

# Social Attention in Nonhuman Primates: A Behavioral Review

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## Abstract

Social attention involves attention directed toward other individuals, as well as the coordination of attention among individuals. This topic has been the focus of much recent research with nonhuman primates. In this review, we focus on the behavior of the participants in this research—both the animals and the humans—rather than on its cognitive implications. After briefly reviewing theoretical issues and the sensorimotor constraints on primate attention, we describe the ethological and experimental work that has been done. The former, involving observational studies in field and captive settings, focuses on the functions of social attention and on differences in traditional and contemporary micro-ethological techniques. The experimental work is organized in terms of the types of social relationships—solicitous, competitive, collaborative—that the various paradigms establish between subjects or between subject and experimenter. These include co-orientation (gaze-following) tasks, food-sharing tasks (such as conditional begging, donor choice, and object choice tasks), conspecific competition (such as occluder and informed leader tasks), and collaborative cue production (where subjects must cue an ignorant experimenter). In all of these tasks, we report the relative effectiveness of various attentional cues, including use of the hands (e.g., touching, pointing) and orientation of the body, head, and eyes. In our final discussion, we consider differences in focus in the observational vs experimental approaches (on negotiating social relationships vs access to food, respectively) and suggest ways in which the methods in these two arenas might be successfully integrated. We also discuss the advantages of considering the “ecology” of the laboratory setting and how recognizing the social and perceptual configurations established by different protocols can aid in their interpretation and design. Finally, we discuss the prevalence of individual differences in this research and how this underscores the importance

of rearing history and other contextual factors in primate social attention.

**Key Words:** social attention, primate behavior, ethology, micro-ethology, experimental methodology, ecological validity

## Introduction

The goal of this paper is to review the methods employed, and the results observed, in the study of social attention in nonhuman primates. Social attention refers to attention being directed toward another as well as to the coordination of attention between interacting individuals. As such, it doubtlessly plays a critical role in social learning and communication. In this review, we consider the full range of social attention research, both experimental and observational, conducted with nonhuman primates, the class of animals most extensively studied on this topic. We conclude with a discussion of concerns in laboratory and field studies, and discuss how an integration of the methods from these two arenas may advance the study of social attention in all social animals.

## Theoretical Issues

In 1957, Chance suggested that the “attentional structure” of a social group—that is, the distribution of who pays attention to whom—may reflect, and even determine, the dominance relationships in that group (see Chance & Jolly, 1970; Chance, 1976; Pitcairn & Strayer, 1984). He proposed, for example, that in a species that adheres to a strict linear hierarchy, the attentional structure of the group would be asymmetric, with subordinates looking to dominants more than vice versa. On the other hand, species that achieve their group coherence through more flexible, affiliative displays should be distinguished by a more symmetrical attentional structure (see also de Waal, 1989b). While some evidence in support of these predictions has been

found, the results are often more complicated than this early model had anticipated.

In a contemporary treatment of this issue, Coussi-Korbel & Fragazy (1995) proposed that something akin to the attentional structure of a group should also be expected to influence the nature of the social learning observed in that group. They suggested that the degree of behavioral coordination, which varies with social structure and is mediated largely by social attention, should affect the patterns of information flow through each group. They proposed, for example, that in egalitarian systems, where social attention is relatively evenly distributed, new skills are more likely to spread through the whole group, compared to more despotic systems, which would show a greater asymmetry of information flow and thus of skill distribution. While little data have yet been generated to address this proposal (although see Kawai, 1965; Chance & Larsen, 1976), much contemporary work does focus on the attentional skills that would mediate such learning.

In some primate social systems, attentional structure may show additional complexity given the prevalence of polyadic interactions in these animals. In coalitional behavior, for instance, two animals that individually are each subordinate to a third may, in forming a coalition, prevail against that dominant individual. Thus, animals that engage in such polyadic interactions must keep track not only of their own relationships but of the relationships between others as well, rendering the observation of exchanged attention particularly pertinent. Since attentional cues such as mutual gaze or other types of shared attention may be indicators of a propensity to collaborate, detecting such cues can become an important skill in this context.

Furthermore, when animals operate within a "fission/fusion" society, where subgroup membership frequently changes (such as in chimpanzees), this may introduce yet another layer of complexity. In such a system, payoffs can arise for individuals who can keep track of who was present to witness particular actions or events. Changing subgroup membership also means a variable distribution of information across the group at large, and any individual capable of tracking that distribution might be able to exploit information about what others have or have not seen. If, in addition, the individual is capable of modifying its behavior depending on its audience, and especially upon what its audience has seen, it might also be capable of manipulating what information it makes available to others.

Some researchers speculate that it was under conditions such as these that humans came to specialize in the assessment and manipulation of the

knowledge of others (see Byrne & Whiten, 1988; Tomasello & Call, 1997). Human-typical traits, such as language, perspective taking, deliberate deception, and "theory of mind" may well have arisen and proved adaptive under these conditions. As a result, primatologists interested in attentional behavior often position their work in terms of its implications for their subjects' abilities to read not just the attention, but also the intention, of others. Attention in even the simplest creatures tends to predict subsequent behavior (e.g., an animal looking where it is going or orienting to a target before it strikes) and thus, in some sense, advertises its intentions. But primatologists tend to be concerned with a more elaborate notion of intentionality in their large-brained subjects. This more elaborate notion includes the understanding of the intentions of others as mental states.

For instance, an individual who looks at something other than its actual focus of interest—for example, feigning indifference or doing what has been called a "distraction display" to lead the attention of others away from a coveted commodity (see Whiten & Byrne, 1988)—are presumed to have intentions that are not immediately predictable from their behavior. Thus, the capacity to inhibit one's outwardly observable attentional behavior and, under audience-specific circumstances, to generate overtly misleading behavior, are taken as more cognitively complex abilities. These tend to be a special interest because they are similar to what humans can do. Such an approach is the focus of much controversy, however. Any given incident of apparent deception is subject to multiple interpretations in regards to the mental states that may underlie it. Even in humans, whether such behavior is a result of a deliberate plan formulated on premises concerning the knowledge of others or whether it is a habitual or emotional response to a particular situation, is not always discernable. In fact, whether such inferences to internal mental states are ultimately falsifiable (e.g., Churchland, 1981; Heyes, 1993; Johnson, 2002) is a recurrent issue in this area of research.

An alternative theoretical approach emphasizes the embodied nature of social cognition (e.g., Varela et al., 1991; Clark, 1999; Johnson, 2001, 2002) over the role of inferred mental states such as "theory of mind." In this view, following the work of developmental psychologist Lev Vygotsky (1978; see also Wertsch, 1985), individuals learn about a domain like social attention through repeated participation in a variety of different interactions. Once they have mastered the various roles in such interactions, they are presumed to "internalize" these behaviors and thereafter can generate them appropriately in novel

contexts. By insisting that such activity is at first public, embodied, and distributed across multiple individuals, and that the later internalized models are based on this activity, researchers from this perspective often treat visible interactions themselves as distributed cognitive events (Hutchins, 1995). From this view, researchers can investigate the media of information flow through such a system and how those media constrain and support one another. Such media, in the domain of social attention, would include observable behaviors like relative head and body orientation, pointing gestures, and the direction of eye gaze. This approach is particularly useful when dealing with nonhuman subjects that cannot readily be queried about their intentions or other mental states. It also provides a common metric for interpreting research from both the laboratory and the field since descriptions of behavior, and especially of changes in behavior over time, are available in both of these settings (see Forster & Rodriguez, this volume).

Whether adopting a mental state model of social attention or a more embodied view, much of the most recent work in this area focuses on identifying the extent and limits of the relevant component skills. The remainder of this paper examines the methodologies used to investigate these skills as well as the data that they generate. In this way, we aim to keep our focus on the behavior of the individuals involved, rather than the cognitive implications of this work.

### Primate Sensorimotor Constraints

Before examining social attention studies, it is important to recognize that certain sensorimotor constraints specific to primates have structured this research. For example, primates have good hearing and produce a variety of vocalizations in social contexts (Owren et al., 2003; Gouzoules & Gouzoules, 2006). These include, in some species, territory calls (to repel competitors), food calls (to attract conspecifics), alarm calls (to alert group members to the presence of predators), as well as more intimate vocalizations that are used to negotiate social interactions. Since these vocalizations can both draw and direct the attention of others, auditory cues would certainly be pertinent to any study of primate social attention.

Another feature that distinguishes primates is their hands. The articulation and opposability of primate digits allows them to grasp and manipulate objects as well as one another. The extended range of movement of their forelimbs, and the facultative bipedalism and upright posture that not only frees their hands but makes the hands of conspecifics more obvious, make reaching and touching pertinent behaviors to observe. Such

movements, especially in conjunction with body and head orientations, can provide models from which novice animals can learn, enable predictions about a conspecific gaining access to resources, and promote opportunities for the emergence of gestural communication (see Gallese et al., 2002). As we shall see below, attention-getting behavior that occurs in multiple modalities—including auditory, haptic, and visual—will tend to be the most effective in these animals.

Vision is the dominant mode of information acquisition in primates. In their evolutionary divergence from other mammals, it was the expansion and differentiation of the neural substrates for vision that most distinguish primate brain development (see Allman, 2000; Gallese et al., 2002). As the ancestral primates moved up into the trees, a shift to forward-facing eyes and the resultant binocular disparity provided the critical depth perception that enabled them to thrive in that arboreal environment. This shift from laterally positioned eyes also provided a distinctive cue in terms of head orientation as to the direction of their visual attention. In fact, cells have been identified in the primate cortex that differentially respond to the image of another primate's face and/or eyes oriented toward or away from the subject (Gross et al., 1985; Perrett et al., 1985). Additional research indicates that the eyes are a special focus of interest in primates viewing the faces of others (Keating & Keating, 1982; Nahm et al., 1997; Sato & Nakamura, 2001). Primates have also developed a progressive motility of the face—from the tethered lips of the primitive prosimians to the richly muscled face of the apes—making this an increasingly important source of social information. Consequently, primates are primed to notice and learn about the contingences that exist between head and eye movement, emotional expression, and various states of the social and physical worlds as perceived through the visual modality. As a result, the study of social attention in primates is largely the study of visual attention (see Emery, 2000).

### Ethological Studies

#### *Functions of Social Attention*

Traditional ethological studies of primate behavior have long recognized the important role that the eyes play in communication in these animals (Hinde & Rowell, 1962; Altmann, 1967; van Hooff, 1967; Kummer, 1968; Plooj, 1978; see Jolly, 1985). Signals involving the eyes inevitably appear among the many gestures and facial expressions included in primate ethograms (van Hooff, 1962; Redican, 1975; Zeller, 1986; de Waal, 1988; Kano, 1989), and some commonalities in gaze-related behavior

have been reported. In many species, for instance, a socially directed stare is used as a threat, and gaze aversion—what Chance (1962) called “cut-off” behavior—is a common tactic to preclude engagement. When a baboon, for example, does not look directly at the “threat yawn” produced by another, this low-level threat is less likely to escalate than if it is acknowledged by a look from the target animal. Eye contact, especially if accompanied by affiliative postures and facial expressions, can likewise be required for positive interactions to proceed. In rhesus monkeys (*Macaca sp.*), for instance, animals attempting to solicit sex or other affiliative contact were observed to wait until the eyes of the target animal were directed at them before they produced the solicitous “lip smack” display (Jolly, 1985; Smuts, 1985).

In complex primate social systems, third parties may also be in a position to make use of the gaze interactions that occur between others. For example, upon detecting others in their group engaging in mutual gaze, especially in conjunction with proximity or contact, baboons (*Papio hamadryas*) (Kummer, 1971) and chimpanzees (*Pan troglodytes*) (de Waal, 1982; Nishida & Hiraiwa-Hasegawa, 1986) will sometimes interfere to prevent possible coalition formation between rivals. In contrast, chimpanzees are also observed to mediate reconciliation between others in their group who do not show co-attention or other signs of probable engagement (de Waal & van Roosmalen, 1979; de Waal, 1982; de Waal & Aureli, 1996).

In coalition-forming primates, recruiting the aid of another against a conspecific often involves the recruiter looking back and forth between the ally and their potential target (Kummer, 1967; Packer, 1977). The ally, who may be monitoring this activity peripherally, can choose to follow the gaze of the recruiter and join in the threat or can fail to look at either the recruiter or the target, effectively “cutting off” the interaction. Note that the occurrence of peripheral monitoring—where a primate observes others without directly facing them—certainly complicates the task for the researcher. While primate peripheral vision does not afford high acuity, it is particularly sensitive to motion and, thus, can be a fairly effective means of tracking activity. Thus, head orientation alone is not always a reliable cue to the focus of social attention. In such cases, multiple cues, repeated observations, and typical precursors and consequences can help disambiguate these events. For example, an ally who, after apparently cutting off a recruitment, consistently looks up immediately after the recruiter abandons its efforts, might provide reliable evidence of its detection, and rejection, of those efforts.

#### *Observational Studies of Social Attention*

Despite the social importance of gaze in primates, relatively few observational studies in which social attention was the primary subject of interest have been conducted. One set of such studies was designed to address Chance's (1967) proposal concerning the “attentional structure” of primate groups. For example, early studies of social attention in rhesus monkeys (*Macaca mulatta*) (Virgo & Waterhouse, 1969) and talapoin monkeys (*Miopithecus talapoin*) (Dixson et al., 1975) supported the hypothesis that subordinate animals attend dominants more than vice versa (see also Emory, 1976; Keverne et al., 1978; McNelis & Boatright-Horowitz, 1998). As more studies were done, however, it soon became clear that the matter was more complicated. In several species, while lower-ranking and younger animals did tend to do more social monitoring overall, the distribution of their gaze did not necessarily map onto the dominance hierarchies in their groups (Haude et al., 1976; Pitcairn, 1976; Torres de Assumpcao & Deag, 1979; Strayer & Garipey, 1986). Other factors, such as kinship, gender, behavioral context, and other social relations, could also play a role. For example, Keverne et al. (1978) found that in talapoin monkeys, dominant animals directed more attention to the opposite sex while subordinates directed more attention to their own. In a recent study on female gorillas (*Gorilla gorilla*) (Watts, 1998), among whom unidirectional rank relationships do not exist, females were more likely to focus their gaze on other females with whom they had antagonistic relationships than those (mainly kin) with whom they had more affiliative relations.

More recently, a few studies that focus on ritualized uses of gaze have also been reported. Bonobos (*Pan paniscus*), for instance, engage in a “peering” behavior in which one animal stares intently, from just centimeters away, at the food in the mouth (or sometimes the hand) of another (Idani, 1995; Johnson et al., 1999; Stevens et al., 2005). Probably derived from begging in infancy, this behavior rarely results in the exchange of food between older animals. It does, however, occur most often in females and is more often directed from younger and subordinate animals toward older and dominant ones. In a species like bonobos, where female coalitions enable these animals to dominate even the males in their groups, such an interaction may not only acknowledge female rank differences (Johnson et al., 1999) and/or resource holding potential (Stevens et al., 2005); it also may function to establish positive affiliations.

A behavior similar to “peering” has also been observed in male gorillas (Yamagiwa, 1992). Although less obviously linked to eating, these

“stares” from only centimeters away are preceded by a friendly approach and characterized by a lack of negative response by the target. While they also tend to be directed most often by young and subordinate animals toward older and dominant ones and thus may serve to confirm rank relations, they can also play a role in greeting, appeasement, and the solicitation of play. Note that in both ape species, the target averts its gaze, not making eye contact during this peer/stare. Thus, at least in some species, even highly intense social gazing can become sufficiently ritualized to lose its threatening quality.

Other ethological studies have focused on primates’ tendency to follow one another’s gaze. In a study of Patas monkeys (*Erythrocebus patas*), Rowell & Olson (1983) found that these animals, who do frequent head-turning “scans” of their surroundings, closely monitor one another and co-orient in the direction of any fixated gaze by a scanning animal. In this way, they establish a “scanning network” that can transmit both social and environmental information rapidly through the troop (see also Caine & Marra, 1988, and Alberts, 1994, on patterns of primate vigilance). Such a network could enable one animal to make use of another’s discovery of food or other resources, or to take advantage of its vigilance for predators. Gaze-following has also been documented to play a role in social learning as seen in developing primates whose attention is entrained by the intent activity of elders engaging in tool use (McGrew, 1992; Russon & Galdikas, 1993) or in social interactions (Altmann, 1980; Goodall, 1986). Gaze-following, as we shall see shortly, has become a primary focus of interest in contemporary experimental studies of primate social attention.

#### *Traditional Methods and Micro-Ethology*

One reason observational studies of social attention have been relatively limited is that coding gaze in “real time” is extremely challenging. Most of the studies described above were conducted on captive groups of primates, ranging from 4 to 40 animals per group. In a given observational session, a single focal animal is selected and, typically, instantaneous scan samples (e.g., at the onset of each 1-min interval) are taken on that animal’s relative head orientation. These data tend to include who the focal is oriented toward and, in some cases, the duration (e.g., “glance,” “look,” or “watch”) and general context (e.g., foraging, grooming, etc.) of that behavior. This practice is then repeated in the next session with another focal animal, and so on. These data must then be correlated with other observations on the same group, gathered at a different time, typically on the distribution of antagonistic vs affiliative behaviors.

Given that shifts in attention can occur in milliseconds and that potential targets can be moving, grouped, and/or a varying distances from the focal data on head orientation are difficult to gather consistently. Inter-observer reliability, when reported (Strayer & Garipey 1986; McNellis-Boatright & Horowitz, 1998), is often lower for these observations than for those of other social behaviors. Plus, no data on the state or response of the other animal, on multi-animal interactions, or on what may be critical details of social context are available in such an approach.

With the recent developments in digital video technology, however, more and more research on attentional behavior is done via video analysis. This offers significant advantages since it allows the detailed assessment of attentional behavior *in situ* for multiple animals simultaneously. Micro-analysis involving slow-motion and repeated-playback viewing can be used to track subtle changes in head orientation, gaze, and other social behaviors. In this way, researchers can compare, for example, the immediate consequences of met vs unmet gaze or examine some of the social functions of an animal turning its head toward or away from another. Of course, as with any methodology, there are limits to this approach. Frame-by-frame analyses are arduous and time-consuming, with each minute of videotape potentially requiring as much as hours to score. While this reduces the total number of minutes that can feasibly be analyzed, however, this approach provides a richness of detail and a means of directly assessing the relations between the animals’ activities as they proceed.

Observational studies using micro-ethological techniques include recent work on mutual gaze (eye contact) in mother-infant pairs of chimpanzees. Bard and her colleagues (2005), for example, videotaped interactions between animals at two different research facilities, sampling at 1-mo intervals, and recording the number of incidents of mutual gaze per hour. They found that mutual gaze between mothers and infants was much more common at the facility in which the adult animals had significantly more interaction with humans and, in addition, were more likely to engage in eye contact with one another. Mutual gaze was also inversely related to the time the mothers spent cradling their infants, suggesting that “mutual engagement in primates is supported via an interchangeability of tactile and visual modalities” (p. 616), especially during infancy.

In a micro-ethological study of adult interactions in bonobos, Johnson and colleagues (2004) looked at gaze interactions in a group of three animals. Videotapes of this triad were taken *ad libitum* at the San Diego Zoo and sampled for head turns

by one animal toward another. Data on the relative position of all three animals' heads during such events, as well as the precise timing of subsequent changes in head orientation by any animal, were recorded. Analyses showed that the best predictor of whether the first animal would maintain its head position or immediately turn away was not the relative head orientation of the animal toward which it had turned but of the third party. That is, if the third bonobo had good visual access to the first animal's head turn, that animal was more likely to turn away quickly than if the third animal had not been in a position to attend. Similarly, in situations when the initial head turn brought all three animals into a state of high visual access to one another, the latency until the next head turn by any animal was significantly shorter than the mean latency between head turns in the original random samples. Such analyses confirm that these animals can monitor and adapt their behavior on the basis of the distribution of attention in others.

In total, these ethological studies highlight the complexities and subtleties of social attention in primates. Observations of social interactions in natural or semi-natural environments, and especially with the aid of micro-analysis techniques, provide important information on the functions of social attention and can help generate ecologically valid hypotheses to be further addressed in the laboratory.

### Experimental Studies

Most contemporary research on visual attention in primates has taken place in the laboratory. Experimental tasks have been of four general types: (1) co-orientation studies, (2) the cooperative use of experimenter-given cues, (3) conspecific competition, and (4) informative cueing. Much of this work was designed to test hypotheses about how the animals represent the knowledge or intentions of others based on their attentional behavior. In this review, our emphasis is not on the theoretical underpinnings or cognitive implications of this work, however. Instead, we adopt a more ethological approach to describing this research. That is, our focus will be on the behavior—of both experimenters and subjects—in these laboratory interactions. While the intriguing and controversial theoretical issues are a vital aspect of this research (for excellent reviews, see Emery, 2000; Itakura, 2004), by focusing on behavior, we hope to highlight the relationships between these experimental findings and those predicted by and observed in the sensory physiology and naturalistic behavior of nonhuman primates.

### *Co-orientation Tests of Gaze-Following*

In Co-orientation studies, "gaze-following" is defined as looking at another individual and then immediately looking where that individual is looking. Subjects are typically presented with a model who directs attentional behavior, such as eye direction, head orientation, or pointing, toward a particular location or object. The goals of this work are to identify the cues that facilitate co-orientation and to determine the accessibility of potential targets.

Some Co-orientation studies used still photographs of models, either human or conspecific, displaying a particular orientation (e.g., Perrett & Mistlin, 1991; Vick et al., 2001). Other studies used videotaped (Emery et al., 1997) or live conspecific models (Tomasello et al., 1998). Most studies, however, involved the animals responding to live human experimenters, positioned in front of them, who would systematically vary the available attentional cues. For example, as a comparison of the effectiveness of head vs eye orientation, on one trial, an experimenter might face the subject and then turn his head and eyes to a target off to the side, while on another trial, the experimenter's head would remain oriented toward the subject while his eyes alone shift toward the target (as in Povinelli & Eddy, 1996a). The location, and the possible occlusion of the targets relative to the subject, could also be varied.

Many of the primates tested for gaze-following were able to use head orientation as a cue. These include New World monkeys (Santos & Hauser, 1999; Neiwirth et al., 2002), Old World monkeys (Emery et al., 1997; Tomasello et al., 1998; Anderson & Mitchell, 1999; Vick et al., 2001) and apes (Itakura, 1996; Povinelli & Eddy, 1996a, 1997; Call et al., 1998; Tomasello et al., 1998; Okamoto et al., 2002). Some monkeys tested did not respond consistently to either head orientation or pointing (Itakura, 1996). Lemurs, which, as prosimians, are most closely related to the original primate ancestor, have not been shown to respond to these cues (Itakura, 1996; Anderson & Mitchell, 1999). Interestingly, success at using a change in eye direction only (i.e., no head turn or other cues) was relatively rare. Of the many animals tested with human models, only an occasional ape (Povinelli & Eddy, 1996a; Okamoto et al., 2002) and, often after prolonged training, a few individual monkeys (e.g., Vick et al., 2001) could use the eyes-only cue. This was somewhat surprising given that several monkey subjects have demonstrated that they can discriminate eyes-only cues in static displays, mainly of conspecifics (Perrett & Mistlin, 1991; Lorincz et al., 1999; Ferrari et al., 2000; Sato & Nakamura, 2001). Overall, multiple, consistent, simultaneous, and dynamic cues were

the most effective in eliciting gaze-following and probably reflect the situation the animals are most likely to encounter in the wild.

The specificity of line-of-sight following was tested by the injection of distracters and barriers into the basic paradigm. To determine whether gaze-following is “geometric,” distracter objects were placed along the path between the subject’s beginning orientation and the target location. When chimpanzees were tested in this paradigm, they tended to pause at these distracters, but then moved on to look at the appropriate target. When a target was positioned behind a visual barrier, chimpanzees shifted their position to look behind the barrier (Tomasello et al., 1999). Similarly, if the experimenter oriented toward an opaque barrier, chimpanzee subjects looked at the barrier and not at a point, along the human’s line of sight, beyond it (Povinelli & Eddy, 1996b). Human infants can follow gaze to a target outside their field of view starting at about 12-month old and do not reliably follow gaze past distracters until after 18 months of age (see Butterworth & Jarrett, 1991; Corkum & Moore, 1995). Among nonhuman primates, only apes have been shown to follow attentional cues to targets outside their fields of view (Itakura, 1996; Povinelli & Eddy, 1997; Call et al., 1998; Tomasello et al., 1999).

Finally, in those cases where there was no target in the location toward which the experimenter directed his attention, the animals would frequently look back at the experimenter’s face as if seeking additional information (Call et al., 1998; Tomasello et al., 2001). In fact, adult rhesus monkeys and chimpanzees tended to decrease their likelihood of gaze-following when the experimenter repeatedly looked at “absent” objects, further suggesting that they expected to find something of interest at the experimenter’s focus of attention (Tomasello et al., 2001). Interestingly, juveniles of these species were not as likely to decrease their gaze-following behavior under those conditions, although they, too, often looked back at the experimenters. This developmental difference suggests that learning is involved in the emergence of gaze-following. Other data indicate that young primates often engage in “social referencing”—that is, checking the faces of older animals, especially their mothers, when faced with novel or frightening stimuli, presumably to determine and mimic their reactions (Mineka et al., 1984; Itakura, 1995; Russell et al., 1997; see also Gomez, 1996). Given that some of the most effective tests of gaze-following depend upon the experimenter first securing the subject’s full attention to his face (see especially Itakura, 1996; Povinelli & Eddy, 1996a), it may be worth investigating whether looking to the face of others

for cues as to how to respond also plays a role in primates’ learning to follow attentional cues.

While many of the primates tested readily co-orient with others, their use of attentional cues in problem-solving contexts has proved more complicated. These tasks have been of two general types: (1) cooperative and (2) competitive. In the cooperative tasks, an experimenter shares food with the successful subject. In the competitive tasks, the experimenter or a conspecific is placed in competition with the subject for that food reward. Questions concerning the ecological validity of these tasks, and other interpretive issues, will be addressed below.

#### *Cooperative Tasks*

Cooperative tasks are of two basic types. In the “Conditional Begging” and “Donor Choice” tasks, the experimenters typically direct attentional cues toward or away from the subject, and whether or how the animal then begs from the experimenter is observed. In the “Object Choice” tasks, the experimenter directs attentional cues toward a baited container, and the animal must, based on those cues, select that target over the others available. In all these tasks, the subject and experimenter are engaged in a collaborative activity that can gain the subject access to food if it can effectively respond to the human’s attentional cues.

*Conditional Begging and Donor Choice Tasks*—Conditional Begging tasks address the question of how the subject responds to the attentional state of a potential food donor. In these tasks, the subject is generally positioned across from a single experimenter from whom it must solicit help to acquire food. Various attentional cues are provided by the experimenter, including orientation of the body, head, or eyes with respect to the subject or the food. The frequency, duration, latency to onset, and modality (auditory or visual) of begging behaviors provided by the subject are recorded (Call & Tomasello, 1994; Hostetter et al., 2001; Povinelli et al., 2003; Kaminski et al., 2004; Leavens et al., 2004; Liebal et al., 2004; Russell et al., 2005). A related test of sensitivity to attentional cues is the Donor Choice task. For this task, two experimenters are present, each giving a different attentional cue simultaneously. The dependent measure in these tests is from which experimenter the subject begs first (Povinelli & Eddy, 1996b; Reaux et al., 1999; Theall & Povinelli, 1999). To date, such food solicitation experiments have only been done with great apes, especially with chimpanzees. In both types of study, some common patterns have emerged.

An experimenter oriented with body, head, and eyes all directed toward a subject is the cue most likely to elicit begging. Body turned toward the

subject and head turned away is less effective, but, interestingly, if the experimenter's body is turned away but his head is turned towards the subject, this is less effective still. The situation concerning eye direction as a cue is even more complicated. On the one hand, direct eye contact by a forward-facing experimenter promotes begging (Povinelli & Eddy, 1996a), yet, in combination with other head and body orientations, the eyes being open or closed does not tend to make a significant difference in performance (Povinelli & Eddy, 1996b; Theall & Povinelli, 1999; Kaminski et al., 2004). One striking exception to this was the performance of a "human-enculturated" orangutan, participating in a Conditional Begging task, who readily differentiated between the eyes-open and eyes-closed conditions. A more traditionally reared captive orangutan in that same study also learned to respond to the eyes-only cue after extensive training (Call & Tomasello, 1994).

These findings indicate a hierarchy of cue effectiveness, with body taking precedent over head, and head over eyes. This has been suggested to reflect the animals' assessment of the humans' "disposition" and/or physical ability to share (see Kaminski et al., 2004). That is, an experimenter's body oriented toward the subject is the most predictive cue of that experimenter's ability to reach out and give food. The availability of the head (and potentially the eyes) as indicators of the experimenter's ability to perceive the begging gesture may only become relevant when the body already indicates a disposition to share.

Other factors have also been shown to facilitate begging. Orienting and leaning toward an object elicits a reliable response, but additionally handling that object tends to elicit immediate and prolonged gestural solicitation (Povinelli et al., 2003). In addition, a "head bob" by the experimenter—a move similar to a solicitous signal made by excited chimpanzees—has also been shown to facilitate begging in that species (Povinelli & Eddy, 1996a; Reaux et al., 1999). This may be due to its general arousal effects or to its interpretation as an incitement to participate.

The modality of begging behavior—that is, whether the ape is more likely to vocalize or use visual cues such as gestures or facial expressions—also appears to be responsive to the attentional state of the experimenter. For example, an experimenter with his back to the subject (Hostetter et al., 2001) or one who was facing another chimpanzee (Leavens et al., 2004) was more likely to engender vocal begging, while one facing the subject was more likely to elicit visual or multi-modal signals. In a few studies, the location of the begging behavior—that is, where the animal positioned its body or gesturing arm—was

examined. For example, when presented with an experimenter oriented towards or away from the subject, in conjunction with the food being positioned in front of or behind the experimenter, Liebal et al. (2004) found that chimpanzees and bonobos tended to move to gesture in front of the experimenter. In contrast, the gorillas and orangutans they tested tended to gesture toward the location of the food. Similarly, Povinelli and colleagues (2003) found that whether the experimenter was oriented toward the food or toward a distracter object, the chimpanzees tended to gesture toward where the human was oriented, even when the food was located elsewhere. Overall, the results of these food solicitation studies indicated that many apes can adjust their begging behavior based on the attentional state of a cooperative experimenter.

*Object Choice Tasks*—The majority of attentional research involving cooperative tasks have been conducted with the Object Choice paradigm (Anderson et al., 1995, 1996; Itakura & Anderson, 1996; Povinelli et al., 1997, 1999; Itakura & Tanaka, 1998; Itakura et al., 1999; Peignot & Anderson, 1999; Vick & Anderson, 2000; Vick et al., 2001; Byrnit, 2004; Inoue et al., 2004; see also Itakura, 2004, for review). For the most part, these tasks were conditional discriminations in which the subject was required to select one of two presented containers based on attentional cues given by a single human informant. Typically, one container was baited with food and the other was not. The subject was either given no visual access to the baiting process or could watch the experimenter move about while baiting (and sham-baiting) containers that were concealed behind a barrier. Once the containers were revealed, variations in the cues provided by the informant included orientation of the body, head, and eyes; hand actions such as touching, tapping, and pointing; body proximity; and various vocal and nonvocal auditory cues.

As with the Conditional Begging and Donor Choice results described above, there seems to be a hierarchy of cue success in these tasks. Pointing is generally a more effective cue than head orientation (Anderson et al., 1995, 1996; Itakura & Anderson, 1996; Peignot & Anderson, 1999; Povinelli et al., 1999; Byrnit, 2004), and head orientation is, in turn, more effective than eye direction alone (Itakura & Anderson, 1996; Itakura & Tanaka, 1998; Povinelli et al., 1999; Vick & Anderson, 2000; Byrnit, 2004). Pointing may be a more accessible cue because an extended arm tends to bring the experimenter's hand into proximity with the appropriate container, maximizing the chances that the animal's visual field will include both cue and container. This interpretation is reinforced by



the finding that a midline point—where the opposite arm was used to point across the body so that the gesturing hand was equidistant from both containers—failed as a cue (Povinelli et al., 1997). Pointing may also be associated, for the animals, with reaching and grabbing, both of which are particularly pertinent to food-getting activity. Interestingly, tapping—that is, making dynamic, audible contact with the container—has been shown to be the most reliable hand-based cue (Itakura & Anderson, 1996; Itakura & Tanaka, 1998; Peignot & Anderson, 1999; Vick & Anderson, 2000; Byrmit, 2004). In fact, many researchers simply assume this cue's potency and use tapping during "pretraining" as a way to ensure that the subjects attend and learn that they will be rewarded for selecting one of the containers.

The finding that head orientation is a better cue than eye direction might stem from its also being more accessible. That is, unlike a shift of the eyes, a head turn is a relatively large motion that can be perceived at a distance and from many angles. Additionally, motion of the head may be easier to detect via peripheral monitoring, allowing the animal to detect changes in attention without having to orient its own gaze directly at the other individual. Given the observations from the field of the role of socially directed gaze in solicitations, threats, or other types of engagement, detecting attention without looking directly at another could certainly have its advantages.

On the other hand, other laboratory data indicate that primates tend to preferentially examine the eyes over all other facial features, at least in static photographs (Keating & Keating, 1982; Nahm et al., 1997). Eye contact has a stimulating effect on a primate's sympathetic nervous system (see Emery, 2000), and it may be that such arousal can facilitate attention to attention. In fact, the potency of eye contact for gaining a primate's attention is so widely recognized that most Object Choice studies explicitly require that eye contact be established before the onset of each trial. Given the salience of the eyes, then, the general ineffectiveness of a shift in eye direction in both Object Choice and Co-orientation tasks is somewhat surprising. Further work is needed to determine if this indicates a real difficulty in extrapolating line-of-sight from the eyes alone or is a result of a competition between predictors in which head orientation tends to win out. (For discussion, see Emery, 2000; Itakura, 2004.) Perhaps eyes, as signals, play more of a role in neural circuits that assess social attitudes than in circuits related to joint exploration of the environment. In any case, it may be important to recognize that, in many of these studies (e.g., Povinelli & Eddy, 1996a; Itakura & Tanaka, 1998; Call et al., 2000; Vick & Anderson, 2000; Inoue et al., 2004), single

individuals of various species were capable of responding to an eyes-only cue (see discussion of individual differences below).

Motivational factors also play a role in these attentional tasks. Barth et al. (2005), for example, found that the performance of chimpanzee subjects was significantly better when they were required to leave the test area after each trial. In the "leave" condition, a subject was engaged in the act of approaching the stimulus when the cue was presented, which may have renewed its motivation to attend to that cue. In contrast, in the "stay" condition, the relevant cues were embedded in a stream of task-irrelevant, nonsocial behaviors exhibited by the experimenter during the inter-trial interval, which may have attenuated the subject's attention to the critical cues.

Other cues have also been shown to facilitate success on Object Choice tasks. The inclusion of vocalizations, such as "food barks," for example, have led to more reliable performance on these tasks in chimpanzees (Itakura et al., 1999; Call et al., 2000); however, since even relatively unemotional, language-based vocalizations also offer an advantage, perhaps just recruiting multiple modalities (i.e., visual and acoustic) in a food-seeking context is sufficient to alert an attention-to-attention response. Other work suggests that multifaceted cues, such as the experimenter approaching, lifting, and peeking under the container, were also highly effective with all the animals tested (Itakura et al., 1999; Call et al., 2000). Not only do such cues include multiple components (head orientation, proximity, touch, etc.), but the experimenter's actions are also organized in such a way as to present a coherent sequence that presumably "makes sense" to the animals and is pertinent to their own concerns regarding gaining access to the hidden food. All of these variations suggest that the best way to motivate effective performance on these tasks may be to tap into existing schemes from the animals' own multifaceted experiences.

#### *Comparing Co-orientation and Cooperative Tasks*

While, overall, the straightforward gaze-following tasks and the somewhat more complex food-sharing tasks show similar profiles in terms of cue effectiveness, there are also some marked differences between them. For one, success on the Co-orientation tasks—if it happens at all—can be spontaneous and immediate. In contrast, when success occurs in the Cooperative tasks, it tends to follow a significant period of training. Furthermore, many primates, especially apes, show a high level of success on Co-Orientation tasks in response to changes in head orientation; however, several subjects of the same species (and even, in some cases, the same individuals) failed

to respond appropriately to head-turning cues in the food-sharing paradigms. For example, one group of baboons tested on Object Choice tasks were unable to use either head or eye turns as cues, despite their earlier discrimination of these cues in static photographs (Vick et al., 2001). Why a capacity for gaze-following does not readily translate into one for selecting an indicated container or potential food donor is not immediately obvious, but various proposals are being considered.

One argument for the overall poorer performance on the food-sharing than on Co-Orientation tasks has been that the cooperative nature of the former tasks may be less "natural" to these subjects than competitive negotiations over food would be. Hare (2001), for example, has suggested that since selection pressures to out-compete conspecifics may have helped shape primates' attentional abilities, those abilities might best be demonstrated in a competitive context. Such arguments have led researchers to devise attentional tasks that are more competitive in nature.

In an ingeniously simple variation of the Object Choice task, for example, Vick & Anderson (2003) changed this traditionally cooperative task into a competitive one. Instead of specifying the "correct" response as choosing the object toward which the experimenter looked, these authors made the other object—the one not looked at—the "correct" one. To do this, they allowed the animal to obtain the hidden food from the container towards which the experimenter did not orient. In addition, when the subject attempted to obtain food from the looked-at container, the experimenter quickly pulled that container from the animal's reach.

This competitive study produced many of the same types of findings, and same types of problems, that characterize the previous Object Choice work. Four baboons—two females and two males—were tested in this paradigm. After considerable training in this task, only one female was able to use eyes alone as a cue. Both females, but not the males, were successful with head orientation, responding more readily to a moving head cue than to a static one. On subsequent tests, even the animal that had previously responded to the eyes-only cue failed to differentiate between closed and open eyes in conjunction with a head-turning cue. This study also showed that simple changes in the protocol, such as adding covers over the foods or imposing a screen during baiting, detracted from the animals' performance, suggesting that factors such as these may have played a role in the extensive number of trials required (especially with monkeys) in other studies of this kind. The authors speculated that the poor performance of the males in this study may have been due to their being "less accustomed to losing competitions for

resources" (Vick & Anderson, 2003, p. 214) than the female baboons would be.

#### *Conspecific Competition*

Another possible factor in the sometimes contradictory findings described above may concern using humans versus conspecifics as models. Nearly all of the above studies involved negotiations between a human experimenter and a nonhuman subject. Tasks that enable these animals to interact with conspecifics may reveal more about how the animals normally exploit attentional cues. In keeping with this, several recent studies have shifted to tasks that involve competitions between conspecifics in an attempt to increase their overall ecological validity (Hare et al., 2000, 2001, 2003; Hirata & Matsuzawa, 2001; Karin-D'Arcy & Povinelli, 2002; Coussi-Korbel, 2004). These paradigms include the Occluder task and the Informed Leader task.

*Occluder Task*—The Occluder task sets a pair of animals against one another in a competition for the retrieval of food. The participants were conspecifics who were identified, in pair-wise food competitions, as dominant and subordinate to one another. Typically, two food items were placed in a room between the holding cages of the subordinate on the one side and the dominant on the other. In the critical tests, one piece of food was visible to both participants while the other, hidden behind an occluder, was visible only to the subordinate. The researchers hypothesized that subordinates who obtained the hidden food more often than the visible food would do so based on an appreciation of which food the dominant was able to see. That is, since food visible to both was liable to be more in contention, the subordinate was predicted to more often obtain food that it saw that the dominant could not see. Subordinates, in both chimpanzees and capuchin monkeys (*Cebus apella*), demonstrated this tendency to retain more hidden food (Hare et al., 2000, 2001, 2003; Karin-D'Arcy & Povinelli, 2002).

The difficulty in such a complex, multifaceted task is, of course, knowing which factors are responsible for which effects. The proportion of hidden vs visible food that the subordinate retained, for example, could be a function of the subordinate being actively intimidated away from the visible food by the dominant animal. Methodological variants have been employed to address this possibility. In one study, the food the subordinate first reached for, instead of the food retained, was taken as the primary measure. In that study, the hidden food was not consistently preferred (Karin-D'Arcy & Povinelli, 2002). In another manipulation, the access that the dominant had to the baiting process, which the subordinate could observe, was varied. In these

tasks, subordinates tended to delay entry into the testing room more when the dominant had access to the whole baiting process; however, when the dominant had access to one food item being hidden but not the other, the subordinate did not preferentially approach the one the dominant had not seen (Hare et al., 2001). In addition, a subordinate's apparent failure to alter its behavior under different conditions might not necessarily indicate an inability to discriminate those changes. Capuchin subordinates, for example, seemed to develop a sufficiently profitable technique early in the course of these tests—they gained a greater share of the food than chimpanzee subordinates did—that it was not clear whether they could not, or just did not, make use of the additional information they were provided in later tasks (Hare et al., 2003).

Even when subjects did behave differently in, and thus appeared to discriminate between, diverse access conditions, it was often difficult to determine just what use they were making of the complex information available. Although “visual access” was often manipulated in the Occluder tasks, virtually no data were taken on the role that attentional cues, such as head, body, or eye orientation, actually played in these interactions. That is, this work does not report, for example, whether the dominant made use of its access, what sorts of orientation cues the subordinate observed, or whether differences in how such cues were used by the animals was predictive of the variable success. This suggests that such complex experimental tasks might benefit from an integration of micro-ethological methods that could provide valuable information on such details.

*Informed Leader Tasks*—In related work in which conspecifics were given differential access to information about a hidden food—called Informed Leader tasks—a combination of experimental and ethological techniques was employed (Menzel, 1974; Hirata & Matsuzawa, 2001; Coussi-Korbel, 2004). In these studies, only a subordinate member of a social group was shown the location of hidden food in a familiar compound. The group was then released all together and the behavior of the informed animal and any individual dominant to it was carefully observed. By combining systematic manipulation of the subjects' access to information, with detailed accounts of how their (videotaped) interactions changed over time, researchers were able to document how the animals adapted to one another's food-finding and other attentional behaviors.

In both mangabees (*Cercocebus torquatus*) (Coussi-Korbel, 2004) and chimpanzees (Menzel, 1974; Hirata & Matsuzawa, 2001), the informed subject, in early trials, moved directly to the hidden food and was followed by the dominant

animal who generally acquired the food. Once the dominant animal began to anticipate the destination of the informed animal, based on its trajectory, and beat that animal to the food, the informed animal's behavior began to change. Upon release, it would inhibit its movement toward the baited container and even head off in another direction. Researchers uniformly reported that the informed animal appeared sensitive to the dominant's attentional state, waiting until the dominant follower was headed away or occupied elsewhere before shifting to move toward the food. In addition, the dominant animal likewise tended to adapt to this change by eventually shadowing the informed animal more closely. Hare et al. (2001) reported a similar type of “shadowing” by the dominant animal in one version of their Occluder task in which both food items were hidden from the dominant rival but visible to the subordinate. It may not be trivial that this shadowing behavior emerged in the third experiment of this series, after many of the subjects had extensive experience in both social roles and with various Occluder combinations. Interestingly, in the Hirata & Matsuzawa (2001) study, it was only after a particular chimpanzee had experienced both the “ignorant” and the “informed” roles that, in her role as an ignorant dominant, she began to follow the informed animal.

#### *Informative Cue Production*

One final class of experimental studies includes both cooperative and competitive elements. A key feature of this work is that one of the experimenters involved does not know the location of the food being sought, and yet the subject is still dependent on that experimenter to procure that food. Thus, in these complicated collaborative tasks, the subject must either inform an ignorant experimenter about the food's location by producing the appropriate attention-directing cues, or she must choose between cues given by an informed vs an ignorant, or a cooperative vs a competitive, experimenter to uncover the food for herself.

In the Informant Choice or “Guesser/Knower” task (Povinelli et al., 1990, 1991; Call et al., 2000), two human informants were involved, each with different visual access to the baiting of containers. While the subject watched, one informant (the Knower) stood with body, head, and eyes directed towards an experimenter who was baiting a container, while the other informant (the Guesser) was out of the room or had his back turned during that process. As in the Object Choice tasks, the subject was not allowed to see which container had been baited. Since the two informants would subsequently use identical cues to indicate different containers, the researchers hoped to determine

whether the informants' attentional states during the baiting process would influence the subjects' choice.

While none of the rhesus macaques tested learned to reliably choose the Knower in these tasks (Povinelli et al., 1991), a few of the chimpanzees did (Povinelli et al., 1990; Call et al., 2000). Even the latter required extensive training, however, including the aid of nonsocial markers of role (e.g., a cap worn by the Knower during training; Povinelli et al., 1990). The chimpanzees' performance in these tasks appeared to be facilitated when the Knower actually conducted the baiting so that he not only oriented toward but also handled the food and containers himself. Note that the evidence provided in these tests is insufficient to determine if the animals themselves represented the informants in terms of their different knowledge states as Guesser and Knower. The finding that some chimpanzees could learn to use attentional cues, such as orientation and handling, to choose an informant is consistent with the data collected on other choice studies, however.

In other informative cueing experiments, the subjects knew the location of the hidden food while the experimenters did not. Thus, unlike all of the above-described choice tasks, the experimenters in these studies did not direct an attentional cue toward one or the other container but, rather, waited for a cue from the subject and then selected a container based on that subject-given cue. In one version of these tasks, comparisons were made between the subject's behavior when it was confronted with a "Competitive vs a Cooperative Experimenter" (Woodruff & Premack, 1979; Mitchell & Anderson, 1997; Anderson et al., 2001). That is, on Competitive trials, if the subject indicated a container that was baited, the experimenter took the food for himself. On Cooperative trials, the experimenter gave the food to the subject. If the subject indicated an unbaited container, no food was found or eaten, and a new trial was begun. In these experiments, the competitive experimenter was distinctively dressed and masked, in part to conceal his identity and in part to help the subject predict his competitive behavior. In variants of this task, the subject also played the role of uninformed chooser on some trials (Woodruff & Premack, 1979).

All of the capuchin monkeys (Mitchell & Anderson, 1997) and squirrel monkeys (*Saimiri sciureus*) (Anderson et al., 2001) tested in this paradigm took hundreds of trials to learn the initial phase of this task—that of pointing to the baited container for the Ignorant Experimenter. Since the experimenter was providing no cues and had not been observed by the subject in association with (i.e., hiding or handling) the food, this part of the

task was apparently even more challenging than the standard Object Choice task. The one group of chimpanzees trained in this paradigm (Woodruff & Premack, 1979) mastered this part of the task much more quickly. (For interesting discussions of the emergence of "pointing" behavior in primates, see Gomez, 1991; Leavens et al., 2005).

Despite these initial species differences, once the basic task was in place, the behaviors that emerged were strikingly similar. In all three species, some individuals eventually inhibited their (by that time well-learned) pointing response in the presence of the Competitive Experimenter. Furthermore, at least one individual in each group came to consistently indicate an unbaited container for that competitor. Anderson and colleagues (2003) even found that when their monkeys had four containers to choose from, they would point to the one farthest from the baited container when the competitor was present. These results are consistent with the data described above on the informed subject "misleading" a competitor away from a hidden food.

One final study involved an ignorant, cooperative experimenter for whom the subjects not only had to indicate the location of a hidden food but, when necessary, a hidden tool used to retrieve that food as well (Call & Tomasello, 1994). In this task, the orangutan (*Pongo pygmaeus*) subjects watched while food was hidden in one of two containers by a first experimenter, who then left the room. When the second, Ignorant Experimenter entered, the subjects—who had previous experience pointing out desired foods to their trainers—immediately and consistently pointed to the baited container. To complicate this task, the food hidden in one of the containers was out of reach and required a rake-like tool to retrieve. After a small set of "pretest" trials, during which the animals could observe the experimenter using the rake, the critical test trials were run. During those trials, the first experimenter, after baiting the hard-to-reach container, would hide the rake behind one of three screens at the rear of the testing area and then leave. The researchers were interested in whether the animals would indicate the rake's location to the second experimenter.

One subject—a "human-enculturated," language-trained orangutan (see further discussion of enculturation below)—pointed only to the baited container and not to the screen hiding the tool on the first two test trials. On both these trials, as the subject watched, the experimenter tried and failed to retrieve the food from that container, then paced and looked around for up to 3 min, and finally left the room. Thereafter, this orangutan consistently pointed to the screens as soon as that experimenter entered the room. The other orangutan, who did

not have the same intensive background with humans, at first failed to point to the screens at all, despite the experimenter's repeated failure to retrieve the food. She did, however, spontaneously point to the visible rake on subsequent training trials. Eventually, with additional experience on this task, she too came to point to the appropriate screen when the rake was hidden (Call & Tomasello, 1994).

Although most of the experimental studies described above have only been conducted in the last decade, they represent a rich and varied body of work that provides many insights into primates' use of social attention cues. In conjunction with developments in observational research, this two-pronged approach can do much to elucidate the nature and function of these subtle and complex interactions.

### Discussion

The experimental studies presented in this review were organized according to the social relationships that they obtain. The tasks were classified as competitive or cooperative, depending on whether they engaged the animals in negotiations that were solicitous, contentious, or collaborative. As such, this organization cuts across some of the more typical boundaries for grouping these studies in terms of their theoretical motivations. For example, both the Occluder tasks (Hare et al., 2001; Karin-D'Arcy & Povinelli, 2002) and the Informant Choice tasks (Povinelli et al., 1990; Call et al., 2000) were originally designed to investigate whether or not the subjects understand the "knowledge" of others based on their attentional behavior. Similarly, we have deemphasized what are often considered critical cognitive issues in this work, such as whether these animals understand the referential nature of a pointing gesture or intentionally manipulate the knowledge available to others (for discussion, see Tomasello, 1995; Vick & Anderson, 2001; Povinelli & Vonk, 2003; Itakura, 2004). While these are certainly interesting and legitimate issues for study and debate, our efforts to shift the focus of this survey to a more ethological description of these tasks aimed to accomplish two things. One was to facilitate a more direct comparison with observational studies of naturalistic behavior. The other was to make explicit a fact that is sometimes overlooked in experimental work—namely, that any interaction between experimenter and subject is a social one. This shift in emphasis can shed a revealing light on some of the more perplexing results reported as well as motivate new directions for research on social attention.

### *Comparing Experimental and Observational Research*

In reviewing the studies conducted in the laboratory vs more naturalistic settings, one of the most striking contrasts concerns the contexts in which social attention has been investigated. All of the laboratory studies focus on negotiating access to food while virtually none of the observational studies do. Social attention, especially gaze-following, is likely to play a role in foraging in the wild, but we have virtually no data on that relationship (although see Goodall, 1986). Similarly, while the observational work often addresses rank relationships, and differential access to resources is certainly one distinguishing feature of rank, we likewise have little explicit information from the field on how this access is mediated by attentional processes. Clearly, observational studies on how animals socially learn about resources in their environment, and use attentional behavior to gain or manipulate access to those resources, is a prime topic for future research in this field.

In the observational work, nearly all the research has focused on the role that attention plays in social relationships—from Chance's (1967, 1976) notion of "attentional structure" through the use of gaze in interactions such as recruitment, threat, or solicitation. This is an important direction for laboratory research that, thus far, has been little pursued. While the begging tasks could arguably be described as negotiating a relationship, most social interactions in primates are intrinsically motivated and do not depend upon, or even entail, the acquisition of food. The Competitive Occluder tasks did make use of basic social variables in the pairing of dominant and subordinate individuals for testing, but these animals were not directly negotiating the nature of their relationships in those tasks. While researchers in the lab are aware of these limitations, logistical constraints have hindered the development of experimental treatments of social negotiation. Relationship variables, such as conflict, alliance, indebtedness, etc., are notoriously difficult to manipulate, or even calibrate, in the lab (although see Cords, 1994; de Waal & Aurelli, 1996). Nonetheless, we suggest that by marrying observational and experimental questions and techniques, there is much to be gained in the study of social attention.

For example, might we be able to design experimental tests of Chance's (1967, 1976) "attention structure" hypothesis to learn more about the relationship between rank and information acquisition? Could other types of relevant information, besides the location or availability of food, be manipulated? Perhaps "playback" studies using videotape of animals engaged in real or fabricated gaze-mediated interactions could be used. Just as playbacks

of vocalizations have been used to assess primates' knowledge of the social relationships of others (Cheney & Seyfarth, 1990; Cheney et al., 1995), perhaps video playbacks could test primates' expectations about attention and rank, or about other social relationships. In addition, micro-ethological techniques offer a means of studying the media of information flow in both laboratory and field situations, providing insights on what the critical attentional variables in different contexts may be (see Johnson 2001, 2004; Herzing, this volume). Clearly, additional communication and collaboration between field and laboratory researchers can profitably expand the range of research opportunities in both settings and help maintain a high level of ecological validity in the research that is done.

#### *The "Ecology" of the Laboratory*

Ecological validity is not just about implementing research that is relevant to the demands that subjects face in their natural lives (although that is, by all means, an important goal, and one that should always guide experimental design). Ecological validity also demands recognizing that the laboratory setting, itself, constitutes an ecology—that is, a complex set of relationships between the subject and its social and physical environment. This entails, in part, acknowledging that every trial is a social interaction, especially given the fundamental physiological and behavioral similarities between primate experimenter and subject. We have tried to make this clear by organizing the tasks in this paper according to the types of social relationships that they embody. Laboratory ecology also entails recognizing that each experimental treatment does not, as is generally assumed, present a single, manipulated variable against a homogenous and, thus, "invisible" backdrop. Instead, each such presentation is a configuration, where variables that are held theoretically constant may nonetheless interact in different ways in each manipulation. Especially in cognitively sophisticated species like primates, the relations between elements in a configuration can often themselves be meaningful.

Consider, for example, the configuration presented in a typical social attention experiment. An experimenter stands in front of his subject, starting at a neutral point in space, until a prescribed moment at which he turns only his head, for a fixed period of time, and then returns to a neutral, non-interactive position. To the scientist, this is the careful isolation and independent manipulation of the variable of head orientation, but to the animal, this presents a bizarre social configuration, very unlike the ones that it normally encounters. It may not be at all clear to the subject what the appropriate rules for interacting under such circumstances

are. The often high number of trials required to reach criterion on these tasks may be more a function of the subjects having to learn those rules, than of the subjects' propensity to attend to attentional cues.

The notion of configuration also comes into play in evaluating the skills that the animals bring to the laboratory situation. One reason, for example, that social relationships are so difficult to address in the laboratory is that, especially in the long-lived, communal primates, these relations depend on the history that the participants share (see Forster & Rodriguez, this volume). That sort of history, which depends on recognizing individuals, and getting to know idiosyncratic tendencies (e.g. aggressive, supportive, playful, aloof), is just the sort of thing that many experimental protocols aim to eliminate. Human informants, for example, are often required to wear identical white lab coats or are randomly cycled through different roles, with the aim of acting as uniformly as possible regardless of the identity of the subject. Perhaps the attention of strangers, or of humans that act like strangers, is not adaptive for primates to notice or learn about.

Another configural issue concerns the dynamics of particular interactions. Consider the unresponsive experimenter who is constrained by the rigors of his protocol to prevent his own behavior from becoming contingent upon that of the subject. Yet, surely, whatever it is that the subject in its lifetime has learned about social attention has occurred in the course of dynamic, contingent interactions. Suppose, for example, that not just arousal, but shared arousal, is a critical component of such interactions. Similarly, perhaps the synchrony or the complementarity of behaviors over the course of a developing interaction are prerequisites for the emergence of shared attention. If such relational factors are indeed relevant, eliminating them from laboratory interactions detrimentally masks their importance.

In general, then, from such an ecological perspective, we are prompted to ask if the rich, multifaceted nature of normal social interaction is, in itself, a required condition for primate social attentional abilities to become manifest. If this is indeed the case, then clearly the typical experimental protocols will underestimate or even misrepresent the animals' capacities. As described above, recent experiments examining the effects of richer, multi-cue contexts (Itakura et al., 1999; Call et al., 2000; Barth et al., 2005) indicated, by their high success rates, that the animals can readily respond to attentional cues when they are embedded in a relevant social configuration. Similarly, approaches that combine ethological and experimental aspects (e.g., Hirata &

Matsuzawa, 2001; Coussi-Korbel, 2004; Johnson, 2004) are more liable to be in a position to assess the complexities that are inherent to such situations. It seems likely that not only our methods but our models for investigating social attention need to become more sensitive to ecological factors in order to adequately address the issues involved.

### *Individual Differences*

One final issue that arises from a behavioral analysis of research on social attention concerns individual differences. Comparative cognition traditionally attempts to describe differences in the ability of species, genera, or other taxonomic categories. This involves the generalization of results to a larger population. Research on relatively large-bodied and expensively housed subjects like primates typically involves only small numbers of subjects, however. As a result, authors often pool data from their subjects and report, for example, the mean likelihood of responses to various cues. In fact, the statistical methods most commonly used are, in general, better suited to differentiating between populations than between individuals. One striking characteristic of the data on attention-based task performance, however, is that significant individual differences are often observed (for discussion, see Itakura & Tanaka, 1998; Vick & Anderson, 2000; Karin-D'Arcy & Povinelli, 2002).

Such differences range from the success of only particular individuals on cues like eyes only (Call et al., 2000; Vick & Anderson, 2000), to markedly different learning rates (Call & Tomasello, 1994; Anderson et al., 2003), to "personality" differences that affect the problem-solving strategies the animals adopt (Mitchell & Anderson, 1997; Hirata & Matsuzawa, 2001). Such individual differences swamp species differences, weakening any claims to a group-specific ability. They also make it necessary that data on individual performance be conscientiously reported. That is, while a study may report "failure" on a given task because, on average, the subjects did not perform above chance, such reports can mask the consistent success of particular individual subjects.

When such individual differences are reported, one ends up with an unsettling catalogue of results that conclude, for example, that some chimpanzees respond to pointing and some do not, some respond to head cues and others do not, some respond to eye direction while others do not, and so on. While the heterogeneity of these data may make drawing solid, generalizable conclusions difficult, such variability is, in itself, an intriguing result. That such individual differences arise in primate cognition research should not be surprising. Primate brains are highly complex, with

multiple interacting systems such as those controlling haptic output, assessing spatial relationships, interpreting facial expressions, and making strategic judgments based on reinforcement contingencies. In such multifaceted neural organizations, even subtle differences in processing efficiency or intersystem communication could produce significant individual differences in task performance. Plus, individual differences in experience, especially in animals so heavily dependent on learning, can produce significant differences in adult capacities. Given the prolonged period of development seen in many primates, the years spent learning in a complex social environment surely shape each individual's propensities and sensitivities in ways that are peculiar to that experience. The interesting cognitive question thus becomes what is it about certain subjects' rearing histories that affects their perceptual, motivational, and reasoning abilities enough to enable them to respond to particular cues better than their conspecifics do.

One answer to this question, offered in the literature, concerns the level of exposure the subjects may have had, especially early in their development, to human "enculturation" (Itakura & Tanaka, 1998; Call et al., 2000; Inoue et al., 2004). For example, it has been repeatedly observed that primates raised by, or closely engaged with, humans over extended periods tend to be capable of using an eyes-only cue on social attention tasks. While human enculturation is not the only explanation for such results (see Vick & Anderson, 2000), it does indicate that the animals are capable of learning about such subtle cues when those cues are relevant to the individuals with whom they regularly interact. Thus, differences that are observed in animals with different rearing histories may reflect the value or usefulness of a given ability within the rearing community, rather than any innate, species-specific capacity. The broad range of adaptability illustrated by these differences reinforces the notion that "enculturation"—as the social establishment of a set of practices and values—is not just a human phenomenon. The cognitive flexibility of primates both enables and requires them to learn what matters in their community, be that in the wild, in captivity, or in the laboratory.

In conclusion, we believe that the integration of field and laboratory research, incorporating the demands of ecological validity and expanding the use of new technologies and techniques, represents a principal direction in which social attention research can profitably develop.

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