuals were present and were found to vary significantly with social status (ANOVA, normalized RT by subject status by congruence by cue duration). Gaze-following dynamics of low- and high-status monkeys were probed separately using ANOVA (normalized RT by congruence by cue duration with subject ID as variable of no interest).

We additionally examined the responses of low- and high-status subjects to cues from monkeys of differing social status. We first separately analyzed low- and high-status individuals pooled across cue viewing times (ANOVA, normalized RT by cue social status by congruence with subject ID as variable of no interest), and then examined the overall responses of pooled low- and high-status monkeys as a function of time (ANOVA, normalized RT by cue social status by cue duration with subject identity as a variable of no interest).

Finally, we examined the impact on gaze-following of low-level cue features, including luminance, contrast, head area, and saturation, using multiple regression and found no significant effects. Although we examined the distribution of eye positions during cue fixation, both from each monkey and relative to each specific cue image, we

were unable to find any systematic differences relating to either social status or reaction time. However, we do not currently exclude the possibility that fixations toward the cuing monkey's eye region may correlate with subsequent gaze-following (e.g. (Dalton et al. 2005)): We note that for the images and fixation windows used in this experiment, successful task performance generally positioned at least part of the cuing monkey's eye-region within the subject's fovea.

Onset and offset of task-related saccades were defined using a velocity criterion (onset, $\geq 60^\circ/s$ for ≥ 8 samples; offset, $\leq 30^\circ/s$ for ≥ 3 samples). We gathered 1000-7000 successful trials from each macaque, excluding saccades initiated faster than 90 ms or slower than 280 ms. The average number of successful trials collected in a single session was 754, with no session contributing more than or 35% the subject's total. "Incidental" successes, defined as successful trials that occurred despite a $\geq 50\%$ fail rate within ± 2.5 -minute time window, were excluded from analysis. To minimize the variance in reaction time due to transient spatial biases or changes in motivation, we normalized our data by subtracting the mean successful reaction time for each monkey and target direction across a 15-minute moving window within each dataset.

All monkeys had extensive experience with nonsocial visual orienting tasks. However, to investigate the effects of experience in this specific paradigm, we parameterised the training history at every data point by noting the log chronological order in which each data point was gathered from a given subject. Neither training

history nor the local (± 2.5 -minute) success rate interacted with gaze-following or the temporal dynamics thereof as continuous predictors of normalized reaction time in a homogeneity-of-slopes general linear model (training history on congruence, $p=0.3$, training history on cue duration by congruence, $p=0.09$; local success rate on congruence, $p=0.3$, local success rate on cue duration by congruence, $p=0.4$). We found an identical pattern of subject status effects using only the first 500 correct trials from each monkey, confirming that training history was not responsible for the subject effects reported here.

Morphometric data was recorded in one day while monkeys were anaesthetized for a routine physical exam. To estimate circulating testosterone, we used callipers to measure the testicles of each subject across their longest axis: these measurements, cubed, estimate testicular volume and thus the rate of testosterone production (Bercovitch and Ziegler 2002).

6. Mirroring of attention by neurons in macaque parietal cortex

6.1 Introduction

People naturally and intuitively share attention with each other. In a laboratory setting, humans respond more quickly to targets that are the object of another's attention, even when this social cuing is brief or consistently misleading (Friesen and Kingstone 1998a; Driver et al. 1999b; Langton and Bruce 1999a). Monkeys' attention also follows the gaze of others (Emery et al. 1997), and the similar magnitude and time-course of gaze following by rhesus macaques and humans (Deaner and Platt 2003) implicates shared neural mechanisms. The ability to follow gaze is believed to be an important foundation for theory of mind (Baron-Cohen 1994; Perrett and Emery 1994a); thus, the neural processes governing gaze following are relevant both to the evolution of social cognition (Tomasello and Farrar 1986; Hare and Tomasello 2004; Tomasello et al. 2005) and to clinical disorders, such as autism, associated with social attention deficits (Baron-Cohen et al. 1995; Pelphrey et al. 2002; Pelphrey et al. 2005; Ristic et al. 2005). Though gaze following involves automatic "mirroring" of other's mental states, mirror neurons (di Pellegrino et al. 1992; Rizzolatti and Craighero 2004) for visual orienting have not previously been identified.

Current evidence suggests that identification of where other individuals are looking is accomplished by neurons along the superior temporal sulcus (STS) (Puce et al.

1998; Wicker et al. 1998; Hoffman and Haxby 2000; Tsao et al. 2003) and in the amygdala (Kawashima et al. 1999; Hoffman et al. 2007). In primates, signals from these brain areas (Tsao et al. 2003) ramify to multiple targets in the visual orienting system, including, within one or two steps, posterior parietal cortex (7A and lateral intraparietal area, LIP; Seltzer and Pandya 1991), prefrontal cortex (supplemental and frontal eye fields, SEF and FEF; Seltzer and Pandya 1989), and subcortical visual areas (pulvinar nucleus of the thalamus, Romanski et al. 1997; and superior colliculus, Fries 1984). Neuroimaging studies have corroborated the finding that perception of faces with averted gaze activates populations of neurons in the STS region and the amygdala, as well as the parietal cortex (Calder et al. 2007). These observations suggest that gaze-following behaviour might be mediated by a relatively straightforward system, beginning with the STS and proceeding through parietal cortex to attention- and gaze-control networks.

Because the fastest reported gaze-following behavior in monkeys is evoked at very short latencies (100 ms after gaze cue onset, see Shepherd et al. 2006), the processing stream that discriminates gaze direction and relays this information to visual orienting areas must operate quite rapidly. Thus, while neuroimaging techniques can identify cortical areas sensitive to the direction of observed gaze, their temporal resolution is too coarse to determine whether these areas are capable of mediating fast gaze-following behavior. In principle, such questions could be answered by recording

the activity of neurons in this putative social gaze processing stream in behaving macaques.

To address these issues, we probed the impact of social gaze cues on the firing rates of LIP neurons in monkeys performing a simple visual orienting task. Previous studies have linked LIP activity to both covert and overt orienting of attention, with neuronal activity tracking visual saliency, saccade likelihood, and target value (Colby and Goldberg 1999; Platt and Glimcher 1999). Our primary goals were to determine whether LIP neurons are sensitive to observed gaze direction and, if so, whether this sensitivity could mediate gaze-following behavior. We were particularly interested in whether the response dynamics were quick enough to mediate the fastest behavioral responses in observed in standard gaze-following probe (Figure 9) (Friesen and Kingstone 1998a; Deaner and Platt 2003; Shepherd et al. 2006). To our knowledge, no prior studies have linked the responses of single neurons to gaze-following behavior or reported the latency at which observed gaze *direction* is represented in the brain. Though several prior studies have contrasted eye-contact with averted gaze (e.g. Perrett et al. 1985), they have not explicitly reported deictic signals, i.e. those that “point” out specific spatiotemporal targets.

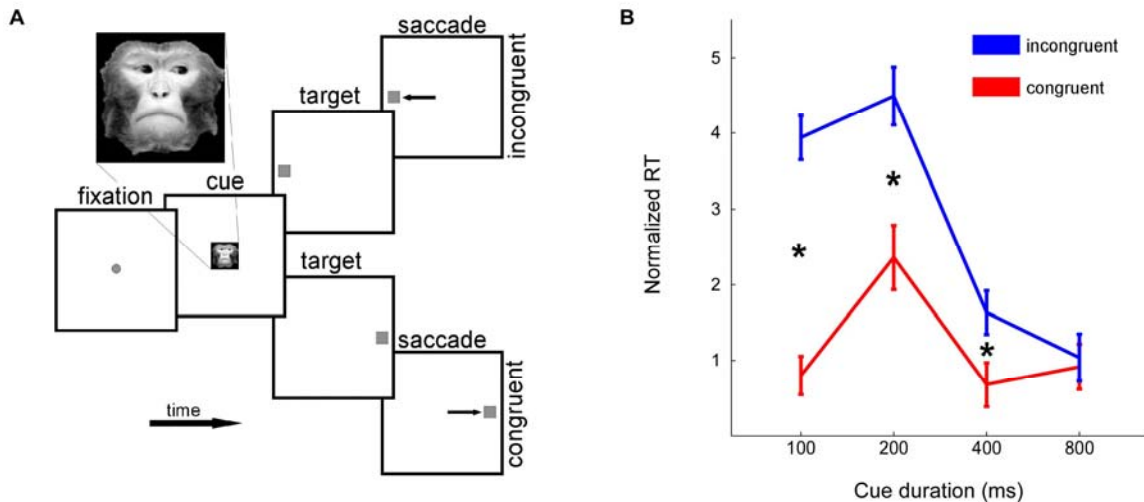


Figure 9: Visual Orienting Task and Behavioral Dynamics.

(a) The impact of social gaze cues on the activity of single neurons in area LIP was probed while monkeys shifted gaze to a peripheral target after viewing an image of a familiar monkey looking toward the RF or away from it. Macaques first fixated a central yellow square ($\pm 3^\circ$) for 200-500 ms. The yellow square was then extinguished and a monkey face, shown here in inset, was illuminated centrally for a variable duration (100, 200, 400 or 800 ms). If the monkey maintained fixation, the face was extinguished and a peripheral yellow square simultaneously illuminated at one of two fixed positions located symmetrically within, or opposite, the measured neuronal RF. Gaze shifts to the peripheral target within 350 ms were rewarded with a small squirt of juice. (b) Gaze following was observed after 100-400ms face viewing durations. The average normalized saccade latency observed across all neurons and cue durations are here plotted for congruent (red) and incongruent (blue) cue conditions. Normalization was to the average response latency for all cue conditions for each given neuronal recording session, cue duration, and target location. Both the main effects of cue validity and cue duration were significant, with the interaction significant at $p=10^{-5}$. Effect size was significant by t-test at 100, 200, and 400ms ($p=3 \times 10^{-10}$, 0.0002, and 0.03 respectively).

We found that the activity of 30 of 106 neurons recorded in LIP (28%) was modulated by social gaze cues, even when these cues were presented outside their classical response fields. Of these, 43% behaved like “mirror neurons”, becoming more

active both while directing attention toward a region of space, and while observing other monkeys do the same. Moreover, we report that temporal dynamics of neuronal responses to social gaze cues predicted the time-course of gaze-following behavior. These findings suggest the hypothesis that parietal cortex mediates gaze following. While confirming this hypothesis requires functional techniques, such as reversible inactivation or microstimulation, these correlative findings support a role for LIP in social mirroring of both orienting behavior and associated attentional states.

6.2 Results

Overall, monkeys followed gaze during physiological recordings, initiating saccades faster when a photographed monkey had also looked toward their target. Gaze-following behavior was strongest at short delays between cue onset and target appearance, as has been previously reported (Deaner and Platt 2003; Shepherd et al. 2006). Monkeys showed significant gaze following for the shortest three cue durations (Figure 9b; ANOVA, average normalized saccadic reaction time per neuron, by congruence X cue duration, $p=0.00001$. Post-hoc t-test of neuronwise effect size at 100ms, $p=3*10^{-10}$; at 200ms $p=0.0002$; at 400ms, $p=0.03$; at 800ms, $p=0.8$).

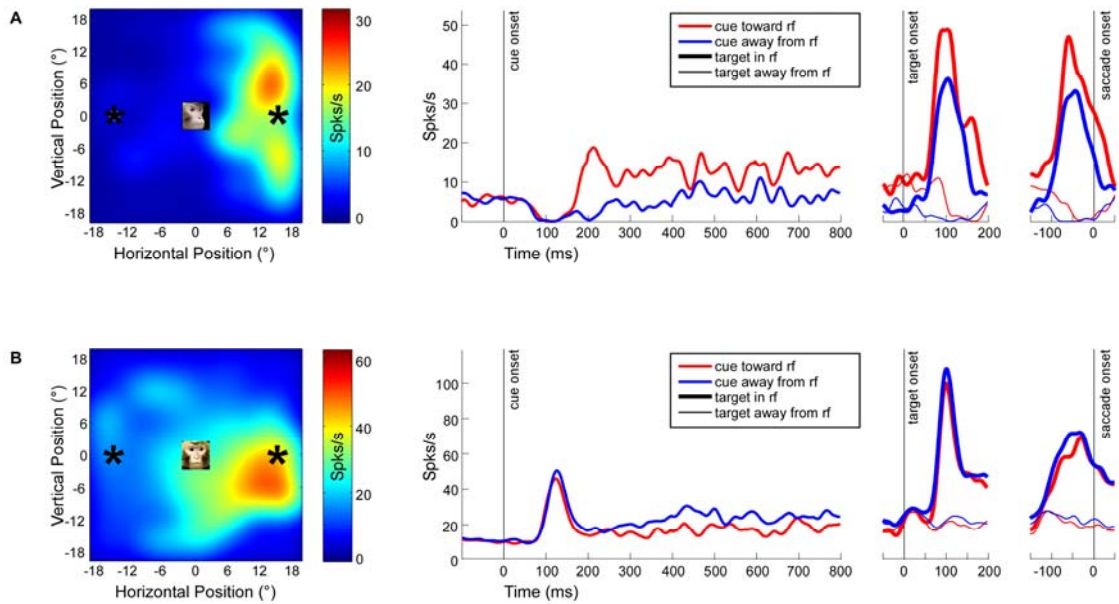


Figure 10: Single LIP neurons are sensitive to social gaze cues.

(a) Example neuron showing firing rate enhancement by social gaze cues. (b) Example neuron showing firing rate suppression by social gaze cues. Response field plots (left panels) illustrate firing rates for saccade targets across the visual field, recorded during an independent set of simple or delayed-saccade mapping trials. Cue image and target locations are superimposed on this map at scale. Right panels show neuronal activity as a function of time, synchronized to cue onset, target onset, and saccade onset, respectively. Cue and target location are indicated by color (red for cues gazing toward the response field; blue, away) and line thickness (thick lines for saccades toward the response field; thin, away). Gaze modulations were robust across time for both neurons.

In total, 153 neurons were recorded, of which 106 were confirmed post-hoc to strongly differentiate between saccade targets located in their estimated response fields (“in RF”) and those reflected through the origin (“outside RF”) (t-test with Bonferroni-corrected $\alpha=.05/153$, over the interval 20-120 ms following target onset). Although faces subtended only the central 5° of visual space, were static, and were presented outside

the classical response field of the recorded neurons, the firing rates of some neurons were systematically modulated by observed gaze direction (Figure 10). For example, Figure 10a presents data for a neuron that increased firing following presentation of a monkey face gazing towards the right side of the monitor—the same direction preferred by the neuron when monkeys oriented to a visual target during simple response field mapping trials. By contrast, other neurons fired more strongly when the observed monkey face was gazing away from the classical response field (Figure 10b). Thirty (28%) of 106 neurons differentiated faces looking toward from those looking away from their RF (Figure 11a, see also Figure 12). About half of these neurons showed systematic increases in firing rate (n=13), while the other half showed systematic decreases in firing rate (n=17), in response to faces gazing toward the RF. These firing rate increments and decrements persisted from face presentation through saccade initiation. Thus, area LIP appears to spontaneously receive information about where other individuals are looking, despite the fact that monkeys were not trained to discriminate these cues or associate them with rewards, and despite the fact that face cues did not predict the location of saccade targets.

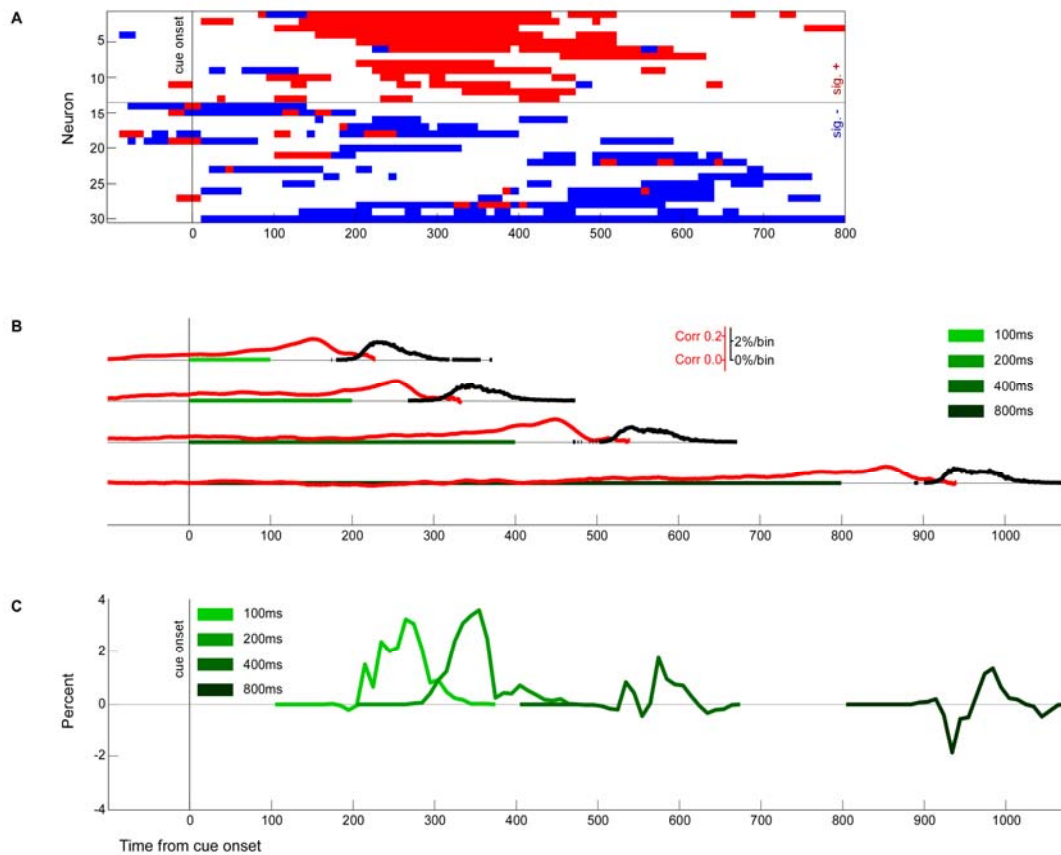


Figure 11: Population response to social cues predicts gaze following.

(a) **Neural cue responses:** Significant neuronal responses to observed gaze direction in 10ms bins. Neurons enhanced by social gaze cues (red) are temporally clustered at the time windows for which gaze-following behavior is strongest, while those suppressed by social gaze cues maintain tonic decreases in activity throughout the fixation period (b) **Task dynamics:** cue fixation, saccade preparation, and saccade latencies are shown for each cue duration. Green bars illustrate the duration of the cue fixation period, red curves indicate correlation of LIP activity with decreased saccade latency, and black curves indicate saccade onset density as a function of time. Thus, the red curves indicate the moment-to-moment correlation of observed LIP activity with decreased stimulus response latency, and range from nearly 0 to as high as 0.2 approximately 30-50 ms prior to saccade initiation. Similarly, the black curves indicate when saccades were observed to begin, with a peak of approximately 2% occurring in any given one-ms bin. (c) **Saccadic response latency distributions:**

differential saccade-onset density for congruently-cued versus incongruent trials show early gaze following which later fades. We here attempt to indicate exactly when gaze-following behavior is evidenced in behavior. To do this, we separately generated histograms of saccade onset time for congruent and incongruent responses— analogous to black curves in the above panel. We then integrated these curves and examined the difference between these cumulative histograms, to illustrate the precise times at which congruent saccades occur faster than incongruent. Thus, positive deflections indicate that more responses have occurred to congruently-cued than incongruent trials, and negative deflections indicate the opposite. In summary, while suppressed neuronal responses are fairly uniform, the excitatory neuronal responses (panel a) are maximal while the 100-400ms cue responses are being generated (panel b) and during the time period in which the largest behavioral effects are observed (panel c).

We next compared the time course of LIP social gaze cue sensitivity to the time course of behavioral gaze following. As we have shown previously, gaze-following behavior develops quickly, then fades, and at longer cue durations may even reverse sign, a phenomenon dubbed inhibition of return (IOR) (Deaner and Platt 2003; Shepherd et al. 2006). Looking exclusively at those trials in which a spatially-neutral gray square appeared, rather than a directional gaze cue, we found that LIP population activity was negatively correlated with saccade latency from 148 ms prior through 115 ms after the time of cue offset / target onset (all trials, Figure 11b; neutral only, Figure 13). This finding is consistent with past observations of ramping LIP activity approximately 100-50ms prior to initiation of a gaze shift toward the neuronal response field (Roitman and Shadlen 2002; Ipata et al. 2006). Note these correlations do not necessarily imply that peak firing rates correlate with saccade latency—rather, we suspect these correlations

may reflect a change in the latency of a short, stereotyped burst of activity which, in turn, correlates with saccade latency.

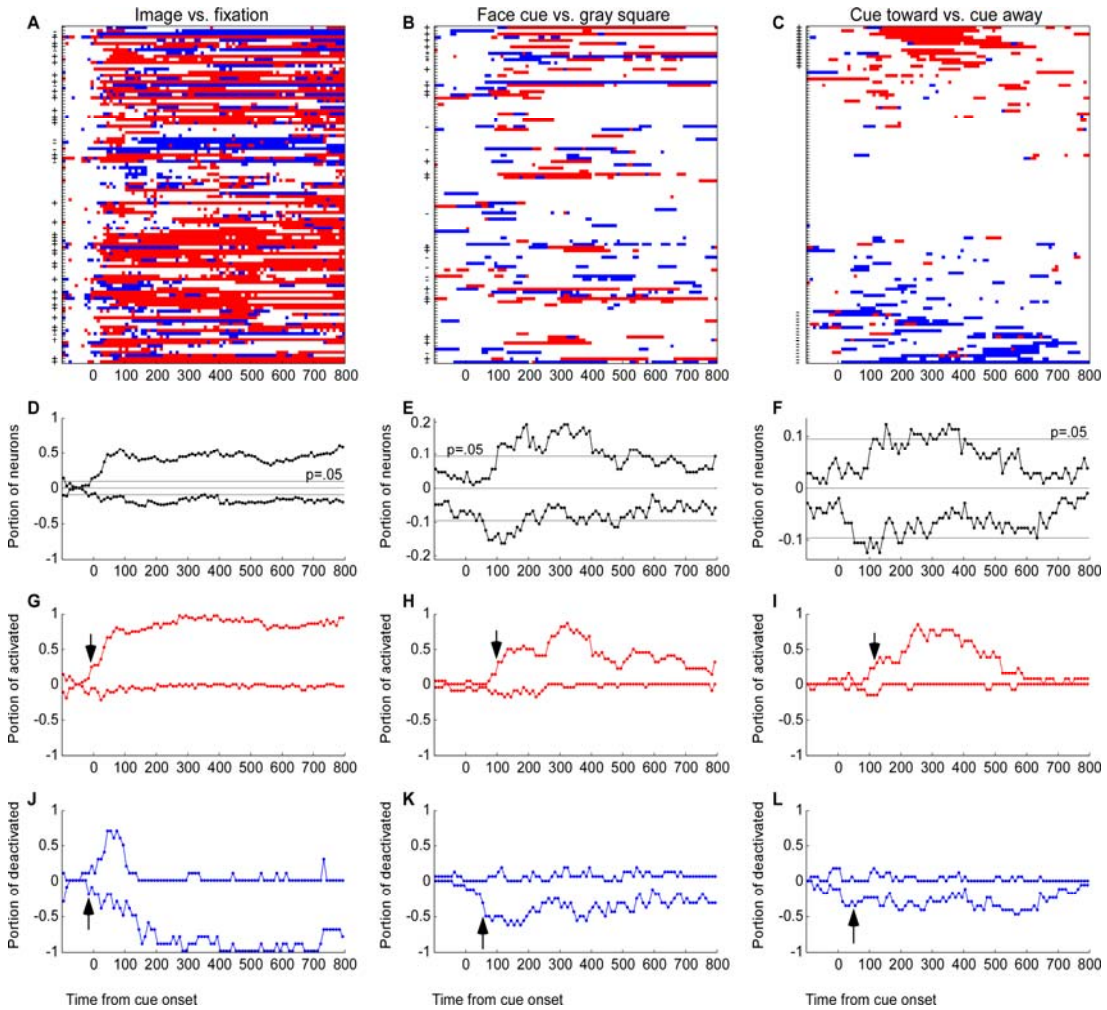


Figure 12: The LIP population develops sensitivity to lower- before higher-level visuosocial cue dimensions.

Columns plot, from left to right, the time course of significant modulation by (A) image fixation, (B) image type, and (C) social gaze cue direction. Population responses first differentiate image onset, then social images, and lastly respond to deictic signals. This holds whether looking across the population (black, D-F); at only neurons which significantly preferred image onset, social images, or cues toward RF (red, G-I); or at only neurons significantly suppressed by image onset, social images or gaze cues (blue, J-L). On these lower plots (G-L), arrows mark the time at which

the population response became significant (two-tailed alpha $p=0.05$). Across all contrasts, suppressive neurons (blue, J-L) appeared to be activated earlier, but with lower temporal coherence.

Based on these data, in order for LIP to directly mediate gaze-following behavior, neurons in this area must be sensitive to social gaze cue direction in the 250ms time window surrounding target onset and during subsequent saccade preparation. Intriguingly, we found that social gaze cues directed toward the RF most strongly excited neurons at latencies 100-500ms after cue onset. In fact, nearly all neurons significantly activated by gaze cues toward their RF differentiated between toward-rf and away-from-rf gazing faces in the period from 250 to 400 ms after cue presentation (Figure 11a, see also rightmost panels of Figure 12). Thus, socially-cued increases in LIP activity occurred in roughly the same time period in which we observed the strongest gaze-following behavior (Figure 11). Conversely, neurons that were significantly deactivated by gaze toward their RF showed no such pattern, with suppression persisting throughout the fixation period (Figure 11a, see also rightmost panels of Figure 12)—a temporal pattern consistent with a role in maintaining fixation (Schiller and Tehovnik 2001).

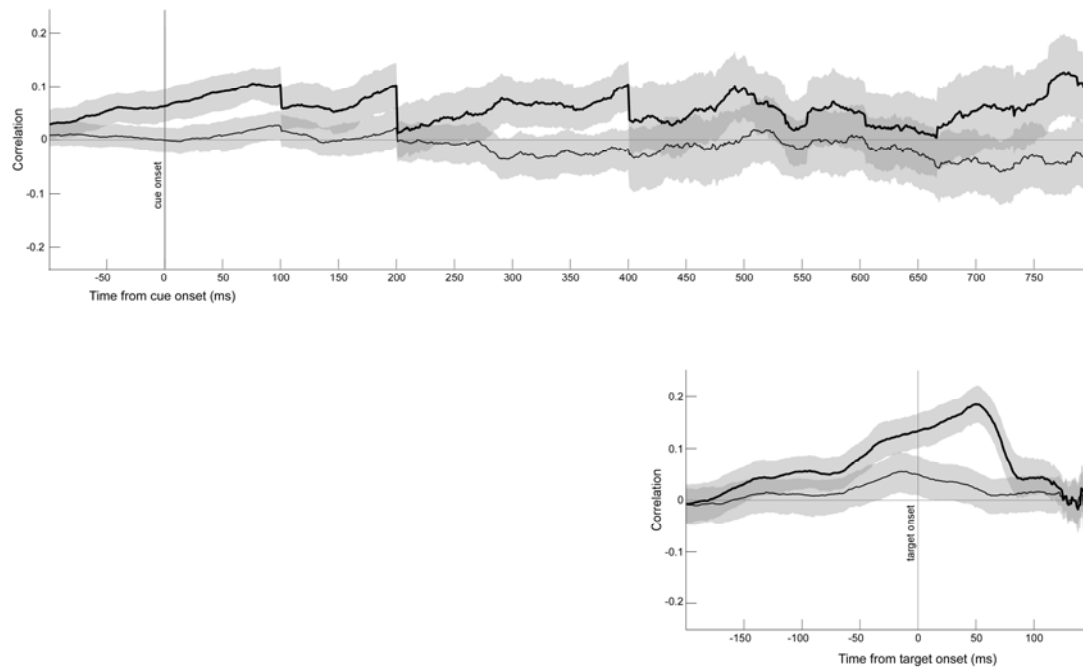


Figure 13: Population activity predicts decreased saccade latency.

Firing rates in neutrally-cued trials predicted decreased reaction times both (a) during the cue period and (b) during saccade preparation. Using only trials in which a grey square appeared rather than a social gaze cue, firing rate strongly predicted decreased saccade latency near the end of a cue duration (before 100, 200, 400, and 800 ms). Peak correlations, however, were achieved during the period intervening between target onset and saccade onset. These correlations were pronounced only when the target appeared in the neuron’s response field (thick lines). Thus, additional neuronal activity in LIP would result in gaze following primarily if it occurred immediately before target onset or during saccade preparation.

To refine our understanding of social attention effects in LIP, we contrasted the latency with which neurons signaled image onset, the latency with which they distinguished social gaze cues from neutral gray squares, and the latency with which they distinguished social gaze cue direction (Figure 12). We looked both at overall population responses and at subpopulations that were significantly enhanced or

suppressed by image onset, image type, and cue direction, respectively. We found that latencies increased systematically: Image-independent responses to cue onset plateaued after only 50 ms, presumably reflecting an overall change in luminance of the display. By contrast, distinctions between social gaze cues and a gray square control image arose between 60 ms (for those neurons that preferred large gray square) and 100 ms (for those neurons that preferred faces). Finally, distinctions between social gaze cue directions arose last, with gaze-cued activations beginning between 100-200 ms and gaze-cue deactivations remaining fairly constant during the cue fixation period. These results are consistent with LIP receiving feed-forward information from successively higher levels of the ventral stream, with deictic social gaze signals arriving last. These findings are also consistent with the idea that LIP mediates both social salience assessment (Klein et al. 2008a) and oculomotor reward contingencies related to task demands (Platt and Glimcher 1999). We speculate that gaze-cue enhanced neurons signal the increased value of acquiring information about regions of space where other monkeys are looking. By contrast, we speculate that gaze-cue suppressed neurons contribute to active fixation required for successful task performance; in order to successfully complete the trial and receive juice reward, any overt gaze following must be suppressed, and fixation maintained, throughout the entire cue period.

6.3 Discussion

This report unifies past literature on mirror neurons, thought to participate in the imitation and interpretation of observed action (di Pellegrino et al. 1992; Rizzolatti and Craighero 2004), with literature on gaze following, thought to mediate the sharing of attentional states between individuals (Baron-Cohen 1994; Friesen and Kingstone 1998a; Driver et al. 1999b; Tomasello et al. 2005). Mirror neurons are motor neurons that discharge not only during enactment but also during observation of a particular behavior (di Pellegrino et al. 1992; Rizzolatti and Craighero 2004). LIP, while not classically a motor area, is active in gaze-related sensorimotor transformations (Gnadt and Andersen 1988; Platt and Glimcher 1997; Snyder et al. 1997, 2000), and its activity contributes to both overt (Thier and Andersen 1998) and covert shifts of attention (Colby and Goldberg 1999; Bisley and Goldberg 2003). We here report that neurons in LIP respond not only when monkeys orient attention toward their response fields but also when other monkeys are observed orienting in the same direction. These effects are detectable despite the irrelevance of social gaze cues to the behavioral task and despite the fact that faces were presented outside the neurons' classical response fields. We find further support for gaze mirroring in the common modulation of gaze-following behavior (Shepherd et al. 2006; Deaner et al. 2007) and mirror system activity (Kilner et al. 2006) by social relevance. Though only a small population of LIP neurons demonstrate mirror neuron behavior in this experiment, this number is consistent with

past studies of mirror neurons. In their initial description of mirror neurons in area F5, di Pellegrino et al. identified 29 of 184 (16%) as having visuomotor mirror properties (di Pellegrino et al. 1992).

Furthermore, we report that those neurons excited by gaze toward their response field were most strongly activated during the period in which the strongest gaze-following behavior was observed. This evidence supports the notion that these neurons may contribute to the reflexive sharing of attention between individuals demonstrated by diverse gaze-following tests (neurotypical humans: (Friesen and Kingstone 1998a; Frischen et al. 2007), other species: (Emery 2000; Deaner and Platt 2003; Itakura 2004), dysfunction in human pathology: (Klin et al. 2002b; Ristic et al. 2005)). Although social gaze cue effects on neuronal activity were small, they were statistically significant even when driven merely by small, static, repetitive digital pictures. While previously-described mirror neurons are activated by the observation of specific actions (di Pellegrino et al. 1992; Rizzolatti and Craighero 2004), LIP neurons here responded to the observation of a sustained attentional state. We anticipate these neuronal responses would be even more robust for dynamic social gaze cues, paralleling the phasic responses observed in other mirror neurons during observation of movements (di Pellegrino et al. 1992; Rizzolatti and Craighero 2004).

Nonetheless, a number of factors militate for caution in the interpretation of these results. While our data show that LIP neurons are sensitive to social gaze early

enough to mediate fast gaze-following behavior, we cannot confirm a causal role. Indeed, the activation of LIP neurons in response to observed gaze comes quite late in the preparatory window for 100ms-cue-duration saccades, despite the fact that gaze following of these cues is nearly as strong as gaze following of cues presented for 200ms. We cannot currently exclude the possibility that activity in other brain areas is crucial for these fast gaze-following responses. In fact, modulations in the activity of LIP neurons may result from inputs from subcortical or frontal circuits that process social gaze cues. In this view, the observed modulations in LIP activity reflect the integration of social gaze cue information with calculations of salience (Colby and Goldberg 1999) or reward (Klein et al. 2008a) associated with acquiring behaviorally useful visual information. Alternatively, LIP may act to bind together observed conspecifics with the objects of their attention, operating in an analogous fashion to the spatial binding of co-activated response fields across saccades (Duhamel et al. 1992).

Indeed, though Calder and colleagues have reported activation in human parietal cortex that differentiates the direction of observed gaze (Calder et al. 2007, see also Hietanen et al. 2006; Materna et al. 2007), other evidence suggests this is not the only pathway through which gaze following may operate. For example, Vuilleumier and colleagues demonstrated that spatial neglect associated with parietal lesions in humans is ameliorated when social gaze cues are directed into the neglected hemifield (Vuilleumier 2002b). This observation suggests that not only is parietal cortex not

necessary for gaze-following behavior, but that social gaze cues can override parietal dysfunction. Conversely, lesions of right superior temporal gyrus (Akiyama et al. 2006b), amygdala (Akiyama et al. 2007), or orbitofrontal cortex (Vecera and Rizzo 2004) each have been reported to disrupt gaze-following behavior. A subordinate role for LIP in gaze following would be consistent with the time-course of microstimulation-evoked saccades across the gaze control network: stimulation of LIP is 20-40ms slower to evoke saccades than stimulation of the frontal eye fields (FEF) or the superior colliculus (SC): FEF, 15-25 ms (Robinson and Fuchs 1969; Bruce et al. 1985); LIP, 30-50 ms (Shibutani et al. 1984; Kurylo and Skavenski 1991; Thier and Andersen 1998); SC, 13-20 ms (Robinson 1972; Stanford et al. 1996).

In order to tease apart the causal pathway through which gaze following emerges, further study will need to better quantify the dynamics of gaze mirroring throughout the attentional control network, and to potentially disrupt this mirroring through targeted inactivations. Thus, tracing neuronal activity from purely perceptual representations of gaze direction through behavioral readouts of attentional state will define not only how we recognize the actions of others, but how we empathize with the minds that animate them.

6.4 Methods

Four pair-housed male rhesus monkeys (*Macaca mulatta*) from our colony at the Duke University Medical Center served as subjects. All animals were originally reared in naturalistic social groups. To enhance motivation, subjects' water access was controlled outside of the experimental session. All procedures were approved by the Duke University Institutional Animal Care and Use Committee and were designed and conducted in compliance with the Public Health Service's Guide for the Care and Use of Animals.

All experiments were conducted using a PC computer running custom software (ryklinsoftware.com). Monkeys viewed stimuli on a dark background on 24" CRT monitor positioned at approximately 45 cm distance. Eye position was monitored using a magnetic search coil surgically implanted beneath the conjunctiva of one eye and sampled at 500 Hz (Fuchs and Robinson 1966; Judge et al. 1980) or via an Eyelink II optical gaze-tracking system. Head position was maintained with a surgically implanted stainless steel prosthesis (Crist) (cf. (Dean et al. 2004)).

To permit electrophysiological recordings, macaques were additionally implanted with a stainless steel recording chamber (Crist) over posterior parietal cortex (LIP) (cf. (Platt and Glimcher 1997; Klein et al. 2008a)). Prior to each session, the chamber was aseptically opened, rinsed thoroughly with sterile saline, and fit with a plastic grid (Crist) (cf. (Dean et al. 2004)). A 23-gauge hypodermic guide tube containing a tungsten

steel 7-12M Ω electrode (Frederick Haer) was inserted through the grid; an X-Y micropositioner (Crist) and hydraulic microdrive (Kopf) were then mated to electrode and chamber. Electrophysiological recordings were amplified and filtered of line noise and search coil system interference (passband ~500-5k Hz). Action potentials were identified in hardware (BAK, PLEXON) by time and amplitude criteria or by template-based spike sorting. The electrode was then lowered until visual or saccade-related activity was recognized on an audio monitor. As the monkey performed visually- and memory-guided saccade trials, the electrode was lowered further at 2.5-20 μ m/s until the waveform of at least one neuron could be isolated and its response field (RF) localized. Data was recorded by custom software (ryklinsoftware.com) and imported into Matlab for further analysis by custom scripts. All surgical procedures were performed aseptically, followed with appropriate analgesics and antibiotics, and in all other ways followed standard protocols described previously (Deaner and Platt 2003; Klein et al. 2008a).

Once a neuron had been isolated and spatially characterized, macaque subjects performed a modified Posner cuing task (Posner 1980; Deaner and Platt 2003; Shepherd et al. 2006) in which they first fixated a central target, followed by a static, centrally-presented social gaze cue. Each cue image consisted of a photograph of a familiar macaque gazing either toward or away from the mapped response field; photographs were 115 pixels square and subtended approximately 5°. Randomly, in one third of

trials, a neutral gray square appeared instead of a social gaze cue; this allowed an independent measure of how LIP activity predicted oculomotor response time. The direction faced by the cue image was randomly determined on each trial, and in each session cue images were selected so that one of the pair faced the response field of the neuron. After a variable duration (100, 200, 400, or 800 ms), the gaze cue abruptly offset, and a target appeared randomly either in the same or the opposite hemi-field as cue gaze. Target locations were chosen so that one target was in the response field of the neuron, while its complement was reflected through the origin to the spatially opposite location; gaze directions and target locations were independently randomized across each session. Subjects shifted gaze from fixation to this peripheral target as quickly as possible and maintained fixation for at least 300 ms to receive a juice reward.

Gaze following was operationalized as a decrease in reaction time to congruently-cued versus incongruent stimuli (Deaner and Platt 2003; Shepherd et al. 2006). Spikes were recorded continuously from 100ms prior to task onset until task completion, and were convolved with a 10ms Gaussian smoothing window to preserve fine latency information while enhancing statistical power at low firing rates (Ipata et al. 2006). To determine the relationship between neuronal activity and decreases in reaction time, we measured, for each neuron, the correlation between the ms-to-ms activity and decreased latency (calculated by subtracting the time of saccade onset from the time of target presentation).

Latency information was further analyzed by re-binning into 10ms bins from 100ms prior to cue presentation through the end of the cue period, and comparing spike counts using Matlab's ranksum function (equivalent to a Mann-Whitney U-Function, e.g. as used in (Coe et al. 2002)). Three latencies each were tracked, using two different metrics. First, we checked all bins of all neurons to find which, if any, significantly differentiated (a) cue images relative to fixation baseline (b) faces relative to a neutral gray square (c) faces looking toward the RF relative to those looking away. Bins that were significantly positive were distinguished from those that were significantly negative. We then applied the following latency metrics: first, we looked at the raw sum of neurons with significantly increased and with decreased firing rates across time, and recorded when either sum was above the binomial expectation (two-tailed $\alpha=0.05$). Second, we separately analyzed neurons that showed significant increases and decreases in activity, and tracked the time course of significant modulations across time for each of these subpopulations.

Neurons were considered significantly sensitive to a variable if they passed a permutation test designed as follows: the total number of bins significantly increased/decreased by a particular variable during the cue period had to exceed the 97.5th percentile total modulated by the presumably meaningless contrast of odd versus even trials. This threshold was set by permutation test, rather than by binomial distribution, to control for statistical dependencies between adjacent timepoints in a

given recording session. For comparison of cue period activity to baseline, a slightly different permutation was appropriate: the threshold number of significant bins had to exceed the 97.5th percentile observed when ongoing activity was compared to a randomly-determined 100ms time window.

7. Conclusion and Future Directions

Social cognition was constructed through long evolutionary and developmental history, but relies upon something so simple and fundamental that we easily overlook it: because minds are metaphysical, our faith in them arises solely from our careful attention to the subtle physical indicators of another's private internal state. In the early chapters of this work, I described the human tendency to attribute mental experiences to others, building in a large part on our observations of how others orient to the world. In chapter one, I described the evolutionary and developmental origins of theory of mind, and suggested a course by which we might learn to attribute mental experiences to another. In chapter two, I reviewed past work on human and nonhuman gaze following behavior, by which we automatically mimic the attentional outlook of others.

In chapter four, I reported our novel behavioral study of naturally-interacting prosimians, arguing that gaze-following abilities exist even in primitive primates and may be widespread among animals living in social groups. In chapter five, I describe our work indicating that these responses, however reflexive, are by no means simple: in both human and nonhuman primates, gaze following is not informationally encapsulated, but is instead contingent upon the social significance of those with whom we interact. Together, these findings suggest that while primate gaze following is built upon common, innate mechanisms, it is expressed via a tightly integrated social

processing network that is influenced both by intrinsic biological factors and by external social context.

I next reviewed known neural mechanisms subserving social perception and attentional responses, followed by a description of our most recent work, investigating the role of the lateral intraparietal area in mediating gaze-following behavior among macaques. This work suggests that observation of gaze leads to changes in visual saliency maps lying in the dorsal frontoparietal attention system, and furthermore, that these changes may be mediated in part by cognitive “mirror neurons”.

In the following pages, I summarize our findings regarding social orienting behavior, its adaptive significance, and its neural mechanisms.

7.1 Attention: Psychology, Ethology, and Neuroscience

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 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 1981b; Posner and Cohen

1984)—one fast and reflexive (exogenous) and the other slow and voluntary (endogenous)—mediated by partially-overlapping neural circuits (Mangun 1995; Egeth and Yantis 1997; Corbetta and Shulman 2002).

Outside the laboratory, observational studies in natural settings indicate that social stimuli are intrinsically salient and strongly attract attention (Keverne et al. 1978; Caine and Marra 1988; McNelis and 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 (Friesen and Kingstone 1998a; Driver et al. 1999a; Deaner and Platt 2003). 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, 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.

7.2 Evolution of visual specialization

Fish evolved the ability to move their eyes, most likely to stabilize the visual world as they moved, but also to center the most behaviorally relevant objects in the field of view (Walls 1962). In terrestrial vertebrates, who experience more light and a more distant visual horizon, visual abilities became correspondingly more important.

Among mammals, primates are particularly remarkable for 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 (Barton and Dunbar 1997; Allman 1999). 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 (Gilad et al. 2004) such as coloration, poise, gesture, facial expression, and gaze (de Waal 2003), as well as affective and referential vocalizations (Cheney and Seyfarth 1990; Seyfarth and 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.

7.3 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 1967a). 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 (Figure 14). 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.

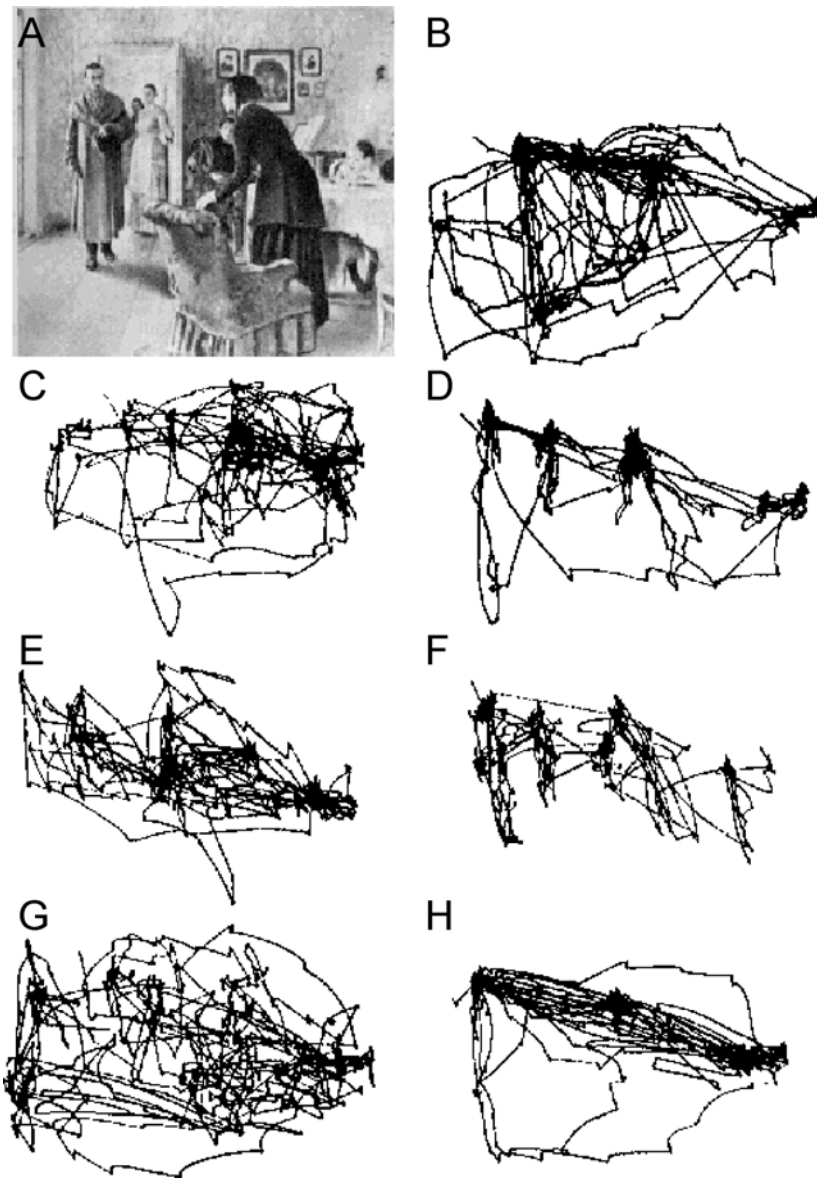


Figure 14: Social context and behavioral goals alter pattern of free viewing.

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 1957.

Recently, Land and Hayhoe (Land and Hayhoe 2001) reported similar context-dependence using non-invasive 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 can serve as external indicators of the shifting internal goals governing an individual's moment-to-moment behavior (Shepherd and Platt 2008).

To make sense of natural orienting patterns, then, requires not just the sophisticated understanding of behavioral repertoire and ecological 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 (Tversky and Kahneman 1981; De Martino et al. 2006) to the intrinsic reward of watching other individuals (Aharon et al. 2001; Hayden et al. 2007).

7.4 Social attention in natural settings

Observational data support the idea that visual attention in nonhuman primates is also biased towards social stimuli (Keverne et al. 1978; Caine and Marra 1988; McNelis and 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 and Keating 1982), and look preferentially toward the regions around the eyes and mouth (Keating and Keating 1982; Kyes and Candland 1987; Guo et al. 2003). They also look more often toward higher-ranking animals than lower-ranking animals (Keverne et al. 1978; McNelis and 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 ringtailed lemurs (*Lemur catta*) interacting in large three-dimensional environments. We used a lightweight telemetric optical gaze-tracking device (Figure 7, see Chapter 4, Shepherd and Platt 2006) operating at 0.22° x 33ms 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 and Platt 2008). Ringtailed lemurs, prosimian primates that diverged from the ancestors of “higher” primates some 60 million years ago, were chosen as subjects based on their tolerance of handling and their availability at the Duke Lemur Center. Ringtailed lemur social groups are similar to those of many higher primates, comprising 10-20 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 ringtailed lemurs fixated their human handlers—as would be expected given we had just suited them, temporarily, into recording equipment. More importantly, they fixated their social companions, and did so more often than they fixated small food rewards (Figure 2, Chapter 4). 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 (Peters et al. 2005; Carmi and Itti 2006). 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 (Figure 3, Chapter 4). 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 (Yarbus 1967a; Land and Hayhoe 2001), 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.

7.4.1 Dominance, sex, and social salience

Our ongoing field studies of orienting in ringtailed 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 which 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 oft-studied anthropoid primates 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 (Keverne et al. 1978; Caine and Marra 1988; McNelis and 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 (Figure 15). The attraction of attention 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 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.

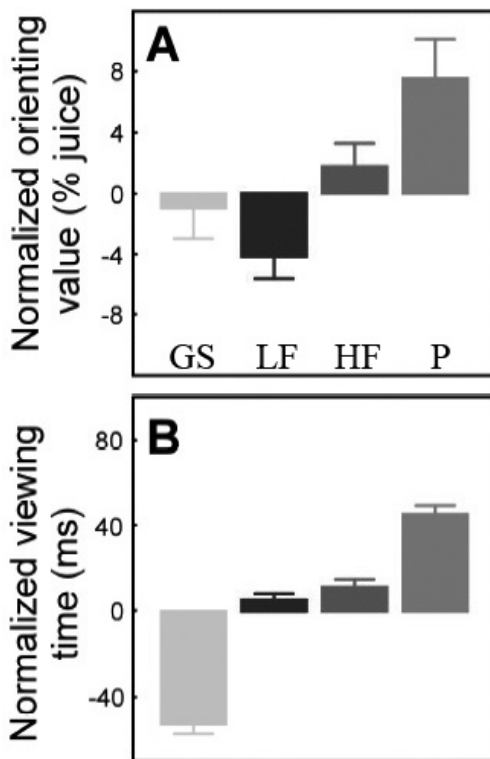


Figure 15: Monkeys sacrifice juice to view important social stimuli

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 perineia (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 grey 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 et al. 2005.)

7.5 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 (Cartmill 1972; Allman 1999). Primates, too, have focused, binocular visual fields (Martin 1990; Allman 1999), 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 and 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 (Chance and Jolly 1970) 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 “[E]ven 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 (Keverne et al. 1978; Cheney and Seyfarth 1990), 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 (Chance and Jolly 1970) describe 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 and 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 aesthetically pleasing, even when they could not recall having seen them (Zajonc 1968, also reviewed Bornstein 1989). More recently, two studies have generalized this effect from “mere exposure” to attentional state. Raymond and colleagues (Raymond et al. 2003) found that stimuli that were presented, but ignored, accrued negative associations in a variety of task conditions. Shimojo and colleagues (Shimojo et al. 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 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.

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 ready to mate (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.

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 governs 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 and 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 a 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.

7.6 Attending to intentions

Ralph Waldo Emerson wrote (Emerson 1876) “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 and Seyfarth 1990; Emery 2000; Tomasello et al. 2005). Subtler still, humans (and perhaps other primates, particularly apes; see 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 they intend 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 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 1981b; Muller and 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 (Friesen and Kingstone 1998a) 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 105ms (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 and Bruce 1999a), and social cuing persisted even when the target was 80% likely to appear in the direction opposite viewed gaze (Driver et al. 1999a). 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 and Emery 1994b).

To test this hypothesis, we contrasted the socially-cued orienting responses of rhesus macaques and humans (Deaner and 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 incompletely suppressed drive to overtly orient in the same direction (Hafed and Clark 2002; Engbert and Kliegl 2003). The temporal dynamics with which attention followed observed gaze were highly similar in the two species (Figure 16), suggesting shared neural mechanisms.

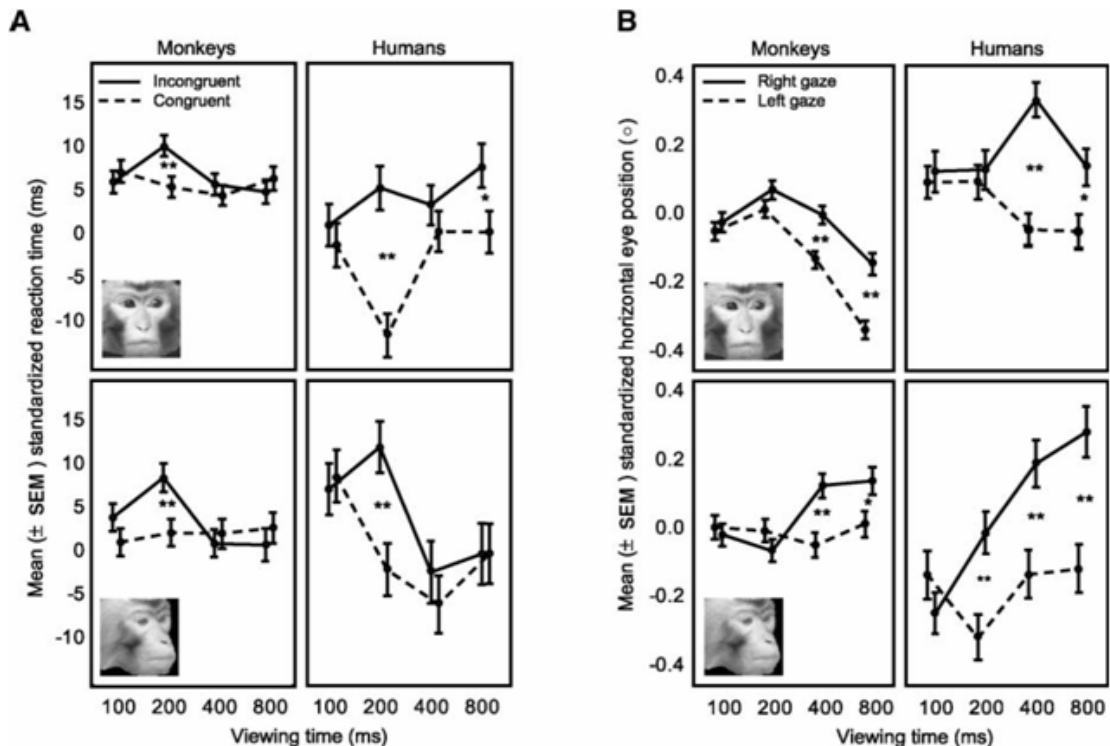


Figure 16: Gaze-following by monkeys and humans shares psychophysical features.

Monkeys and humans show similar magnitude and time-course of gaze-following in response to non-predictive monkey gaze cues presented continuously for 100, 200, 400, or 800ms 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 and Platt 2003.)

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 Emery 2000; Itakura 2004).

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 ringtail lemurs with an infra-red 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 (Figure 5, Chapter 4). 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 (Figure 6, Chapter 4). The temporal sequence of gaze alignment supports the conclusion that lemurs actively follow the gaze of other individuals (Shepherd and Platt 2008). Our results stand in sharp contrast to at least two prior observational studies (Itakura 1996a; Anderson and Mitchell 1999) that concluded prosimian primates do not follow the gaze of human observers.

7.6.1 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 (Driver et al. 1999a; Deaner and Platt 2003). 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 (Figure 17) (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.

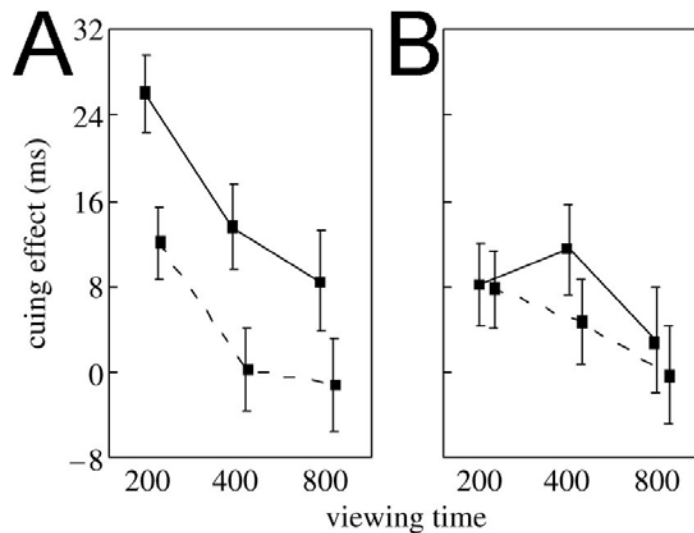


Figure 17: Sex differences in the effect of familiarity on gaze following.

Mean cuing effect (\pm s.e.m) for male (dashed lines) and female (solid lines) subjects from (A) within the same department (familiar) as the gaze models or (B) from outside the department (unfamiliar). (Deaner et al. 2007)

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 7 male rhesus macaques in response to 4 rightward- and 4 leftward-looking photos of each of 4 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 (Figure 18a, see also Figure 8, Chapter 5), while dominant monkeys followed gaze later, and then only in response to other dominant monkeys (Figure 18b, see also Figure 8, Chapter 5). 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 both internal and external factors govern macaque gaze following, comprising both biological variables like testosterone and ecological variables like relative social status.

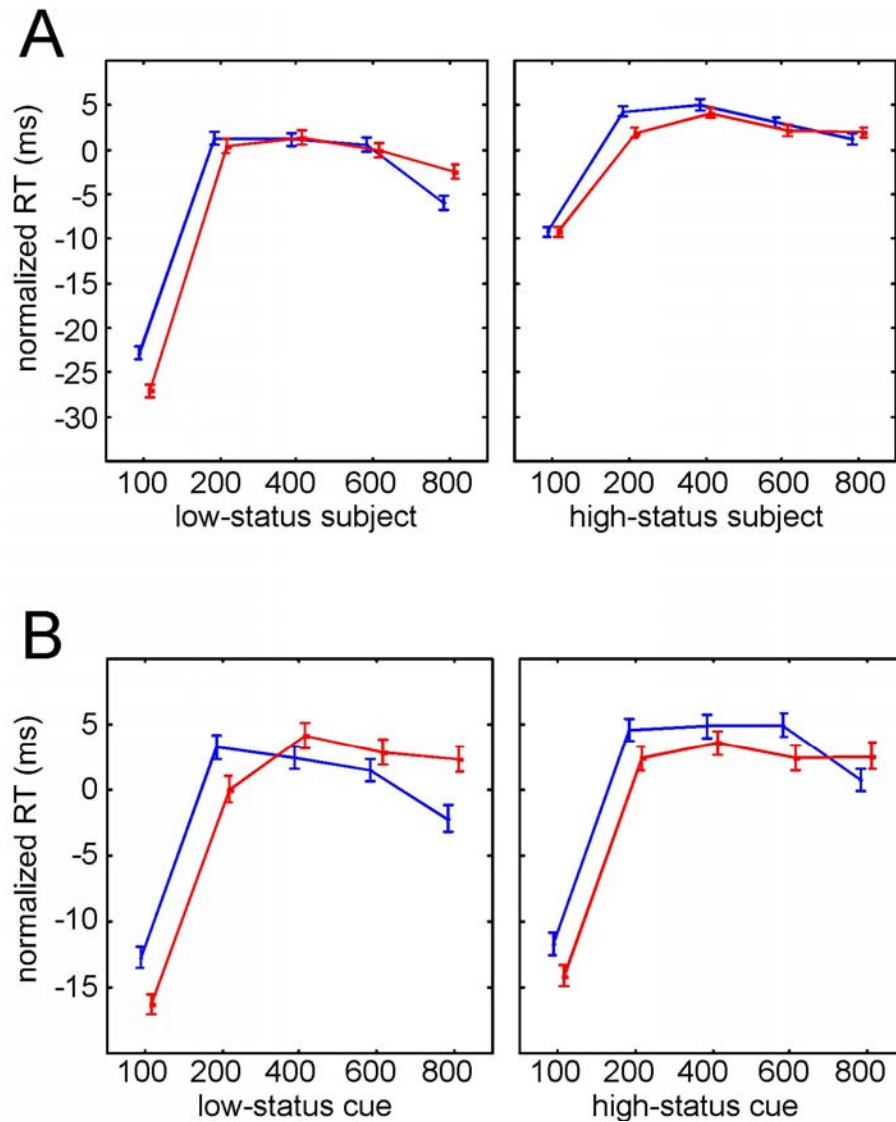


Figure 18: Social identity and context influence gaze-following in macaques.

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 100ms 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 et al. 2006.)

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 (Mathews et al. 2003; Hori et al. 2005; Holmes et al. 2006; note also Hietanen and Leppanen 2003; 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. Bradley et al. 1997; Bar-Haim et al. 2005). 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 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.

7.7 Gaze as a strategic social signal

As described above, 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 un-crowded 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 and Whitten 1987) 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 turn-taking in conversation (Argyle and 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 and Tomasello 2004). The importance of social gaze for facilitating increased cooperation among human ancestors may even have led 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 and 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, 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 (Haude et al. 1976; Deaner et al. 2005), extinguishing gaze following of lower-ranking animals (Shepherd et al. 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.

7.8 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 (van der Geest et al. 2002) found the fixation patterns of the two groups could not be distinguished when they viewed simple cartoons including human figures. In contrast, Pelphrey and colleagues (Pelphrey et al. 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; Swettenham et al. 2003; Kylliainen and Hietanen

2004; but see Bayliss et al. 2005; Ristic et al. 2005), they consistently show severe disruptions in social orienting in more natural contexts. When Klin and colleagues (Klin et al. 2002b, 2002a) 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 (APA 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). 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 (Raleigh et al. 1991; Edwards and Kravitz 1997), 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.

7.9 Neural mechanisms of social attention

To develop a biologically plausible, ethologically motivated model of attention in primates, what features are essential? 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 (Peters et al. 2005; Carmi and Itti 2006). 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 they rely heavily on image motion to assign saliency to humans and animals. Without undervaluing either their 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 identifying and tracking animate objects have proved challenging 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 (Serre et al. 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 animals within images. The processes that link object recognition by the ventral visual processing stream to target localization within the dorsal stream remain largely unknown, even though 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”, 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”.

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 evidence has begun to reveal how social variables, such as dominance status and reproductive state, are processed in primate brains. While social cognition involves most of brain, in some manner or

another, it can largely be simplified into two streams (Figure 19): a streamlined but inflexible subcortical pathway, and a nuanced—and labyrinthine—cortical network (Adolphs 2002; Vuilleumier 2002a).

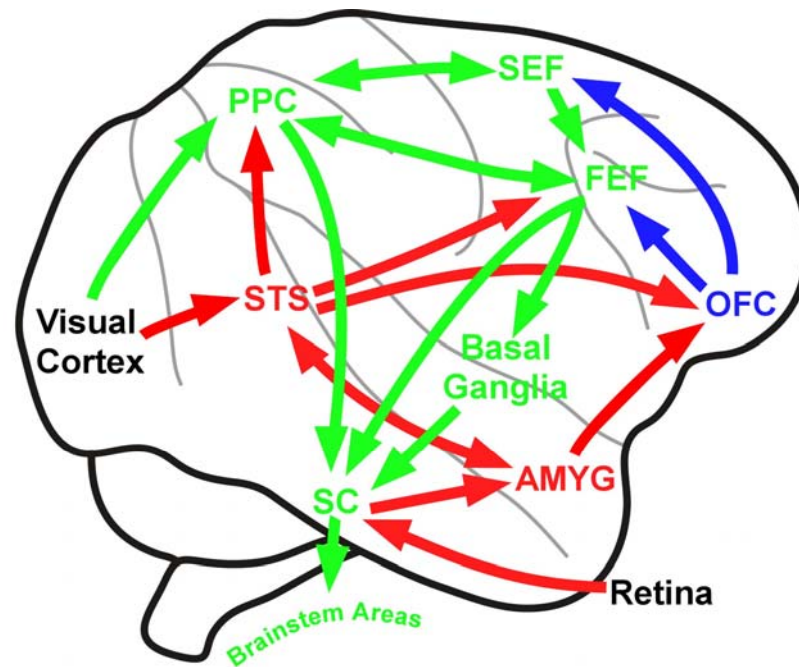


Figure 19: Key circuits involved in social attention.

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. Abbreviations: 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.

7.9.1 The Subcortical 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 be 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 and Swards 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; Swards and Swards 2002; Johnson 2005). Just such a relay of social threat signals, from retina to superior colliculus (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 (Kawashima et al. 1999; Gothard et al. 2007; Hoffman et al. 2007). 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 2002a).

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 and Whitten 1987). Thus, eye-contact responses in amygdala may not only serve to indicate 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 (Goldstein et al. 2001; Hamann et al. 2004; Bayliss et al. 2005; Deaner et al. 2007) as well as psychosocial disorders (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. 2003b). While the 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.

7.9.2 The Cortical Network

7.9.2.1 Gaze Perception

In parallel to the subcortical pathway, a slower, more nuanced, and more recently evolved cortical pathway leads from V1 through the ventral visual stream. Recent 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 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 maybe part of the primordial visual cortex that was present in stem primates (Tootell et al. 2003; Rosa and Tweedale 2005) and perhaps others mammals as well (Kendrick et al. 2001).

It remains unclear whether these areas assess subordinate-level distinctions between hierarchically-classifiable objects or are optimized for processing animate objects or, specifically, 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 (Sewards and Sewards 2002; Johnson 2005; Schultz 2005). It is known, however, that each of these ventral-stream visual areas are 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 (Vuilleumier 2002a; Sabbagh 2004).

It is important to note that both orienting to others and gaze following are 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, orbitofrontal cortex (OFC) and hippocampus form a functional circuit that is important for associating emotional and social salience with mnemonic and perceptual information (Vuilleumier 2002a; Sabbagh 2004; Smith et al. 2006), and all 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 that fetal testosterone negatively impacts both social attention and social relationships in human juveniles (Knickmeyer and Baron-Cohen 2006).

7.9.2.2 Gaze Orienting

Ultimately, signals from these ventral (“what”) areas must relay social information to dorsal (“where”) orienting and attention control systems. Three neural tissues 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 (FEF), and the superior colliculus (SC). 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 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). 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 and 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 and Hikosaka 2003; but not FEF, Leon and Shadlen 1999).

Critically, we have recently shown that in the “pay-per-view” paradigm discussed above, 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. 2008b). 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 towards 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 processing 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.

7.9.2.3 Gaze Mirroring

One intriguing possibility is that gaze following may be supported by specialized neurons that 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 Rizzolatti and 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 et al. 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 (Gnadt and Andersen 1988; Colby et al. 1996; Platt and 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 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.

7.10 Summary

Laboratory research using arbitrary tasks and stimuli has 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 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, 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.

7.11 Closing thoughts and future directions

Our belief that other beings are conscious is a leap of faith. Yet solipsism, however rational, is hardly a viable alternative: too much of our enjoyment of life is wrapped up in our ability to share it with others. For many of us, even our more personal goals—our hobbies and peregrinations, our quest to better ourselves physically and mentally—are understood through the standards and approbation of others. When our ability to relate to other individuals is handicapped—for example, by psychopathologies such as autism—it wreaks havoc not only upon our interpersonal relationships, but upon our existential enjoyment of life.

Yet humans are hardly alone in this. We have shown that even primitive primates naturally mirror the mental focus of others: ringtailed lemurs use the observed looking behavior of other lemurs to guide their own visual exploration. We have described how this behavior is not mindless, but in fact influences (and is influenced by)

our social relationships and our knowledge regarding our shared world. Finally, we have discovered tantalizing hints as to how this shared experience arises in the brain, through changes in our mental representation of surrounding visual space.

However, many challenges remain. Results from both typically-developing and autistic individuals suggest that initiation and response to joint attention may be mediated by different neuronal systems and may have differential implications for our ability to bond with others. We do not know whether differences in our ability to respond to joint attention—that is, to follow gaze—are modulated by our dynamic social context, or whether they merely reflect perceptual fluency (in the case of familiarity) or low-level stimulus features (in the case of dominance).

Furthermore, we have only just begun to relate even a simple and well-defined joint attention behavior, gaze following, to its possible neural underpinnings. Critically, we cannot say whether LIP activity is causal or consequential to attentional mirroring of observed gaze. We do not know whether it is the primary site at which attention is modulated by gaze cues, or whether it is one of many. We do not know what role, if any, subcortical systems have in directing spatial attention in response to deictic social cues, nor where these perceptual computations or behavioral responses might take place within the colliculus, pulvinar, and amygdala. Finally, we do not know how biological factors which vary across individuals (with gender, with status) impact these behaviors,

nor how different components of this system interact in typical and atypical development.

Answering these questions is important not just because they provide some hope of understanding, and perhaps even ameliorating, aspects of the autism spectrum disorders. They are important because they address, in a concrete way, what it means to be human and to recognize the humanity in others.

8. APPENDIX: Noninvasive telemetric gaze tracking in freely-moving socially-housed prosimian primates

8.1 Introduction

At the start of the last century, scientists noted that subjects do not accurately describe the eye movements they make while reading, suggesting that subjective reports cannot provide an accurate assessment of visual orienting (Dodge and Cline 1901). Since then, various means of quantitatively measuring eye movements have been developed, relying initially on tracked contrast boundaries (*ibid*) or corneal reflections (Jasper and Walker 1931), electrooculography (Fenn and Hursh 1934), current induction through magnetic search coils (Robinson 1963), and digital video oculography (Nakayama 1974).

In the 1960's, Alfred Yarbus dramatically demonstrated that visual orienting reflects the interaction of stimulus-driven perceptual variables with behavioral goals (Yarbus 1967a). Although his work revolutionized our understanding of the ethology of visual orienting, its scope was constrained by technical limitations. Most significantly, Yarbus tracked gaze using light reflected by mirrors, affixed by suction to the sclera of each subject, onto photo paper placed beside each picture. This technique made heroic demands on both the subjects and the experimenter, and required that subjects' heads be firmly fixed in position. Consequentially, recordings were brief, focused on static two-dimensional images, and were conducted from a single vantage point with no opportunity for interaction or locomotion.

Due to its spatial accuracy and temporal precision, the magnetic search-coil technique has become widely used to study visual orienting in both humans and nonhuman primates (Collewijn 1998). This technique involves attaching a loop of conductive wire to the sclera so that it circumscribes the iris, the orientation of which can be measured by recording the current induced through the loop by a cycling magnetic field of known strength. The loop is surgically implanted near the conjunctiva in animal experiments but is also used in humans through the application of wire-implanted contact annuli placed directly on the eye. Much as for Yarbus's optical technique, use of a magnetic search coil poses substantial design constraints that limit application to conditions outside the laboratory. First and foremost, the search coil technique requires subjects to be held rigid within a controlled and spatially uniform magnetic field. As a result, the search coil technique has been used to measure visual orienting only under decidedly non-naturalistic conditions (e.g. Deaner and Platt 2003; Guo et al. 2003; Deaner et al. 2005; Guo et al. 2006). Eye movements in the laboratory are generally evoked through operant conditioning, pairing salient but artificial stimuli with explicit juice or food rewards.

Unfortunately, these limitations have resulted in a gulf between laboratory measurements of gaze behavior and the natural contexts for which gaze control systems evolved (Walls 1962; Lipps and Pelz 2004). For example, gaze behavior in social settings has been largely inaccessible to both laboratory scientists and field researchers (but see

(Keating and Keating 1982; Tomasello et al. 1998); for overview see (Emery 2000; Itakura 2004)). In the laboratory, gaze can be measured accurately, but only under conditions that typically fail to approximate the subject's natural social environment. In contrast, observations of animals in their natural social context typically rely on spatially and temporally imprecise measurements of orienting: for example, noting approximate head direction at regular intervals (e.g. Keverne et al. 1978; McNelis and Boatright-Horowitz 1998; Watts 1998; for general ethological techniques see Martin and Bateson 1993).

It has recently become possible to use portable, dual-camera, optical gaze-tracking devices to quantitatively measure the visual behavior of freely-moving human subjects. This research has focused on performance of simple goal-directed tasks, for example making sandwiches or tea (Land and Hayhoe 2001), washing hands or filling a cup (Pelz and Canosa 2001), copying block designs (Pelz et al. 2001), and driving (Shinoda et al. 2001). This research has shown that task-irrelevant fixations are rare, that fixations tend to be "just-in-time" with a buffer length of 100 to 1000ms, and has reconfirmed Yarbus's finding (1967) that both expectations and instructions influence the top-down constraints shaping gaze.

We aim to extend this approach to the study of visual orienting behaviors in nonhuman animals, specifically a prosimian primate, the ring-tailed lemur (*Lemur catta*). Ring-tailed lemurs provide excellent subjects for several reasons. First, lemurs branched from the main primate lineage in the early Eocene (50 million years ago) but are believed

to retain many traits of ancestral primates and thus hint at the evolution of primate visuosocial behavior (Jolly 1966; Richard 1995; Sauther et al. 1999). Second, lemurs are trichromats (Sauther et al. 1999), have a large binocular field of 114-130° and are diurnal, despite the presence of a *tapetum lucidum* (Jolly 1966; Richard 1995; Sauther et al. 1999). They live in open scrubland in societies whose complexity approaches that of anthropoid primates (Jolly 1966; Richard 1995; Sauther et al. 1999). Specifically, they form bisexual aggregations of 10-20 individuals which are characterized by well-defined social hierarchies and extensive use of auditory, olfactory, and visual communication (Jolly 1966; Richard 1995; Sauther et al. 1999). The importance of both olfaction and vision to social communication in this species is strikingly embodied by the large, high-contrast, musk-loaded ringtail that serves as the species' namesake. The tails are used in ritualized combat to flick scent toward the heads of rivals (Richard 1995) and appear also to facilitate group cohesion—on the ground lemurs lift their tail high, while in the trees they allow their tails to hang; in both poses, the tails are conspicuous. Finally, the species is trainable, moderately sized, and tolerant of both experimenters and equipment, and subjects are readily accessible through the conservation and research programs of the Duke Lemur Center, a naturalistic but experimentally tractable setting (e.g. Nunn and Deaner 2004).

8.2 Approach

8.2.1 Gaze-Tracking Equipment

To record gaze in freely-moving nonhuman animals, we implemented a prototype optical telemetric gaze-tracker developed by Iscan, Inc. (ETL-200 Primate Research Eye Tracking Laboratory with Telemetry Upgrade). To our knowledge, this is the lightest of the few telemetric gaze-tracking systems yet developed; most competing systems are designed for human use and rely on portable recorders (e.g. the RIT Wearable Eyetracker, see Babcock and Pelz 2004) rather than wireless transmitters. The Iscan system consists of head-mounted eye and scene imaging systems, imported through the included RK-726PCI card into a Dell computer system for processing by raw eye-movement data acquisition software, and echoed for display to an eye and a scene monitor.

Optical gaze-tracking relies on the differential reflection of invisible infrared light by the pupil and retina relative to the sclera and iris. Gaze recording systems either track a bright pupil or dark pupil depending on their design; we used a dark-pupil system that is more resistant to changes in ambient infrared illumination than existing bright-pupil alternatives. The Iscan gaze-tracker uses two small head-mounted CCD cameras: a color “scene camera” to record the 76° x 52° view directly in front of the subject’s head, and an infrared “eye camera” to record the position of the eye via a small head-mounted dichroic (“hot”) mirror. An infrared LED, mounted directly beneath the eye camera,

ensured adequate illumination. These components were mounted on a thermoplastic helmet specially fitted for *Lemur catta* (Figure 20a). An insulated wire connected this headgear to the power supply and a radio-frequency wireless transmitter (Figure 20b), which were worn in a backpack made from a modified primate vest (LOMIR), pouch (LOMIR), and velcro support belt.

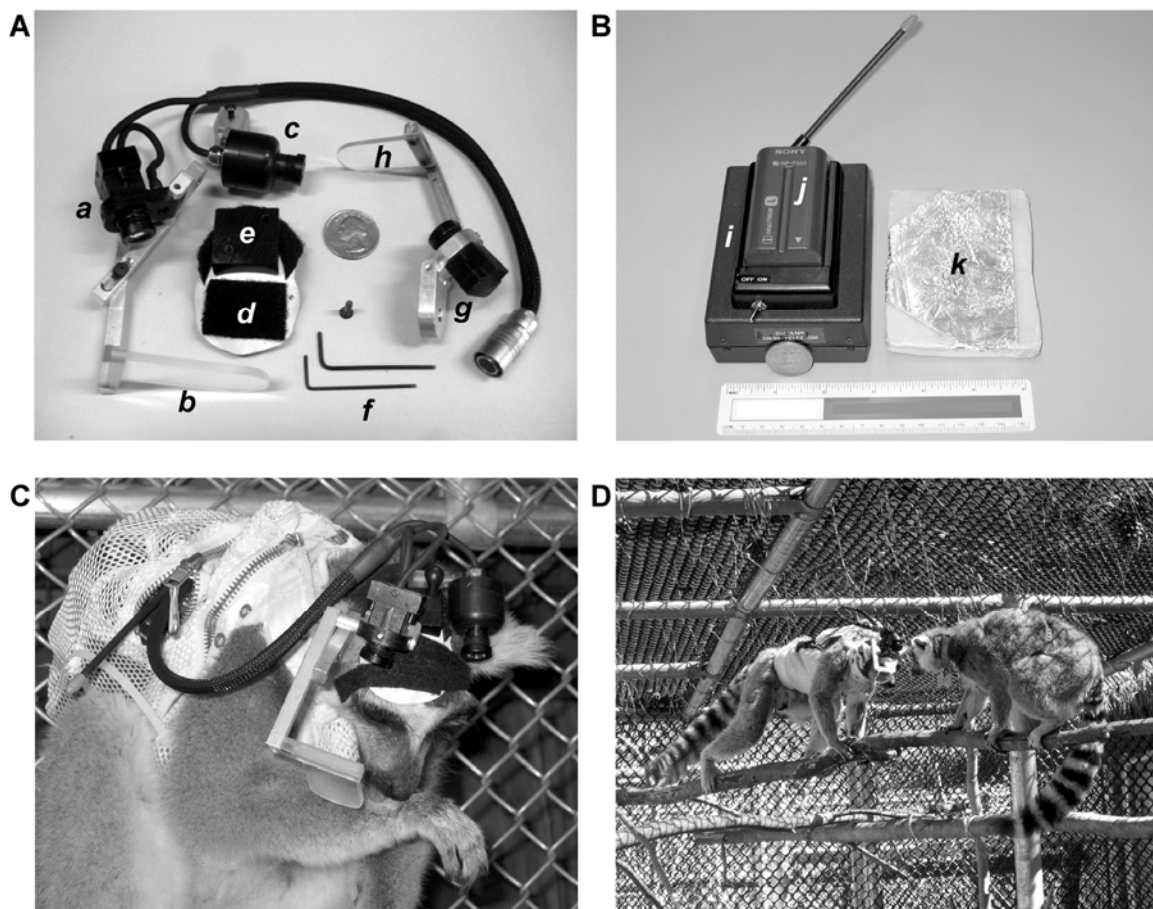


Figure 20: The Gaze-Tracking Assembly

Panel A displays the parts of the head assembly: the eye camera (a), dichroic mirror (b) and scene camera (c); the thermoplastic helmet (d) and camera mount (e), allen keys for headgear assembly (f), and the training camera (g) and mirror (h). An American quarter is shown for scale. B displays the transmitter (i), battery (j) and heat

shield (k), with a quarter and a ruler for scale. C and D show the subject lemur during active gaze-tracking: C shows the fit of the vest and headgear to the lemur, while in D, the gaze of the lemur subject is recorded as he walks along a branch toward a conspecific female.

Eye position was computed at the receiving station. First, the camera image was thresholded in software to isolate the dark pupil from the brighter iris and cornea surrounding it. Optional use of a corneal reflection (the first Purkinje image) to track eye position was abandoned, both because it is inaccurate at eccentric eye positions (Rikki Rasdan, Iscan, personal communication) and because it was easily disrupted by glare from direct sunlight. The Iscan system was then calibrated to 5 locations in the visual field (see below), thus relating the centroid of the thresholded pupil region to its corresponding point of regard in the scene video. Intermediate pupil positions were mapped to intermediate scene coordinates using a proprietary method (Iscan) analogous to cubic interpolation, and pupil coordinates were smoothed across frames to increase image stability. (Throughout this article, we shall describe eye orientation using two terms: first, “point of regard” or “POR”, denoting the attended region of the scene camera image and thus reflecting the orientation of eyes in the head; second, “gaze”, denoting the attended region of the world and thus reflecting the orientation of eyes and head in allocentric space.)

These data were combined into one video stream, with the point of regard marked by a white crosshair, and with pupil diameter and POR coordinates displayed in a black bar near the lower edge of the screen. Video was monitored for online

confirmation of data quality and recorded to videocassette for subsequent offline analysis. Additional video outputs could be used to access the raw eye and scene videos for later re-analysis, and a digital data file recorded horizontal pupil diameter, pupil centroid coordinates, and POR coordinates.

In part because the digital data file was not time-stamped in the same manner as the video output, we found it did not reliably synchronize with our video record under telemetric recording conditions. Instead, we relied on the processed video recording, which indicated the POR both by onscreen crosshair and with coordinates displayed on the lower part of the screen. However, the processed video did not display the POR crosshair when it was located near the edge of the scene image. Together, this meant that the scene data was incomplete (it was occluded by POR data) and that the POR data was incomplete (near the edge of the screen) and needed to be manually positioned or synched from the digital file.

For future recordings, we hope to obviate these problems by recording the raw eye and scene camera outputs to digital video. We found that a relatively long (200ms) smoothing window was necessary for online calculation of POR, but we believe we can dramatically increase the accuracy and precision of our gaze records by performing post-hoc re-analysis of the eye video. One potential improvement would be the use of an ellipsoid fit to reduce pupil centroid misalignments due to encroachment by sun glare, shadow, or tapetal reflection. Another improvement would be the implementation of

direct oculometric measurements distinguishing fixations and pursuit movements from saccades (Gajewski et al. 2005).

8.2.2 Harness Design

Since the deployed weight of the gaze-tracking system was a significant fraction of our subjects' masses (about $\frac{1}{4}$ *Lemur catta* bodyweight) it was critical that the equipment be comfortably and securely harnessed. Fittings were required both for the transmitter assembly worn on the back and the camera assembly worn on the head.

To secure the transmitter and power pack to the lemur's back, we used two LOMIR products: first, a small primate vest (LOMIR Biomedical, PJ01) to distribute transmitter weight across the lemur's back; second, a small pouch (LOMIR Biomedical, JP01) to hold the transmitter itself. The vest fit over the front shoulders around the arms and zippered closed along the back. We attached the pouch to the back of the vest using plastic tie-wraps, removed from the vest a plastic reinforcement ring intended to support a cannula, and added attachment points for a Velcro stabilizer belt. In addition, we added a quarter-inch styrofoam and aluminum-foil heat shield to protect the lemur from the unexpectedly large heat output of the transmitter.

To secure the camera assembly to the head, we used a customized thermoplastic helmet. To make the helmet, we cut a slightly oversized patch from a sheet of thermoplastic resin (AbilityOne Corp.'s Ezeform Light or Polyform Light), heated it in boiling water, and molded it over an adult lemur skull covered with a damp cloth. After

the resin had cooled, we added screw holes for attachment of the camera assembly. The helmet was later custom-fit to each subject by trimming and smoothing the helmet to ensure a comfortable fit with adequate clearance for each lemur's eyes and ears and adding Velcro attachment points. The helmet was temporarily secured to the subject's head during recording using two thin Velcro straps, which ran from the front of the helmet to the back, crossing under the jaw.

In total, the roving portion of our system massed 660g. Component masses on the body totaled 539g from the vest (193g), transmitter (239g), battery (103g) and heatshield (4g). Component masses on the head totaled 120g from the thermoplastic helmet and straps (11g), mirror (10g), and the cameras and mount (99g). This total was approximately equal to the mass borne by a lemur mother weaning twins. Our subjects, both adult males, massed approximately 2.5 kg each at the time of these experiments.

Weight reduction from both head and body would likely improve recording quality and promote natural behaviors; these reductions might most easily be accomplished by eliminating the mirror or by reducing the weight of the vest. An alternate vest design might provide additional improvements by enhancing the stability of the "backpack". Because a lemur's torso is ellipsoid in cross-section, the pouch had a tendency to rotate to the side during recording sessions. One possible solution would be to eliminate the vest and anchor the pouch directly to the shoulders and hips—we have

avoided this, however, because free movement of the lemur's muscular hind legs appeared to preclude useful attachment.

8.2.3 Telemetry

To communicate eye and scene video data from the free-ranging subject to a computer for analysis, data was broadcast up to 300m by a 900MHz, 500 mW transmitter with a 7.2V, 10W lithium battery serving as a one-hour power supply (both Iscan). Peak range and data quality varied substantially with the local environment, with particular types of enclosures and electrical interference causing distinctly different broadcast characteristics. In order to increase the range over which we could collect data, we mobilized our receiver and computer. We accomplished this using an uninterruptible power supply (APC Back-UPS XS 1500, Model BX1500) capable of powering the receiver itself as well as a desktop computer, computer CRT monitor, and separate eye and scene CRT monitors. The UPS was capable of maintaining this equipment unplugged for up to half an hour, about one third the battery life of the deployed transmitter system. The receiver system was mounted on a cart, which in turn was loaded into a small all-terrain vehicle to provide maximal mobility.

This prototype telemetric system could be improved both in versatility and portability. Transmissions were badly disrupted in some local environments, notably by types of wire or chain-link animal housing. Erratic signal fluctuations in these areas caused video flicker and partial deregistration of telemetric data. Because these

fluctuations grew worse with decreasing signal strength, they could be reduced, if not obviated, by decreasing transmission distance to several meters. Strikingly, transmission problems were more severe within some outdoor enclosures than between electrically shielded areas surrounding our laboratory. In laboratory recordings using rhesus macaque, digital data desynchronized from our video record by only 17 samples (280ms) over 32 minutes. In our second-best recording from a moving lemur, we lost 800 digital samples (13 seconds) over 54 minutes; in our best, we lost 65 samples (1.0 second) over 22 minutes. In our worst recording sessions, we abandoned digital data altogether, as up to 21% of the normally stable video data stream was lost as flicker.

Because of this limited transmission range in certain fenced environments, versatility could also be improved by an increase in portability at the receiver. This could be accomplished by using a smaller computer and more space- and energy-efficient monitor, for example a "lunchbox" design with integrated LCD screen (e.g. ACME SKD Industrial Portables). It would also be very helpful to route eye and scene video directly to the computer for digital recording and display. Computerized display would eliminate the eye and scene video CRTs, and digital recording of these raw data streams would facilitate post-hoc reanalysis while obviating the need for additional digital video recorders.

8.2.4 Training

Each lemur was habituated to the gaze-tracking equipment over the course of one to two months. Modular equipment design allowed us to gradually increase the mass and awkwardness of recording gear both on the back and on the head. In addition to the components described above, we used a dummy camera and mirror to facilitate habituation to headgear at the reduced mass of 48g (40% normal). Compliance was reinforced with food rewards, typically grapes and raisins, either hand-fed to the lemur or placed proximally in the local environment. In this manner, we were able to progressively habituate the lemur to handling and increased encumbrance while simultaneously encouraging normal mobility.

Habituation can be completed in four to six weeks (one hour, thrice weekly), and two to three training sessions were sufficient to regain habituation after hiatus. Subjects exhibited a reduction in spontaneous behavior, contingent on the ease with which animal handlers performed the initial capture, but normal movement capabilities were maintained and food rewards were accepted. Two behavioral changes were deemed detrimental. First, the weight of the headgear decreased spontaneous activity: at times, and particularly after protracted handling, subjects rested with head declined relative to the body. This was best avoided by limiting handling to the minimum possible duration. Second, subjects occasionally shook their heads, particularly when stressed, for example by the threat of conflict with rival males during the mating season. Nevertheless,

equipment was fastened to the head securely enough that these bouts did not displace the camera system, and normal recording resumed without intervention as soon as the bout ended. Companion lemurs exhibited no marked change in behavior in response to the recording equipment.

Initially, we also trained one lemur to orient toward an audiovisual cue in return for food rewards. This was performed to assist in calibration; however, we discovered an alternative and more effective method not requiring conditioning (see below). This aspect of training was therefore discontinued in the first subject and omitted in the second.

8.2.5 Calibration

The primary challenge to field recording of gaze behavior in a habituated subject is proper calibration of the eye position to a point of regard in the visual scene.

Calibration may shift across sessions, due to variations in lighting conditions and in the specific relative positions of eye, helmet and mirror. It is therefore necessary to recalibrate the subject at the beginning of each recording session. In humans, this can proceed through simple instruction and verbal confirmation. Our first approach was to train lemurs to orient on cue, much as monkeys with scleral search coils are trained in a laboratory environment (Fuchs and Robinson 1966).

First we attempted to draw each subject's attention using a clicker made for training dogs, rewarding them with food after each successful fixation. However, we

found that prolonged handling induced or exacerbated a state akin to learned helplessness (Seligman 1972), in which the lemur was minimally inclined to orient toward the clicker even when rewarded. We then attempted to train the lemur to orient toward a bright yellow squeeze-ball, with limited success. Additionally, we were concerned that the use of a visual orienting cue might influence the subject's orienting behavior during the subsequent recording session.

Luckily, a simpler and training-independent method proved more effective. The lemur was released without calibration, and the equipment was allowed to settle into its resting position. Once the lemur had recovered from handling and was resting comfortably, one experimenter (the "trainer") approached with food rewards from the direction of the various calibration points: center, upper-right, upper-left, lower-right, and lower-left. As the trainer entered the subject's field of view, the lemur typically glanced at the approaching human. At the same time, the experimenter at the computer entered calibration points. This experimenter entered the calibration points when he observed maximal deflection of the lemur's pupil in the direction of the trainer's approach and heard the trainer's verbal confirmation of eye contact. Because the eyes orient quicker than the head, and because calibration was triggered by maximal excursion of the eye in its orbit, head movements did not substantially impede the process of calibration.

Once all calibration points had been entered, we confirmed successful calibration in two ways. First, we hand-fed the lemur several raisins and observed smooth pursuit of the treats as the subject monitored their approach. Second, we attained eye contact with the lemur from within each quadrant of the scene video. Humans are very skilled at discriminating mutual gaze, and so once the trainer's verbal report of eye contact matched the subject's gaze in the scene display, we initiated data collection.

Ideally, we would perform a more thorough calibration, using the 9 or more points typical of human studies. This would require sophisticated manipulation of the subject's eye movements, however it is critical that any manipulation not distort the intrinsic gaze behavior under study. One possibility would be to evoke fixations using an isolated flash of light, for example, a laserpointer directed to the wall of an otherwise dark room. Autocalibration systems of this type have been developed for human children (Trueswell et al. 1999; Ramlohl et al. 2004) but have not yet been adapted to animals.

8.2.5 Gaze Recording

In the early phase of this research, we successfully measured pupil position and gaze during hand restraint and free movement, both in isolation and in visual contact with other lemurs. In later phases, we recorded these data while subjects ranged freely through interactive social environments in their home enclosure or outdoors. Recordings from lemur "Licinius" took place in one to three connecting indoor rooms (1.4 x 2.0 x 3.4

m each) with branches, potential food sources, platforms, and one heterospecific lemur (*Eulemur fulvus*, "Maurice"). Recordings from lemur "Aracus" took place during free movement between two indoor (1.8 x 1.6 x 2.4 m each) and one outdoor (3.7 x 3.9 x 2.4 m) enclosure, and also in one large, unroofed, treeless pen (5.6 x 85 m). These areas were shared with up to seven conspecifics: three adult females, three juveniles, and one older male. Sessions for both lemurs included terrestrial and arboreal locomotion, leaps, foraging, and social interaction.

Recordings were robust against movement and outdoor releases were primarily limited by weather and risk of climbing. In bright sunlight, the high contrast between direct sun and shadow decreased video quality in both the scene and the eye camera. Environments that permitted the lemur to climb limited the ability of the experimenters to recapture the lemur to fine-tune the recording assembly, replace discharged batteries, or remove the recording equipment at the end of the session. By contrast, in enclosed environments with human-accessible perches, our subjects were quite tolerant of human approach for each of these manipulations.

To date, we have gathered data from freely-moving lemurs during eight recording sessions requiring 1-3 hours for setup, calibration, and data collection. Of these, six sessions resulted in gaze signal robust enough for analysis, and of those, 5-20 minutes per session appeared to be of optimal quality. We have fully analyzed 30

minutes of this data, during which gaze was calibrated to a location in the scene video for 67% of those 30 minutes.

Failure to assign gaze to a location in the scene video could have resulted from a loss of signal, a dead zone in our calibration, or from fixations outside the $76^{\circ} \times 52^{\circ}$ window recorded by the scene camera. To some extent, these possibilities could be distinguished in the digital data: a valid measurement of pupil diameter in the absence of valid POR coordinates suggests that gaze is directed outside the scene video. Analyzing Iscan digital data files drawn from two sessions with minimal flicker, a validly recorded pupil (59%-67% over 42 minutes) was calibrated to an onscreen position in 76%-94% of the samples.

8.2.6 Data Coding

We coded point of regard and regions of interest (ROIs) using integrated POR on scene video output. The processed video was digitized for analysis at $0.22^{\circ} \times 33\text{ms}$ resolution using InterVideo WinDVD Creator, and included both a crosshair representing the point of regard and a set of POR coordinates stamped in the lower part of the video screen.

After a recording session had been digitized, it was segmented into one-minute clips and visually inspected to evaluate data quality. In addition, a small number of putative ROIs were selected for coding based on their putative reward value, locomotor relevance, or social relevance. Clips were analyzed in order of data quality using a

custom-designed open-source Matlab environment (Skriatok Videoscore, www.duke.edu/~svs/skriatok). Videoscore provides a graphic user interface by which experimenters can browse and annotate video data and also track various targets, entering their coordinates by mouse-click. In this manner, POR and hypothesized ROI were manually located on each frame, and recorded frames were categorized as moving or stationary. In addition, some high contrast environmental landmarks were tracked to determine head movements relative to the external environment; these movements could be compensated over short periods to produce a scanpath in world-centered coordinates. For videos with minimal flicker, we were sometimes able to import and synchronize digital data representing POR, expediting at least part of the data coding process. The end result of this coding was a marked video sequence from which we could derive gaze scanpaths, head-centered eye position, and the proximity of gaze to the various categories of ROI. Examples drawn from a 2-second clip are shown in Figure 21. During this period, the lemur subject “Licinius” looked up at a researcher’s face and then at an offered raisin during the process of system evaluation. The gaze scanpath displayed has been stabilized to reflect world coordinates—the POR within the scene video was less motile. This stabilization was performed using just two environmental reference points, coded in the upper right and lower right corners of a small window in the near wall.

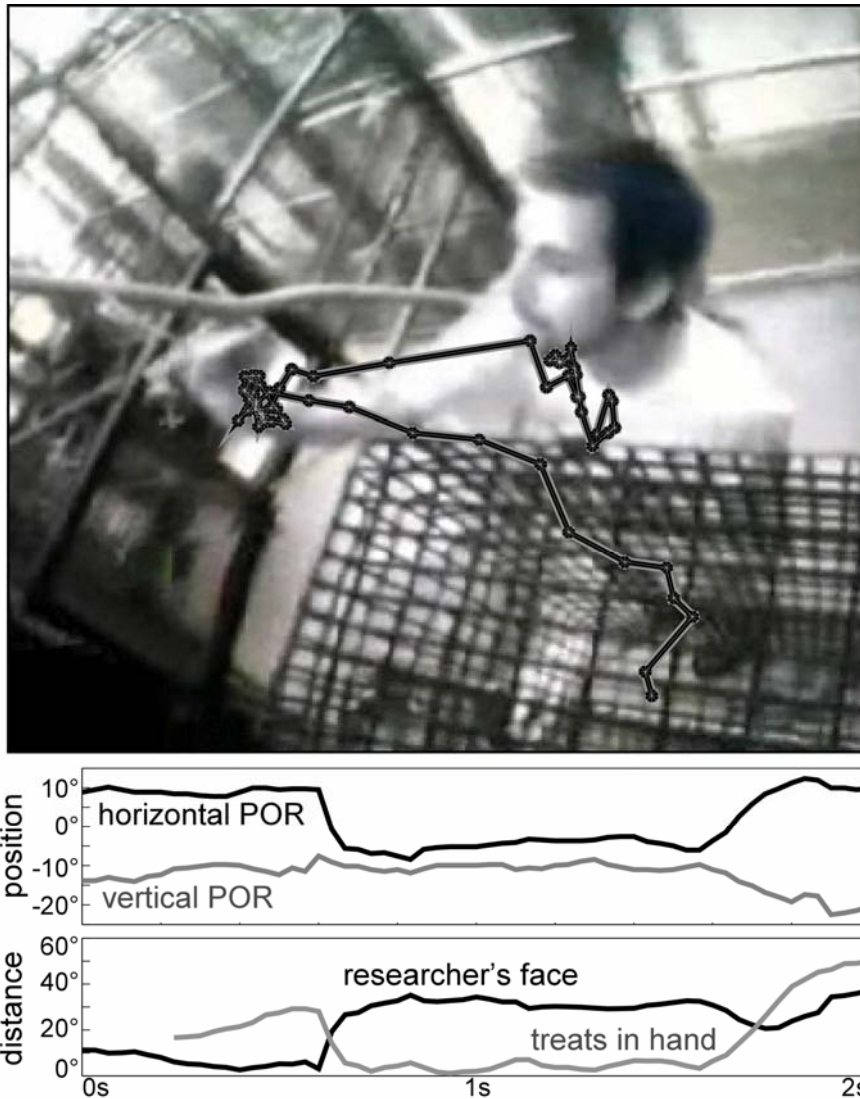


Figure 21: Lemur gaze throughout time.

The upper panel shows a two-second gaze scanpath, projected onto the environment reconstructed from multiple scene video frames (blurred by combining images across head angles). The initial point-of-regard record, coded in camera coordinates, was transformed to world coordinates by comparison with stable reference points marked digitally along the rear wall. Below, this data is plotted as a function of time: first as horizontal and vertical POR coordinates within the camera (that is, relative to the head), and then below as the distance between recorded gaze and two putative regions of interest, the researcher's face (black) and handheld treats (gray).

Once several static points in the environment have been coded throughout the video, it is possible to stabilize the video across camera rotations and translations caused by lemur movement. Future upgrades to Videoscore could potentially incorporate this information as coordinates are coded, compensating head movements and thus facilitating coding of ROI coordinates across larger time steps. In environments with well-defined fiducial landmarks, this may permit accurate extraction of head location and orientation (e.g. using ARToolKit from the HIT Lab, University of Washington; see also Rothkopf and Pelz 2004).

8.3 Quality Assessment: Post-Hoc Data Confirmation

We performed several post-hoc analyses to confirm data quality. Direct observations suggested that recordings were robust. We often observed the subject's gaze shift along a contour, for example the bright orange loops of an extension cord or twisting contours of a branch. These complex scanpaths seemed unlikely to arise by chance. Likewise, we regularly saw smooth pursuit of food rewards as the experimenter hand-fed the subject treats.

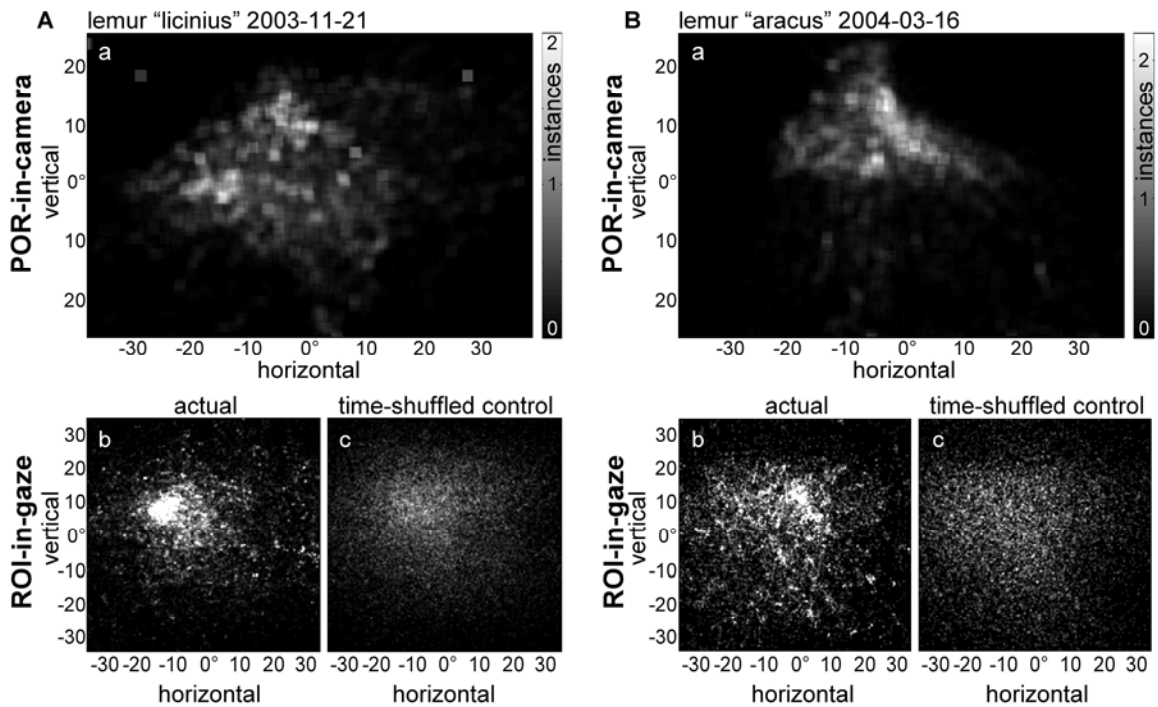


Figure 22: Post-hoc calibration check.

Post-hoc calibration controls are shown for two recording sessions, one from each of our lemur subjects (left, “Licinius”, right, “Aracus”). In the upper panels, point-of-regard histograms (smoothed over 2 degrees) are shown for the coded portion of the recording sessions. POR was well distributed across the central portion of the scene camera, although blank areas in the upper corners suggest weaker calibration in these areas on these days. Below, putative regions of interest are plotted relative to the point of regard (left) or, as a control, to a time-shuffled point of regard (right). Regions of interest are notably more clustered in the former than the latter case, confirming that recorded gaze is attracted to these putatively salient regions.

More formally, we analyzed the distribution of POR both within the camera and relative to putative regions of interest. We generated histograms of recorded POR positions within each data session, finding that distributions were stable across different clips from any particular recording sessions, but different between recording sessions. Good calibrations tended to result in broadly gaussian fixation distributions, while

poorer calibrations were suggested by distributions with missing quadrants, sometimes accompanied by abnormally dense fixation in adjacent regions. Overall, POR was well distributed across the central portion of the scene video (Figure 22a).

Though blank areas were evident in some sessions, suggesting weak calibration in these regions on these days, other regions appeared to accurately represent gaze. To confirm this intuition we measured the distribution of ROI relative to gaze. We reasoned that if our coded ROI accurately described the salient locations in the visual field, gaze should be drawn to these locations, and they should cluster tightly when plotted against gaze coordinates. To measure this, we generated histograms of the position of all ROIs versus gaze.

As expected, ROI clustered tightly when plotted in gaze coordinates (Figure 22b). The location of this peak suggests the accuracy of our calibration was, on average, accurate to within 5-10° degrees, and that any calibration error was systematic within a recording session and thus likely to effect all categories of ROI similarly. Furthermore, ROI failed to tightly cluster when plotted relative to time-shuffled POR data, that is, to POR observed at *other times* within the same one-minute clip (Figure 22c). To quantify this, we measured the proximity between observed POR and the closest ROI, and compared to a repeat analysis substituting time-shuffled POR data. In 26 of 30 clips, mean distances were smaller for the recorded data than for the time-shuffled control. Overall, proximity was 6% greater in our actual data than predicted by a time-shuffled

control, suggesting that the recorded gaze was attracted to the contemporaneous regions of interest ($p < 0.003$, paired t-test, 30 clips). This confirmed both that our *a priori* judgments of ROI relevance were reasonable, and that our telemetric data successfully captured the attraction of the subjects' gaze toward these regions.

We also analyzed the properties of frame-to-frame POR shifts within the camera. The lengthy period over which eye positions were smoothed (200ms) precluded any neat segmentation of gaze shifts into fixations, saccades, vestibulo-ocular reflex and optokinetic nystagmus; however, it was still possible to examine the pattern of POR shifts across time. First we examined fixation behavior, plotting histograms of relative eye position across intervals of one frame, two frames, four, eight, and so forth, up to 4.3 seconds (Figure 23). The vast majority of successive frames show minimal shifts in eye position, as can be seen in the tight clustering of relative POR locations at 0° distance in the single-frame (33ms) offset comparison. As comparison time doubles to 66ms, 132ms, and so forth, this clustering becomes much less apparent, largely disappearing after two seconds. As can be seen in the first panel, direction and magnitude of frame-to-frame POR shifts were generally gaussian. No clips were observed with abnormal peaks, such as might derive from a transient, but characteristic, misidentification of the pupil boundary. These observations suggested that our gaze record was composed of a mix of fixations and saccades and represented the smoothed, but essentially accurate, pattern of lemur eye movements.

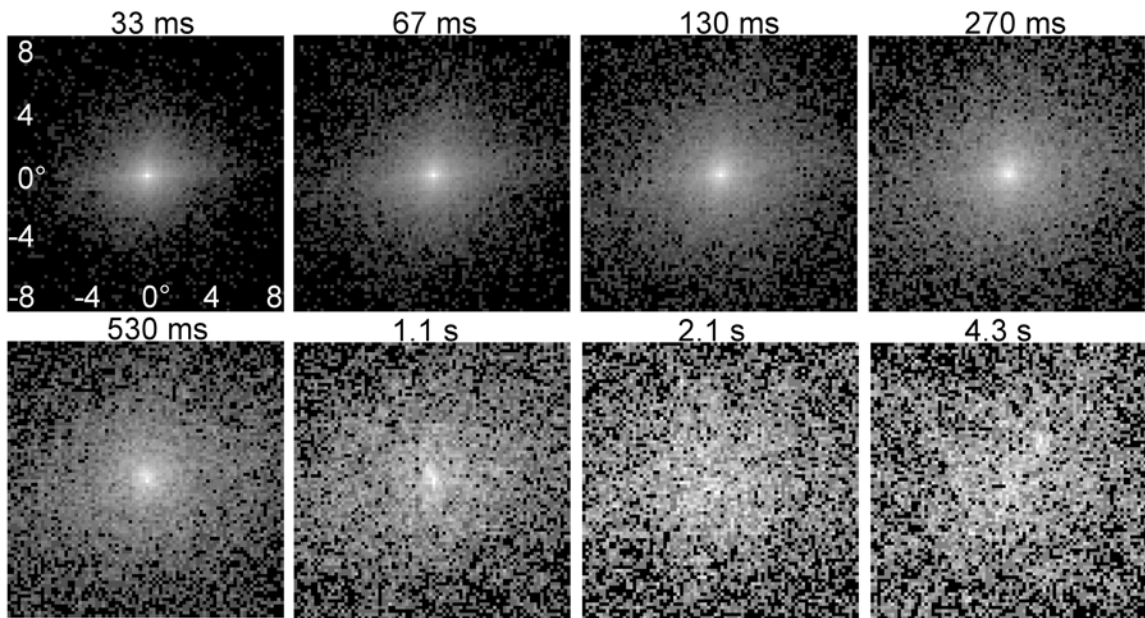


Figure 23: Post-hoc gaze jitter density

Two-dimensional histograms plot relative POR position across different time shifts. POR locations are tightly clustered near 0° in the 33ms (one frame) comparison, but as comparison time doubles to 66ms, then 132ms, and so forth, the cluster relaxes. Beyond one second, the peak has largely disappeared. (Note the first three panels are within the 200ms smoothing window used in these experiments.)

We also examined our data for evidence of saccades; that is, for coherent shifts in gaze position across time. We compared the direction of successive POR shifts as a function of their magnitude, plotted here as polar histograms (Figure 24). For the smallest observable POR shifts, single-pixel jitter during fixation resulted in aliasing along the cardinal angles; nonetheless, a slight increase at 0 radians suggests oriented movements. This becomes increasingly obvious for larger POR shifts of 15-60°/s ($\frac{1}{2}^\circ$ - 2° shift between successive frames) and 60-240°/s (2° - 8° between frames) respectively. These POR shifts seem likely to reflect large saccades, during which eye movement

direction is strongly correlated across successive frames resulting in a sharp peak at 0 radians. For the POR shifts exceeding $240^\circ/s$ (8° between frames), this coherence decreases. These shifts were rare, and their diminished coherence may suggest a correlation between increased noise and rapidly shifting POR.

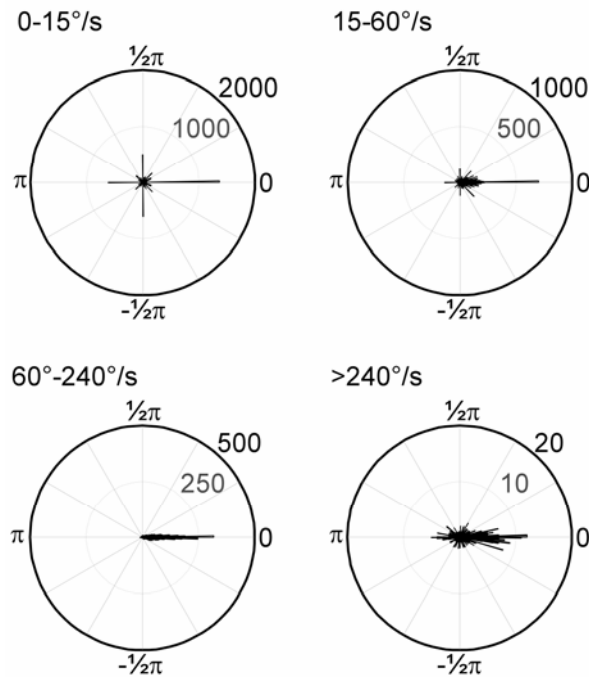


Figure 24: Post-hoc gaze jitter direction.

Polar plots indicate relative direction of frame-to-frame POR shifts across different magnitude ranges. In frame-to-frame POR shifts of a moderate size, direction was very stable over time, suggesting saccadic eye movements.

Finally, we contrasted oculomotor behavior between *Lemur catta* and *Macaca mulatta*, a species with very well defined oculomotor behavior similar to that of humans. A single male macaque with known and species-typical eye movement patterns was specially fitted with a thermoplastic cap; headgear was attached as described above and

the power supply and transmitter were firmly strapped to the outside of his primate chair. The macaque was calibrated using methods analogous to those we employed in the field, and sat comfortably in a primate chair with his head unfixed while free-viewing his home colony. We compared 22 minutes of macaque POR data to our full 30 minutes of coded lemur data, and measured relative POR position as a function of time lapse. Comparing the 80th percentile distance between eye positions as a function of their separation in time, we found that fixations relaxed asymptotically into a more uniform distribution, and that this relaxation had a similar time course in the two species. However, we found that at asymptote the macaque eye positions were more widely distributed than the lemurs (Figure 25). We speculate that this distinction may correlate with the broader binocular field of monkeys (140-160°) versus lemurs (114-130°) (Richard 1995).

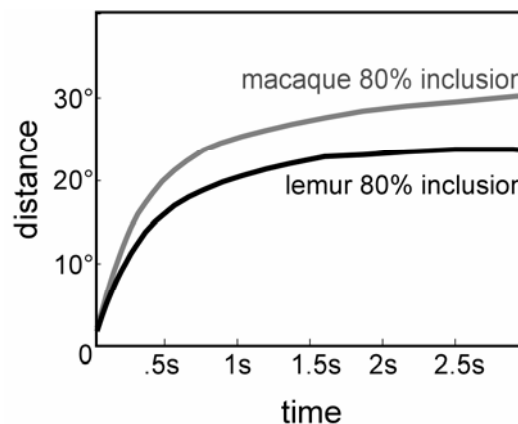


Figure 25: Eye-gaze range utilization for macaques, lemurs.

Here we plot distance between POR data as a function of time, as recorded for lemur and macaque subjects. Each line reports the radius from the current POR position in which 80% of fixations will be included after a given amount of time has

passed. For both lemurs and macaques, this distance is minimal for short time lapses (within fixations), but rapidly increases to asymptote. Both species approach asymptote with a similar time course, but eye positions distribute more broadly in macaques than in lemurs. These differences may reflect the larger binocular field of *Macaca mulatta* relative to *Lemur catta*.

8.4 Conclusions

We report the implementation of a telemetric infrared-video gaze-tracker to measure visual orienting by freely-moving *Lemur catta*. Two lemur subjects tolerated system mass of approximately $\frac{1}{4}$ their body weight, permitting successful measurements of gaze behavior during social interaction, foraging, and locomotion in both terrestrial and arboreal landscapes. We found that lemurs displayed visual orienting behaviors similar to those of macaques and humans, suggesting that much primate gaze behavior evolved earlier in the lineage. The described techniques thus provide a quantitative method of examining gaze behavior as nonhuman animals navigate, forage, and interact within their natural environments. Future technological development will doubtless improve the versatility, subtlety, and accuracy of telemetric gaze tracking; however, we found that current technology is sufficient to study control of eye movements in the strategic contexts for which they evolved.

8.5 Appendix: Equipment and Supply List

AbilityOne Corp / Sammons Preston Rolyan

<http://www.sammonspreston.com>

- *Polyform Light, 1/16th x 12 x 18 inch perforated sheets*
- *Ezeform Light, 1/16th x 12 x 18 inch perforated sheets*

ACME Portable Corp.

<http://www.acmeportable.com.tw/>

- *SKD Industrial Portable*

APC

http://www.apcc.com/resource/include/techspec_index.cfm?base_sku=BR1500

- *Back-UPS XS Series, Model BX1500 (apparently discontinued, but similar to BR1500)*

ISCAN, Inc.

<http://www.iscaninc.com>

- *ETL-200 Primate Research Eye Tracking Laboratory with Telemetry Upgrade*

LOMIR Biomedical

http://www.lomir.com/jackets_vests.php

- *Primate Vest - PJ01*
- *Jacket Pocket - JP01*

The MathWorks

<http://www.mathworks.com/products/matlab/>

- *Matlab Software*

University of Washington

<http://www.hitl.washington.edu/artoolkit/>

- *ARToolKit*

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Biography

Stephen Shepherd was born in Marshalltown, Iowa in 1978. He received his BS in Biology (focused on Computational and Neuronal Systems) in 2000 from Caltech, and received his PhD in Neurobiology from Duke in 2008. He has authored 11 technical publications, listed below. While at Duke he was supported by an NIH Grant for Basic Predoctoral Training in Neuroscience and by a NAAR Predoctoral Fellowship entitled “Neural Basis of Social Gaze-following Deficits Explored in an Animal Model”, and held memberships in the Society for Neuroscience, the Cognitive Neuroscience Society, the Human Behavior and Evolution Society, the Vision Science Society, the American Society for Primatology, and the Steering Committee for Graduate Training in Neurobiology. He has profited from his experiences working with Professors John Allman Shin Shimojo, and Michael Platt, and leaves Duke to work as a postdoctoral scholar in the laboratory of Professor Asif Ghazanfar at Princeton.

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