

Thesis
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Approaches to Studying
Gaze Monitoring in
Nonhuman Primates

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Abstract

This thesis explored the gaze monitoring abilities of monkeys. A review of previous studies indicated that the face is a valuable source of information for nonhuman primates. When viewing faces, nonhuman primates can recognise conspecifics, individuals and emotional expressions. Within the face, the eyes are a particularly salient feature; nonhuman primates are extremely sensitive to the eyes and gaze is an integral component of all primate expressions. However, where another individual is looking potentially allows a primate access to a wealth of information about their environment; another's visual orientation can indicate important objects or events. It is this informational value of gaze, rather than responses to self-directed gaze, that is the focus of this thesis. Previous research has indicated that nonhuman primates' responses to gaze are fairly inconsistent across tasks. Therefore, the studies reported here explored monkeys' responses to gaze within a number of experimental paradigms in order to better evaluate their abilities. Approaches included spontaneous responses to another individual's visual co-orientation, picture discrimination, object-choice tasks, a competitive task and a computer-based cueing paradigm.

The data reported in this thesis are consistent with previous research in this field. Nonhuman primates spontaneously follow gaze within a simple visual co-orientation paradigm, but they do not readily use gaze as an informational cue within other paradigms, such as the object-choice task. Explanations of this pattern of results are suggested, and mainly focus on the ecological validity of the tasks and general procedural issues. In addition, nonhuman primates do not demonstrate preferential responding to eye gaze, in fact, head orientation seems to be the more salient cue. These findings are not readily accommodated by Baron-Cohen's (1994) model that proposes that the eyes

are the pre-eminent source of information regarding another individuals' gaze direction.

Directions for future research are identified. There is considerable need for further research on a wider range of primate species, and for a consideration of the ontogeny of behaviours. A more detailed analysis of the role of gaze in nonhuman primates' natural interactions is considered desirable and other paradigms are also suggested.

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Declaration

Publications based upon the work contained in this thesis:

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Sarah-Jane Vick, Dalila Bovet & James R. Anderson (2001). Discrimination of gaze cues by olive baboons (*Papio anubis*). Animal Cognition, 4 (1) p 1-10.

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Chapter One

Visual Communication in Nonhuman Primates:

Looking at Faces and the Role of Gaze

‘Other people’s faces provide us with a wealth of social information. We are highly skilled at recognising the faces of people we know, and we can assess characteristics such as age or sex fairly accurately even when a face is unfamiliar. We are also adept at interpreting facial expressions and make much use of these in regulating patterns of social interaction’ (Ellis & Young, 1988, p 87).

While the above quotation refers to human social cognition, many nonhuman primates also inhabit complex social environments where the face is an important source of information about other individuals (van Hooff, 1967; Perrett & Mistlin, 1990). It has been proposed that the development of group living in primates was accompanied by a progressive increase in the utilisation of visual forms of communication, with vision replacing olfaction and vocalisation as the primary means of transmitting social information (Allman, 1982; Anderson, 1998; Andrews, 1963; Brothers, 1996; Emery, 2000). Visually attending to conspecifics allows group living primates access to important social information (Kummer, 1967) and attending to faces is likely to be an integral component of this social monitoring (Pascalis, Petit, Kim & Campbell, 1999; Perrett & Mistlin, 1990). Indeed, morphological changes in the primate face have enhanced its value as an information source; as Emery (2000, p 583) states, ‘the primate face has evolved an elaborate system of facial musculature that aids in producing expressive facial movements.’

As stated above, faces contain information concerning the identity and emotional states of other individuals and this chapter will consider the evidence that nonhuman primates are able to recognise and respond to this information appropriately. Following a general overview of nonhuman primates' responses to faces, this review will present a detailed consideration of the role of the eyes in particular and examine responses to other individuals' gaze. However, it is first necessary to offer a brief overview of the various methodologies employed within this field of research as the issues raised are relevant to this and subsequent chapters.

1) How has face processing in nonhuman primates been studied?

1.1) Responses measured

Studies investigating the face processing abilities of nonhuman primates are somewhat eclectic in nature; approaches range from behavioural to neurophysiological and employ various forms of stimuli. Behavioural methods may use either trained or untrained responses. Untrained measures are naturally occurring responses; amount of attention, visual scanning patterns and emotional or behavioural responses may vary, and consistent variations in these measures reveal that subjects are able to discriminate perceptually between stimuli. Visual scan patterns may differ between two sets of stimuli with subjects showing a preference for one type of stimulus over another or displaying different inspection patterns in terms of number, duration or areas fixated (Keating & Keating, 1982; Swartz, 1983). Behavioural or emotional responses may differ according to the content of the stimuli, for example, the intensity of a given behaviour, such as an appeasement gesture like lip-smacking, may differ according to the stimulus presented (Perrett & Mistlin, 1990; Plimpton, Swartz & Rosenblum, 1981; Sackett, 1966). Such patterns of responding allow the conclusion that the individuals are perceiving salient differences between the stimuli presented (Bovet & Vauclair, 2000).

Nonhuman primates may also be trained to make an arbitrary response to one stimulus and not another; again the capacity for differential responding reveals an ability to discriminate between the stimuli. Individuals may be required to discriminate between two stimuli according to some criterion in order to obtain a reward. Such a discrimination might take the form of 'respond to individual A' (Rosenfeld & van Hoesen, 1979), or to match-to-sample by selecting a stimulus from the options presented that matches (according to some criterion) a sample stimulus, which can either precede or be presented simultaneously with the choice (e.g. Dasser, 1988; Parr, Winslow, Hopkins & de Waal, 2000). Trained responses include lever-pressing in order to view an image. For example, one paradigm requires a lever press to view an image which then disappears when the lever is released, but depressing the lever again within 10 seconds leads to the same image reappearing, while a longer delay results in a new image being presented (Fujita & Matsusawa, 1986). This method provides two measures of preference (amount of time viewing the image and number of times an image is viewed) and although dependent upon an arbitrary behaviour, it taps into an untrained measure of preference for, and habituation to, stimuli.

Neurophysiological and physiological methods allow more direct measures of perceptual processing to be taken. At the neurophysiological level, the activity of visual neurons can be measured as a means of exploring the cortical or subcortical mechanisms underlying face-processing abilities. As with behavioural measures, differential responses indicate that stimuli are perceived as distinct from one another in some manner. Cells may be sensitive to a single feature or to a combination or configuration of features. For example, neuronal responses may reveal selectivity for particular facial features which are generalisable across stimuli and are thus not explicable in terms of other incidental aspects of the stimuli presented, such as lumination or colour (Perrett, Mistlin, Chitty, Smith, Potter, Broenniman & Harries, 1988). In addition to single cell recording, evoked related

potentials (ERPs) have been used to examine brain activity in response to facial stimuli (Pineda, Sebestyen & Nava, 1994). Autonomic measures such as heart rate also may be indicative of differential psychophysiological responding to various stimuli; this measure can complement overt behavioural responses and offers additional insight into the affective salience of the stimuli presented (Boysen & Bernston, 1986).

The dependent measure in face-processing studies with nonhuman primates can therefore be a natural (untrained response), an arbitrary trained response aimed at tapping some underlying ability and allowing overt measurements, or a neurophysiological or autonomic measure which is indicative of covert processing.

1.2) The form and content of the stimuli presented

Most research into face processing in nonhuman primates has used two-dimensional stimuli, ranging from video images to various forms of static image, while the content may be conspecific or human models. It is worth briefly considering how these variations might influence the results obtained.

The range of stimuli employed to examine face processing varies considerably; line drawings (Dittrich, 1994), colour photographs (Tomonaga, 1994), black and white photographs (Keating & Keating, 1982) and video (Nahm, Perrett, Amaral & Albright, 1997) have all been used to allow the systematic presentation of easily manipulated stimuli. However, the use of such two-dimensional images is based upon the premise that responses to these images somehow equate with natural patterns in primate facial perception (Keating & Keating, 1993; Nahm et al, 1997), a premise which has not gone unchallenged (see Bovet & Vaclair, 2000, Deregowski, 1999, & Fagot, Martin-Malivel & Dépy, 1999, for recent reviews of picture perception). The use of two-dimensional stimuli in the study of primate social cognition raises certain issues; it has been highlighted that the ability to discriminate between two pictures does not necessarily mean that the subject is

perceiving the image in any meaningful manner as opposed to a 'complex artificial configuration devoid of any social significance' (Zayan & Vaclair, 1988, p 92). However, if this were the case then subjects should not display socially appropriate behaviours in response to the stimuli (e.g. Overman & Doty, 1982). In addition, the wider social matrix of the subject and stimulus individual should have no influence on the responses observed, but several studies have found that this is not the case. For example, an electrophysiological study on one chimpanzee (*Pan troglodytes*) found that heart rate measures differentiated responses to photographs of aggressive, companion and unfamiliar chimpanzees (Boysen & Bernston, 1989).

Even if these social stimuli are somehow meaningful, it is not clear at what level nonhuman primates understand the representational quality of the images (Bovet & Vaclair, 2000; Fagot, Martin-Malivel & Dépy, 1999; Kyes, Mayer & Bunnell, 1992; Pascalis et al, 1999; Zayan & Vaclair, 1988). That is, do they realise that the stimulus is only a representation of an individual, or do they perceive the picture as if it were the actual individual? Some of the studies in which animals display socially appropriate behavioural responses to two-dimensional stimuli may be suggestive of image-object equivalence. For example, Overman and Doty (1982) reported that pigtailed macaques (*Macaca nemestrina*) displayed emotional responses to socially relevant colour photographs such as humans and monkeys, but not to less salient images (e.g. flowers, insects and landscapes). Furthermore, the social status of the tested or stimulus primate may influence response patterns to socially meaningful stimuli. For example, colour slides of potentially threatening stimuli elicited responses dependent upon Java monkeys' (*Macaca fascicularis*) own social status; aggressive and submissive gestures for high and low ranking individuals, respectively (Kyes, Mayer & Bunnell, 1992). Indeed, social factors may even influence post-test social behaviours, suggesting that nonhuman primates may not show any meaningful distinction between real and pictorial stimuli (Capitano, 1987). In neurophysiological studies, so-called

face cells are found to respond to both real, model and two-dimensional faces (Desimone, 1991; Perrett, Smith, Potter, Mistlin, Head, Milner & Jeeves, 1985).

In contrast, it has been suggested that nonhuman primates may modify their social behaviours when presented with pictorial stimuli; the absence of a social context may allow subjects to become dis-inhibited, for example, displaying prolonged fixation even to images of threatening conspecifics without fear of behavioural repercussions (Nahm et al, 1997). This could be explained in terms of 'interest' being a more powerful determinant of viewing preferences than whether the images are associated with rewarding or aversive cues (Humphrey, 1972). However, if nonhuman primates do alter their behaviour as a consequence of the lack of interactive contingency of pictorial stimuli, then the validity of using photographs as a means of gaining insight into the social perceptions of nonhuman primates may be questioned, except possibly at a very low level. On the other hand, the absence of interaction could allow animals to express their natural behaviours more freely; Nahm et al (1997) in their study of viewing patterns, argue that the patterns observed are only quantitatively not qualitatively different from natural viewing behaviours; indeed, it may be parsimonious to assume that the underlying processes are similar.

The fact that nonhuman primates respond differentially to pictorial stimuli does not offer further insight into the representational status of such stimuli; it may only be indicative of the animal's awareness that the 'conspecific' does not display contingent or congruent behaviour patterns, and not that they comprehend the representational nature of pictures at some level. A similar distinction has been made regarding nonhuman primates' understanding of reflections (Anderson, 1994). Neurophysiological studies indicate a considerable degree of functional equivalence between real and two-dimensional faces; some cells respond in a qualitatively identical manner to real and two-dimensional faces. However, the presentation of pictures produced a reduction in activity in the majority of cells in the superior temporal sulcus that were responsive to faces (Perrett et al, 1985). This

suggests that although two-dimensional images are processed in a similar manner to real faces the two are not entirely equivalent. Conceivably, the absence of perceptual cues such as stereoscopic disparity and motion reduce the activity of cells which specialise in processing complex visual stimuli.

The medium of stimulus presentation itself may have some relevance to how the nonhuman primate perceives and processes the image. Three dimensional model heads have been used as a means of studying face perception; stump-tailed macaques (*Macaca arctoides*) were shown to display appropriate behavioural responses to such a model, suggesting that this is a salient, albeit neglected, form of stimulus for nonhuman primates (Mistlin, 1984). Intuitively, in terms of examining social perception in nonhuman primates, video may seem the most complete two-dimensional stimulus form as the image includes motion and is therefore closest to a live model. Early research showed that monkeys prefer dynamic over static images (Butler, 1961). Moreover, neurophysiological studies have found motion responsive cells in the superior temporal sulcus close to cells which are responsive to moving visual stimuli, underlining the importance of motion in facial expressions; indeed some are identified as being responsive to dynamic components of expressions (Perrett & Mistlin, 1990). However, in one study of the perception of facial displays in rhesus macaques (*Macaca mulatta*), there were no differences in scanning patterns for static and dynamic stimuli (Nahm et al, 1997); this finding suggests that photographs are valid as a means of presenting social stimuli, although the effect could be due to the artificial and context-devoid nature of the stimuli. Nonetheless, photographs are the most commonly used medium for presenting stimuli to nonhuman primates as a means of studying face processing, and as highlighted above, photographic stimuli generally do seem to produce meaningful behavioural, autonomic and neurophysiological responses (e.g. Boysen & Bernston, 1986; Kyes, Mayer & Bunnell, 1992; Perrett et al, 1985).

Indenti-Kit faces have been presented to nonhuman primates as these materials allow controlled and systematic variations of features and configuration. The use of these composite photographic stimuli may be justified: rhesus monkeys spontaneously categorised these images as 'faces' as opposed to 'non-face' stimuli on initial presentations (Keating & Keating, 1993). Line drawings have also been used on the basis that these stimuli allow the information presented to be more stringently controlled; it has been argued that such control is crucial in feature analysis studies where systematic variation is required (Dittrich, 1994). A lexigram-trained chimpanzee was able to label familiar individuals presented as line drawings (Itakura, 1994), but the data suggest that the chimpanzee did not spontaneously respond to these stimuli as representations of familiar individuals. That is, the chimpanzee may simply have learned to label the line drawings with the symbols referring to familiar individuals without attributing any real meaning to the images. However, infant pigtailed macaques demonstrated a preference for normal faces over scrambled faces when these were presented as line drawings of conspecifics; thus, even at a young age, line drawings of faces seem to have some salience as social stimuli (Lutz, Lockard, Gunderson & Grant, 1998).

Dittrich (1994) reported that Java monkeys learned to discriminate schematic drawings of four species of monkey more quickly than geometrical or 'non-natural' stimuli, which indicates that the line drawings possessed some social salience. Furthermore, the monkeys generalised from lateral to frontal facial views of the stimulus monkeys, and recognition was largely independent of transformations in size and orientation. However, the stimuli differed in terms of shape, texture depicted and shading, and the use of such physical cues as a basis for discrimination and generalisation may not be ruled out. Moreover, rhesus macaques were shown to attend less to schematic than photographic faces (Keating & Keating, 1982) and neurophysiological evidence shows that line drawings produce weaker neuronal responses (Perrett, Rolls & Caan, 1982), suggesting that the two

forms are not equivalent as 'social' stimuli. However, Dittrich (1994) has argued that the representational status of the stimuli is not important in that even if nonhuman primates are unaware of the relationship between reality and pictorial representations, the efficient classification and discrimination abilities displayed suggest a predisposition for processing these types of stimuli regardless of the manner of presentation.

As highlighted above, studies of nonhuman primate face-processing vary greatly in terms of methods used and stimulus type; one variation of the latter is the content of the stimuli. Studies use either human or nonhuman primate faces as discriminanda and it is important to consider whether this variable has implications for the outcomes. Studies utilising both forms of stimuli have sometimes produced divergent results, perhaps suggesting that different species are not equivalent as stimuli. For example, studies of face recognition (Tomonaga, Itakura & Matsuzawa, 1993; Phelps & Roberts, 1994; Pascalis & Bachevalier, 1998) and physiological responses (Pineda, Sebestyen & Nava, 1994) have reported variations according to whether a human or nonhuman primate face is presented. To increase validity, therefore, it would seem advisable to utilise conspecifics as stimuli whenever possible; if primate social perceptions are being examined then the use of more socially meaningful stimuli should be prioritised.

However, studies have found that nonhuman primates display appropriate behavioural responses (Overman & Doty, 1982; Perrett et al, 1985) and similar visual scan patterns (Nahm et al, 1997) to human and nonhuman primate stimuli. Rhesus monkeys performing a sequential same/different categorisation task produced errors which indicated that monkey and human faces were being placed in one category while fruits and flowers were placed in another, suggesting that the monkeys were perceiving some level of relationship between monkeys and humans (Sands, Lincoln & Wright, 1982). When interacting with humans, nonhuman primates often display behaviours which are homologous with those exhibited in conspecific engagement (Exline & Yellin, 1969;

Kummer, Anzenberger & Hemelrijk, 1996; Thomsen, 1974) suggesting that nonhuman primates perceive humans as socially meaningful interactants. Moreover, physiological studies using both human and conspecific images found that a chimpanzee displayed differential pattern of heart-rate responses according to the familiarity status of the depicted individual (Boysen & Bernston, 1986; 1989). Pineda et al (1994), though highlighting differences in squirrel monkey (*Saimiri sciureus*) ERP responses to conspecific and human images, stated that both elicit *qualitatively* similar responses, with monkey images evoking enhanced responses. At the neurophysiological level, face cells in the macaque anterior superior temporal sulcus respond to both human and nonhuman primate faces, suggesting that the underlying neural mechanisms for processing these stimuli are similar (Desimone, 1991) though the strength of some cell responses may be affected by stimulus species (Mikami, Nakamura & Kubota, 1994).

To summarise: several types of stimuli have been used in order to evaluate face processing in nonhuman primates. Though there is much debate concerning the nature of picture recognition in animals, it would seem that two-dimensional images are able to elicit appropriate behavioural and physiological responses; the representational status of the images is therefore of tangential interest here. However, it would seem adroit to use the most realistic form of stimulus available; while video and photographic images seem to be adequate modes of presentation, the status of more degraded stimuli such as schematic drawings is less clear. While there is some evidence that humans and conspecifics are not entirely equivalent as social stimuli, it appears that both are capable of eliciting behavioural and physiological responses in nonhuman primates.

2) What information do faces provide?

'Important visual signals arise from the face. The face provides a plethora of social information about an individual's gender, age, familiarity, emotional expression and potentially their intentions and mental state' (Emery, 2000, p 582).

As Emery (2000) identifies, the face can be a source of much information important to any group-living primate. The following sections will consider the role of the face in the recognition of identity and expressions in nonhuman primates, before examining the role of the eyes in expression and communication.

2.1) Species level recognition

At the most basic level, nonhuman primates need to discriminate conspecifics from other species inhabiting their environment (Pascalis et al, 1999). Humphrey (1974), using a habituation paradigm, concluded that rhesus monkeys could distinguish pictures of members of their own species from other mammals, that is, 'rhesus macaques appear to perceive their own species as a separate perceptual category worthy of more attention than other groups of animals' (Perrett & Mistlin, 1990, p 194). For sympatric species, investing time and effort in an appropriate mate, for example, requires that conspecifics be distinguished from allospecific individuals. Many nonhuman primate species have idiosyncratic markings which differentiate one species from an otherwise similar species (Kingdon, 1980) and also demonstrate an ability to identify conspecifics visually (see Table 1).

Rhesus monkeys were successfully trained to discriminate pictures of conspecifics from Japanese macaques (Yoshikubo, 1985). However, training in picture discrimination is not required for many examples of species recognition. For example, Fujita (1987) found

that four of five species of macaques, bonnet (*Macaca radiata*), pigtailed, rhesus and Japanese, discriminated pictures of conspecifics from other macaques in terms of preferential lever-pressing to view images, (although one species, stumptailed macaques, showed a preference for pigtailed macaques and conspecifics were of lesser interest).

Table 1: Studies of species level recognition

Task/Method	Species	Stimuli	Results	Author
Viewing preferences for conspecifics and other species.	Stumptailed macaques	Photographs	Preference for conspecifics.	Demaria & Thierry, 1988
Discrimination of four different species of monkey.	Java monkeys	Line drawings	Successful discrimination	Dittrich, 1994
Viewing preferences for conspecifics and other species.	Macaques (5 species)	Photographs	Discrimination of species.	Fujita, 1987
Viewing preferences for conspecifics and other species.	Japanese and rhesus macaques	Photographs	Discrimination of two species of macaques.	Fujita, 1990
Viewing preferences for conspecifics and other species.	Pigtailed macaques	Photographs	Preference for viewing conspecifics.	Fujita, 1993
Viewing preferences for conspecifics and other species.	Sulawesi macaques	Photographs	Preference for viewing conspecifics.	Fujita & Watanabe, 1995
Viewing preferences for conspecifics and other species.	Rhesus monkeys and Humans	Photographs	Preference only for novel conspecific images.	Pascalis & Bachevalier, 1998.
Viewing preferences for conspecifics and other species.	Infant rhesus monkeys	Photographs	Preference for viewing conspecifics.	Sackett & Rupenthal, 1973
Viewing preference for different species.	Infant pigtailed macaques	Photographs	Differential viewing of different species.	Swartz, 1983
Viewing preference for different species.	Rhesus monkeys	Video	Preference for viewing conspecifics.	Swartz & Rosenblum, 1980
Individual recognition of human and chimpanzees.	Chimpanzee	Photographs	Advantage for conspecific faces.	Tomonaga, et al, 1993
Viewing preference for different species.	Japanese macaques	Photographs	Discrimination of two species of macaques.	Tomonaga, 1994
Discrimination of conspecifics.	Rhesus monkeys	Photographs	Successful discrimination of conspecifics.	Yoshikubo, 1985

Sulawesi macaques (*Macaca nigra*, Fujita & Watanabe, 1995) and pigtailed macaques (Fujita, 1993) were also found to prefer to view pictures of conspecifics using the same paradigm. Similarly, young adult pigtailed macaques discriminated three species of macaques (pigtailed, Java and stumptailed) in terms of differential habituation to pictures (Swartz, 1983). Demaria and Theiry (1988) found a preference for images of conspecifics (over non-primates or even other macaque species) in female stumptailed macaques. Bonnet macaques pressed a lever to view a videotaped conspecific more than videos of other species; though only one example of each species was shown so that individual rather than species characteristics may be responsible (Swartz & Rosenblum, 1980). Moreover, three-month-old macaques displayed preferences for conspecifics, suggesting that this ability is innate or early to emerge in infant primates (Sackett & Rupenthal, 1973). In contrast to a straightforward preference for conspecifics, both Fujita (1990) and Tomonaga (1994) report that Japanese macaques showed a preference for viewing images of rhesus monkeys over conspecifics; nevertheless, these results also demonstrate an ability to discriminate between species.

Within a face recognition paradigm, Tomonaga, Itakura and Matsuzawa (1993) found an advantage for conspecific faces in a recognition task with a language-trained chimpanzee (human participants were better with human faces). Rhesus macaques and humans demonstrated recognition of conspecifics, but not allospecific individuals, in a paired comparison task; sensitivity to recognition was inferred from the tendency to preferentially fixate a novel stimulus more than a familiar image (Pascalis & Bachevalier, 1998). While the face is not the only available source of identification, it is probably the most important. Fujita (1993) examined preferences for photographic stimuli in pigtailed monkeys and found that the preference these monkeys showed for their own species over Japanese macaques diminished when head or head and tail regions, but not body, background or colour, were removed from the image. Similarly, the face was also found to

be important in a study using line drawing to investigate species discrimination by Java monkeys (Dittrich, 1994).

2.2) Individual recognition

While differentiating allo- from intra-specific individuals is undoubtedly an important task for primates, a critical feature of interactions among nonhuman primates is the ability to recognise individual conspecifics. This capacity confers an adaptive advantage for species in which social status is largely dependent upon kinship (e.g., Cheney, Seyfarth & Smuts, 1986). However, nonhuman primates may also form varyingly transient social units such as coalitions, alliances and friendships, making the primate social world an extremely complex environment (Cheney & Seyfarth, 1990a; Harcourt, 1988; de Waal, 1989). Thus, 'as groups became larger, the ability to garner social knowledge by recognizing and remembering familiar individuals and their relationships with other group members became highly advantageous' (Parr et al, 2000, p 47). The importance of this relationship between efficient recognition and successful social manoeuvring has been highlighted by the finding that brain lesions which impair individual recognition can also lead to severely impaired social interactions (Hasselmo, Rolls & Bayliss, 1989).

General features such as gender, age and rank may be determined from another individual's appearance. For example, Sackett (1966) found that isolation-reared rhesus macaque infants showed high levels of interest in slides of infant conspecifics and that their behavioural responses to these images were distinguishable from those to other categories, such as images of older conspecifics resting or exploring. Similarly, juvenile rhesus macaques' viewing preferences were found to be particularly sensitive to images of coeval (in comparison to infant and adult) conspecifics with various facial expressions (Redican, Kellicut & Mitchell, 1971). Thus, identifying another individual's age may be a function of face recognition. However, systematic variations according to the age and gender of the

stimulus conspecific are not frequently reported in face recognition tasks and this is an area that would benefit from experimental clarification.

The ability to recognise individual conspecifics has been demonstrated in several nonhuman primate species (see Table 2). As noted previously, Itakura (1994) reported that a lexigram-trained chimpanzee recognised familiar individuals represented in line drawings. Capitano (1987) demonstrated that pigtailed macaques of intermediate rank were able to recognise familiar conspecifics on video; exposure to images of conspecifics showing behaviours that were inappropriate (in terms of the dominance relationship between the subject and stimulus monkey) led to heightened levels of group aggression following experimental sessions. Hamadryas baboons (*Papio hamadryas*) presented with slides of familiar conspecifics displayed viewing preferences that were consistent with the dominance rank of the depicted individual (Kyes & Candland, 1984). In addition, rhesus monkeys (Rosenfeld & van Hoesen, 1979) and Java monkeys (Bruce, 1982) discriminated faces of individual conspecifics, and chimpanzees were able to match photographs of familiar conspecifics with their vocalisations (Bauer & Philip, 1983).

Two Java monkeys performing a simultaneous discrimination task identified novel views of a familiar conspecific after a few trials, whether presented with pictures of a full body or just the face, while another monkey was able to match images of different body parts of familiar group members (Dasser, 1987). Further research revealed that Java monkeys could also, after considerable training, match slides according to the relationships between the individuals depicted: two monkeys successfully identified mother-offspring pairs (Dasser, 1988). A face recognition study conducted with chimpanzees and rhesus monkeys showed that both species readily learned to match pairs of photographs of several other unfamiliar individuals, with the chimpanzees performing above chance on their second exposure to the images (Parr et al, 2000). Chimpanzees were also able to match unfamiliar mother-son, but not mother-daughter or unrelated individuals pairings,

providing some evidence for phenotypic matching based on physical, facial cues (Parr & de Waal, 1999). As highlighted above, identifying relationships between individuals is a crucial skill within complex primate societies (Cheney & Seyfarth, 1990a); further studies regarding these abilities and replication of these initial findings would be welcome.

Physiological measures such as event-related potentials (ERPs) and heart-rate have also been used to investigate individual recognition in nonhuman primates. In a study with squirrel monkeys, ERPs were sensitive to the familiarity of conspecifics (but not humans) depicted in photographs (Pineda, Sebestyen & Nava, 1994). Boysen and Bernston (1986, 1989) found that a chimpanzee's heart rate differentiated between familiar and unfamiliar conspecifics and humans. Neurophysiological studies have also located a small number of cells that are responsive to an individual's identity; these cells seem to be based upon feature combinations or configurations and generalise across viewing conditions (Hasselmo, Rolls & Bayliss, 1989; Perrett et al, 1984; Perrett & Mistlin, 1990). Thus, across a variety of measures (behavioural and physiological) nonhuman primates have demonstrated acute sensitivity to identity.

Table 2: Studies of individual recognition

Task/Method	Species	Stimuli	Results	Author
Matching vocalisations to facial images of familiar conspecifics.	Chimpanzees	Photographs	Correct cross-modal matching.	Bauer & Philip, 1983
Heart rate measured in response to humans.	Chimpanzee	Photographs	Differential response to familiar and unfamiliar humans.	Boysen & Bernston, 1986
Heart rate measured in response to conspecifics.	Chimpanzee	Photographs	Differential response to familiar and unfamiliar conspecifics.	Boysen & Bernston, 1989
Individual recognition of conspecifics.	Java monkeys	Photographs	Successful discrimination.	Bruce, 1982
Behavioural responses to conspecifics.	Pigtailed macaques	Video	Appropriate spontaneous behavioural responses.	Capitano, 1987
Matching various views of familiar conspecifics.	Java monkeys	Photographs	Correct matching.	Dasser, 1987

Task/Method	Species	Stimuli	Results	Author
Identifying conspecific mother-offspring pairs.	Java monkeys	Photographs	Correct matching or categorisation of pairs.	Dasser, 1988
Neuronal responses to conspecific faces.	Macaques (2 species)	Photographs	Cells responsive to expression and identity of face stimuli.	Hasselmo et al, 1989
Viewing preferences for various stimuli.	Rhesus monkeys	Photographs	Differential viewing of individuals and species.	Humphrey, 1974
Recognition of familiar conspecifics.	Chimpanzee	Line drawings	Successful recognition of individuals.	Itakura, 1994
Discrimination and visual scan pattern of human face.	Rhesus monkeys	Identikit faces	Successful discrimination. General fixation on eye-region.	Keating & Keating, 1993
Viewing preferences of familiar conspecifics.	Hamadryas baboons	Photographs	Choice consistent with status of conspecific.	Kyes & Candland, 1984
Simultaneous match to sample and behavioural responses to humans and conspecifics.	Pigtailed macaques	Photographs	Correct discrimination. Appropriate spontaneous behavioural responses.	Overman & Doty, 1982
Identifying mother-offspring pairs in unfamiliar conspecifics.	Chimpanzees	Photographs	Successful matching of mother-son, but not mother-daughter pairings.	Parr & De Waal, 1999
Recognition of unfamiliar conspecifics (match-to-sample).	Chimpanzees Rhesus monkeys	Photographs	Successful matching of images.	Parr et al, 2000
Neuronal responses to familiar human faces.	Rhesus monkeys	Photographs	Cells sensitive to identity.	Perrett et al, 1984
Delayed match-to-sample and discrimination learning of humans and nonhuman primates.	Squirrel monkeys	Photographs	Successful matching and discrimination.	Phelps & Roberts, 1994
Event related potentials (ERPs) in response to viewing faces of humans and monkeys.	Squirrel monkeys	Photographs	ERPs differentiate familiar and unfamiliar monkeys but not humans.	Pineda et al, 1994
Picture discrimination of unfamiliar conspecifics. Behavioural responses.	Rhesus monkeys	Photographs	Successful discrimination. Appropriate behavioural responses.	Rosenfeld & van Hoesen, 1979
Individual recognition of human and chimpanzees.	Chimpanzee	Photographs	Advantage for conspecific faces.	Tomonaga, et al, 1993

2.3) Recognition of facial expressions

Face perception also facilitates the rapid perception of the emotional state of conspecifics (see Table 3). Nahm et al (1997) investigated how monkeys looked at conspecifics and humans displaying various facial expressions. The eye movements of four adult rhesus monkeys were recorded as they viewed photographic and video images; the face was foveated more than other body parts or surrounding objects, again highlighting the salience of facial stimuli (Fujita, 1993). The expressive content of the images was found to affect viewing patterns with agonistic and affiliative images evoking different scan patterns. For example, the eye region was fixated more than the mouth region when threatening or fear-related stimuli were presented, but this pattern was not evoked by submissive expressions. Thus, according to the authors: ‘the emotional and behavioral salience of a facial expression can be delineated on the basis of viewing patterns – that is, how monkeys look at the face’ (Nahm et al, 1997, p 620). These results are also reflected in visual scan pattern studies with rhesus monkeys; when viewing human and conspecific faces, facial expression affects the pattern of eye movements observed (Keating & Keating, 1982). For example, on-face fixations increased when a human model was showing a threatening expression compared to a neutral expression (Sato & Nakamura, 2001).

Other studies have examined behavioural responses to the emotional content of images. Plimpton, Swartz and Rosenblum (1981) observed the responses of juvenile bonnet macaques to video recordings of unfamiliar conspecifics. They reported appropriate behavioural responses to the images; for example, the monkeys behaved submissively when presented with a threatening male. Infant rhesus monkeys reared in isolation responded differentially to pictures of conspecifics according to facial expression, exhibiting behavioural disturbance in response to threatening (but not neutral or fearful) expressions, and also reducing lever-pressing responses when this resulted in threatening images being

presented (Sackett, 1966). Thus, responses to facial expressions seem to be at least partially 'hard-wired' and not dependent upon social learning.

Table 3: Studies of recognition of expressions

Task/Method	Species	Stimuli	Results	Author
Visual exploration of conspecifics in a choice chamber.	Infant stumptailed macaques	Photographs	Differential viewing of different expressions.	Anderson & Chamove, 1984
Discrimination of different monkey facial expressions.	Java monkeys	Line drawings	Successful discrimination.	Dittrich, 1990
Neuronal responses to conspecific faces.	Macaques (2 species)	Photographs	Cells responsive to expression and identity of face stimuli.	Hasselmo et al, 1989
Visual scan patterns of conspecific, chimpanzee, human and schematic faces.	Rhesus monkeys	Photographs & schematic drawings.	Differentiation of expressions and non-face schematics receive less attention.	Keating & Keating, 1982
Visual scan patterns of human and monkey faces.	Rhesus monkeys	Video & Photographs	Viewing differentiates expression depicted.	Nahm et al, 1997
Neuronal responses to faces.	Rhesus monkeys	Photographs	Cells sensitive to expression.	Perrett et al, 1984
Neuronal responses to faces.	Rhesus monkeys	Photographs	Cells sensitive to expression.	Perrett & Mistlin, 1990
Event related potentials (ERPs) in response to viewing faces of humans and monkeys.	Squirrel monkeys	Photographs	Sensitivity to perceived threat of individual.	Pineda, et al, 1994
Behavioural responses to conspecifics.	Juvenile bonnet macaques	Video	Appropriate spontaneous behavioural responses.	Plimpton et al, 1981
Viewing preferences for conspecific facial expressions.	Rhesus monkeys	Photographs	Differential response to expression for coeval conspecifics.	Redican et al, 1971
Viewing preferences and behavioural responses to conspecifics.	Infant rhesus monkeys	Photographs	Viewing preferences. Appropriate spontaneous behavioural responses.	Sackett, 1966

Socially reared juvenile rhesus monkeys decreased lever pressing in order to avoid pictures of conspecifics of similar age displaying threat expressions relative to images of more affiliative or neutral expressions (Redican, Kellicut & Mitchell, 1971). Infant

stumptailed macaques also showed differential responses to slide images of conspecifics presented in a choice chamber; they demonstrated reduced exploration of photographs depicting negative expressions (Anderson & Chamove, 1984). Within a discrimination learning paradigm, Java monkeys differentiated monkey facial expressions depicted in line drawings; however, the stimulus set consisted of only four images and subjects had a considerable number of trials in which to learn the discrimination (Dittrich, 1990).

In an ERP study, the magnitudes of the ERPs were taken by the authors to reflect the perceived threat of the human and conspecific individuals presented on colour slides (Pineda, Sebestyen & Nava, 1994). At the neurophysiological level, a small number of cells are sensitive to the facial expressions or elements of expressions of both human and monkey faces presented as static images, while others respond to dynamic components of expressions, such as raising eyebrows (Perrett et al, 1984). Some cells in the superior temporal sulcus respond specifically to mouth movements; differentiating between threatening and appeasing mouth positions (Perrett & Mistlin, 1990). Hasselmo et al (1989) also identified cells primarily in the superior temporal sulcus which were responsive to expressions independent of identity.

Summary

The abilities to recognise conspecifics' identities and expressions involve interrelated but distinct processes: identity remains constant despite a wide range of expressions, while expressions must be interpretable over a range of different individuals (Hasselmo, Rolls & Baylis, 1989). These capacities and their interactions are invaluable to any group-living primate with the need to respond appropriately to conspecifics in terms of both identity and emotional state. As the above review shows, at both the behavioural and physiological level, nonhuman primates make considerable use of facial information in order to identify individuals and their emotional states.

3) The role of gaze

'Gaze, or looking, is of central importance in social behaviour. It is partly a non-verbal signal but more a means of perceiving the expressions of others, especially their faces. However, the act and manner of looking also have meaning as signals, showing for example the amount of interest in another person, and are partly intended as signals. So gaze is both signal and channel, a signal for the recipient, a channel for the gazer' (Argyle, 1988, p 153).

When viewing faces, primates are particularly interested in the eye region. Visual scan patterns of rhesus monkeys have shown that the eyes of stimulus faces are an important feature during a recognition task (Keating & Keating, 1993). Performance of a similar task was impeded by masking the eye region for chimpanzees, and when both eyes and mouth were masked for rhesus monkeys (Parr et al, 2000). In contrast, Dittrich (1990) found that the face outline was the most critical feature for Java monkeys performing a discrimination task with line drawings of conspecifics. However, the discrimination involved only identifying one of four images, and the test to examine feature preferences may not have been a valid measure of the monkeys' true viewing preferences. For example, they eyes depicted all signal direct gaze and seem to form two distinguishable pairs across the four faces, while the outlines show more variation and may present a better discriminative cue when only one feature is available. Moreover, adding the eyes to the outline improved performance more than the addition of other internal features, suggesting that even within Dittrich's (1990) paradigm the eyes were an important feature for discrimination.

The eyes received a disproportionate amount of interest from hamadryas baboons viewing slides of a conspecific male; slide selection and viewing duration were highest for faces containing the eye region (Kyles & Candland, 1987). Although these results could be

specific for viewing dominant male faces, Keating and Keating (1982) also found that rhesus monkeys fixated the eye region more than other facial features when viewing conspecific, chimpanzee, human and schematic faces. Sato and Nakamura (2001) replicated these findings; rhesus monkeys preferentially fixated, in terms of both frequency and duration of fixations, the eye region of a photographed human face. Infant pigtailed macaques were found to preferentially foveate a normal as opposed to scrambled line drawing face of a conspecific; the authors suggest that appropriate eye position may be a determining feature as simple displacement of the eyes diminished levels of looking (Lutz et al, 1998). This indicates that the macaque infants were sensitive to disruption in the eye region and were therefore attending to this feature when scanning conspecific faces. Thus, interest in the eye region seems to be a general phenomenon; 'if the eyes are the window to the soul and forecast intent, they may be critical to monitor in the initial five seconds of face-to-face contact' (Keating & Keating, 1982, p 218).

3.1) Primate eye morphology

Recent research suggests that reading the eyes of nonhuman primates may be difficult due to the morphology of the eye. Nonhuman primates' eyes have an external morphology that is considerably different to that of the human eye: human eyes are elongated, have the largest ratio of exposed sclera in primates, and this exposed sclera is devoid of pigmentation (Morris, 1967; Kobayahi & Koshima, 1997; 2001). Kobayashi and Koshima (1997; 2001) used frontal full-face images to examine these features in 88 species of primate (10 species of prosimians, 26 species of New World monkeys, 43 species of Old World monkeys and 9 ape species). In addition to recording the coloration of the eyes and surrounding area, they measured the width/height ratio of the eye outline (WHR) and also the amount of visible sclera within the eye outline (SSI). Both WHR and SSI increased significantly across primate orders, prosimians having the least visible sclera and smallest

WHR, followed by New World monkeys and then Old World monkeys, with apes having the greatest WHR and most sclera exposed. As identified above, humans have a particularly large WHR and SSI; these were significantly different even from other ape species (Kobayashi & Koshima, 2001).

The relationships between these eye morphology parameters and habitat and body size were examined to explore the possible function of these adaptations. SSIs were found to correlate well with a number of measures of body size, such as weight, crown-rump length, sitting height and walking height; that is, larger exposed sclera is associated with increasing body size (Kobayashi & Koshima, 2001). This may be explained by the increased efficiency of eye movements compared to head or body movements in larger bodied primates; these adaptations allow increased mobility of the eye and thus the extension of the visual field. This is supported by the finding that the amount of scanning by eye movement alone was correlated with SSIs in a study of 18 species of primates. The amount of eye movement used for visual scanning was exceptionally high in humans (with a mean of 61% of horizontal scans being made with the eyes alone). For nonhuman primates, the highest amount of eye movement was found in chimpanzees, the largest species studied (20-35%), with the other primate species having a mean of 10.6% (range 4.3% - 24.4%; Kobayashi & Koshima, 2001).

Kobayashi and Koshima (2001) hypothesise that elongated eyes (WHR) are an adaptation to terrestrial life, where the demand for horizontal scanning exceeds the need for vertical scanning. Elongation is significantly more pronounced in terrestrial primates than in semi-arboreal or arboreal species, with the former also having significantly higher WHR than the latter. In order to test this hypothesis, the frequency and durations of both vertical and horizontal scanning were recorded during feeding in a number of primate species. The ratio of horizontal to vertical scanning was positively associated with the WHR and also differentiated between habitat types, with terrestrial species engaging in

horizontal scanning more frequently and for longer than arboreal or semi-arboreal species. Thus, elongated eyes may be an adaptation for greater eye movement in larger bodied primates and also allows for the increased need for horizontal scanning which accompanies the adoption of more terrestrial habitats (Kobayashi & Koshima, 2001).

While body-size and habitat type may account for the shape of primate eyes (in terms of WHR and SSI), these features do not explain the coloration of primate eyes. Although humans have a white sclera, in almost all (95%) other species of primate studied, the visible sclera is brown or dark brown in colour (Kobayashi & Koshima, 2001). Two explanations for the adaptive function of coloured sclera have been proposed. Firstly, it has been suggested that pigmentation may serve to reduce glare, as coloration is absent in nocturnal species (Duke-Elder, 1985). However, recent research has found that nocturnal species also have pigmentation, and of course, diurnal humans have no pigmentation (Kobayashi & Koshima, 2001). Thus, it seems that the coloration of sclera observed in primates cannot be adequately explained by an anti-glare hypothesis.

The second hypothesis focuses upon the communicative function of the eyes (see subsequent sections); in addition to increased flexibility in terms of visual scanning, visible sclera may render eye movements more visible to others (as in humans). However, the sclera pigmentation in nonhuman primates and many other mammals suggests that the coloration may serve to obscure rather than highlight eye movements (Perrett & Mistlin, 1990). For example, Thomsen (1974) noted that during a study of gaze in several species of primates, lower inter-observer reliabilities for squirrel monkeys in particular seemed to confirm a subjective impression that discerning direction of gaze was difficult for primates with small dark eyes.

In support of the camouflaging hypothesis, Kobayashi and Koshima (2001) found that in over half of 82 primate species studied, sclera coloration was similar to both the iris and surrounding face region making it difficult to determine the position of both the eyes

within the face and the iris within the eye outline. In a further 37 species, the surrounding face colour was readily distinguishable from that of the sclera. For example, in some guenons the eye region (*Cercopithecus mona*, *Cercopithecus cephus cephus*) or brow (*Cercopithecus neglectus*) is highlighted with bright coloration (Kingdon, 1980) presumably reflecting the importance of the eye region during social or sexual signalling (Emery, 2000). However, although the position of the eyes may be visible due to different coloration, even in these species the iris and sclera were of similar coloration making it difficult to determine gaze direction (Kobayashi & Koshima, 2001). Thus, in all but one of the nonhuman species studied¹, the coloration suggests that eye movements are obscured with sclera of a similar hue to the iris and/or surrounding face.

It is argued that concealing eye direction could serve at least two adaptive functions in nonhuman primates: avoiding conflict with conspecifics and avoiding predation. Camouflaging eye direction could help nonhuman primates avoid agonistic encounters with conspecifics that may be precipitated by direct eye contact (Perrett & Mistlin, 1990). In addition, if nonhuman primates can conceal their gaze direction from predators this may be adaptive as predators will be unable to ascertain whether or not their approach has been detected (Kobayashi & Koshima, 2001). Interestingly, in an earlier smaller study, infants were shown to have more visible sclera than adults in all 14 species of primates examined, perhaps suggesting that infant gaze serves some as yet undetermined function within primate species (Kobayashi & Koshima, 1997).

However, as shall be seen, nonhuman primates do detect direct gaze although the underlying mechanism may be a source of speculation: ‘in monkeys the sclera is not usually visible in eye-contact; same species eye gaze computation must therefore depend on other factors, e.g. the relative displacement of the pupil in the (very dark) iris and reflections of incident light from the front of the eye probably determine perceptual sensitivity’

¹ Ruffed lemurs, *Varecia variegata*, who only have a small amount of exposed sclera in any case, SSI = 1.08.

(Campbell, Heywood, Cowey, Regard & Landis, 1990, p 1124). Povinelli and Giambrone (2000) suggest that sensitivity to gaze (in primates and other animals) may derive from the emergence of at least two environmental conditions: predation and group living. The threat of predation would have selected for individuals who were able to detect the presence of a set of eyes in their visual field and rapidly react accordingly. The evolution of sensitivity to gaze in response to increased group living is proposed to result from advantages gained from exploiting others' gaze in order to identify information about the social and physical environment (Kummer, 1967). In the latter case, it is not merely the detection of eyes or direct gaze that is crucial, but a less egocentric form of gaze reading, that is, the identification of non self-directed gaze. Again, as group living is considered to have evolved in response to predation (van Shaik & van Hooff, 1983), it is proposed that gaze reading was initially beneficial in that it allowed reactions to predators detected by other group members (Povinelli & Giambrone, 2000). These two forms of gaze will be discussed in more detail below. The next section will consider nonhuman primates' responses to direct gaze: that is, when monitoring another's eye region, are nonhuman primates sensitive to whether or not they are being looked at?

3.2) Detecting direct gaze

One of the most important things about another's eyes is whether or not they are looking at you: sensitivity to the presence or absence of eye-like stimuli is widespread within the animal kingdom (Baron-Cohen, 1994; Gómez, 1996a; Ristau, 1998). Sensitivity to direct gaze has been revealed through behavioural phenomena such as flight responses in sparrows (Hampton, 1994), injury feigning in plovers (Ristau, 1998), death feigning in snakes (Burghardt, 1991) and tonic immobility in chickens (Gallup, 1972). Some species actively exploit this sensitivity to eyes: for example, some insects (*Lepidoptera*) display false eye-spots as an innate antipredatory tactic (Blest, 1957; Scaife, 1976). It has been suggested

that direct gaze may be a special form of stimulus: a 'distinct percept' that receives rapid processing due to its salience (Kummer, Anzeberger & Hemelrijk, 1996). For example, in studies with humans using a visual search paradigm, straight gaze targets were detected faster than equivalent but less eye-like stimuli or averted gaze targets (von Grünau & Anston, 1995).

For nonhuman primates, gaze is an extremely important communicative signal; all their facial expressions include gaze direction as an integral component (Bertrand, 1969; Emery, 2000; van Hooff, 1967). Sustained eye contact has been identified as being central to threatening gestures for many primate species (Hinde & Rowell, 1962; Redican, 1975), while lateral gaze aversion is associated with submissive gestures (Chance, 1962).

Disengaging gaze may serve to 'cut-off' aversive stimuli such as a threatening facial expression (Kummer, 1968; Altmann, 1967; Johnson, 2001). However, such a simple dichotomy is not sufficient to explain the social communicative role of eye direction. For example, eye contact has also been implicated in triggering sexual arousal in stump-tailed macaques (Linnankoski, Grönroos & Pertovaara, 1993) and in appeasement gestures, such as lip-smacking (van Hooff, 1967). Within the great apes, eye contact serves a variety of social functions; it can be both a threat and part of an affiliative social interaction, such as reconciliation following an aggressive encounter in chimpanzees (de Waal, 1989). As Mitchell (1972, p 56) notes, 'affection, fear and hostility... are differentially related to various frequencies and durations of looking.' Thus, gaze may have various motivations and as a communicative gesture it should therefore be understood within the matrix of wider facial characteristics such as head posture and mouth configuration (van Hooff, 1967; Perrett & Mistlin, 1990).

Nevertheless, the importance of direct gaze in social communication suggests that nonhuman primates are adept at detecting this facial feature and, indeed, there is considerable evidence to support this view. The eye region received a disproportionate

amount of attention from rhesus monkeys viewing conspecific and human faces, especially when threatening facial expressions were presented, leading Nahm et al (1997) to comment upon 'the perceptually compelling nature of direct eye contact.' Similarly, rhesus monkeys were shown to visually fixate images of conspecifics displaying direct eye contact (even within neutral faces) more than those depicting averted gaze (Keating & Keating, 1982). Sato & Nakamura (2001) also reported that rhesus monkeys gazed for longer durations and more frequently when looking at a photograph of a human face with direct gaze than when presented with averted gaze.

Like humans (Hains & Muir, 1996; Lasky & Klein, 1979; Vecera & Johnson, 1995), from early infancy nonhuman primates respond differentially to images or observers displaying eye contact or averted gaze. Very young rhesus macaque infants display considerable sensitivity to gaze (Mendelson, Haith & Goldman-Rakic, 1982). By week three, infants exhibited higher levels of emotional disturbance when confronted with images of conspecific faces exhibiting direct eye contact than faces in profile with averted gaze. Furthermore, during the first week of life, the infants fixated monkey faces displaying direct and averted gaze an equal amount, but during weeks three and seven they inspected the direct gaze images less. However, visual scan patterns revealed that the monkeys foveated the eyes proportionally more during the direct gaze condition. While the authors suggest that this may simply be an artefact of the proximity of the eyes to the central field location, it would be interesting to control for the actual eye position in order to examine whether the effect was due to direct gaze per se. Kalin and Shelton (1989) showed that six- to twelve-month-old rhesus monkeys (briefly separated from their mothers) responded to an observer's gaze; staring with a neutral expression resulted in hostile responses, while an observer turned in profile with averted gaze produced behavioural inhibition and freezing. Similarly, a study with younger rhesus infants (aged nine- to twelve-weeks) identified differential responses to an observer's gaze direction; frequency of barking and lip-

smacking increased in a direct gaze condition, while freezing behaviours were highest when gaze was averted (Kalin, Shelton & Takahashi, 1991). In both these studies head orientation was confounded with eye direction, making it difficult to draw any conclusion regarding sensitivity to eye gaze alone, however, it seems reasonable to assume that eye direction played at least some role in invoking the behavioural responses observed.

Adult rhesus macaques are extremely sensitive to eye contact; in a forced-choice task with paired photographs of a human model, the monkeys were able to discriminate direct gaze from gaze averted by as little as 5 degrees laterally (Campbell et al, 1990). Head orientation of the model was manipulated independently, but analysis revealed that responses were not made on the basis of head direction. In a subsequent study, rhesus monkeys were able to differentiate pairs of human eyes looking through a slit, indicating that eye gaze alone was sufficient for the discrimination (Eacott, Heywood, Gross & Cowey, 1993). As with human participants, performance diminished as the degree of angular deviation from frontal gaze decreased. Furthermore, behavioural responses indicated that the monkeys perceived the human faces as salient social stimuli; initial presentations elicited lip-smacking responses (Campbell et al, 1990). Stumptailed macaques are also sensitive to both head and eye direction; they exhibited spontaneous behavioural responses to direct eye contact even when the head was turned laterally (Perrett & Mistlin, 1990). Similarly, lesser mouse lemurs (*Microcebus murinus*) responded with gaze aversion when presented with eye-like stimuli but not when presented with various control images (Coss, 1978).

Adult male rhesus monkeys responded with mildly threatening behaviours when a human experimenter stared and tried to establish eye contact; these diminished if the human then lowered his gaze, but escalated if staring was maintained, and were absent in all but the most aggressive monkey in a control condition where the experimenter's eyes were closed (Exline & Yellin, 1969). Moreover, direct gaze from a human wearing a hood also

led to little reaction from the monkeys, suggesting that the eyes needed to be within a face, that is, in a meaningful context (Exline, 1971). Within a similar paradigm, Thomsen (1974) studied responses to a staring human in a few species of nonhuman primates; readiness to engage in eye contact, measured in looking frequencies, not duration, varied across species. Overall, talapoins (*Miopithecus talapoin*), patas (*Erythrocebus patas*) and Java monkeys all looked at the observer more than rhesus, stumptailed or squirrel monkeys. Gender and age also seemed to be influencing factors, for example, young rhesus monkeys looked as much as adult talapoins and patas monkeys, with young females being the most willing to engage in eye contact (nearly twenty cases of eye contact recorded per minute at a distance of 61 centimetres from the observer). However, because only frequency of eye contact and not duration was recorded, it is difficult to interpret these differences in gaze patterns; frequent eye contact could suggest that the monkeys were monitoring the human, while prolonged bouts of eye contact might be indicative of affiliative or agonistic gestures (Emery, 2000).

Finally, in a study of hiding behaviour in Java monkeys, a human observer first trained the monkeys by threatening them with a direct stare and vocalisation whenever they attempted to drink from two juice bottles (Kummer, Anzenberger & Hemelrijk, 1996). During this training phase, three of the four male monkeys tested threatened the experimenter before drinking, or responded to his threats with lip-smacking. Although there were more general postural cues and vocalisations as components of the human's threat behaviours, it seems probable that the monkeys were responding at least partially to the observer's direct stare.

Autonomic physiological responses to eye contact have been reported in macaques (Wada, 1961); the experimenter's gaze was consistently found to depress EEG responses. In addition, neurophysiological research has identified cells in the anterior superior temporal sulcus respond to certain orientations of the head and to eye gaze (Desimone et al, 1984; Perrett et al, 1985; 1992; Perrett & Mistlin, 1990). For example, some cells were

sensitive to profile views of the face and their responses diminished as the face was rotated horizontally to a frontal facial view while others demonstrated the opposite response pattern (Perrett et al, 1985). Most face responsive cells were responsive to specific face views (such as a profile) rather than to all face views, suggesting that determining the direction of another individual's gaze may be the function of these neurons (Perrett et al, 1992). The majority (64%) of cells responsive to head orientation have also been shown to be sensitive to eye direction (Perrett et al, 1985).

Sensitivity to gaze was compatible with, but could be independent of, responsiveness to head orientation; cells selective for frontal faces also responded to direct gaze, while cells sensitive to profile views were also selective for averted gaze. Responsiveness diminished according to angular deviation from the preferred orientation for both head and eyes, and for cells responsive to compatible head and eye direction, eyes in an incompatible direction had an inhibitory effect compared to the same face with eyes closed (Perrett et al, 1985). Furthermore, ablation in this area reduces the ability to discriminate efficiently between gaze aversion and direct eye gaze in stump-tailed macaques (Campbell et al, 1990). However, lesions to this area do not only affect the discrimination of facial stimuli but two-choice visual discriminations in general (Eacott et al, 1993).

Single cell recordings have also identified sensitivity to gaze information in other areas in the macaque brain; cells in the amygdala were also sensitive to direct gaze (Brothers, Ring & Kling, 1990; Brothers & Ring, 1992). As Perrett and Mistlin (1990, p 93) summarise 'it is apparent that macaque monkeys are extremely sensitive to the direction of gaze of another individual. They are also sensitive to the direction in which the head points and these two parameters interact in the signalling of expressive intent.' Thus, at the neurophysiological level, there is evidence that the direction of another individual's gaze undergoes extensive processing, at least in terms of discriminating self-directed and averted gaze.

In summary, nonhuman primates demonstrate a particular interest in the eye region and are sensitive to whether or not they are the target of another's gaze; direct and averted gaze are differentiated in terms of spontaneous behavioural responses, looking preferences, discrimination learning and neurophysiological activity.

3.3) Mutual gaze

'Eye contact or looking into each other's eyes seems to be a privileged way to transmit communicative intent, to turn any behaviour into an ostensive behaviour' (Gómez, 1996b, p 133).

The previous section considered nonhuman primates' sensitivity to direct gaze, however, eye contact need not simply be a component of facial expressions to which nonhuman primates respond. Gaze could also play a more flexible role in communication; eye contact may also be an ostensive behaviour, both expressing and assessing communicative intent. According to Gómez (1991; 1996a; 1996b) great apes use eye contact in an ostensive manner, for example, in order to gain attention of human interactants and make requests. Thus, gaze informs others of one's intentions and also enables the attention of the other to be monitored; as highlighted above, gaze is both signal and channel (Argyle, 1988).

Within social interactions, nonhuman primates may monitor the gaze of conspecifics. Menzel (1974) remarked that when a knowledgeable chimpanzee was leading others to hidden food locations, looking into the addressee's face was an important component of communication; suggesting that establishing eye contact was necessary for the interaction. Similarly, captive chimpanzees utilised visual gestures only when conspecifics were oriented appropriately; when recipients were not visually oriented, chimpanzees made more non-visual gestures, such as touching the other individual or

making noises to gain their attention (Tomasello, Call, Nagell, Olguin & Carpenter, 1994). However, both of these studies only identify that chimpanzees respond to another's general orientation and not necessarily that they are sensitive to the direction of gaze per se. In another study, young chimpanzees demonstrated little appreciation of another's ability to see; only one of four chimpanzees removed a blindfold from a human who was assisting with carrying a container across an enclosure (Premack, 1988).

Studies of pointing abilities in nonhuman primates have also noted that nonhuman primates often spontaneously look to the trainer's face during pointing, perhaps indicating sensitivity to another's visual orientation. For examples, rhesus monkeys (Blaschke & Ettlinger, 1987) and chimpanzees (Leavens, Hopkins & Bard; 1996; Woodruff & Premack, 1979) have all been reported to look towards a trainer when pointing. Furthermore, one orangutan with extensive experience of human interactions was found to point differentially according to whether or not the trainer's eyes were open (Call & Tomasello, 1994). However, these pointing studies do not generally examine mutual gaze per se (and do not identify the trainer's responses to direct gaze) and it may simply be that captive nonhuman primates learn that a trainer's face is a good indicator of behaviour, for example, that when a trainer's face is visible their behaviours are more likely to be contingent with one's own.

Gómez (1996b) reports that hand-reared juvenile gorillas would engage in more attention getting behaviours when presented with an inattentive than attentive human, for example, eyes closed versus eyes open. However, as Povinelli and Giambrone (2000) identify, there is a crucial procedural bias in Gómez's study. During inattentive trials, the human did not respond to the chimpanzees' requests for food (and therefore attention-getting behaviours were prolonged) whereas during attentive trials the interactant immediately responded to any requests. In a similar study, chimpanzees were confronted with an experimenter engaging in one of four behaviours for a 20-second interval before

awarding the chimpanzee a food item: making and maintaining direct eye contact, making direct eye contact and 'attentive' head movements, waiting with their eyes closed or looking above and behind the chimpanzee (Theall & Povinelli, 1999). The authors predicted that an appreciation of visual orientation would result in the chimpanzees making more non-visual attention getting behaviours (such as vocalising) when the interactant was not oriented appropriately. In contrast, if the chimpanzees were concerned only with behaviours and outcomes, there would be no differences between visual orientation conditions. The results supported the latter position as there were no differences between conditions with respect to the amount or latency of attention-getting behaviours exhibited (Theall & Povinelli, 1999).

In a systematic study of gaze comprehension, Povinelli and Eddy (1996a) conducted a series of experiments with a group of young chimpanzees (aged 5-6 years). In all experimental conditions, the chimpanzees were required to determine whether or not they were in a human interactant's line of regard. The chimpanzees were presented with two trainers, one looking at the chimpanzee and another not visually oriented towards them, and had to choose which trainer to make a begging gesture towards. For example, in one condition one trainer faced the chimpanzee while the other had his/her back turned; the chimpanzees displayed an immediate and consistent disposition to gesture to the trainer facing them. In contrast, during all other conditions, the chimpanzees failed to demonstrate any appreciation of whether or not the trainer could see them; that is, both trainers turned away with one looking over his shoulder, one trainer attending and the other distracted, eyes open versus eyes closed, and various conditions where the eyes of one trainer were occluded with hands, a screen, a buckets or a blindfold.

The authors concluded that although the chimpanzees were able to improve their performances, they did so by learning a series of simple associative rules such as 'choose the experimenter with face visible or unobscured' (Povinelli & Eddy, 1996a). The

performance in the initial condition, where one trainer's back and head were turned away from the chimpanzee, could feasibly have been the result of having already learned through daily interactions that humans are usually unresponsive when their backs are turned (Povinelli & Eddy, 1996a). It should be noted that within this paradigm, the chimpanzees were required to respond on the basis of two potential interactants' behaviours, and that perhaps this made the task more cognitively demanding. Moreover, in all conditions, although one trainer could see the chimpanzee and the other could not, the trainers did not try to engage in eye contact: that is, they did not stare directly into the chimpanzees' eyes but rather fixated a central target. Thus, although the task required that the attending trainer be distinguished, this is not the same as the mutual gaze described by Gómez (1996a, 1996b).

Povinelli and Eddy (1996a) suggested that the distinction between being able to see another and engaging in mutual gaze may be suitably be distinguished in terms of 'hot' and 'cold' social stimuli, with 'hot' social stimuli having an emotional valence and 'cold' stimuli being interpreted on a more cognitive level (Brothers & Ring, 1992). In a subsequent study, the chimpanzees were tested in a condition where one trainer tried to engage the chimpanzee in mutual gaze; they showed an immediate preference for the trainer engaging in eye contact, indicating that mutual gaze is a salient component of social interactions (Povinelli & Eddy, 1996b). However, further conditions demonstrated that head orientation and movements also influenced preferences, suggesting that there may be more to chimpanzees' gaze monitoring abilities. One potential problem with these studies was the age of the chimpanzees; perhaps they were too young to demonstrate the abilities being investigated. However, a follow-up study of the same chimpanzees aged 7 years indicated that they were still responding on the basis of learned behavioural rules and did not seem to understand the role of visual orientation (Reaux, Theall & Povinelli, 1999).

In a recent review, Povinelli and Giambrone (2000) propose that sensitivity to direct or mutual gaze does not necessarily indicate an understanding of internal mental states. While Gómez (1991; 1996b) suggests that gorillas are utilising gaze ostensibly in order to communicate intent, Povinelli and Giambrone (2000) argue that the behaviours reported reveal nothing more than a sensitivity to behavioural configurations. As identified above, it may be that these apes are demonstrating an awareness of the contingencies of successful interactions with humans, more specifically the relationship between orientation and probability of responses to the apes' own behaviours.

In summary, these lines of research suggest that although nonhuman primates may effectively use and monitor eye contact during interactions, they may not understand that looking somehow connects the other to what is perceived. As Povinelli and Eddy (1996a, p 126) state, 'knowing that someone is looking at you might be one of the most primitive arenas in which we could expect to find a mentalistic appreciation of seeing if it existed. Notice, however, that the mere fact that attention to eye gaze and eye contact exists and play a causal role in social interactions does not by itself guarantee that such an understanding is present.' While nonhuman primates seem to be sensitive to eye contact and may engage in mutual gaze, it is not clear what the underlying mechanisms of such behaviours are. Moreover, all of the research reported in this section pertains to the great apes, there is no comparative information available concerning the potential of mutual gaze in monkey communication (Gómez, 1996a).

3.4) Non-self-directed gaze

‘The ability to follow the direction of conspecifics’ visual gaze would seem to be a social skill with immediate adaptive benefits. Following the gaze of others might help individuals perceive important entities in the environment such as food, predators, and certain kinds of social interactions among group mates’

(Tomasello, Call & Hare, 1998, p 1063).

Of course, another individual’s gaze has the potential to impart a great deal more information than simply whether or not they are looking at you. Where another individual looks may signal important objects or events, so gaze monitoring could also enable nonhuman primates access to a wealth of information about their physical and social environment (Kummer, 1967; Povinelli & Eddy, 1996c; Tomasello, Call & Hare, 1998). Indeed, visual orientation is a function of social relationships: Chance (1967) identified that primate social groups display an ‘attention structure’ whereby looking preferences reflect the social structure of the group. Within this hierarchy, dominant individuals receive the greatest amount of visual interest but spend less time monitoring others, while the reverse pattern is observed for subordinate group members. Chance (1967) suggests that not only is this attention structure a function of a group’s hierarchy, but also that group members extrapolate information regarding rank from the amount of attention an individual receives. While this latter hypothesis would be difficult to examine, studies have addressed the attention structures of nonhuman primate groups.

McNelis and Boatright-Horowitz (1998) measured social monitoring in patas monkeys and verified the pattern outlined by Chance (1967); subordinate monkeys spent more time looking at dominant individuals than vice versa. Watts (1998) found that female mountain gorillas (*Gorilla gorilla berengei*) also monitored group members in a pattern

consistent with the social relationships within the group; females looked at males more than other females, and looked more to females with whom they had antagonistic, as compared to affiliative, relationships.

Species differences in the attention structure of primate groups have also been examined. In an interspecies study, a dominant male gelada (*Theropithecus gelada*) monitored his harem more than a mandrill (*Mandrillus sphinx*) alpha male, and the gelada harem also looked at their male more than the mandrill harem (Emory, 1976). Although the author related this to the different social structures of the two species, the study only examined one group of each species, and it may be that individual differences rather than species differences were responsible for the data obtained. However, the overall pattern of attention was similar to that found in studies with other species, that is, higher ranked individuals were monitored more than subordinate group members.

Moreover, species differences in the type of looking behaviours observed in relation to the attention structure have been identified. Two groups each of red-capped mangabeys (*Cercocebus torquatus*) and grey-cheeked mangabeys (*Cercocebus albigena*) were studied (Blois-Heulin, 1999); again, status was related to social attention, with subordinates monitoring their group members more than dominant individuals. In addition, the type of looking used in social monitoring differed for the two species with grey-cheeked mangabeys glancing (very brief fixation) more and red-capped mangabeys usually fixating for longer durations.

Although the informational content of the attention structure of group members is difficult to examine, accurately determining the direction of another individual's gaze would be invaluable for allowing a nonhuman primate to take advantage of social and environmental information. The tendency to co-orient with conspecifics has been noted in wild nonhuman primates including hamadryas baboons (Kummer, 1967) and chimpanzees (Plooij, 1978). However, there are problems with these observations. Firstly, it is unclear

what cue the nonhuman primates are responding to; for example, general bodily orientation, head orientation, eye direction, or some combination of these, could all be the basis for co-orienting responses (Lorincz, Baker & Perrett, 1999). Secondly, in such a setting the possibility that the shift in visual orientation was caused by some external stimulus may not be excluded. Both individuals may simply be independently responding to a sound or movement which the human observer has not noticed (Tomasello, Call & Hare, 1998). Visual co-orientation has therefore been examined more systematically with captive primates (see Table 4).

3.4a) Gaze following

Itakura (1996) explored gaze following (Scaife & Bruner, 1975) in eleven species of primates, including two species of lemur, four macaque species, chimpanzees and a human-raised orangutan. A human experimenter stood in front of the enclosure and waited for subjects to approach, the experimenter then attempted to gain eye contact before turning his head and eyes to look behind and to the side of the nonhuman primate. When gaze shifts were accompanied by a pointing gesture, monkeys tended to either make no response at all, or to fixate the hand, or move in the direction gestured towards. In contrast, chimpanzees and the orangutan usually responded appropriately to a combination of looking with pointing, the orangutan doing so on all trials. In the head orientation only condition, only the chimpanzees and orangutan responded; the chimpanzees oriented in the correct direction on 20% of trials while the orangutan responded correctly on 70%.

This study therefore suggests that while monkeys do not co-orient with a human, great apes are able to do so, especially if they have had extensive experience of interacting with humans. However, during this study motivation may have been a problem; the human observer did not attempt to engage and maintain the primates' interest, for example, by feeding them. This may be an important consideration as amount of time spent oriented

toward to the trainer was related to response rates. Moreover, although the observer attempted to obtain eye contact, it is not clear whether or not he succeeded or if this influenced performance. Indeed, this in itself may have impeded the performance of the monkeys in particular; as highlighted above, monkeys may find such abrupt instances of direct gaze aversive.

In a similar study of gaze following in response to a human interactant, stumptailed macaques, but not black lemurs (*Eulemur Catta*), showed visual co-orientation (Anderson & Mitchell, 1999). In contrast with Itakura's (1996) study, the experimenter attempted to engage the monkeys in a sustained interaction; the human fed small pieces of fruit to the monkeys and alternated between mutual eye contact and fixating on the ground or food items. Within this context, the macaques were more likely to visually co-orient with the observer than not to respond, while the lemurs were more likely to make no response. Moreover, the authors report that on some trials the macaques displayed delayed co-orientation (more than 2 seconds following the experimenter's gaze shift): after a short delay they clearly looked to the experimenter's face before turning their head. In this study, as with the orangutan studied by Itakura (1996), the experimenters were familiar with the subjects and it may be that the social relationship between interactants influences visual co-orientation and other social behaviours (Anderson & Mitchell, 1999; Coussi-Korbel & Fragaszy, 1995).

In the only study to date to use conspecific interactants, Tomasello, Call and Hare (1998) studied five species of primate: chimpanzees, sooty mangabeys (*Cercocebus atys torquatus*), rhesus, stumptailed and pigtailed macaques. An experimenter (located in an observation tower) waited until two conspecifics were oriented appropriately; one facing the other and positioned so that one was oriented towards the experimenter and the other's back was towards the experimenter. The experimenter then induced the individual facing toward them to fixate on a desirable food item (e.g. an orange) and then observed the

response of the other individual in the dyad. Control trials were identical except that the experimenter started a trial when only one individual was present, sitting with its back towards the experimenter. All five species responded to the conspecific's change in visual orientation by immediately (usually within 1 second) co-orienting, while they did not turn during control trials. In this study, because the models were conspecifics, the precise nature of the initial orientation could not be controlled; for example, the primates may have been responding to a change in head orientation or more specifically to eye gaze (Tomasello, Call & Hare, 1998). These authors also suggested that previous negative results with monkeys may reflect a motivational problem in interacting with a human, as some of the same species who readily demonstrated gaze following had failed to do so in an inter-specific interaction (e.g. Itakura, 1996).

A study by Tomasello, Hare and Fogleman (2001) which used both cross-sectional and longitudinal methodology to examine the ontogeny of gaze following, reported that both rhesus macaques and chimpanzees developed the capacity to visually co-orient with a human interactant's orientation (head and eyes) during mid-late infancy (5.5 months and 3-4 years, respectively). This study also demonstrated that only older individuals (rhesus monkeys from 2-years old and chimpanzees from 4-years old) learned to ignore uninformative cues; when presented with successive trials, they were significantly less likely to co-orient during a second 5-trial block than during the initial presentation (Tomasello, Hare & Fogleman, 2001). The emergence of a capacity to visually co-orient could serve as an adaptive function as young animals become more independent and are at more risk from predation. It has been suggested that increasing predation risk may lead to the development of a sensitivity to others' direction of gaze (Povinelli & Giambrone, 2000; Tomasello, Hare & Fogleman, 2001). However, while nonhuman primates may learn to visually co-orient with others at an early age, as they mature their behaviour becomes more flexible as they learn to control the co-orienting response.

In Tomasello et al's (2001) study there was no attempt to sustain an interaction between the experimenter and study animals, so Itakura's (1996) negative results cannot be entirely explained by the absence of any ongoing interaction. Perhaps an alternative explanation could be found in the environments the study animals were tested in. While Anderson and Mitchell (1999) and Tomasello et al (2001) used nonhuman primates housed in research facilities, Itakura (1996) tested zoo-housed primates; perhaps zoo-housed animals are so habituated to human observers who engage in non-contingent behaviours that they are unlikely to respond to the experimenter's actions.

The role of eye gaze itself is unclear in these studies: gaze following was studied in response to changes in head direction and while the eyes may be a salient factor in evoking co-orientation these studies do not address this issue directly. The cues used by monkeys when co-orienting have been examined in more detail using photographic images of conspecifics (Lorincz, Baker & Perrett, 1999). The tendencies of two rhesus monkeys to co-orient were studied in response to the body posture, head orientation and eye direction of a static image of a conspecific. The monkeys responded to head orientation over body posture when these conflicted and although the monkeys responded to eye gaze alone, they were more likely to do so when head and eye orientation were consistent with each other. However, Sato & Nakamura (2001) failed to replicate the gaze following response to depicted eye direction; rhesus monkeys did not demonstrate more visual scanning of the area congruent with depicted eye direction.

Another recent study has also addressed the role of eye gaze in visual co-orientation in macaque monkeys in response to a human interactant (Ferrari, Kohler, Fogassi & Gallese, 2000). The tendency to follow another's gaze was assessed in juvenile/adolescent (2-6 years) and adult pigtailed macaques. Eleven monkeys were tested in their home cages and presented with the following four conditions: head and eye both oriented together, eye orientation alone, a postural cue (movement of the experimenter's

trunk) and a non-social control (movement of a box). Combined head and eye movement invoked a gaze following response more readily than eye gaze alone, although both were significantly likely to lead to co-orientation in adults (Ferrari et al, 2000). However, while juvenile monkeys also responded to the combined head and eye orientations, they did not respond to eye gaze alone. Correlations showed that tendency to respond to both head and eyes and eyes alone increased significantly with age. Moreover, the looking patterns of two head-restrained adult monkeys were measured in response to various gaze signals given by a human (head and eyes, eyes and a non-social control condition). Both monkeys reliably followed the experimenter's gaze to look at the same quadrant of space in both the head and eyes and eyes alone condition, but not during the control condition. Thus, monkeys respond to both combined head and eye orientation and eye gaze alone when presented with images of conspecifics or a human interactant.

In their study into gaze comprehension in young chimpanzees (discussed above) Povinelli and Eddy (1996a) briefly reported that when the chimpanzees encountered a 'distracted' trainer who was looking to one side rather than oriented towards the chimpanzee, they would turn to examine the area to which the trainer was oriented. Thus, these chimpanzees demonstrated visual co-orientation in response to a human's static head direction. Povinelli and Eddy (1996c) explored chimpanzees' gaze following further; a human trainer looked to a predetermined location, either moving both the head and eyes or simply changing the direction of eye gaze alone. In both conditions, the chimpanzees changed their visual orientation more than during a control condition when the trainer looked directly at the chimpanzee. The direction of the trainer's gaze was above and behind the chimpanzee, this ability to follow another's gaze to a location outside their own visual field is considered significant because human infants do not demonstrate this ability until they reach about 18 months of age and some interpret it as an important landmark in perspective-taking (Butterworth, 1995; Moore, 1999; but see Tomasello, 1995). In addition,

the authors examined how the chimpanzees would respond to barriers which intersected the trainer's line of regard (Povinelli & Eddy, 1996c). When the trainer glanced toward the partition, the chimpanzees responded by attempting to examine the partition and not the wall behind themselves. That is, the chimpanzees acted as though they understood that the partition obstructed the trainer's view, an ability that human children have developed by the age of around two and a half years of age (e.g. Flavell, Everett, Croft & Flavell, 1981).

While the chimpanzees tried to examine the trainer's side of the partition, perhaps indicative of an appreciation that the target of fixation was there, it could also be that this was simply an expression of interest in the partition generally (Tomasello & Call, 1997). Thus, although the responses to the partition may reflect a sophisticated level of understanding of gaze, it could also be that the chimpanzees simply co-orient in line with another's change of visual orientation and examine whatever they encounter visually while doing so. In this case, during the first experiment the chimpanzees continued to turn until reaching the back of their enclosure simply because they failed to perceive anything of interest while turning, while in the second study they examined the partition because they encountered it while co-orienting (Butterworth & Jarret, 1991). In a replication and extension of their earlier study, Povinelli and Eddy (1997) addressed the selectivity of the chimpanzee's gaze following. Again, the chimpanzees responded to a trainer's change of orientation (head and eyes) by turning in the same direction and more specifically to the same quadrant in space. In contrast, they did not visually scan their enclosure in response to a control 'no glance' condition nor in response to irrelevant movements by the trainer.

An ingenious experiment was conducted to further examine chimpanzees' gaze following in response to a human's change of orientation; their appreciation of a trainer's perspective was addressed both by a more systematic study of responses to barriers and by introducing distractor objects (Tomasello, Hare & Agnetta, 1999). If the chimpanzees simply followed another individual's gaze until they encountered something of interest then

they should have fixated the barrier and the distractor object, while a more sophisticated level of gaze following would have led them to investigate the experimenter's side of barriers and to continue co-orienting even after their gaze reached the distractor object. The chimpanzees looked around the barriers more during the experimental trials (when an experimenter was fixating them) than on control trials when the experimenter fixated an irrelevant location. In the distractor study, when the human was oriented towards the 'distractor' object the chimpanzees also fixated this object. However, when the trainer fixated a location beyond the distractor the chimpanzees continued to co-orient after encountering the distractor object. The chimpanzees therefore demonstrated an ability to follow gaze 'geometrically', that is, to accurately project another's line of sight (Butterworth & Jarret, 1991).

Call, Hare and Tomasello (1998) report that when gaze following in response to a shift in head and eye orientation, chimpanzees would sometimes look back to the human's face once they had co-oriented to a distal location and found nothing of interest there, before co-orienting again. This 'checking back' is considered an important facet of child socio-cognitive development, though there is some debate regarding its meaning; some consider it indicative of a mentalistic appreciation of gaze while others suggest that simpler processes may underlie this behaviour (Corkum & Moore, 1995). As the authors note, it is possible that the chimpanzees simply returned to a central orientation once they had finished gaze following, and the second gaze tracking observed was simply an independent co-orientation response (Call, Hare & Tomasello, 1998).

Table 4: Gaze following studies

Task (cue)	Species	Method	Results	Author
VCO (head & eyes).	Stumptailed macaques Black lemurs	Human interactant	Only Stumptailed macaques showed VCO.	Anderson & Mitchell, 1999
Visual scan patterns (head & eyes).	Rhesus macaques	Video of conspecific	VCO to fixate target object more than distractor object.	Emery et al, 1997
VCO (head & eyes/eye gaze) Visual scan patterns.	Juvenile and adult pigtailed macaques	Human demonstrator	VCO to head orientation. Only adults VCO with eye gaze alone.	Ferrari et al, 2000
VCO (head & eyes).	2 Species lemur 4 Species macaque Chimpanzees An orang-utan	Human demonstrator	Only chimpanzees (20%) and the orangutan (80%) demonstrated VCO.	Itakura (1996)
Visual scan patterns (head & eyes/eye gaze).	Rhesus macaques	Photographed conspecific	Scanned location congruent with depicted gaze.	Lorincz, et al, 1999
VCO (eyes).	Chimpanzees	Human interactant	VCO with eye direction alone.	Povinelli & Eddy, 1996b
Gaze following (head & eyes).	Chimpanzees	Human interactant	Demonstrated geometric gaze following (barriers and to area behind them).	Povinelli & Eddy, 1996c
VCO (head & eyes).	Chimpanzees	Human interactant	VCO to appropriate quadrant of space	Povinelli & Eddy, 1997
VCO (head & eyes ²).	Sooty mangabeys 3 Species macaque Chimpanzees	Conspecifics	All species demonstrated VCO.	Tomasello et al, 1998
Visual scan patterns (eye gaze).	Rhesus macaques	Photographed human face	Did not scan area congruent with eye direction	Sato & Nakamura, 2001
Gaze following (head & eyes).	Chimpanzees	Human interactant	Demonstrated geometric gaze following (barriers and distractors).	Tomasello et al, 1999
VCO (head & eyes).	Chimpanzees Rhesus macaques	Human interactant	Develop VCO during infancy and habituate to uninformative gaze in adulthood.	Tomasello et al, 2001

Note: VCO = Visual Co-Orientation response.

Emery et al (1997) used conspecific models and a video presentation to examine rhesus monkeys' responses to another's target directed gaze. The eye movements of two monkeys were recorded while they viewed an image of a conspecific looking at a target. In this study, there were several cues available to the monkeys; the eye and head direction and body posture of the model monkey were all oriented towards the target object. The monkeys did fixate a target object that the model monkey was oriented towards more than an identical distractor object, and the authors state that their results identify an ability to follow gaze and engage in joint visual attention. However, the monkeys also fixated the target location before any objects appeared and failed to demonstrate maintained interest in the object once the model monkey was removed from the image. Thus, it may be that the results reflect an ability to follow gaze but it is not clear whether or not the monkeys were looking at the object specifically or simply fixating the location in space where the object was located.

3.4b) The object-choice paradigm

Another approach to studying gaze perception in nonhuman primates is the object-choice paradigm (Anderson, Sallaberry & Barbier, 1995). The object-choice task requires the nonhuman primate to use experimenter-given cues, such as pointing or looking, to locate a hidden food item in, under or behind one of two objects presented. Ostensibly, this task could be solved using simple co-orientation, that is, looking where the experimenter looks should heighten the probability of choosing the first object encountered and retrieving the food item. Thus, while there may be a distinction between tracking another's gaze to a location in space and following gaze to a perceived object (see Section 4 for a discussion), the former could be sufficient for successful performance in an object-choice task. However, this does not seem to be the mechanism invoked by the object-choice task; in

spite of their ability to track gaze, most primates tested have serious difficulties in mastering the object-choice task (Call, Agnetta & Tomasello, 2000; Hare 2001).

Anderson, Sallaberry and Barbier (1995) presented three capuchin monkeys (*Cebus apella*) with an object-choice task, with head and eye direction combined and pointing plus head and eye orientation as the experimenter-given cues. Pointing was found to be necessary and sufficient for the monkeys to perform the task successfully. After over 1000 trials with head and eye orientation available as a cue, the monkeys failed to use this information to choose the correct container but were able to use pointing as a cue within 300 trials. A study with rhesus monkeys reported similar results; none of the monkeys responded correctly to head and eye cues but two of the three showed improved performance with manual gestural cues (Anderson, Montant & Schmitt, 1996). The study also addressed the possibility that reduced distance between cue and objects might explain the advantage for manual gestures; one monkey performed significantly above baseline levels when a gaze (head and eyes) cue was presented at a closer range, suggesting that some of the discrepancy between facial and manual cues may be due to the cue-stimulus distance. However, the monkeys did not perform above chance levels when presented with an eye gaze cue, even though this was also presented in close proximity (about 15cm) to the object.

In a single case object-choice study with a capuchin monkey (Itakura & Anderson, 1996), the capuchin received scaffolding with manual gestures before proceeding to gaze cues, and a correction procedure and time-outs following errors were introduced. The monkey successfully mastered (80% correct criterion level) all of the cues presented except for an eye gaze only condition: these included tapping, pointing and head and eyes oriented at both near and far proximity to the object (15cm and 60cm respectively). Thus, this explicit training seemed to facilitate cue use by a monkey up to but excluding eye gaze alone.

In a similar study with great apes, Itakura and Tanaka (1998) reported an ability to respond to all cues including eye gaze. Two chimpanzees, an orangutan and a group of two-year old children were all tested in a succession of conditions, as used by Itakura and Anderson (1996), and responded successfully to all experimenter-given cues. However, although able to exploit eye direction, performance in this condition was lower than in all preceding conditions suggesting that this was a more difficult cue for these subjects to use. Gorillas were also able to use experimenter-given cues but did not respond to eye gaze alone; in fact, when presented with eye gaze alone, the gorillas failed to complete the task appropriately (Peignot & Anderson, 1999). Although it is conceivable that there is some underlying species difference which accounts for the failure of gorillas to read eye gaze, it could be due to different amounts of experience of interacting with humans; while the other apes studied had extensive experience with humans, the gorillas in this study did not. Indeed, rearing histories and experience with humans have been highlighted as important factors in nonhuman primates' responses to a human interactant (e.g. Call, Hare & Tomasello, 1998; Tomasello & Call, 1997).

Chimpanzees who had previously shown an ability to gaze follow in response to a shift in a trainer's head and eye orientation, were shown to use the same information less reliably in an object-choice task (Call, Hare & Tomasello, 1998). Interestingly, one of the factors which appeared to determine performance was the container in which the food was concealed; while the chimpanzees used experimenter-given cues to locate food hidden in a tube or behind a barrier, they failed to do so when the objects were upturned bowls. These results exclude any simple gaze following mechanism (whereby nonhuman primates co-orient and are more likely to respond on the congruent side or continue co-orientating until encountering something of interest) as the basis for performance, as this would lead to similar levels of performance across all conditions. It has been suggested that such a co-orientation in combination with foraging tendencies might be sufficient to explain the

chimpanzees' behaviour; perhaps the chimpanzees are accustomed to foraging in holes and behind natural barriers but not beneath objects (Call, Hare & Tomasello, 1998). However, it would be reasonable to assume that chimpanzees have experience of looking under things, for example, beneath stones where insects can be found, making this explanation less feasible. In addition, the chimpanzees had participated in earlier experiments and thus had considerable experience of finding food under opaque containers.

The authors suggest that the crucial difference may be that in the former two conditions the experimenter could actually see the food item while giving the cue, while in the bowl condition the experimenter was unable to see the food item. According to this hypothesis, the chimpanzees have some understanding of what others can and cannot see; they are able appreciate the experimenter's perspective and understand that with certain occluders the experimenter can see things that the chimpanzee cannot. However, there is no evidence of an appreciation that seeing leads to knowing; the chimpanzees would have recognised that the experimenter witnessed the baiting procedure in all conditions and knew the location of the food item regardless of the type of occluder (Call, Hare & Tomasello, 1998). This study does raise interesting issues in that methodological details may have important implications for performance in the object-choice paradigm. For example, had only upturned bowls been presented, the conclusion might have been that the chimpanzees were unable to use experimenter-given cues, a conclusion that is incorrect given performance with the alternative occluders.

In addition to addressing the issue of occluder type, Call, Agnetta and Tomasello (2000) considered the type of cues that chimpanzees would use to find hidden food items. Vocalisations and other noises, or an experimenter approaching, touching or lifting and looking under the container, facilitated performance in a minority of chimpanzees, but these factors did not enhance performance for most chimpanzees. Across the various conditions, seven chimpanzees responded to head and eye direction combined as a cue and

only four responded at above-chance levels when only eye gaze was available. The authors suggest that the approach and vocalisation cues may assist some chimpanzees by engaging them in a 'foraging mode' and may change the functional context of the task (Call, Agnetta & Tomasello, 2000). This is an interesting concept as there seems to be something about the object-choice task which nonhuman primates find particularly challenging; while able to gaze follow they do not seem to exploit gaze readily within this paradigm. Call et al (2000) state that gaze following may be a simple mechanism whereby nonhuman primates survey their environment for information, while the object-choice task is a communicative situation where the relevance of the trainer's behaviour to the task at hand must be understood. Thus, the superiority of cue reading by nonhuman primates with considerable experience with humans may be due to greater understanding of communication and interactions with humans (Tomasello & Call, 1996).

In contrast to evidence that chimpanzees are fairly precise when following another's gaze (see Tomasello, Hare & Agnetta, 1999), Povinelli, Bierschwale and Čech (1999) report that chimpanzees were insensitive to whether or not a trainer was actually looking at a container presented during the object-choice task. Seven chimpanzees were tested in three experimental conditions: the trainer fixated the baited container with eyes alone, or oriented both head and eyes either towards or above the container. The chimpanzees performed at chance levels when eye gaze alone was available as a cue, but above chance in both head and eye orientation conditions. It is interesting that the chimpanzees did not use eye gaze as a cue as they had previously demonstrated an ability to visually orient in response to eye direction (Povinelli & Eddy, 1996b). In addition, the chimpanzees' responses were not influenced by whether the cues were static or included motion; most object-choice studies present a static cue so any benefits for more active cues would have perhaps indicated that abilities had previously been underestimated. Thirdly, the authors suggest that responding to both on and off-target gazes (head and eyes)

indicates that the chimpanzees do not have a high level appreciation of seeing (Povinelli, Bierschwale & Čech, 1999).

Conceivably, the chimpanzees either have an understanding of attention which is amodal or independent of gaze (Povinelli & Eddy, 1996a), or they respond to simple behavioural indicators (a low-level account of their abilities). The above chance performance in the above-object gaze condition could be a consequence of co-orienting with the trainer's gaze direction which subsequently led to a response on the congruent side. Indeed, the authors suggest that success in both head orientation conditions (and failure in the eye gaze only condition) could have been due to bias towards the trainer's face; if the chimpanzees were drawn to the human's face this could result in the response pattern obtained (Povinelli, Bierschwale & Čech, 1999). It does seem that the chimpanzees were not insensitive to gaze direction as they consistently followed the trainer's gaze during off-target trials and examined the direction to which the trainer was oriented (i.e. demonstrated visual co-orientation). Perhaps given the situation, the chimpanzees were making the only response to be expected; although the trainer was effectively not cueing either object, their orientation in the general direction of one container would at least seem to differentiate the objects on offer as it is unclear what alternative response was available. However, in a comparative study with human children (3 years old), the children responded randomly when presented with a 'distracted' trainer, that is, the author's conclusions have some basis (Povinelli, Bierschwale & Čech, 1999).

As with gaze following, only one study has attempted to examine nonhuman primates' responses to conspecific gaze cues within an object-choice paradigm. In a study that used both human and conspecific informants, chimpanzees performed similarly under both circumstances (Itakura, Agnetta, Hare & Tomasello, 1999). A local enhancement cue, whereby the informant approached the location of the baited object and remained there, was used by all four chimpanzees when given by a conspecific and by three when the

interactant was human. Only one chimpanzee successfully used a gaze (head and eyes) and point cue condition but only when this was presented by a human trainer. However, the chimpanzee's initial performance was random, suggesting that an appreciation of the informative nature of the gesture was learned during the study (Itakura et al, 1999).

In addition, twelve chimpanzees were presented with a human informant who vocalised while cue-giving; the human made a vocalisation while giving a head and eye orientation cue which alternated between the chimpanzee and baited container for about 10 seconds before the objects were presented. Vocalisations enhanced performance for six individuals, while three chimpanzees performed above chance even without any vocal component to cues. As previously stated, the authors suggest that vocalisations may facilitate gaze following by highlighting the foraging component of the task (Itakura et al, 1999). While it may be that the perceived direction of the vocalisation (rather than the gaze cue) facilitates success on the object-choice task, this is unlikely as another study found that directed vocalisations alone were insufficient for above chance performance (Call, Agnetta & Tomasello, 2000). Overall, Itakura et al (1999) found that approaching or vocalising engaged the chimpanzees in the foraging task while gaze cues alone were less likely to facilitate correct choices. The authors propose an interesting hypothesis whereby gaze following is demonstrated in social monitoring rather than within a foraging context; locating food may require cues other than or in addition to gaze (Itakura et al, 1999).

3.4c) Alternative paradigms

In addition to the two main paradigms (gaze following and object-choice) outlined above, there have been some other approaches used in the study of gaze comprehension in nonhuman primates (see Table 5). Santos and Hauser (1999) used an expectation violation paradigm (commonly used with pre-linguistic human infants) to study cotton-top tamarins' (*Saguinus oedipus oedipus*) responses to a human's gaze. The tamarins observed a human

looking at one of two items presented before reaching for one of the objects; reaching for the looked at item is considered to be consistent with expectations while choosing the other item would be a violation of expectancies. The dependent variable was the amount of attention each event received from the tamarins, with greater amounts of looking predicted when expectancies were not fulfilled; this was found for head and eye orientation combined but not to eye gaze alone (Santos & Hauser, 2000).

However, these results are weakened by the small amount of data collected; the effect was a less than 1-second increase in looking for sixteen subjects during one trial within a total of five 12-second trials; perhaps the reliability of these results should be examined with further testing. In addition, Emery (2000) identifies another possible problem with this technique; duration of looking may not be the most appropriate measure of interest. Emery et al (1997), in their study of gaze following in rhesus monkeys, found that frequency rather than duration was the significant measure and it is suggested that vigilance may result in a number of brief inspections rather than a prolonged bout of interest in an object. Emery (2000) also suggests that the tamarins may have been responding according to a specific rule rather than attributing mental states (more specifically, an intention to reach for the attended object) to the experimenter (Santos & Hauser, 2000). The tamarins received three familiarisation trials and may have simply associated head orientation (they did not respond to eye gaze alone) with a subsequent response to the congruent side/object. It is also possible that simple co-orientation led to the experimenter and monkeys being oriented towards the same object and the subsequent action with the alternative object led to increased visual exploration. Such a behavioural mechanism does not require an understanding of looking behaviour as a predictor of subsequent actions.

Studies of hiding in nonhuman primates have addressed the issue of perspective-taking, on the premise that hiding requires an appreciation of what another can see. Field

observations have suggested that hiding is one of the more common forms of 'tactical deception' displayed by nonhuman primates; for example, concealing mating behaviours to avoid conflict arising from dominance imposed restrictions on access to mates (Byrne & Whiten, 1988; Whiten & Byrne, 1997).

In a study of hiding behaviour in Java monkeys, a human observer threatened any animal that tried to gain access to a desired drinking source. Subsequent testing involved the introduction of partitions that could conceal the monkeys when they were drinking, but the monkeys did not demonstrate any preference for concealed locations (Kummer, Anzenberger & Hemelrijk, 1996). Gyax (1995; 2000) also studied hiding in captive group-living Java monkeys; mating and aggressive situations were analysed in order to determine whether individuals concealed themselves from group members. Within the context of mating, low- and middle-ranking males and their partners were more likely to mate near occluders than in visibly open areas. However, Gyax (1995) suggests that trial and error learning may be the underlying mechanism as there was little evidence that the monkeys were appreciating another individual's perspective; there was no preference for well concealed (solid partitions) over more poorly camouflaged locations (panels offering only partial concealment). In contrast, behaviour following aggressive encounters did not indicate any hiding tendency for either individuals or rank-sex classes (Gyax, 2000). Thus, evidence for hiding abilities in monkeys is limited, and may be limited to specific social situations such as mating. Furthermore, positive results are not necessarily indicative of perspective-taking as simpler mechanisms may be sufficient to explain the behaviours observed. For example, avoiding another's direct gaze or simply moving so that the (perhaps threatening) other is no longer visible may lead to hiding behaviours without invoking any perspective-taking abilities.

Cheney and Seyfarth (1991) found that rhesus and Japanese macaques interacting with an infant were sensitive to whether or not the mother of the infant was visually

monitoring the encounter. Behaviours were observed across three experimental conditions which differed according to the mother's ability to perceive the interaction; the monkeys were separated by either a glass partition, an opaque barrier or a one-way mirror which allowed the monkey and infant to see the mother but not vice versa (a relationship which the monkeys had the opportunity to learn with prior exposure to the mirror). Measures of approaches, retreats and agonism revealed that interactions between monkeys and infants were not simply affected by the mother's presence (one-way mirror) but rather by whether the mother was able to perceive the interaction (glass condition). The authors propose that the monkeys were sensitive to the mother's visual orientation, whether in terms of general bodily, head or eye orientation, and altered their behaviour accordingly (Cheney & Seyfarth, 1991). However, it is unclear what behavioural indices the monkeys were using; contingency between the interacting monkey's behaviour and the mother's responses would have been absent in the one-way mirror condition. This lack of contingency may have been the determining factor rather than a response to the mother's orientation, or an appreciation of what the mother could actually perceive (which was dependent upon understanding the nature of the one-way mirror).

A recent study examined whether chimpanzees are able to appreciate a conspecific's line of regard within a competitive situation (Hare, Call, Agnetta & Tomasello, 2000). Two chimpanzees were put into competition over two desirable food items placed within a communal area; the food items were placed in various locations so that only the subordinate chimpanzee could see both items, and the behaviours of both chimpanzees when given access to the area were recorded. The behaviour of subordinates suggests that they were aware of their competitor's visual perspective; subordinates consistently chose the food item which they could see but their rival could not rather than a food item which both chimpanzees could readily see. In contrast, dominants would first secure the openly visible item before taking one to which they alone had visible access.

This finding was robust across a number of manipulations, for example, when tyres or barriers were used to conceal food items. These behaviours were not observed when a transparent barrier was introduced, that is, choices were not simply made on the basis of accessibility or proximity of food items to objects.

Moreover, by manipulating pairings chimpanzees could be tested as both the dominant and subordinate individual, and their behaviours were dependent upon their status relevant to their competitor. Chimpanzees' modified their choices according to whether or not they were dominant, rendering simple rule learning regarding occluders an improbable explanation for the behaviours observed (Hare et al, 2000). The ability to readily use a conspecific's orientation to choose between two available food items contrasts with the results of the object-choice study reported above (Itakura et al, 1999). This suggests that it is not the foraging situation per se which impedes sensitivity to another's attentional status gaze, but that the context may be more important (Hare, 2001). Chimpanzees appear to readily use information regarding another's looking behaviour as a means to solve a competitive food problem, but may not do so within the 'co-operative' context of the standard object-choice task. Thus, a paradigm shift from co-operative to competitive experimental contexts may lead to a productive new direction for research into nonhuman primates' socio-cognitive abilities (Hare 2001, see Chapter Five for further discussion).

A recent study by Fagot and Duruelle (submitted) used a cueing paradigm, that has identified a gaze-induced reflexive orienting response in human adults, to examine baboons' responses to gaze (e.g. Langton & Bruce, 1998; see Chapter 6 for further details). Schematic and photographic faces were presented in the centre of a monitor before pupils were added to the eye outline in order to depict a direction of eye gaze (left or right). After a brief interval (300ms), a target would appear either on the side congruent with the depicted eye gaze or on the opposite side of the monitor. In humans, responses to

congruent targets (whether detection, localisation or identification of targets) are significantly faster than responses to targets which appear in a location incongruent with the gaze cue. However, the baboons' response times did not differentiate between cued and uncued targets (Fagot & Duruelle, submitted). In contrast, after extensive exposure to a condition in which gaze consistently predicted target location, the re-introduction of incongruent trials revealed that the baboons were faster to respond to congruent targets. That is, the baboons had learned to use the depicted eye direction to locate targets. These results do not therefore support the view that nonhuman primates reflexively orient to gaze as humans do, but rather that the baboons learned as association between the gaze cue and subsequent target location. Note that this association does not require that the baboons perceived the central images as faces at all (Zayan & Vauclair, 1998). Although the authors of this study concluded that baboons did not demonstrate any inherent sensitivity to another's direction of eye gaze, several methodological issues need to be considered before drawing strong conclusions (see Chapter 6 for further discussion).

At the neurophysiological level, while there is considerable evidence that gaze receives extensive processing, it is not clear whether this sensitivity extends beyond detecting self-directed gaze. While cells which are sensitive to another's actions in the environment (such as walking towards or reaching for an object) have been located in the amygdala (Perrett et al, 1990), analogous cells coding another's visual orientation towards an object have not yet been identified (but see Jellema, Baker, Wicker & Perrett, 2000). Emery (2000) investigated the responses of single cells (in the area of the brain containing gaze sensitive cells) when presented with head orientation in combination with a target object. The cells were tested with the profile view of the head alone, the object alone and the head and object together either in congruent or incongruent positions (head turned towards the target object or head turned in the opposite direction). None of the four cells examined demonstrated any sensitivity to the relationship between head orientation and a

target object. This suggests either that the number of cells sampled was insufficient or possibly that a different area of the brain, perhaps the amygdala, is implicated in the processing of this level of gaze (Emery, 2000).

Table 5: Alternative paradigms

Task	Species	Method	Results	Author
Behavioural observation	Java monkeys Rhesus macaques	Various partitions introduced	Some evidence that the monkeys were sensitive to whether or not they could be seen by group members.	Cheney & Seyfarth, 1991
Go no-go task with central gaze cues before targets.	Guinea baboons	Computerised cueing task	Did not demonstrate reflexive orienting, but did show evidence of learning.	Fagot & Duruelle, submitted.
Hiding during mating	Java monkeys	Controlled observations	Low and middle ranking couples preferred concealed locations.	Gygax, 1995
Hiding during aggression	Java monkeys	Controlled observations	No preference for concealed locations.	Gygax, 2000
Competitive food acquisition	Chimpanzees	Conspecific competitor	Evidence that chimpanzees know what competitors can see.	Hare et al, 2000
Hiding to gain access to desired drink source	Java monkeys	Human interactant	No evidence of any hiding behaviours.	Kummer et al, 1996
Expectancy violation, looking preferences	Cotton-top tamarins	Human interactant	Responses discriminated between objects based on looking behaviours.	Santos & Hauser, 1999

Gaze processing at a more sophisticated level than detecting direct gaze may require connectivity between gaze direction processing in the superior temporal sulcus and an area which processes spatial information, such as the intraparietal sulcus (Emery, 2000): there is some evidence for reciprocal connections between neurons in these areas (Harries & Perrett, 1991). Moreover, Emery (2000, p 595) suggests that ‘motion in relation to an object may provide a more salient cue for neural response, compared to the ambiguous

relationship between two static objects (head and object).’ Thus, neurophysiological processing of non-self directed gaze has yet to be adequately identified and explored.

3.4d) Seeing and knowing

Do apes know what they have seen? Initially, this may seem a somewhat strange question – but before advancing to whether nonhuman primates appreciate seeing as a mental state in other individuals, it is important to consider how their own perception influences subsequent behaviours. To date only one study has addressed this issue. Call and Carpenter (2001) examined the visual search patterns of orangutans, chimpanzees and human children (aged 2 ½ years) looking for a hidden item; two or three tubes were presented but only one of these contained the desired item (food for orangutans and chimpanzees, stickers for the children). The study measured responses in two ways: choice of tube (they could only indicate one) and looking behaviours, that is, did they visually inspect the tubes before making their choice? In some trials, the subjects witnessed the baiting procedure while in others baiting was concealed behind a screen. The results indicate that when they had witnessed baiting, apes and children were more likely to locate the reward and less likely to visually inspect the tubes. Thus, when they had inadequate information (concealed baiting condition), they gained information by visual exploration.

A study within the competitive paradigm (Hare et al, 2000) demonstrated that chimpanzees are also able to keep track of what competitors have previously seen; the chimpanzees responded differentially according to whether or not a dominant competitor had witnessed a food item being hidden or moved to a new location (Hare, Call & Tomasello, 2001). The subordinate chimpanzees obtained significantly more food items when their competitors were uninformed or misinformed about the location of food items, but when dominants were informed of the food’s location subordinates were less likely to approach the food items. Furthermore, chimpanzees demonstrated an ability to recognise

what different individuals had seen by responding appropriately when knowledgeable competitors were replaced by naïve dominant competitors (who had not witnessed the food items being concealed).

Other studies investigating the relationship between seeing and knowing (Premack, 1988; Povinelli, Rulf & Biershwale, 1994; Povinelli, Parks & Novak, 1991; Call, Agnetta & Tomasello, 2000) have shown that chimpanzees and rhesus monkeys seem to be unable to discriminate those who have seen the baiting process (Knower) from those who have not (Guesser). Although an earlier study had reported that chimpanzees recognised the relationship between seeing and knowing (Povinelli, Nelson & Boysen, 1990), a critical review by Heyes (1994) led to a re-evaluation of the findings. The chimpanzees showed a preference for the Knower when the Guesser was not in the room during baiting, but did not demonstrate an immediate transfer to a condition in which both trainers remained in the room, but the Guesser wore a paper bag over their head (so that they could not see the baiting procedure). Although the chimpanzees quickly learned to use this new information to successfully perform the task, they did not discriminate between the trainers immediately.

It may be that the presence of two trainers simply makes the task overly complex (Povinelli & Eddy, 1996a). Alternatively, it may be that nonhuman primates do not understand seeing as an epistemic state, but rather use simpler rules. For example, after many trials chimpanzees could distinguish the Knower from Guesser in terms of recognising which individual was present when baiting occurred (Povinelli, Nelson & Boysen, 1990), but this does not require any appreciation of seeing per se. A similar interpretation of the competitive study (Hare, Call & Tomasello, 2001) would be that the chimpanzees were sensitive to the presence, or proximity, of individuals during baiting and not to what they could perceive (and thus know). In a further competitive experiment in which two food items were presented, the chimpanzees did not seem able to discriminate

between those items which the dominants had seen hidden and those which they had not (Hare, Call & Tomasello, 2001). This suggests that any appreciation of the seeing-knowing relationship was somewhat limited. It could be that the availability of two food items reduced the level of competition and changed the nature of the task or that this addition simply placed too many cognitive demands on the chimpanzees (Hare, Call & Tomasello, 2001).

Other attempts to test whether nonhuman primates appreciate seeing as an epistemic state have also failed to provide positive evidence (see Table 6). Gómez (1998) offers a brief report of a ‘false-belief’ task that examined whether an orangutan was sensitive to the relationship between seeing and knowing. The orangutan witnessed a ‘Provider’ bait a container with food before fetching a key to lock it, and then replacing the key. The orangutan would then indicate the baited container when a trainer (‘Giver’) entered; the trainer would then fetch the keys, open the box and reward the orangutan with its contents. For probe trials, the Provider would place the keys in a new location following the baiting procedure; the orangutan was therefore required to indicate the new location of the keys to the ignorant (did not see the relocation) trainer. That is, she had to recognise that the Giver’s knowledge about the key’s location were false. The orangutan failed to indicate the new location of the keys to the Giver on the six trials presented. However, Gómez (1998) reports that having a third individual (stranger) relocate the keys may have enhanced performance, although learning over trials may also be a factor. Heyes (1998) argues that the flaw of this study is that it does not promote using ‘seeing’ as a cue; for example, in the standard trials, the Giver knows where the keys are located even though they did not see them being placed there. This methodological issue could be circumvented by combining the role of Provider and Giver and having a second individual to move the keys.

A similar study was conducted with orangutans (Call & Tomasello, 1994); a trainer would use a rake to reach a baited container, but on the crucial trials the rake would not be returned to its original location but instead would be 'hidden' behind a curtain. A naïve trainer would then enter and be unable to reach the baited container without the rake: would the orangutans recognise their ignorance and provide information regarding the rake's whereabouts? The authors report that both orangutans quickly learned to indicate the rake's location. However, the results may indicate that the orangutans understood the relationship between trainer, rake and food; their responses do not necessarily indicate that they appreciated seeing as an epistemic state (Tomasello & Call, 1997). For example, would they have also pointed to the hidden rake if the experimenter who hid the tool returned and did not immediately start the task, that is, were they responding on the basis of knowledge states or simply indicating the rake's location as a means of cueing food delivery?

Another attempt with a non-verbal false belief task also produced negative results. Call and Tomasello (1999) presented children (aged 4-5-years old), two orangutans and five chimpanzees with a trainer who would indicate where they had seen a food item placed by identifying the baited container with a marker. The task required subjects to recognise that when the containers were moved during the trainer's absence, the placing of the marker would not be informative. Using extensive pre-testing, the authors were able to ensure that subjects were able to perform the basic task requirements. Thus, they demonstrated an ability to use the marker to locate the food item, follow the movement of the food item in both visible and invisible displacements, and to ignore the marker when they knew its location to be incorrect. However, only the children performed successfully on false-belief trials, that is, the apes did not ignore the marker when the trainer had not witnessed a displacement and therefore held a false belief regarding the reward's location. In fact, the apes' performance can be explained by the following: if they saw the location of a food

item then they would choose that location, if the food cue was unavailable they would use the marker. It may be that the pre-trial training actually reinforced these simple rules and therefore seeing was not identified as a relevant factor. Alternatively, although the apes were able to perform the pre-test tasks, perhaps the combination of tasks on the critical trials was too cognitively complex (Call & Tomasello, 1999).

Table 6: Studies of seeing and knowing

Task	Species	Method	Results	Author
Recognition of seeing-knowing relationship	Orangutans	Human interactants	Not convincing evidence of appreciation of ignorance.	Call & Tomasello, 1994
Recognition of seeing-knowing relationship	Humans, orangutans and chimpanzees	Non-verbal false belief	Only children showed appreciation of seeing as epistemic state.	Call & Tomasello, 1999
Recognition of seeing-knowing relationship	Rhesus and Japanese macaques	Presence of food or predator	No evidence of an appreciation of seeing as epistemic state.	Cheney & Seyfarth, 1990
Recognition of seeing-knowing relationship	Orangutan	Human interactants	No evidence of appreciation of ignorance.	Goméz, 1998
Competitive food acquisition	Chimpanzees	Conspecific competitor	Evidence that chimpanzees know what competitors have and have not seen.	Hare et al, 2001
Recognition of seeing-knowing relationship	Chimpanzees	Human interactants	Chimpanzees prefer knower over guesser.	Povinelli et al, 1990
Recognition of seeing-knowing relationship	Rhesus macaques	Human interactants	No preference for knower over guesser.	Povinelli et al, 1991
Recognition of seeing-knowing relationship	Chimpanzees	Human interactants	Failure to replicate preference for knower.	Povinelli et al, 1994

Cheney and Seyfarth (1990b) examined whether rhesus and Japanese macaque mothers would inform their offspring of the presence of either food items or a potential threat. While mothers witnessed the hiding of food or a hiding trainer with a net in an adjoining cage, they did not try to communicate this information to their offspring who

had not witnessed these events. That is, they failed to demonstrate that they had any appreciation of the relationship between seeing and knowing as it applied to their offspring. Thus, to date there is no convincing evidence that nonhuman primates understand gaze as an epistemic state. As all the studies in this section highlight, designing an appropriate task to examine whether nonhumans appreciate that seeing leads to knowing is indeed challenging (Heyes, 1998).

Summary

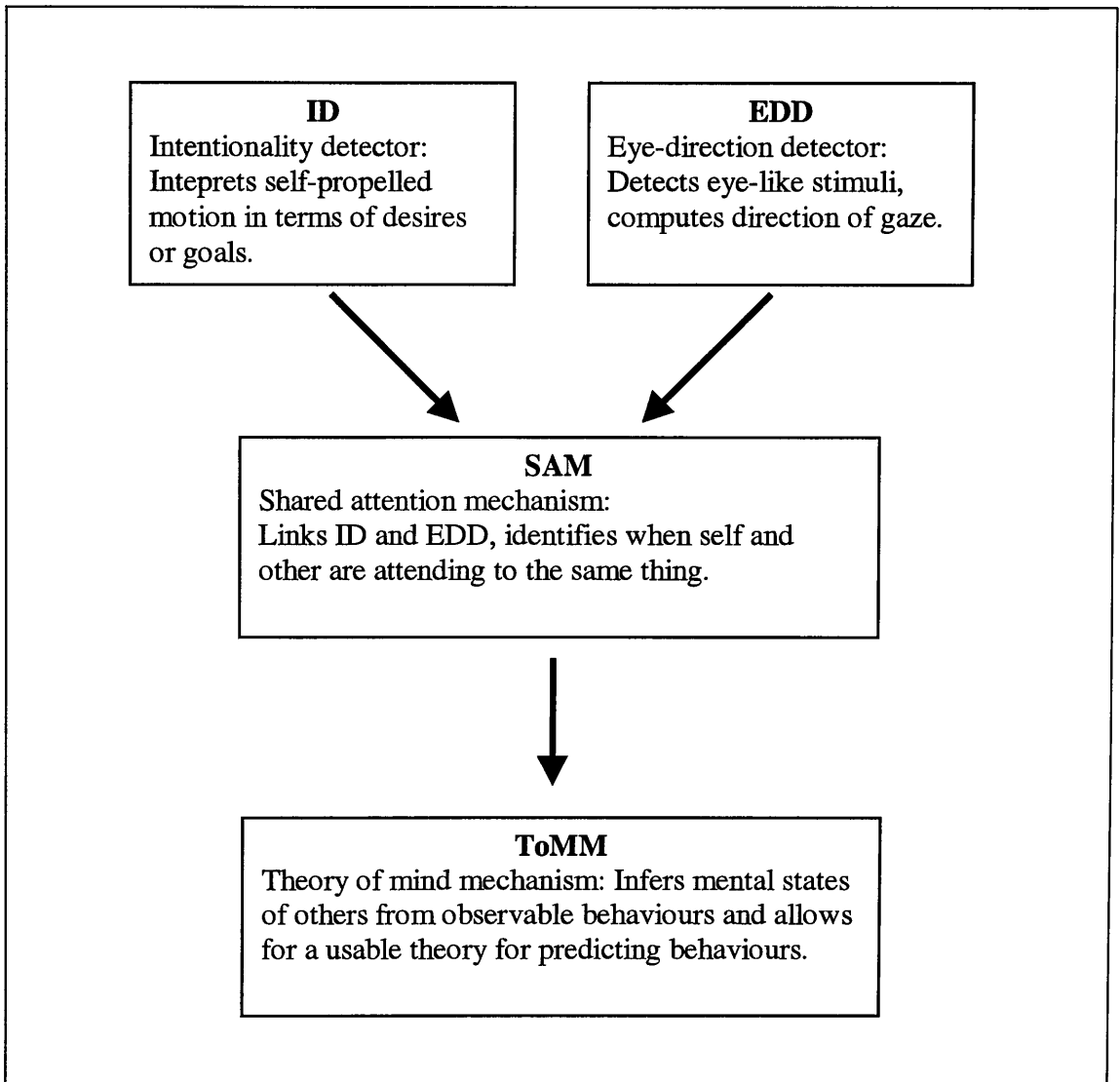
To summarise: type of occluder, vocalisations, experience with humans, relationship with interactant (familiarity, context) and context (competitive or co-operative) may all influence the visual co-orientation and gaze-reading abilities of nonhuman primates. However, while nonhuman primates readily follow gaze, responses in object-choice tasks are far more variable. Moreover, explicit training in object-choice gaze exploitation may be required; nonhuman primates are usually given prior experience with manual gestures such as pointing before they master gaze orientation as a cue (Anderson et al 1995; 1996; Itakura & Anderson, 1996; Itakura & Tanaka, 1998). What is apparent is that visual co-orientation is not the mechanism underlying behaviour during the object-choice task; while gaze following is a spontaneous response, responding to gaze as an informative cue is not so readily demonstrable in nonhuman primates. Alternative paradigms have also been outlined, the competitive task in particular seems to be an interesting approach to investigating nonhuman primates' abilities to read other individuals' attention. To date, attempts to determine whether nonhuman primates appreciate the relationship between seeing and knowing have produced negative results.

4) Gaze, Attention and Theory of Mind

‘Evidence that visual attention is monitored and manipulated in self and others during primates’ social manoeuvring is of particular interest given the role currently ascribed to a capacity for shared attention in the ontogeny of the human mindreading system (Whiten, 1997, p 167).

Sensitivity to gaze has been identified as playing an integral role in the development of mental state attribution in humans. Baron-Cohen (1994) has proposed a model for mind-reading abilities which is based upon the interactions between separate modules, with sensitivity to the eyes and looking behaviours being the basis for the development of mental state attributions (see Figure 1). The Eye Direction Detection (EDD) module initially functions to detect the presence of eye-like stimuli and later to detect the direction of another’s gaze (eye direction) while the Shared Attention Mechanism (SAM), which represents whether the self and another individual are attending to the same object or event, emerges later (between the ages of 9-14 months). The Intentionality Detector (ID) processes another’s goal-directed behaviours, for example, movement towards an object. Of particular interest is Baron-Cohen’s proposition that sources of information other than eye gaze which may also indicate another’s direction of attention (such as head orientation and postural cues) would be processed by ID and not EDD. That is, eyes are seen as a unique stimulus and ID and EDD are only integrated at the SAM level. Thus, Baron-Cohen’s model is based upon the precedence of eye gaze as ‘eye direction is a more reliable indicator of attentional state than head-angle’ (1994, p 740).

Figure 1: An adaptation of Baron-Cohen's mindreading model (1994)



Baron-Cohen (1994) cites evidence for the detection of eye-like stimuli function; the eyes are extremely salient stimuli across wide genera of species and from early infancy in humans. However, it is not clear that the second function of EDD, namely, detecting the direction of gaze, is necessarily part of the same module. It has been proposed that the EDD module may be inappropriate; while detecting eye-like stimuli may be one function of such a module, detecting the direction of another's gaze could be based upon a range of

cues including not only eyes but also head and body orientation. Thus, it has been proposed that such a mechanism would be better described as a 'Direction of Attention Detector' (DAD, Perrett & Emery, 1994). For DAD, when various indicators of attention direction are available their salience is hierarchical, with the eyes being more important than head direction, which in turn takes precedence over bodily orientation (Emery, 2000; Perrett & Emery, 1994; Perrett et al, 1992).

Research with humans has demonstrated that sensitivity to gaze direction is influenced by information regarding head orientation (Gibson & Pick, 1963; Maruyama & Endo, 1983; Vecera & Johnson, 1995). However, recent research has shown that these two features may be processed in parallel rather than in a hierarchical manner. Using an interference task, Langton (2000) found that both head and eye direction interfered with a task requiring directional responses to be made; this indicates that eye and head direction may be mutually influential when determining another's direction of attention. Thus, while the available evidence seems to support Perrett and Emery's (1994) DAD mechanism (rather than Baron-Cohen's EDD), it does not support their hierarchical model. Whatever the precise mechanisms, sensitivity to eyes and others' looking behaviour is proposed as 'foundational for the entire construct of theory of mind' (Povinelli & Giambrone, 2000, p 19; Baron-Cohen, 1994; Premack & Dasser, 1991; Tomasello, 1995).

Are nonhuman primates able to understand what another individual sees? The capacity to comprehend another's perception is one of three levels of mental state attribution identified by Premack and Dasser (1991), the remaining levels being the attribution of intentions (attributing desires or motivations to the other) and attribution of knowledge states (including beliefs). It is important to stress that responding to another's gaze, for example, as in the gaze following studies discussed in the previous sections, in itself reveals very little about the ability to comprehend what another individual can 'see'. Looking (or gaze or visual orientation) is an observable behavioural cue, that is, the eyes

(and/or head) directed towards something. In contrast, 'seeing' is an internal mental state that connects the perceiver to what is being looked at (Csibra, 1998). "Seeing' can be said to be an 'overt' mental state, because it is usually accompanied by observable behaviours (the eyes and other body parts oriented to an object), and in this sense you can see another organism 'seeing'" (Gómez, 1996a, p 333). However, although the behavioural states of looking and seeing are confounded, an appreciation of another's looking behaviours (i.e. using head and eye direction as sources of information) may not indicate an appreciation that the other individual is 'seeing' what is in their line of regard (i.e. that their looking behaviours also indicate an internal state of perception).

If co-orientation occurs in response to general postural cues, either related to or independent of eye direction, the precise visual focus of the other may be irrelevant to the observer. For example, an association could be learned between another individual's head position and the detection of an interesting or salient object or event in the environment upon orienting in the same direction. In other words, head or eye direction is simply a discriminative cue to look in a given direction (Povinelli & Eddy, 1996b; Tomasello, Call & Hare, 1998). A distinction has been made between this kind of simple mechanism for following another's gaze to a location in space and the ability to follow another's gaze to fixate the target of their gaze (Baron-Cohen, 1994; Moore, 1999; Corkum & Moore, 1995). That is, simply co-orienting in the same direction may lead an individual to fortuitously perceive an object, but this is not the same phenomenon as following the direction of gaze in order to mutually fixate an object (Emery, 2000; Povinelli & Eddy, 1996c). However, even sophisticated gaze following (for example, ignoring distractors and taking account of barriers) may not necessarily indicate that nonhuman primates appreciate what the other individual can 'see'. It may be that they are sensitive to the observable gaze cues available and have learned through experience to use this information accurately to identify the focus of another's gaze and how this may be influenced by context. That is, although

geometric gaze following may lead to both individuals looking at the same object, this does not mean that they appreciate that they are both 'seeing' a common object. As Csibra (1998, p 118) suggests, in order to use gaze effectively all that is required is 'an understanding of a particular physical relation between the other person's eyes and certain parts of the environment (similarly to the understanding of the physical relation between a camera and the objects it can 'see') and an associative link between the presence or absence of this relation and the behavioural dispositions of the person.'

In addition to the distinctions between looking and seeing, it is also important to consider what other functions gaze might serve. For example, it is also argued that seeing and attending are not the same phenomenon, and that likewise attention is not the same as seeing as an epistemic state. However, within developmental psychology, there is limited consensus concerning definitions and what various behaviours represent in terms of the underlying psychological abilities (see Dunham & Moore, 1995). Terms such as 'gaze following', 'joint visual attention' and 'shared attention' are often used interchangeably in the literature and in practice it is difficult to determine what different authors mean when using these concepts. For example, 'joint attention' has been defined in very conflicting terms; at one extreme, 'at its most sophisticated level, joint attention is in effect a 'meeting of minds'' (Bruner, 1995, p 6), while at the other, 'deictic gaze, or joint visual attention as it is often called, may be defined simply as 'looking where someone else is looking' (Butterworth, 1995, p 29).

Baron-Cohen (1994) considers the ability to follow gaze in human infants to be indicative of an awareness that the other individual is seeing or attending to something. Others suggest that gaze following does not implicate an appreciation of others as attentional beings. Tomasello (1995, p 104) suggests that understanding 'attention' requires that other individuals are seen as intentional agents: 'attention should be considered as intentional perception.' That is, attention is not the same phenomenon as simply 'looking

at' or even 'seeing'. For 'seeing', the primary representations of another individual and whether that individual is or is not perceiving (that is, whether or not the eyes are open or obstructed) in combination with simple geometric rules are sufficient. However, for any comprehension of another's attention (in Tomasello's terms) it is necessary for some notion of the 'aboutness' of perceiving (Baron-Cohen, 1995; Baron-Cohen & Cross, 1992; Premack & Dasser, 1991).

Tomasello and Call (1997, p 318) propose that simple visual co-orientation may be seen as demonstrating that nonhuman primates see others as 'animate beings who are directed to particular entities in the world – based on readily observable actions.' Thus, the ability to follow gaze (even eye gaze) allows nonhuman primates to predict (at a basic level) another's subsequent behaviour and also to detect important events or objects in their environment. However, they draw a distinction between being able to use another's gaze as an information source and appreciating that other's gaze may indicate attention or even seeing. Such a distinction might help to explain divergent abilities in the simple co-orientation task and object-based paradigms; the former is based on gaze following while the latter may require some level of appreciation that an object is being attended to (Call, Agnetta & Tomasello, 2000).

These distinctions may become less clear when sophisticated gaze following is considered, for example. Does fixating a target object despite the presence of distractors simply indicate a high-level geometric appreciation of gaze or does it also suggest some understanding of gaze as a perceptual or attentional state (Tomasello & Call, 1997)? Furthermore, as seeing and attention may only be deduced from external behaviours, then distinguishing seeing or attention from looking (or providing suitable cues in order to study understanding) is extremely difficult. That is, it may not be possible to differentiate sophisticated appreciation of gaze as a spatial signal, and its relation to subsequent

behaviours, from even a basic appreciation that the other is having any mental experience of perceiving (e.g. Butterworth & Jarret, 1991).

A recent review of this topic has suggested that nonhuman primates may indeed only understand gaze as a behavioural state, without being capable of appreciating seeing as an epistemic state (Povinelli & Giambrone, 2000). This is not to say that nonhuman primates do not have a complex knowledge of other's looking behaviours but rather that it is based upon appreciation of behaviours and not internal mental states. While it has been suggested (e.g. Byrne & Whiten, 1988) that social complexity has resulted in the selection for a capacity to appreciate the minds of others (or theory of mind), Povinelli & Giambrone (2000) suggest that an extensive capacity for reasoning about behaviour is a viable alternative. Thus, behaviours which are overtly similar in human and nonhuman primates need not invoke the same covert mechanisms: 'identical behaviours may be generated and/or attended by different psychological representations' (Povinelli & Giambrone, 2000 p 50).

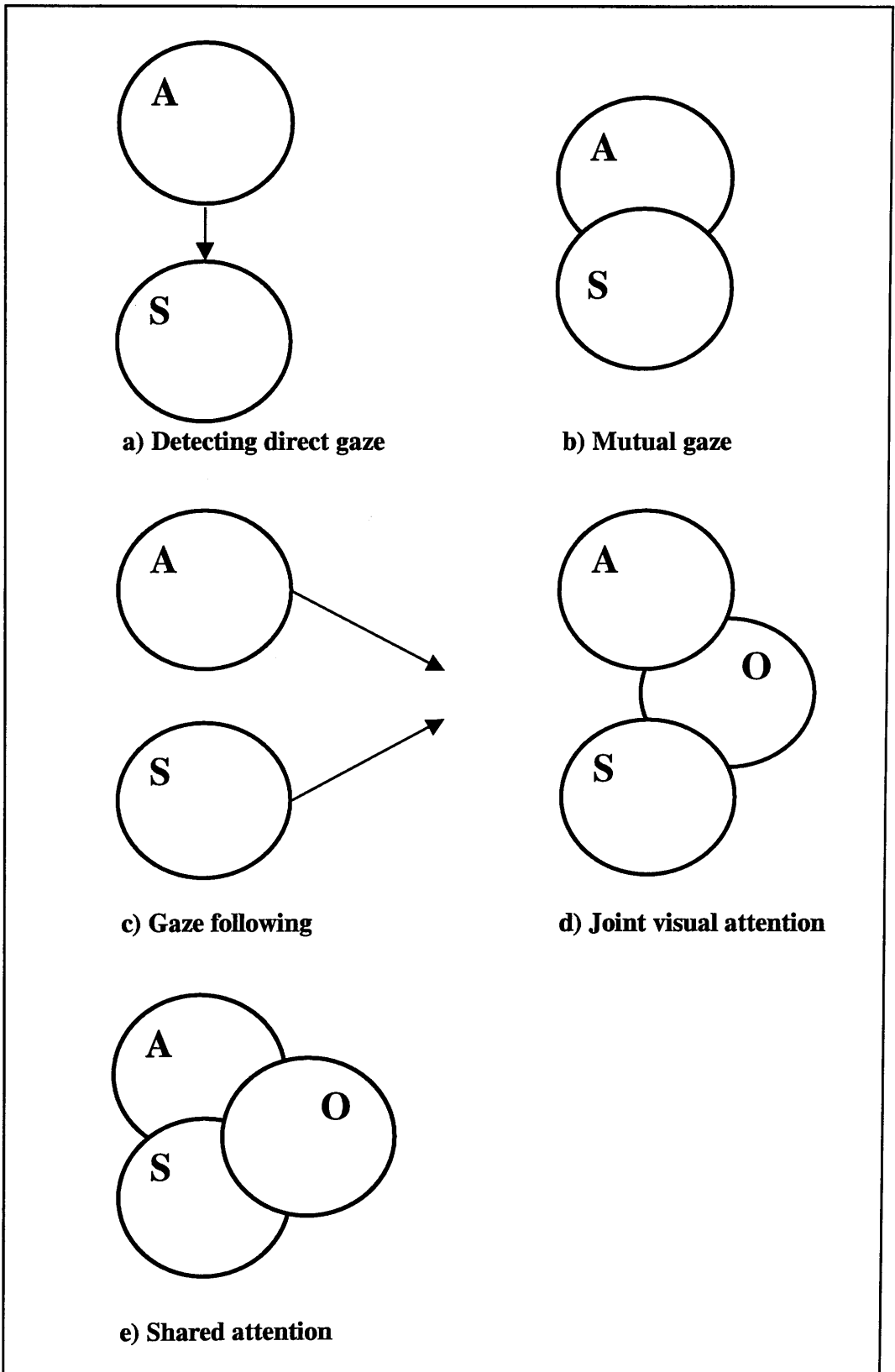
Although the distinctions between seeing as an observable behaviour state, an internal state of perception, or as attending are interesting, a fuller discussion of these issues is beyond the scope of this thesis (see Dunham & Moore, 1995). However, it is important to define some other common terms used in the literature. The following offers an interpretation of what the various labels represent (see Figure 2). 'Gaze following' is used to denote the act of visually co-orienting with another individual, while 'joint visual attention' is considered as involving both individuals focusing their attention on a common object (Tomasello, 1995). Further, 'shared attention' has been differentiated from joint visual attention; the former requiring that the individuals know that they are both attending to the same object and is therefore a combination of joint and mutual attention and considered a triadic interaction (Baron-Cohen, 1994). This shared attention is probably closest to what Tomasello (1995) considers to be joint attention and is seen as providing

the appropriate context for the development of human infants' communicative and other socio-cognitive abilities (Dunham & Moore, 1995; Flavell, 1999; Tomasello, 1995).

Figure 2 illustrates how these various definitions relate to each other in terms of the role of Self (S), Agent (A) and Object (O). This figure is based upon Werner and Kaplan's (1963) representation of triadic interactions between the infant, mother and object of attention. The figure illustrates common uses of the terms given and therefore may not fit with all definitions of a behaviour used in the vast literature on this topic. Although the gaze following component of the figure does not have a common object, this does not mean that gaze following cannot be a highly accurate means of identifying the target of another's gaze, but rather than this behaviour does not invoke an appreciation of anything more than the direction of another's gaze. That is, this response does not imply appreciation of attention or other internal mental states. Although joint attention is often used to denote visual co-orientation to a common object (e.g. Emery, 2000), the notion of 'attention' does not accurately describe the phenomenon under consideration (e.g. Tomasello, 1995). Thus, geometric gaze following is a better definition of visual co-orientation that accurately detects the target of another's gaze.

Figure 2: Illustration to clarify the nature of various gaze-related behaviours.

A = agent, S = self, O = object



As all of the phenomena outlined in this section are all represented by the same observable behaviour of gaze, the studies reported in the following chapters will focus upon the abilities of monkeys to respond to the gaze cues of another individual; that is, to use the looking behaviours of others as sources of information. What mechanisms do monkeys have that enable them to use gaze to anticipate and explain behaviours (Gordon, 1998)? Whenever other cognitive levels of gaze are considered, terms will be used consistently with the definitions outlined above. Thus, although 'the mental connection engendered by visual perception' (Povinelli & Eddy, 1996a) is of theoretical importance, there is still a lack of data concerning the use of gaze cues in nonhuman primates, especially for non-apes (or rather non-chimpanzees). The following studies explore the sensitivity of monkeys to the looking behaviours of others; more specifically, what sources of information monkeys respond to and in what circumstances. By using a variety of approaches to examine these issues, it is hoped that a clearer picture of monkeys' understanding of gaze will emerge and that the strengths and weaknesses of the experimental procedures used will be identified.

Chapter summary

This chapter has reviewed literature concerning nonhuman primates' ability to process faces and especially gaze information. Spontaneous and arbitrary behavioural responses, in addition to neurophysiological responses, indicate that nonhuman primates are able to discriminate faces on a number of levels; they are able to recognise conspecifics, individuals and facial expressions. Nonhuman primates are also extremely sensitive to gaze, especially direct gaze, as indicated by behavioural and neuronal responses. While monkeys and apes, but not prosimians, readily respond to non-self directed gaze by visually co-orienting, they do not consistently use these same behavioural cues to solve object-choice tasks. Alternative paradigms have also generally failed to convincingly demonstrate effective use

of gaze as an information source, although competitive paradigms may be more conducive to gaze cue use. Although nonhuman primates are sensitive to the behaviour of others, there is no convincing evidence of any awareness of seeing as a mental state and there are serious methodological problems with attempts to examine this issue (see Heyes, 1998). However, as nonhuman primates are so adept at monitoring the behaviours of others, whether mental attribution is involved or not (Cheney & Seyfarth, 1991), further investigation of the cues used in such monitoring is of interest. Research to date has primarily focused upon chimpanzees' responses to gaze and there are few comparable data for non-ape species. This thesis explores monkeys' responses to other individuals' gaze using a variety of paradigms.

Chapter Two

Spontaneous Responses to Gaze

This chapter will consider spontaneous behavioural responses to another's visual orientation. The first study is an exploration of gaze following responses in olive baboons (*Papio anubis*), focusing on the cues which evoke visual co-orientation. Baboon responses to a human interactant's changes of visual orientation were studied, more specifically the role of the head and eyes in invoking visual co-orientation were explored. The second study examines whether monkeys are sensitive to qualitative aspects of another's looking behaviours, that is, does the amount of visual interest in objects influence their own responses to the same objects? Novel objects that had received varying forms of visual and manual exploration from a human interactant were presented to capuchin monkeys (*Cebus apella*) and olive baboons and their responses were observed.

Study 1: Visual co-orientation in baboons

As reviewed in the previous chapter (see Chapter One, section 3.4a), nonhuman primates are able to follow the gaze of another individual. It is proposed that such an ability confers an advantage upon group-living primates as they gain access to information about their physical and social environment by monitoring the looking behaviours of others (Kummer, 1967; Tomasello, Call & Hare, 1998). The ability to visually co-orient with another individual's line of regard has not been extensively studied in any species other than chimpanzees. There is evidence that nonhuman primates respond to another's change in head direction (Anderson & Mitchell, 1999; Tomasello, Call & Hare, 1998; Tomasello,

Hare & Agnetta, 1999; Tomasello, Hare & Fogelman, 2001). Chimpanzees have been shown to respond to a shift in a human interactant's eye direction by visually co-orienting (Povinelli & Eddy, 1996b), and more recent evidence suggests that macaques are also able to respond to eye gaze alone (Ferrari et al, 2000; Lorincz, Baker & Perrett, 1999). It is interesting to study the salience of these information sources for nonhuman primates, as there is still some debate about their relative importance (Langton, 2000; Perrett & Emery, 1994). As Corkum and Moore (1995, p 63) state, 'functionally, head and eye orientation are often equally good predictors of direction of attention because they are frequently congruent (i.e., we usually turn head and eyes together). However, there are cases when the two cues are in conflict (e.g., the more subtle movement of turning our eyes but not our head) and in these cases, eye orientation alone provides the most accurate information regarding attention.' Studies with human infants suggest that head orientation is initially the more readily used cue, with sensitivity to eye gaze only emerging later in development (from around 18 months; e.g. Moore, 1999, but see Hood, Willen & Driver, 1998, for evidence of sensitivity to eye direction in younger infants).

This study addresses whether olive baboons demonstrate co-orientation in response to a human interactant's change in direction of visual orientation, and if so, do they respond to shifts in eye direction only? The study is an extension of Anderson and Mitchell's (1999) paradigm with the trainer engaging the monkeys in an ongoing interaction and presenting trials within this context. However, in the present study, the baboons were presented with a variety of orientation cues in order to ascertain the salience of head and eye direction information.

Baboons are an extremely interesting species to study in terms of responses to visual orientation cues, not least because there is currently a complete lack of data concerning their abilities. Although this applies to nearly all species except chimpanzees, baboons have been reported to exploit the visual orientation of others in 'tactical

deception' (Byrne & Whiten, 1988). In addition, they have fairly elongated eyes and are a terrestrial species (Kobayashi & Koshima, 2001). This indicates that horizontal movement of the eyes is important in their visual scanning, and also that such movements should be visible to others (relative to many other primate species). However, Emery (2000) also highlights the importance of facial morphology; in contrast to the relatively flat faces of most primate species, baboons have an extended canine-like snout. It may be that this distinct feature is an excellent indicator of another individual's visual orientation as head direction is very readily determined, even at a considerable distance.

Methods

Subjects

Five olive baboons were studied: three males (Balthazar, Kiki and Stuart) and two females (Freya and Julie) housed at the CNRS Centre de Primatologie, Rousset-sur-Arc, France. Their ages ranged from 4 to 30 years and they had either been born at the centre or were transferred there from a safari park approximately three years before the study was conducted. All baboons were housed in indoor/outdoor enclosures in small social groups. For the purposes of testing, the baboons were restricted to the outside area; dominant baboons were tested in the presence of other group members, but during testing with subordinates, more dominant group members were closed indoors.

The monkeys were fed a diet of commercial monkey pellets, fruit and vegetables, with feeding being postponed until the daily testing sessions were completed. Standard food items (small pieces of fruit and vegetables or grains of maize) as well as dietary treats (nuts, raisins and cereals) were used to maintain the monkeys' participation in the interaction with the experimenter. Sessions were conducted with each baboon at approximately the same time of day, two or three days a week.

Apparatus

A stopwatch was used to time the sessions and a video camera was positioned to record both the experimenter's and monkey's behaviours during the session.

Procedure

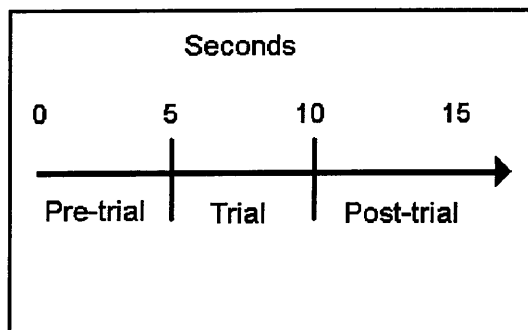
All sessions were videotaped and coded at a later date. The experimenter sat directly in front of the baboon's enclosure at a proximity of around 50cm so that she was at the monkey's eye level. The stopwatch was started and the session commenced. All the baboons were accustomed to interacting with humans and readily accepted food items from the experimenter. During each session, the experimenter gave small food items to the baboons at regular intervals (about every 15 seconds) and engaged in 'natural' behaviours: looking at the baboon, the food items and the immediate environment between the individuals (Anderson & Mitchell, 1999).

To test for gaze following, the experimenter followed a pre-determined schedule and interrupted the feeding bout in order to change their direction of gaze, looking between 60-90 ° to the left or right and maintaining the position for approximately 5 seconds before returning to a central orientation. Three trial types were presented pseudo-randomly within each session: head and eyes both turned to the side, head turned with eyes closed and eyes only oriented to the side. For head only trials, the eyes were closed before the head was turned. All changes in orientation were performed calmly and the experimenter maintained a neutral posture and facial expression. Five test sessions were conducted with each monkey, with three trials within each 10-minute session. Trials per session were kept to a minimum in order to avoid habituation within sessions; as there were no targets, the baboons may have learned to ignore the experimenter's gaze behaviours as uninformative (Tomasello, Hare & Fogelman, 2001).

Video Coding and Data Analysis

Preliminary viewing of the videos was used to identify pre, during and post trial video segments (all of 5 second duration, see Figure 1). These segments of video were coded independently by two individuals (SJV & REB) several months after the data were collected. During coding, the screen was partially covered in order to conceal the experimenter's actions so that the observers were blind to the trial type and direction. All the monkeys' changes in orientation to either the left or right of the central position were recorded. Inter-observer reliability was high (agreement for 253/276 behaviours recorded: 91.67%). Disagreements were reviewed until a unanimous decision was reached by the two observers.

Figure 1: The intervals used for video coding.



As each change in the monkeys' orientation from the central position was recorded, this allowed each interval (pre- post- and during trials) to be re-coded into categories according to the baboons response pattern (see Table 1). One trial could not be coded due to human error.

Table 1: Categories of responses and their definitions.

Category	Definition
No response	The baboon did not turn from the central orientation during the interval.
Congruent response	The baboon turned only in the direction congruent with the human interactant.
Incongruent response	The baboon turned only in the direction opposite to that of the human interactant.
Both	The baboon turned and looked in both the congruent and incongruent direction during the interval.

Results

As can be seen from Figures 2a – c, the baboons' behaviours differed between pre-, during and post trial intervals. Chi square tests were conducted in order to examine whether turns in the congruent direction were more likely during a given trial, that is, were the monkeys co-orienting with the experimenter? In both head orientation conditions, the baboons were more likely to look in the congruent direction during the trial than either immediately before or afterwards. For Head and Eyes: $\chi^2 = 6.609$, 2df, $p = 0.037$; for Head only: $\chi^2 = 8.857$, 2df, $p = 0.012$. However, the same effect was not found for eye gaze alone: $\chi^2 = 3.250$, 2df, $p = 0.197$.

Although this could suggest that the baboons readily co-oriented with another's change in head direction but failed to do so when presented with eye gaze alone, the analysis of only the Congruent category data may underestimate the levels of visual co-orientation. That is, the data also clearly show that the category Both also seems to increase during the trial interval; in this category, the baboons did orient in the congruent direction but also looked in the opposite direction. If these trials are also considered in the analysis the results show that all three conditions facilitated visual co-orientation in baboons: for

Head and Eyes: $\chi^2 = 15.8$, 2df, $p < 0.001$; for Head only: $\chi^2 = 20.759$, 2df, $p < 0.001$; for eyes only: $\chi^2 = 8.727$, 2df, $p = 0.013$.

Figure 2a) Stacked bar chart showing frequency of response categories across time for head and eye direction.

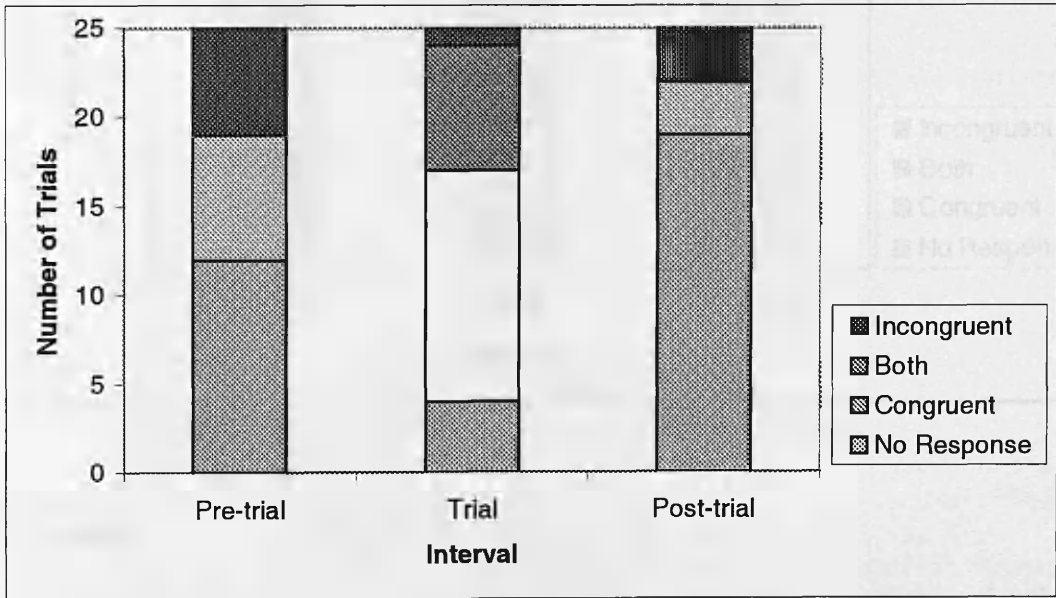


Figure 2b) Stacked bar chart showing frequency of response categories across time for head direction only.

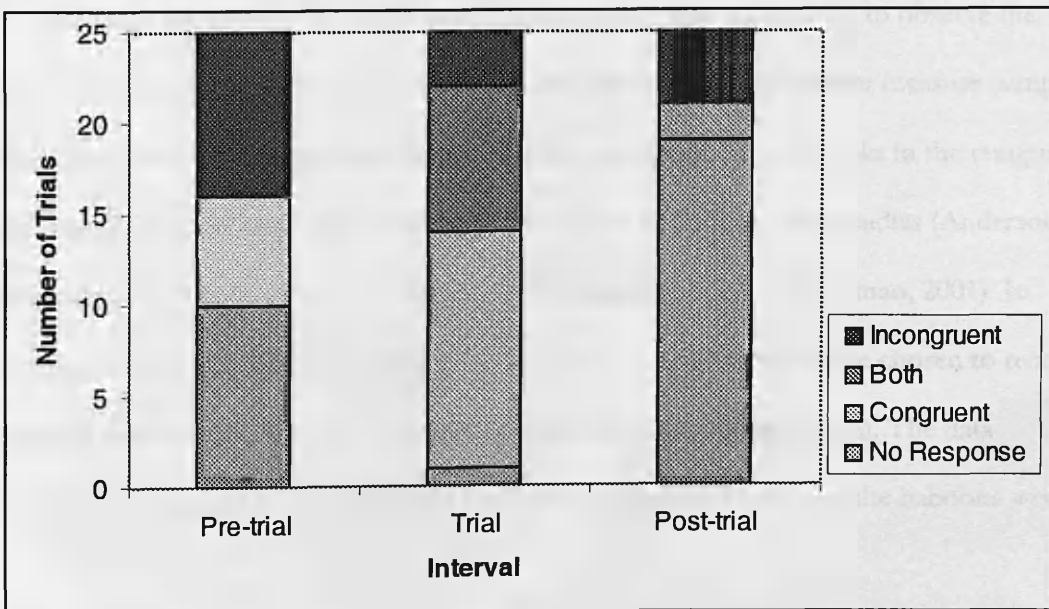
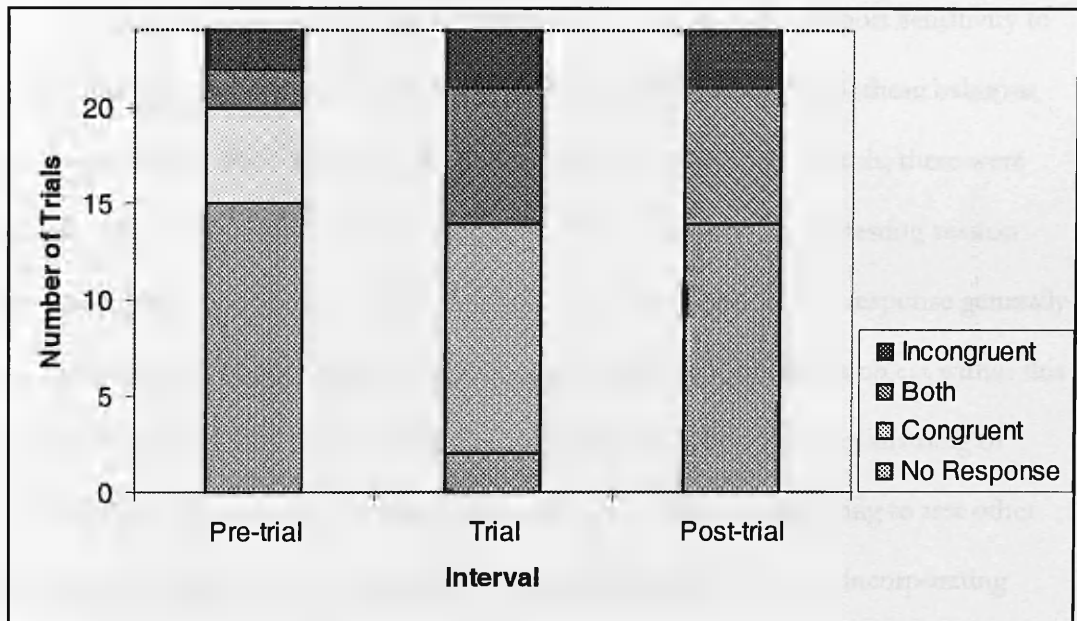


Figure 2c) Stacked bar chart showing frequency of response categories across time for eye gaze.



Discussion

The results show that baboons do respond to another's shift in gaze direction by visually co-orienting in a congruent direction. However, it is apparent that gaze following in response to eye gaze was not as readily demonstrable as gaze following in response to head orientation; a broader definition of gaze following was required in order to observe the effect of visual co-orientation in response to eye gaze alone. This broader measure (simply classifying cases according to whether or not the nonhuman primate looks in the congruent direction during a given interval) has been the unit of analysis in other studies (Anderson & Mitchell, 1999; Tomasello, Call & Hare, 1998; Tomasello, Hare & Fogelman, 2001). In contrast, a more conservative measure has been used by others who have chosen to record only the first look made by the monkey (Ferrari et al, 2000; Itakura, 1996). The data analysis combining the Congruent and Both data suggests not only that the baboons were

likely to visually co-orient in response to another's change in direction, but also that they were likely to show less specific looking behaviours.

It is worth noting that in contrast to the only other studies to report sensitivity to eye gaze in monkeys (Ferrari et al, 2000; Lorincz, Baker & Perrett, 1999), these baboons were tested in their home cages and in the presence of conspecifics. That is, there were plenty of other things which could have caught their interest during the testing session (Tomasello, Hare & Fogleman, 2001). Perhaps the visual co-orientation response generally leads to visual scanning of the environment, or the absence of any target object within this paradigm simply led to general looking when the baboons failed to detect anything of significance following their co-orientation response. It would be interesting to test other species with paradigms previously used with chimpanzees, for example, incorporating target objects, or even targets and distractors, and examining responses to barriers (Povinelli & Eddy, 1997; Tomasello, Hare & Agnetta, 1999).

The baboons responded to head direction even when the experimenter's eyes were closed, suggesting that head direction in itself is sufficient to provoke a gaze following response. This finding coincides with that reported for human infants (less than 18 months old); the infants did not distinguish between shifts in both head and eye direction and those in which only the head was turned and eyes remained centrally fixated (Corkum & Moore, 1995). Thus, whether or not the interactant is actually able to see anything does not seem to be relevant to the visual co-orienting response of baboons. This may suggest that the visual co-orientation response is simply a behavioural response which does not necessitate any understanding of the role of eyes in visual perception; it may even be a reflexive behaviour (see Chapter 6).

However, it could be that once the head is turned in profile, the eyes are a less visible and become a less salient feature (Perrett & Emery, 1994). In fact, perhaps a shift in head orientation renders eye movements fairly irrelevant, while small changes in visual

orientation are usually achieved by eye movements, change in head orientation signals a larger shift in visual orientation (Freedman & Sparks, 1997). That is, if the shift in gaze requires a head turn, then the subtler movements of the eyes may not be particularly informative. In addition, if the movement of the head itself caught the baboon's eye, then they may have missed the closing of the eyes that preceded this action. In addition, the lower response rate to eye gaze alone may be partially due to the study's mixed-trials design; the co-presentation of a more salient cue (i.e., head direction) within sessions may have diminished the tendency to visually co-orient when eye direction alone was available. For example, Corkum & Moore (1995) found that human infants were less likely to respond to eye gaze when a mixed-trials design was used; Moore (1999) has suggested that these mixed blocks lead to the 'de-emphasis' of eye gaze.

The baboons did respond to eye gaze, indicating that they are sensitive to the eyes at some level. Perhaps both are reliable as social cues and invoke the appropriate response without any recourse to a consideration of seeing per se. As Perrett and Emery (1994) highlight, there are several possible sources of information regarding another's visual orientation (eyes, head and body orientation) and these can be used in combination or independently depending upon the circumstances. Indeed, nonhuman primate eye gaze may often be difficult to discern due to the morphology and coloration of their eyes (Kobayashi & Koshima, 1997; 2001), so sensitivity to alternative signs of visual orientation would be adaptive. As noted in the introduction, baboons have an interesting facial and eye morphology and it may be that despite their eye morphology, they primarily rely on head direction as an indicator of another's visual orientation. It would be extremely interesting to test baboon responses to conspecific gaze cues; in order to allow for the control for head and eye movements, a paradigm such as that used with rhesus macaques by Perrett and his colleagues might be enlightening (Emery et al, 1997; Lorincz, Baker & Perrett, 1999).

The analysis used could be considered as underestimating the gaze following response somewhat; co-orientation during the 5-second post-trial interval could also be seen as gaze following. However, as Figures 2a-c reveal, there is little evidence of the gaze cues having any sustained effect on behaviours in terms of visual co-orientation or general scanning in the post-trial interval. In fact, as the shift in attention occurred at the start of the trial interval, the during-trial data is in fact 'post' trial data in itself. That is, perhaps the post-trial 5-second interval is simply too long after the event (gaze shift) for there to be any sustained effects upon behaviour.

A potential problem with the methodology is the dependent variable measured: the baboons had to clearly shift their own visual orientation by turning their heads (Itakura, 1996; Tomasello, Call & Hare, 1998; Tomasello, Hare & Fogleman, 2001). Other studies have measured eye movements and this may be a more accurate assessment of a monkey's responses (Emery et al, 1997; Ferrari et al, 2000; Lorincz, Baker & Perrett, 1999). Indeed, it could be argued that head direction seemed to be more effective than eye direction because of the measure used; perhaps shifts in eye direction by the experimenter resulted in similar shifts in eye gaze by the baboons which were not observed and recorded. As Emery (2000) identified, discrepant results may be dependent upon the measure used (for example, duration versus frequency of looking) and it may be that more fine-grained and accurate measures of looking behaviours are desirable in an analysis of the gaze following phenomenon (see also Johnson, 2001).

Furthermore, the inability to successfully record eye direction may have led to another error in analysing gaze following; it was not possible to determine whether the baboon had actually perceived the interactant's change in visual orientation. This measure has been used to filter data in previous studies; those cases where the monkeys did not fixate the interactant in order to see the gaze shift were excluded from subsequent analysis (Ferrari et al, 2000; Tomasello, Call & Hare, 1998). Moreover, recording the first head turn

following the human interactant's shift in visual orientation may be a more accurate means of monitoring the gaze following response (Ferrari et al, 2000; Itakura, 1996). However, the difficulties in monitoring the baboons' eye movements made determining when they actually noticed the change in visual orientation very difficult, and therefore may have made this an inappropriate measure. Thus, a more sensitive dependent measure, such as eye movement recordings, would better facilitate the study of nonhuman primates' gaze monitoring abilities.

Study 2: Gaze and stimulus enhancement

'Reading the attention of others affords information of those aspects of the environment that will most probably affect their decision-making and thence determine future behaviour (Whiten, 1997, p 162).

When an individual observes another contacting with an object, this can influence the probability of that object being approached or contacted by the observer: an effect known as stimulus enhancement (Spence, 1937). Such a behavioural phenomenon could benefit gregarious animals, such as primates, who are able to acquire information about their environments from observing conspecifics' behaviour (Hall, 1963). For examples, learning to fear predators (Cook & Mineka, 1989), learning about a potential food source (Visalberghi, Valente, & Frigaszy, 1998) or learning about novel or potentially useful objects (Fragaszy & Visalberghi, 1989; Russell, Adamson & Bard, 1997; Wechkin, 1970; Zuberbeuhler, Gyax, Harley & Kummer, 1996), can be facilitated by observing other individuals' responses to their environment.

At the neurophysiological level, cells have been identified which respond to another's actions in relation to objects in the environment, such as walking towards or

reaching for an object (Brothers, 1995; Perrett et al, 1990; Perrett & Emery, 1994). Thus, Perrett and Emery (1994, p 685) state that ‘there is neurophysiological support for the notion that the representation of dyadic relationships underlies the visual analysis of actions and intentional behaviours of others.’ Furthermore, ‘mirror cells’ have been identified in monkeys which respond within a purely observation/execution matching system; these cells respond both whether the subject or another individual performs a particular action, such as grasping an object (Rizzolatti, Fadiga, Gallese & Fogassi, 1996; for a recent review, see Gallese & Goldman, 1998). This indicates that the actions executed upon the environment by other individuals undergo some sort of categorical neural processing and that any resemblance with an individual’s own interactions is also encoded.

In addition to observing others interacting with their physical environment, monitoring the visual orientation of others may be an alternative means of acquiring information about objects or events in the environment. Nonhuman primates are highly sensitive to the behavioural status of other individuals and will modify their own actions in response (Cheney & Seyfarth, 1991). Moreover, the phenomenon of gaze following which has been demonstrated in several species of nonhuman primates (Anderson & Mitchell, 1999; Ferrari et al, 2000; Povinelli & Eddy, 1997; Tomasello, Call & Hare, 1998; Tomasello, Hare & Fogleman, 2001) indicates that primates are responsive to the looking behaviours of others; changing their own visual focus in order to co-orient with another individual. Thus, monitoring both the interaction and visual monitoring afforded to conspecifics, objects and events potentially exposes socially living primates to valuable information regarding their social and physical environment.

Recent neurophysiological research has suggested that visual orientation may indeed play a role in interpreting other individuals’ behaviours. Perrett and his colleagues have identified a population of cells (in the anterior temporal sulcus of macaque monkeys) that selectively respond to the sight of another individual performing actions (such as

reaching) only when the actor's visual orientation is congruent with the action (Jellema, Baker, Wicker & Perrett, 2000). That is, these cells seem to be sensitive to combinations of intentional actions and visual orientation. However, there is no evidence to date that the object of the action is also encoded within such a neural processing system (Emery, 2000); it may be that the function of these cells encodes direction and actions.

Moreover, while gaze following in nonhuman primates is a fairly robust phenomenon, this response could be a simple reflexive response or a learned association between co-orienting with another and being rewarded by perceiving something of interest. That is, gaze following does not necessarily reflect an understanding of gaze as an attentional state, or even a more basic appreciation of how seeing connects the perceiver to the perceived. Even at a behavioural level, gaze following does not indicate that nonhuman primates relate an individual's gaze behaviour to the object or event being looked at. For example, it is not clear whether visual co-orientation plays a role in social learning; can gaze alone lead to stimulus enhancement? If so, what type of looking behaviours are relevant, does it matter what form of visual monitoring is witnessed? Would a brief visual inspection be sufficient or would more a more sustained visual exploration be more conducive to increasing the salience of an object? Moreover, if nonhuman primates use another's visual orientation to predict behaviour, then it is important to distinguish 'irrelevant' looking behaviours from more prolonged visual monitoring which presumably identify more important objects or events: not all behaviours are of predictive value (Montgomery, Bach & Moran, 1998).

Within a more mentalistic framework, although an individual may look at a given object, this does not in itself impart information concerning the intentional status of the perceiver, for example, whether or not the individual intends to act upon the object (as opposed to the object simply falling within the line of regard). Knowledge about what another individual can perceive is only the first of three levels of mental state attribution

identified by Premack and Dasser (1991), with the attribution of intentions and attribution of beliefs being the remaining two. While much research concerning the presence of a 'theory of mind' (Premack & Woodruff, 1978) in primates has focused upon visual perspective taking (Tomasello, Hare & Agnetta, 1999) and the relationship between seeing and knowing or believing (Call & Tomasello, 1999; Hare, Call & Tomasello, 2001; Povinelli, Nelson & Boysen, 1990), there has been less consideration of the understanding of the relationship between perception and looking behaviours as an expression of intention or interest. Baron-Cohen and Cross (1992, p 182) propose that 'visual perception possesses intentionality: it is always *about* something. Eye-direction signals this intentionality by specifying the *target* of visual perception: what perception is about.' However, it is not clear whether nonhuman primates, or even human infants, appreciate gaze at such a level (Corkum & Moore, 1995; Tomasello, 1995).

Santos and Hauser (1999) employed an expectation violation paradigm to investigate cotton top tamarins' responses to a human interactant's gaze. These authors suggest that increased looking reveals that the monkeys were sensitive to the relationship between looking behaviours and intention to act; the monkeys looked more when the experimenter reached for a previously ignored (as opposed to the looked at) object. However, alternative explanations for these findings have been identified, such as associative learning and simple co-orientation (see Chapter One, Section 3.4c). In contrast, if nonhuman primates responded differentially to various, qualitatively different forms of perceptual contact this could be seen to indicate that the relationship between gaze and intentions was indeed being processed on some level (as it is in human children, e.g. Montgomery, Bach & Moran, 1998). Returning to a consideration of observable behaviours alone, differential responses would indicate that nonhuman primates are sensitive to some of the subtleties of other individuals' looking behaviours; how various types of looking behaviours might relate to the salience of an object or event.

In order to avoid possible learning effects, the present study utilised a natural response of primates, namely exploration of novel objects; many primate species display a seemingly intrinsic motivation to manually (and visually) explore novel objects (e.g., Harlow, Harlow & Meyer, 1950; Vauclair & Bard, 1983). Thus, the monkeys' responses to novel objects were recorded to try and determine whether the monkeys would be influenced by the perceptual contact (touching/looking) of a human experimenter. A study with children reported an inability to distinguish 'perception from attention' until the age of six years old, but the task required a verbal response and an interpretation of scenarios regarding a model's desires (Montgomery, Bach & Moran, 1998). It may be that a more simple method of recording monkeys' preferences for objects might be able to demonstrate an ability to distinguish different forms of looking behaviours.

The present study aimed to answer three main questions. Firstly, would monkeys demonstrate differential responses to objects according to whether or not an experimenter exhibited perceptual contact with the objects? Would any preferences be independent of the objects themselves, that is, would there be any difference between preference patterns when identical and non-identical object pairs were presented? Finally, would monkeys distinguish between an experimenter having simple perceptual contact (i.e. brief looks or touches) with an object and engaging in more prolonged visual or tactile exploration?

Methods

Subjects

The monkeys studied (see Table 2) were four capuchin monkeys and eight olive baboons. The capuchin monkeys were housed in a small social group at the Psychology Department, Kyoto University, and were all tested individually. The baboons were socially housed at the CNRS Station de Primatologie, Rousset, France, and these monkeys were tested in the presence of subordinate group members.

Table 2: Subject characteristics of the three groups of monkeys studied.

Capuchins (Look/touch)	Olive baboons A (Look/touch)	Olive baboons B (Glance/look)
Heiji (male, 6 years)	Amie (female, approx. 6 years)	Esperance ^a (female, 10 years)
Kiki-chan ^a (female, 5 years)	Gim (male, 6 years)	Freya (female, approx. 6 years)
Theta ^a (female, 5 years)	Katje (female, 5 years)	Gaspard ^a (male, 9 years)
Zilla ^a (female, 7 years)	Kiki ^a (male, 5 years)	Melchior (male, 11 years)

^a Monkeys with prior experience using a human experimenter's head and/or eye direction as a cue within an object-choice paradigm (at least 9 months had elapsed before the present study commenced).

Apparatus

The apparatus consisted of a wooden tray (measuring 90cm x 16cm for the capuchins and 60cm x 40cm for the baboons) and a cardboard screen (approximately 100cm x 80cm). A wide variety of stimulus objects were used: for examples, small boxes, egg cartons, coloured plastic alphabet letters and shapes, plastic bottles, and metal nuts and bolts.

Procedure

Two stimulus objects were placed 30 to 40 centimetres apart on either side of the midpoint of the tray which was set 50cm back from the enclosures and so out of the monkeys' reach. The objects and their positioning were concealed from the monkeys by means of the cardboard screen. The objects were attached to a length of string that was secured to the table upon which the board lay to prevent the monkeys from pulling the objects into the cage or enclosure. Small, light or rounded objects were secured to the board with

transparent tape in order to avoid uncontrolled movement when the tray was pushed forward.

The stimulus objects presented varied randomly from trial to trial, but on one half of the trials (distributed randomly) a pair of identical objects was presented. In the case of identical objects, care was taken to position them so that the stimulus array appeared symmetrical to the monkey. For non-identical objects, the only constraint was that the objects were approximately similar in size. Some objects appeared in several trials across the forty trials presented to each monkey, but when this occurred the presentations were always separated by at least six intervening trials, and the objects were always paired with another non-identical object.

For the capuchin monkeys, two experimenters conducted each trial, while for the baboons, only one experimenter conducted the trials, both positioning and presenting the objects as described below. One experimenter positioned the two objects and removed the screen and then moved away from the stimulus presentation area. The second experimenter approached and sat down behind the table upon which the stimulus tray lay. The experimenter made eye contact with the monkey, and immediately upon establishing eye contact switched their orientation to one of the objects, either looking at it or touching it, according to the randomised test schedule for that monkey.

When looking at an object, the experimenter clearly oriented his or her head and eyes towards that object and when touching an object, the experimenter looked at it as above while also touching the object lightly with the index finger of the ipsilateral hand. For four of the baboons (Group B), touching the object was replaced with glancing at the object, that is, with the experimenter orienting only her eyes towards the object. With the exception of the initial eye contact between experimenter and monkey, no eye contact occurred. The experimenter's initial orientation to an object lasted for approximately 1 second, after which the experimenter looked briefly at the central point of the board before

switching orientation again to one of the objects, this time glancing, looking or touching it for approximately 5 seconds. After this period of prolonged orientation, the experimenter again briefly looked at the centre of the board before switching for a final time to one of the objects, glancing, looking at it or touching it for 1 second. After the final glance, look or touch, the experimenter looked at the centre of the board, pushed the board forward so that the objects were within the monkeys' reach, then moved away.

The experimenter(s) then discreetly observed the monkey to see which of the two objects was contacted first. As soon as one of the items had been touched, the experimenter approached and retrieved both objects. The screen was put in place and the next trial proceeded after approximately two minutes. There were a total of forty trials per individual; thirty-two experimental trials as described above and eight 'control' trials consisting of a single bout of looking or touching, directed to one of the two objects and lasting either 1 or 5 seconds. Two trials or two separate two-trial sessions (with at least an hour between sessions) were run with each monkey each day, in order to avoid the possibility of habituation to signs of experimenter's actions in rapidly successive trials.

In addition to the 8 control trials, there were four trial types (see Table 3 for details), with presentations counterbalanced to the right and left and according to whether the pair of objects was identical or non-identical. There were eight of each trial type presented (except for LL, $n = 6$, due to human error the data from the remaining two trials in this category could not be analysed). Note that for the second baboon group, 'look' (head and eyes) and 'touch' were replaced with 'glance' (eyes only) and 'look'.

Table 3: Sequences of behaviour presented for each trial type.

Condition		Sequence
look LOOK look	(lLl)	Short look, long look, short look.
touch TOUCH touch	(tTt)	Short touch, long touch, short touch.
look TOUCH look	(lTl)	Short look, long touch, short look.
touch LOOK touch	(tLt)	Short touch, long look, short touch.

Data analysis

The data were analysed on three different levels; overall group data were examined in order to see whether the monkeys responded preferentially to a particular form of behaviour (touching, looking or glancing), group data were also analysed according to the four types of trial, individual data patterns were then explored. Binomial tests were conducted in order to compare performances with chance responding; only control data and all significant or near-significant results are presented.

Results

Capuchins

Control trials: At the group level, the capuchins did not show any tendency to respond to the object that had been looked at or touched rather than the alternative object presented during control trials (see Table 4).

Experimental trials: when presented with a pair of identical objects, the capuchins showed a tendency to respond to the object that was touched last. For one individual this response pattern was significant, Heiji consistently responded to the last object touched.

Table 4: Capuchin responses at the group, trial and individual level.

Control	Group	Trial type	Individual
Look	Same		Same
Short look 3/8	Last touch: 21/32 ^b		Heiji, last touch: 7/8 ^a
Long look 2/8			
Touch			
Short touch 4/8			
Long touch 3/8			

Same/different refers to identical and non-identical object pairings. Subscripts indicate probability (Binomial tests) ^a $p < 0.05$, ^b $p = 0.055$.

Baboons A (look and touch).

Control trials: As a group, the baboons did not show any tendency to respond to the object that was looked at or touched rather than the alternative object presented during control trials. During control trials, one individual demonstrated a tendency to respond to the object which had been touched; Amie chose the item which had been touched on all trials presented (see Table 5).

Experimental trials: When presented with non-identical objects, the baboons showed a tendency to respond to the object which was touched for the longer duration and to respond to the object which had been touched last. On identical object trials, this group (like the capuchin group) demonstrated a preference for the last object touched. For tT trials there was again a tendency to respond to the object which had been touched for the longer duration, when a pair of non-identical objects were presented. When two identical objects were presented on lLt trials, the monkeys showed a preference for the item which had been looked at first or touched last. When presented with identical objects, one baboon (Katje) responded to the object, which was touched for the longer duration. On

non-identical object trials, one baboon (Amie) chose the object that had been touched for the longer duration (see Table 5).

Table 5: Baboons Group A, responses at the group, trial and individual level.

Control	Group	Trial type	Individual
Look	Same	Same ILt	Same
Short look 5/8	Last touch: 21/32 ^b	First look: 12/16 ^a	Katje, long touch: 7/8 ^a
Long look 3/8		Last touch: 12/16 ^a	
Touch	Different	Different tTt	Different
Short touch 6/8	Long touch: 21/32 ^b Last touch: 21/32 ^b	Long touch: 12/16 ^a	Amie, long touch: 7/8 ^a
Long touch 3/8			Control Amie, touch: 4/4 ^c

Same/different refers to identical and non-identical object pairings. Subscripts indicate probability (Binomial tests) ^a $p < 0.05$, ^b $p = 0.055$, ^c $p = .062$.

Baboons B (glance and look)

Control trials: As a group, the baboons did not show any tendency to respond to the object looked at or touched rather than the alternative object presented during control trials (see Table 6).

Experimental trials: When presented with a pair of identical objects, the baboons showed a tendency to respond to the object that was looked at (head and eyes) last. Esperance demonstrated a preference for the object within an identical pair that had been looked at (head and eyes) first or last within the trial sequence.

Table 6: Baboons Group B, responses at the group, trial and individual level.

Control	Group	Trial type	Individual
Glance	Same		Same
Short glance 3/8	Last look: 21/32 ^b		Espe, first look: 7/8 ^a
Long glance 2/8			Last look: 7/8 ^a
Look			
Short look 4/8			
Long look 3/8			

Same/different refers to identical and non-identical object pairings. Subscripts indicate probability (Binomial tests) ^a $p < 0.05$, ^b $p = 0.055$.

Discussion

Firstly, during control trials the monkeys did not demonstrate differential responses to objects according to whether or not an experimenter exhibited perceptual contact with the objects; this suggests that even touching the objects failed to elicit any effect of stimulus enhancement. While Call et al (2000) reported that touching an object in an object-choice paradigm failed to substantially increase subsequent choice of that object, earlier object-choice studies found that manual cues (such as tapping or pointing) did enhance performance (Anderson, Montant & Schmitt, 1996; Anderson, Sallaberry & Barbier, 1995). The current results also contrast with pre-schooler's responses; although young children did not discriminate different forms of perceptual contact they did differentiate between two items when only one had been acted upon by a model (Montgomery, Bach & Moran, 1998). Of course, it may be that another individual's (or at least a human experimenter's) prior perceptual contact simply has no effect on monkeys' responses to novel objects but there are alternative possible explanations for this result.

One consideration is simply that the short bout of contact (only 1 second for half the control trials) was too short and that perhaps the monkeys failed to engage in the interaction and thus monitor to the experimenter's behaviour. A more extended control

trial, for example, a three-action trial (like the experimental trials) with the experimenter only orienting towards or acting upon one of the objects, might be a more appropriate means of assessing sensitivity to these behaviours. Moreover, due to the small sample size and number of trials the statistical power of the tests were low; it would, therefore, be interesting to explore the influence of perceptual contact with further testing. In light of these weaknesses, it seemed adroit to analyse and consider the experimental trial data despite the lack of support (from the control trials) for the hypothesis that perceptual contact would influence responses to novel objects.

In contrast to the control data, during the more extended experimental conditions where both objects were involved, there were some consistent patterns in the responses of the monkeys at the group (but not at the trial or individual) level. For both the baboon and capuchin groups, the monkeys responded in a consistent manner according to the physical contact that the experimenter had had with an object, that is, which objects were touched and when. When two identical objects were presented, there was a preference for the last object touched, indicating that the human model's behaviour influenced the levels of interest for two otherwise indistinguishable items. That is, although there was no consistent preference for touched objects observed during control trials, there was an overall bias towards the most recently touched object when a combination of behaviours were demonstrated.

Furthermore, for the capuchins and Group B baboons, at both the group and individual levels, the only preferences observed were for identical object pairings. The behaviours demonstrated by the experimenter reliably exerted an influence indicating that such social information was sufficient to manipulate levels of interest in an object independently of the object's intrinsic qualities. Or conversely, that the experimenter's behaviours had no influence when intrinsic levels of interest in the objects differed (i.e. on non-identical pairings). However, for the baboons in Group A there was also an effect

when non-identical objects were paired; the monkeys initially manipulated the object touched last or for the longest duration. This suggests that social cues may have been more important than the objects' properties in determining responses to the objects even when the objects presented presumably were of differing interest intrinsically.

For the baboons in the glance/look group, the results were generally similar; when presented with identical objects, the baboons initially contacted the last object which the experimenter had oriented towards (head and eyes). This suggests that while head orientation was ineffective when presented in combination with physical contact with an object, when only presented in combination with eye gaze, head direction became a salient action. As noted in Study 1, it may be that the presentation of mixed cues leads to the less salient source of information simply being neglected (Moore, 1999). One means of counteracting such an effect would be to simply investigate one cue within each session. The results may also indicate that some level of visual co-orientation with the experimenter was occurring (at least in the absence of manual gestures from the experimenter), so that the monkeys were simply more likely to respond to an object presented to the side to which they were already oriented (Povinelli & Eddy, 1997). However, it would seem that responses were also determined by the intrinsic interest in the non-matching objects.

It is not clear whether the monkeys distinguished between an experimenter having simple perceptual contact (i.e. seeing or touching) with an object and engaging in more meaningful contact, such as sustained looking and manual exploration. The baboons in Group A did show a bias towards choosing the item in a non-identical pair which had been touched for the longer (5-second) duration, but they also demonstrated a preference for the object touched last. The other two groups demonstrated no preferences for items which had been the focus of more extended bouts of interest, making it difficult to draw any strong conclusions from the results obtained. However, it should be noted that all of the actions performed by the experimenter were very definite and deliberate: they purposefully

looked or touched both items, albeit briefly in most instances. Perhaps a more naturalistic sequence of behaviours could be used to investigate nonhuman primates' responses to another's interactions with objects, for example, using a scenario with glances or inadvertent touches to one object but more extensive visual or manual exploration of the other (Montgomery, Bach & Moran, 1998). An interesting adaptation of this study would be to manipulate the content of videos of conspecifics engaging with and looking at objects to varying degrees; these could be shown to the study animals prior to exposing them to the same objects (Cook & Mineka, 1989; Emery et al, 1997). That is, would a conspecific's amount of interest in an object influence subsequent exploration of that object by a second animal?

Overall, the most consistent result was to respond to the last object oriented to with the most salient form of cue presented; for the capuchins and Group A baboons this was touching the object, while for Group B baboons this was head orientation. This recency effect suggests that the monkeys may have been monitoring the experimenter's behaviours (or at least the more salient actions presented) and may have still been oriented towards the last object when presented with the objects to explore. It might, therefore, be interesting to vary the interval between the model's demonstration and presenting the objects in order to examine this behaviour more fully. Simple co-orientation with the experimenter's actions (gesture or head orientation) may be sufficient to explain the monkeys' behaviour, at least with identical object pairings. This is interesting because visual co-orientation does not seem to facilitate the choice of a baited object within the object-choice paradigm. Perhaps the presence of food in the object-choice task somehow interferes with gaze following responses (Call, Agnetta & Tomasello, 2000).

It would be interesting to explore these findings further, for example, would latency to contacting the objects reveal any distinct patterns; it is possible that social cues were more readily (quickly) responded to when the objects had no discernible differences.

Alternatively, visual scan patterns could be employed as a dependent measure; perhaps frequency or duration of looking at the objects (Emery et al, 1997; Emery, 2000) would reveal a different pattern to the measure used in the present study (first object explored manually). A further problem with the procedure is that the experimenter's behaviour lacked any meaningful context; for example, although looking behaviours may indicate intention, the experimenter never actually proceeded to engage in any interaction with the objects. Perhaps an expectation violation paradigm similar to that used by Santos and Hauser (1999) could be employed as a means of exploring nonhuman primates' responses to another's gaze; that is, would responses differentiate different forms of looking such as brief glances and extended fixation?

Turning to a consideration of these results within a more mentalistic frame-work, they could be seen as suggesting that nonhuman primates do not distinguish between simply looking at an object and attending to it (Tomasello, 1995). That is, although nonhuman primates may be able to compute the geometry of gaze (i.e., visually co-orient) they may not share another's attention (Baron-Cohen, 1994). Thus, it may be that nonhuman primates do not have any such sophisticated appreciation of looking behaviours and do not distinguish between qualitatively (or even quantitatively) different gaze behaviours. However, an appreciation of looking behaviour at even the most basic level might allow for fairly reliable predictions of another's subsequent actions. As Montgomery, Bach and Moran (1998, p 692) state in reference to young children, 'looking at something may associate the protagonist with an object in a particularly salient fashion, and it is possible that it is this association, rather than conceptual understanding of how visual attention and goal are related, that influences pre-schoolers to infer goal on the basis of line of regard.' Nevertheless, it would be interesting to explore these issues further, whether the underlying mechanism were based upon observable behaviours or some form of appreciation of seeing or attention, this line of research could examine nonhuman

primates' sensitivity to the subtleties of other individuals' interactions with their environments.

Chapter summary

Study 1 demonstrated that olive baboons are sensitive to a human interactant's change in orientation; they changed their own visual orientation in response to shifts in head direction and eye gaze alone, albeit less reliably. In addition, the baboons demonstrated increased vigilance following a change in orientation by the experimenter. The baboons were insensitive as to whether the interactant was able to see anything; head direction was responded to even when the eyes were closed. This suggests that head and eye direction can be used independently when assessing another's visual orientation.

In Study 2, nonhuman primates did not reliably distinguish between items on the basis of a human interactant's perceptual contact with one of the items (during control trials). However, during more prolonged trials there was some evidence of sensitivity to the experimenter's behaviours. The capuchin monkeys only demonstrated significant bias in responses when identical objects were presented, while the baboons showed a less clear pattern of results making any meaningful interpretation of these findings difficult. The monkeys' responses revealed a consistent preference for the object oriented towards last, at least when the experimenter's last action was the more salient of the two actions within a session. Overall, there was little evidence of an appreciation of the varying quality of looking or touching behaviours; the results may reflect some form of simple co-orientation response. This study had considerable methodological weaknesses that make drawing strong conclusions problematic; however, it would be interesting to further examine these issues using a different or at least improved methodology.

Chapter Three

Gaze Discrimination by Olive Baboons

Anthropoid primates are extremely sensitive to eye gaze, or at least to one particular form of eye gaze: direct eye contact (see Chapter One, Section 3.2b). From early infancy, humans and monkeys respond differentially to images or observers displaying eye contact or averted gaze (Hains & Muir, 1996; Kalin, Shelton & Takahashi, 1991; Mendelson, Haith & Goldman-Rakic, 1982; Vecera & Johnson, 1995). There is considerable sensitivity to small deviations in eye gaze from a central position: for example, Symons, Hains & Muir (1998) reported that 5-month-old human infants displayed less looking and smiling to adults who averted their gaze by 5 degrees horizontally (but not vertically). Similarly, infant rhesus monkeys discriminated direct from averted gaze (Mendelson, Haith & Goldman-Rakic, 1982) and adult rhesus monkeys discriminated between photographs depicting direct gaze and gaze averted by 5 degrees (Campbell et al, 1990).

However, it is not clear whether the distinctiveness of direct gaze as a percept reflects a more general capacity for discriminating gaze direction; that is, determining whether or not another individual is looking at you does not necessarily imply an ability to distinguish whether the individual is looking at an object based on eye direction, for example. It has been suggested that direct gaze may be a special form of stimulus that receives rapid processing due to its social salience (Baron-Cohen 1994; von Grunau & Anston, 1995; Kummer, Anzenberger & Hemelrijk, 1996; Muir, Hains & Symons, 1994). In nonhuman primates, direct and averted gaze are a critical element in many social situations; for example, maintained stare is a component of threatening facial gestures in many species of monkeys (Chance, 1967; Perrett & Mistlin, 1991).

At the neurophysiological level, there is evidence that specific areas of the brain are specialised for the processing of gaze information. Single cell recordings in the superior temporal sulcus have identified cells that are sensitive to eyes directed towards the viewer and to averted gaze (Perrett et al, 1985). Furthermore, monkeys with lesions in this area fail to discriminate efficiently between gaze aversion and eye contact (Campbell et al, 1990). Thus, primates respond to direct gaze on both a behavioural and neurophysiological level. However, neurophysiological research has thus far only demonstrated sensitivity to direct and averted gaze (in terms of head and eye orientation) and has not revealed sensitivity to gaze in relation to the fixated object (Perrett et al, 1985, 1988; Emery, 2000). Thus, the function of gaze monitoring in nonhuman primates may serve primarily to detect whether or not another individual is looking at you.

On the other hand, where another individual looks may signal important objects or events, so gaze monitoring could also enable nonhuman primates to access information about their physical and social environment (Kummer, 1967). As reviewed in Chapter One, nonhuman primates do visually co-orient with conspecifics and humans; apes and monkeys but not prosimians have been shown to visually co-orient with another individual (e.g. Anderson & Mitchell, 1999; Emery et al, 1997; Tomasello, Call & Hare, 1998; Tomasello, Hare & Fogelman, 2001). While studies with chimpanzees have demonstrated an ability to co-orient to changes in another individual's eye direction alone (Povinelli and Eddy, 1996b), most studies with monkeys have not attempted to determine whether body posture, head or eye direction cues underlie co-orientation. However, Lorincz, Baker and Perrett (1999) used photographic stimuli in order to separate the cues available and reported that rhesus monkeys also co-orient with eye direction alone. In addition, a recent study has demonstrated that monkeys also respond to a human interactant's change in eye gaze direction (Ferrari, Kohler, Fogassi & Gallese, 2000).

Nonhuman primates therefore appear sensitive to photographs depicting eye directions in that they respond to whether gaze is direct or averted and also visually co-orient with the direction of gaze presented (Mendelson et al, 1982; Lorincz et al, 1999). However, a complementary approach is to examine whether nonhuman primates are able to make less egocentric decisions about the direction of others' gaze. That is, rather than examining whether nonhuman primates distinguish direct from averted gaze or whether they exhibit active co-orientation, do they demonstrate any kind of awareness of when another individual is fixating an object?

Study 3: Discrimination of depicted gaze

The present study uses a simultaneous discrimination learning paradigm to examine the ability of olive baboons to discriminate photographs on the basis of whether or not the portrayed model is looking at or away from a target object (Anderson & Doherty, 1997). While monkeys are known to be extremely sensitive to eye direction when detecting self-directed looking, it is unknown whether they are able to discriminate images on the basis of a concept of visual orientation towards a target.

Methods

Subjects

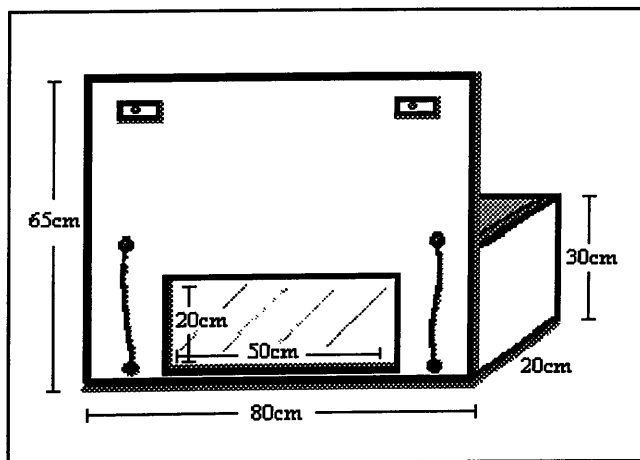
Four olive baboons were studied: two males (Kiki and Gaspard) and two females (Esmeralda and Domi) housed at the CNRS Centre de Primatologie, Rousset-sur-Arc, France. Their ages ranged from 3½ to 10 years and they had either been born at the centre or were transferred there from a safari park approximately two years before the study was conducted. All baboons were housed in spacious indoor/outdoor enclosures in small social groups. For the purposes of testing, the baboons were restricted to the outside area;

dominant baboons were tested in the presence of other group members, while for testing subordinate baboons more dominant members were closed indoors. The monkeys were fed a diet of commercial monkey pellets, fruit and vegetables, with feeding being postponed until the daily testing sessions were completed. Standard food items were used as reinforcers (small pieces of fruit and vegetables or grains of maize).

Apparatus

The apparatus consisted of a large opaque upright wooden panel (65cm x 80cm), which concealed the tester from the baboons' view, with a clear perspex window (20cm x 50cm) at the bottom of the panel which allowed the stimuli to be presented. Two pieces of cord were threaded through holes in the panel and could be pulled from either side of the apparatus, the cords were pulled to the experimenter's side before each trial and the baboons responded by pulling one of the cords towards them. The apparatus could be hooked onto a horizontal cage bar and secured into place with two nuts and bolts modified with small metal bars (see Figure 1).

Figure 1: The apparatus as seen by the baboons.



Materials

Condition One – ‘Direct Gaze’: The stimuli were ten pairs of colour photographs (15cm x 22.5cm) which had been enlarged using a colour photocopier. Each picture consisted of a face-on head-and-shoulder view of one adult person (viewer) in the centre (face approximately 8cm x 6cm), the identity of the viewer changed with each new pairing presented. In each pair, one photograph depicted direct gaze, that is towards the observer, while the other depicted averted gaze (eyes 25° to one side). The positive stimulus was the direct gaze image (see Figure 2).

Condition Two - ‘Head Orientation’: In this set of ten pairs of photographs the viewer was again central. A red ball (diameter 7cm) was suspended with translucent thread approximately 50cm to one side, slightly in front of and above the eye level of the viewer; the position of this target (to the left or right of the viewer) was constant within pairs. Within each pair, the viewer was oriented towards the target in one picture and away from the target in the other so that the head was only seen in profile (see Figure 2). The photograph of the viewer oriented towards the target was always the positive stimulus in this condition.

Condition Three – ‘Eye gaze Fixation’: Ten pairs of photographs again depicted a central viewer and the target object (located as in condition two). However, in the photographs used in this condition the viewer was always face-on, and one of the pair showed the viewer's eyes fixated on the target while the second showed eye gaze averted from the target (both having 25° deviation from centre, see Figure 2). The picture depicting the viewer looking at the target was the positive stimulus in this condition.

Condition Four – ‘Geometrics’: Ten pairs of simple line drawings, the same size as the photographic stimuli, were used in this condition. The drawings consisted of a central geometric shape (e.g. ellipse, rectangle) which were approximately the same size as the

average faces in the photographic conditions (8cm x 6cm). Two smaller symbols (e.g. diamonds or parallel lines, 1.5cm by 2.5cm, that is, approximately the same size as the eyes in the photographs) were placed in what would be the eye positions of a human face. Within each pair, the large shape was constant but the small symbols were different; one member of each pair was chosen to be the correct choice and was always rewarded (see Figure 2).

Design

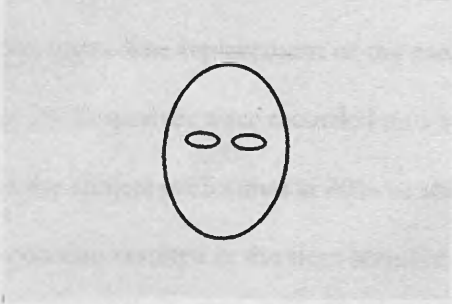
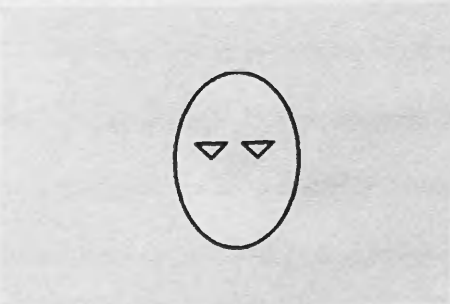
The experiment was designed to allow the baboons to be presented with each of the four conditions in turn, however, due to time constraints, not all the monkeys were tested in all four conditions (as shown in Table 1).

Table 1: Subject characteristics and the experimental conditions encountered by each baboon in Study 1.

Baboon	Condition			
	First	Second	Third	Fourth
Gaspard	Direct gaze	Geometrics	Gaze	Head
Male, aged 6 years			Fixation	Direction
Esmeralda	Head	Direct gaze		
Female, aged 8 years	Direction			
Kiki	Gaze	Head	Direct gaze	Geometrics
Male, aged 5 years	Fixation	Direction		
Domi	Geometrics	Gaze		
Female, aged 10 years		Fixation		

Figure 2. Examples of the stimulus pairs presented:

a) Direct Gaze b) Head Orientation c) Eye gaze fixation d) Geometrics. The images on the right-hand side were the correct choices.



Procedure

Training. Before commencing with the experimental conditions the baboons were trained to meet the response demands required by the task. Firstly, the baboons were trained to pull the cords, secondly, to pull the cords only when stimuli were presented in the window and finally, to perform a simple colour discrimination task using the cords to select one of the two stimuli. Once colour discrimination had been mastered (80% correct for two consecutive 30-trial blocks), the baboons proceeded to the experimental conditions. For Gaspard, this took 2378 and 1950 trials, for Kiki 2284 and 2100 trials, for Esmeralda 1073 and 2794 trials and for Domi 1590 and 2585 trials, for the initial training and colour discrimination tasks, respectively.

Testing. Testing was carried out at approximately the same time each day for each subject but test sessions varied in length depending on the baboons' motivation to perform the task. Basic sessions consisted of 30-trial blocks with the correct stimuli being pseudo-randomly presented to the left or right, with no more than three consecutive baitings to either side. For each trial, an opaque card screen was placed in the window and the pictures were put in place side by side behind this screen; the screen was then removed and the baboon responded by pulling one of the cords. Pulling on the cord next to the correct stimulus was rewarded by the experimenter who delivered a food item directly beneath the centre of the apparatus. The stimuli were then concealed and arranged for presentation on the next trial.

An incorrect response was followed by the immediate replacement of the card screen and a short delay (approximately 10 seconds). Responses were recorded on a score sheet. A problem was considered mastered when the subject performed at 80% or above over two consecutive blocks; attainment of this criterion resulted in the next stimulus pair of the set being presented in the next session. A condition was considered completed if a

baboon reached criterion within two blocks of the problem, that is, 80% correct responses for the first 60 trials presented, for two consecutive stimulus pairs.

Results and Discussion

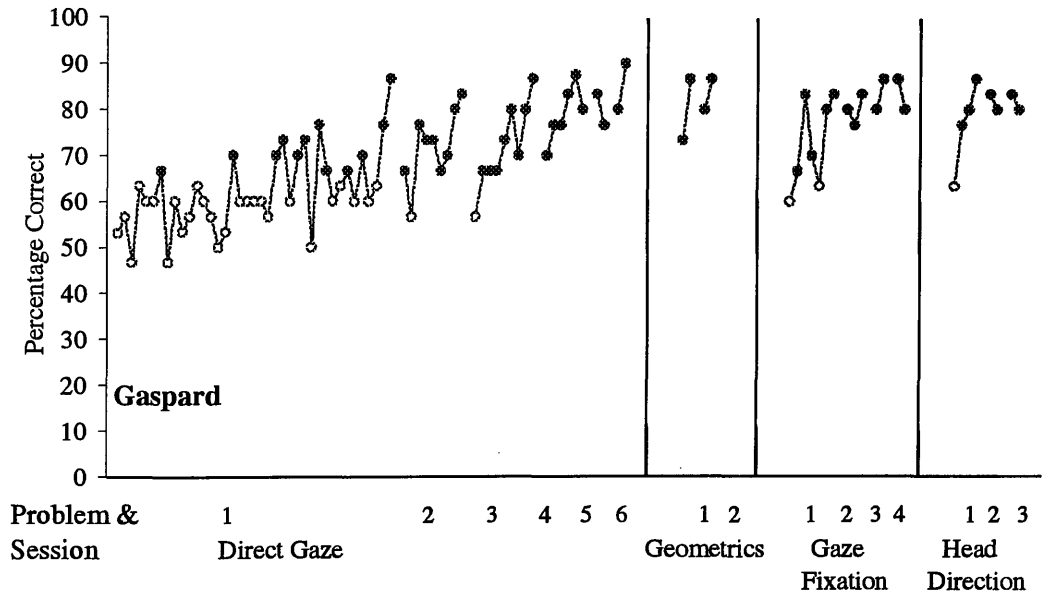
All four baboons reached criterion in at least one of the photographic or line drawing discriminations. In each case the first condition was mastered only after many trials and with marked individual differences in performance. However, two baboons then required only between 2 and 11 sessions to learn subsequent problems. Thus, olive baboons were able to learn to respond selectively to photographs according to the eye and head orientations depicted and showed some evidence of limited transference of this discrimination to novel stimuli. Figures 3a-d shows development of the baboons' performances across sessions in the conditions presented.

Only two baboons (Gaspard and Kiki) completed all four conditions. They both quickly mastered all three conditions presented after the first condition. For Gaspard the first condition was Direct Gaze, which he mastered in 67 sessions; for Kiki the first condition was Eye gaze Fixation, mastered in 59 sessions. In contrast, Esmeralda and Domi both completed their first conditions but failed to complete the subsequent conditions presented even after 48 sessions and 76 sessions respectively. Thus, while able to master the 'Geometric' (Domi) and 'Head Orientation' (Esmeralda) conditions, respectively, these baboons did not reach criterion in a condition requiring that the direction of gaze as indicated by eyes alone be discriminated. This suggests that eye gaze discrimination tasks may have been more demanding, or at least that previous learning during Head Orientation and Geometric conditions did not readily transfer to eye direction discriminations (whereas mastering eye direction problems did appear to facilitate performance on subsequent tasks).

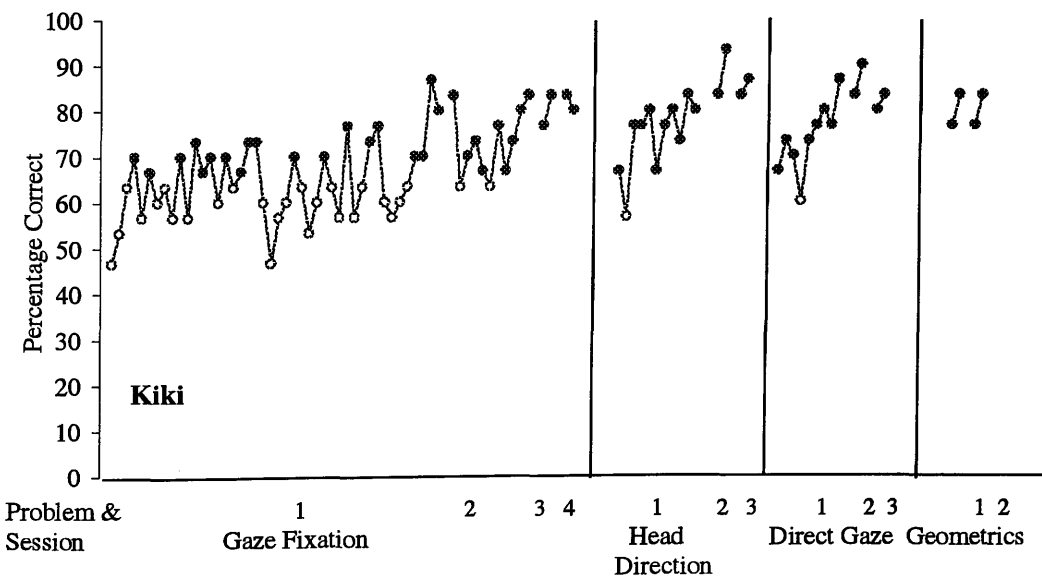
Figure 3. Individual performance on the picture discrimination task for a) Gaspard b) Kiki c) Esmeralda d) Domi.

Solid data points represent above chance performance (Binomial tests, $p < 0.05$) and open data points represent chance performance.

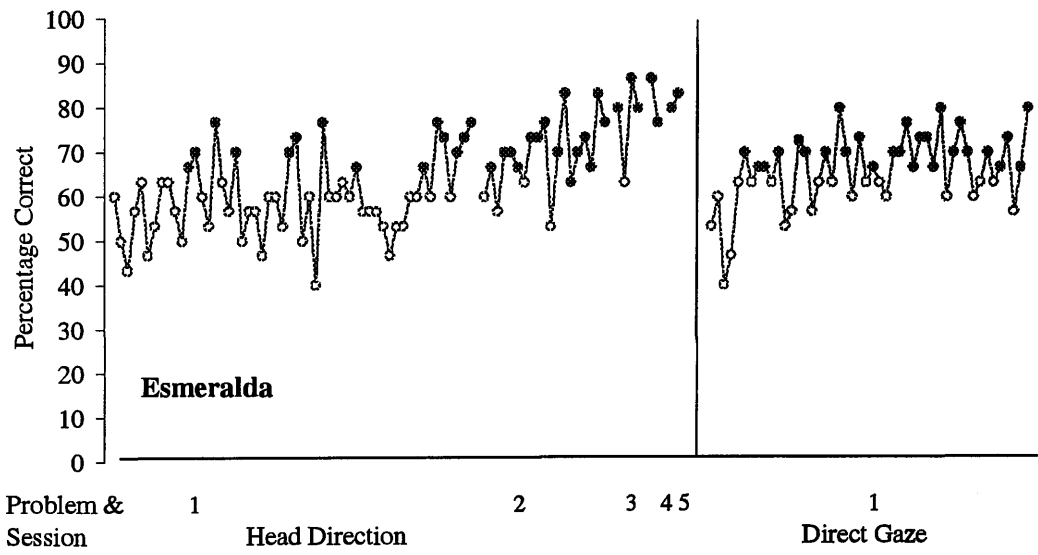
a)



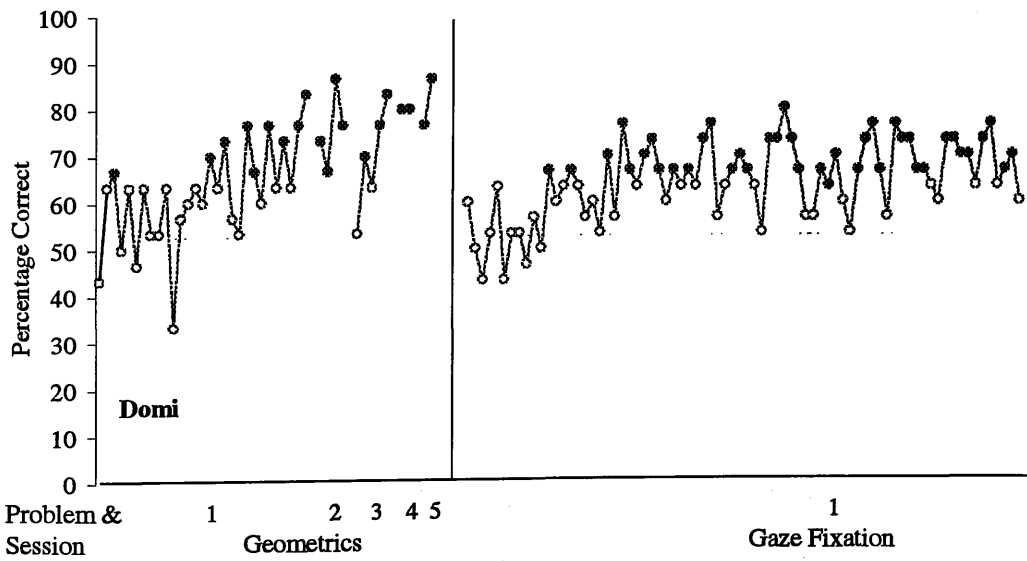
b)



c)



d)



Both Gaspard and Kiki showed fastest learning in the 'Geometric' condition, which in addition to Domi's ability to perform this discrimination is suggestive of lesser cognitive demand in this task, perhaps because the stimuli were simpler. For example, there was no need to consider any target objects for successful responding and the physical differences between the images may have been more salient.

It is difficult to determine exactly how the baboons solved the problems presented. Gaspard and Kiki both showed gradual improvement across successive conditions. While their results could indicate that a concept of 'looking at' had been learned, they could also reflect simple improvement at discriminating complex visual images rather than responding to the photographs as meaningful images. That is, rather than learning to respond to photographs depicting visual orientation to objects, the baboons may have been responding according to more simple rules (Perrett et al, 1988; Vauclair & Zayan, 1988). For example, the photographic problems could be solved using physical cues such as absolute head or eye orientation, or, for the Direct Gaze condition, the detection of a highly salient image; namely direct gaze (e.g., von Grunau & Anston, 1996; Mendelson et al, 1982). However, the fact that even this image was not readily discriminated, requiring 67 sessions for Gaspard and 13 sessions for Kiki, might suggest the absence of any attribution of social meaning to the photographs.

Studies of face processing in nonhuman primates have suggested that face discrimination can be processed in two distinct ways: either holistically or in a piecemeal or feature based manner (Perrett et al, 1988). Task demands have been identified as determining to some extent the method of processing engaged; for example, some face recognition tasks simply do not require any configurational processing and are easily performed on the basis of specific feature discriminations (Keating & Keating, 1993; Perrett et al, 1988). It has been proposed that when monkeys are tested on categorisation tasks, larger stimulus sets preclude piecemeal strategies; the individual characteristics of

images are not learned but rather a more general categorisation (e.g., Schrier & Brady, 1987). The present study used a limited stimulus set for each condition, and only two images within any given problem, which leaves open the possibility that successful baboons may have learned to discriminate key features of the photographs presented, rather than requiring a concept of 'looking at' to guide their responses.

Study 4: Does gaze discrimination transfer to a live model?

Study 4 was designed to investigate further the possible strategies used by baboons showing gaze discrimination in Study 3. If the baboons perceived the photographs as socially salient and encoded something about the looking behaviour (at any level) of the model, then this experience might facilitate subsequent performance on a related task using a real model. A task was presented so that a simple discrimination, such as consistently responding to the absolute orientation of the head or eyes (that would have sufficed for an individual problem in the first study) would not lead to mastering the new experimental conditions. The only way in which such simple rule learning could facilitate performance on the new task would be if it were based on the relationship between a cue and the location of the target object in the photographs, (e.g., visible sclera away from target object). While this would also be simple visual discrimination, it is indistinguishable from identifying 'looking at the object' and indeed such a simple mechanism may not be any different from how nonhuman primates perceive visual orientation. For example, a 'low-level' account of gaze following simply requires co-orientation until something of interest is encountered; eye direction may be a simple discriminative cue to look in a given direction (Tomasello, Call & Hare, 1998). Thus, visual orientation in others could be encoded by the direction of gaze as an arbitrary discriminative cue and the presence of an object or event in the congruent direction.

A simple object-choice task was used in which an experimenter presented the baboons with gaze cues towards the target location (Anderson, Sallaberry & Barbier, 1995). This study aimed to compare the ability of two baboons trained to discriminate the gaze direction of humans in photographs (using head and/or eye direction as cues) with the performance of baboons without such prior learning.

Methods

Subjects

Four olive baboons were studied. Two males, Gaspard and Kiki, had learned to discriminate gaze direction in photographs in Study 3. Two females, Esperance (9 years old) and Ida (5 years old), had no experience of tasks involving facial stimuli but had extensive experience in an unrelated object and picture categorisation task using the same apparatus (Bovet & Vauclair, 1998). None of the baboons had any prior experience of tests in which the experimenter communicated cues. Housing and feeding were as described for Study 3. Dietary treats (raisins) were used as reinforcers.

Apparatus

The apparatus was a wooden rectangular box (80cm x 20cm x 20cm) which could be hooked onto the outside wall of the cage approximately 50cm above ground level. Two shallow food-wells (3cm diameter) were set 60cm apart in the top of the box; these were each covered by a square piece of wood (5cm x 5cm) and secured in one corner and could be rotated to reveal the wells. A large, hand held screen (50cm x 90cm) was used to conceal the baiting procedure.

Procedure

Pre-training: The baboons were familiarised with the apparatus by the experimenter; food items were placed in the uncovered wells, which the baboons were then allowed to retrieve. Gradually, the well covers were moved so as to finally conceal the treats entirely, so that the baboons had to push the covers out of the way to retrieve the food items. The baboons readily learned to do this within one training session.

Testing: During testing, the baiting procedure was concealed from the baboons by the screen; experimenters always rotated the covers of both wells in the same order so that sound cues were not available. The location of the treat was pseudo-randomised between the left and right food-wells with no more than three consecutive baitings on one side. After baiting was completed, the screen was lowered so that the experimenter could be clearly seen by the baboon, while the two food wells remained concealed. The experimenter was already in a static posture according to the cue condition for that trial. Baseline trials showed the experimenter fixated on the centre point between the two food wells and therefore supplying no cue, while in cue conditions the experimenter had either head and eyes or eyes only oriented towards the correct side, according to condition (see Appendix A).

There was a minimum 5-second (extendable up to 10-seconds) observation period to ensure the baboon looked at the experimenter. The screen was then fully removed to allow the baboon to respond; a correct choice revealed a food item which they could retrieve and consume, while an incorrect response was immediately followed by the screen being reinstated and hence the end of the trial. A 10-second time-out followed an incorrect response and a correction procedure was used with the treat remaining in the same location on correction trials until found. Responses were noted on a record sheet. Sessions consisted of 30-trial blocks and the baboons completed one to four sessions a day.

Head orientation and eye direction were used as experimenter-given cues. Each naive female baboon was paired with an experienced baboon; all the baboons were first presented with one block of baseline trials and subsequently one pair was presented with head (and eye) orientation as a cue, while the other pair received only eye direction as a cue. Criterion for mastering the task was set at 80% for two consecutive sessions.

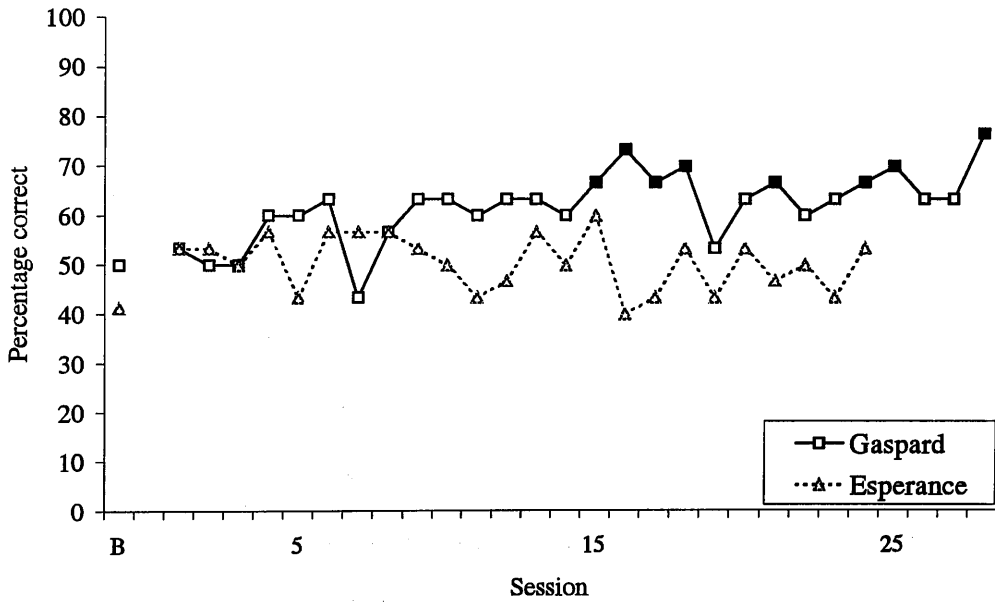
Results and Discussion

None of the baboons succeeded in reaching the 80% criterion level even after over 700 trials (excluding correction trials) with experimenter-given cues available (see Figure 4). Gaspard's performance in the head orientation cue condition did rise significantly above chance levels (Binomial tests, $p < 0.05$) in 8 of the last 14 sessions. In contrast, Esperance, in the same condition, failed to respond above chance levels. While it may be tempting to attribute Gaspard's superior performance to his previous experience with photographic stimuli, the results may simply reflect individual variation. It is clear that he did not perform above chance until after over 400 trials and, furthermore, that his performance remained fairly inconsistent thereafter. This trend is not suggestive of a positive transfer of information acquired in earlier testing to the new situation, but does suggest that he was learning to exploit head orientation as an experimenter-given cue within this new experimental paradigm.

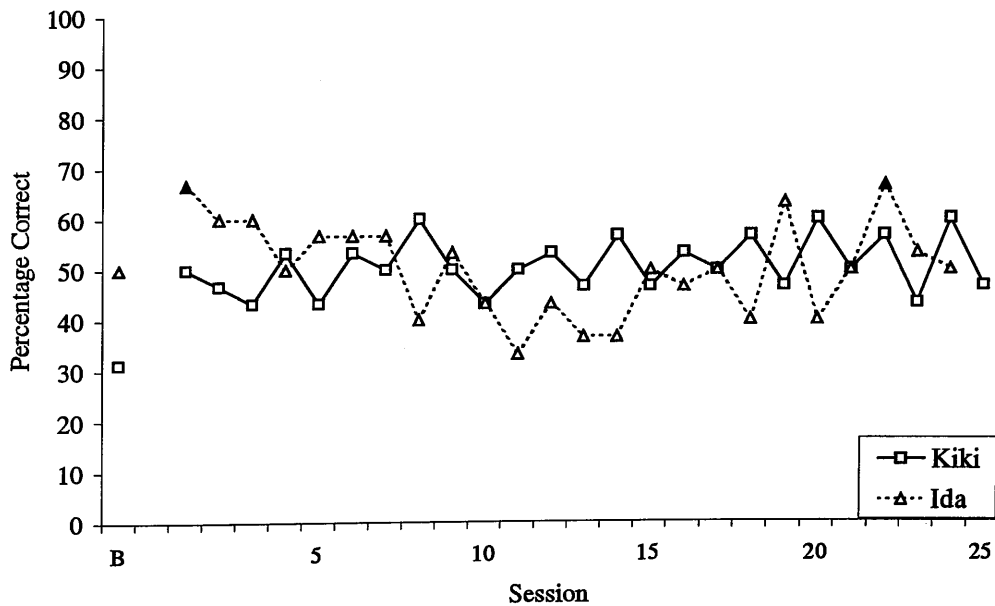
Figure 4. Individual performance in the object-choice task for a) head orientation b) eye gaze.

Solid data points represent above chance performance (Binomial tests, $p < 0.05$) and open data points represent chance performance.

a)



b)



In the eye direction cue condition, neither baboon learned to use this cue in order to locate the food. For Kiki this suggests an absence of positive transfer of any comprehension of attention or gaze direction from his experience with photographic stimuli. Both Kiki and Ida failed to learn the task even after more than 700 trials (excluding correction trials). Although Ida was above chance during her very first session, her subsequent performance suggests that this was not indicative of a cue-reading ability but rather the high score was due to chance.

The results of Study 4 make it difficult to draw any strong conclusions regarding the salience of head and eye direction as experimenter-given cues for baboons. The failure of the baboons to master their initial cue conditions prevented any comparison of the baboons across conditions and therefore individual differences cannot be excluded. It is noteworthy that the only baboon to show signs of learning was tested in the head orientation condition; findings to date suggest that head orientation, rather than eye direction alone, is a more salient cue for nonhuman primates in object-choice tasks (Itakura & Anderson, 1996; Povinelli, Biershwale & Čech, 1999; see also Study 5). However, while head turns by a model may spontaneously produce visual re-orienting in monkeys (Anderson & Mitchell, 1999; Tomasello, Call & Hare, 1998), when it comes to object-choice even this cue may not be readily used without explicit training (Anderson, Montant & Schmitt, 1996; Anderson, Sallaberry & Barbier, 1995; Itakura & Anderson, 1996). While one baboon did learn to exploit head orientation as a cue this required a considerable number of sessions, suggesting that the cue was learned and that the task was not tapping an underlying visual co-orientation mechanism.

General Discussion

A potential problem in integrating the results of studies 3 and 4 concerns the use of different tasks to assess the discrimination of visual orientation towards an object. For example, the target items were visually very different. However, it seems reasonable to expect that any natural ability to discriminate the object of another individual's gaze would be generalisable to a range of contexts, objects and even events, as long as the cues remained explicit. In other words, it could be argued that if the baboons in Study 3 had learned or used a strategy based upon 'looking at' at any level, they should have subsequently exploited the corresponding type of information presented in Study 4 to master the object-choice task.

However, the results of these studies can be interpreted in several ways. Firstly, although nonhuman primates may be adroit behaviour readers, this sensitivity to behavioural cues might not reflect an ability to attribute even basic attentional states, such as seeing, to others or to categorise a behaviour as 'looking at' (Cheney & Seyfarth, 1991; Whiten, 1996). If the visual co-orientation response observed in many primate species is a fairly automatic behavioural response, then maybe they are unable to form a concept such as 'looking at'. Thus, the baboons solved the problems on a cue-learning basis as this was the only means available to them. Alternatively, it may be that nonhuman primates are able to appreciate when another individual is looking at an object, but that the methods used in these studies did not invoke the use of this ability. For example, the relatively slow rates of acquisition and lack of transfer may have been due to motivational problems; basic procedural flaws such as too short a time-out period may have led to less than optimal performances. Moreover, it may be that the use of a small stimulus set in Study 3 favoured the use of a piecemeal processing strategy (Schrier & Brady, 1987; Perrett et al, 1988). Although the signs of positive transfer displayed by two baboons within Study 3 could be

seen as contrasting with such a position, it may be that they had simply started to form learning sets (Drea & Wallen, 1995; Harlow, 1949; Miles, 1965; Schrier & Brady, 1987).

Furthermore, it is possible that the baboons did not perceive the photographs as representations of real objects and could have processed them independently of their representational content. Whether, and at what level, animals perceive a correspondence between objects and their pictorial representations is currently being debated (Bovet & Vauclair, 2000; Fagot, Martin-Malivel & Dépy, 1999). It is also conceivable that during the object-choice task, the baboons did not consider the experimenter as a social interactant. However, as noted in Chapter One, nonhuman primates readily respond to humans with appropriate social gestures (Exline & Yellin, 1969; Kummer et al, 1996), so it is unlikely that the central problem was due to the inter-species nature of the interaction or the stimuli used.

A third explanation for the results obtained is that the baboons did use information concerning looking at versus not looking at in some manner (rather than simple physical cues) during Study 3 but failed to make explicit use of the related information in Study 4. As discussed in Chapter One (Section 3.4b), the object-choice task has produced equivocal results concerning nonhuman primates' abilities in using gaze cues. While many species of primates have been shown to respond by visually co-orienting to the changes in head and/or eye direction of another individual (Anderson & Mitchell, 1999; Ferrari et al, 2000; Tomasello, Call & Hare, 1998; Tomasello, Hare & Fogleman, 2001), performance in the object-choice task often fails to reflect these abilities. For example, chimpanzees that demonstrated gaze following in response to shifts in eye direction alone were subsequently unable to use this same information to solve an object-choice task (Povinelli, Bierschwale & Čech, 1999). Nonhuman primates show at best inconsistent responses across variants of the object-choice task (Anderson, Montant & Schmitt, 1996; Anderson, Sallaberry & Barbier, 1995; Call, Hare & Tomasello, 1998; Call, Agnetta & Tomasello, 2000; Itakura et

al, 1999). That is, it may be that the object-choice task was an inappropriate transfer task (Hare, 2001).

Thus, baboons were able to learn gaze discrimination using photographic stimuli, but it is difficult to ascertain whether this reflects an underlying concept of 'looking at' as they did not demonstrate any positive transfer from picture discrimination to an analogous problem presented by a real model. However, several methodological problems with the present studies have been identified which may account for this failure. In spite of evidence suggesting that baboons may be sensitive to the visual orientation of others (e.g. in "tactical deception", Byrne and Whiten, 1998), it remains to be demonstrated that such behaviours are indeed based upon an ability to appreciate gaze, rather than an appreciation of behavioural contingencies that may or may not be related to their gaze behaviours.

Chapter summary

The ability to discriminate between pairs of photographs according to the portrayed model's visual orientation in relation to a target object was examined in four olive baboons. Two baboons successfully managed to solve the problem, even when gaze was demonstrated by eye direction alone. A third showed an ability to discriminate head direction but not eye direction. In order to investigate further their ability to discriminate gaze, the two successful baboons and two naïve baboons were presented with a simple object-choice task accompanied by experimenter-given cues. There was no evidence of transfer from the photographic stimuli to a real model; only one baboon showed signs of using the experimenter's gaze to choose between two objects, and only after over 300 trials. These results could suggest that the baboons used simple physical cues rather than a concept of 'looking at' to solve the picture discrimination but alternative explanations were also considered.

Chapter Four

Use of Experimenter-Given Cues by Capuchin Monkeys in an Object-Choice Task

In parallel with work on primates' responses to others' changes in visual orientation, studies using an object-choice paradigm, in which the experimenter presents behavioural cues to indicate the location of a hidden food item, have attempted to examine whether nonhuman primates can use gaze information in a problem-solving context. In addition, this paradigm has also attempted to identify the relative salience of potential cues. Initial studies with capuchin monkeys (Anderson, Sallaberry & Barbier, 1995), and rhesus macaques (Anderson, Montant & Schmitt, 1996) found that while monkeys responded to gestural cues (pointing), they were unable to use a gaze cue which consisted of both head and eyes oriented towards the correct object. One consideration in these studies was the differences in cue-stimulus spatial contiguity in the cue conditions presented. The study with rhesus monkeys addressed this issue in a second experiment; even when the experimenter's head and eyes were positioned much closer to the objects, the monkeys did not readily use these cues to achieve above-chance performance levels (although one of the three monkeys did show improvement relative to baseline sessions). Furthermore, a cue condition consisting of eye direction alone in similarly close proximity to the objects produced no improvement in performance above chance levels.

Itakura and Anderson (1996) trained a single capuchin monkey to use several behavioural cues in an object-choice task; the original object-choice procedure was modified to include correction trials and time-out periods following errors, and an enforced observation period. This monkey not only readily learned to use manual cues given by the

experimenter but also learned to use combined head and eye direction presented both at close proximity to and at a greater distance from the correct object. However, when eye direction alone was presented, the capuchin's performance fell to chance levels.

In contrast to the largely negative data regarding the abilities of monkeys to use eye-gaze cues in an object-choice task, there is some evidence, albeit inconsistent, of such an ability in great apes. Itakura and Tanaka (1998) using the same object-choice paradigm as above, found that chimpanzees, an orangutan and human infants (2 years old) were all able to use experimenter-given cues up to and including eye direction alone to locate the baited object. However, a study which presented eye direction as probe trials within a session of pointing trials, found that juvenile chimpanzees, (in contrast to 3 years old children), were unable to use eye direction alone as a cue. Although the chimpanzees were able to use head orientation, they did not differentiate between an experimenter looking at or above the target (Povinelli, Bierschwale & Čech, 1999). In addition, an object-choice study with gorillas found that while performance levels were high when manual gestures or combined head and eye direction were presented, the gorillas would not respond to eye orientation only (Peignot & Anderson, 1999).

The apparent inability of monkeys to use eye direction as an information source contrasts with abundant evidence identifying eye gaze as a highly salient feature of interactions both with conspecifics (Chance, 1967; Emery, 2000) and humans (Exline & Yellin, 1969; Exline, 1972; Thomsen, 1974). Thus, nonhuman primates' display considerable sensitivity to other individuals' visual orientation in general and to eye direction in particular, both in terms of behavioural and neurophysiological responses. This makes their responses to gaze within experimental paradigms intriguing; outside of the gaze following context, there is less convincing evidence that they can make explicit use of such gaze information. Although capuchin monkeys have not been tested within a gaze

following paradigm, the studies reported here aimed to further explore the abilities of capuchins to use experimenter-given cues in an object-choice task.

In addition, the ability to use eye gaze was tested more thoroughly than in previous studies. While eye direction might be expected to be the most accurate means of determining what another individual is looking at (at least in humans, see Kobayashi & Koshima, 1997; 2001 for example), it may be that for monkeys less precise indicators are usually used. For example, following another individual's head orientation may be adequate for detecting important object or events (Perrett & Emery, 1994; Emery, 2000). This present study further examined the importance of various visual cues which monkeys may use to ascertain visual orientation. Gestural cues such as touching and pointing, head orientation and eye direction were presented as experimenter-given cues in a simple object-choice task, with additional conditions aimed at revealing whether monkeys are able to read eye gaze within the object-choice paradigm.

Study 5: An object-choice task

This experiment aimed to replicate and extend Itakura and Anderson's (1996) finding that a single capuchin monkey was able to learn to use cues given by a human experimenter up to, but excluding, eye direction. Might some modifications to the conditions presented reveal effective use of eye direction alone as an experimenter-given cue during an object choice task? More specifically, would a reduction in the distance between the eyes and object or the addition of eye movements be conducive to mastering the use of eye direction alone as a cue?

Methods

Subjects

The monkeys tested were three captive-born, adult female capuchin monkeys: Zilla (6 years old), Theta and Kiki (both 4 years old), members of a social group of five. They were fed a daily diet of fresh fruit and vegetables and commercial monkey pellets. During the study feeding was postponed until after the daily test sessions, with standard food items (small pieces of fruit) being used as rewards during testing.

Apparatus

The monkeys were tested in a clear perspex test cage (47cm x 51cm x 47cm) in a room adjacent to the colony room. A hatch in the front panel (25cm x 27cm) could be secured by a small bolt so that there was a 3cm high horizontal opening along the bottom to allow monkeys to respond by reaching through to touch their chosen object. The test cage was secured on a 75cm high metal frame with a table (40cm x 80cm x 75cm) placed adjacent to the front panel. A wooden tray (40cm x 24cm) on which the objects were placed could be moved along the table; away from the test cage for baiting and toward it for presenting trials. Two identical transparent containers (8cm x 11cm x 6cm) were secured to the tray during pre-training, these were replaced by opaque brown containers during testing; each positioned 4cm from the front edge and 20cm apart. A screen (52cm x 46cm) was used to conceal the baiting process from the monkeys.

Procedure

Pre-training. The monkeys underwent preliminary training in which they learned the basic task of choosing between two objects in order to locate a hidden food item. The experimenter baited one of two transparent containers behind the screen, interposed between the apparatus and the cage front, always lifting and then replacing both containers

in the same order to eliminate sound and movement cues. The screen was then removed and a 5-second observation period was allowed before the experimenter pushed the tray towards the test cage. During these training sessions the experimenter maintained a neutral posture with head and eyes remaining oriented toward the centre of the apparatus midway between the two containers. During the first session (30 trials) a food item was visible in one of the two containers; the monkeys had to touch or push away the baited container in order to be given the reward. If the incorrect container was chosen the tray was withdrawn and a 20-second time out followed before the same trial was represented, that is, a correction procedure was used until a correct choice was made. All three monkeys learned to respond to the baited container and receive the treat within one session. For the next session an opaque brown container was introduced; during this session the clear container was always empty and the monkeys had to respond to the opaque container in order to obtain the food item. All monkeys learnt to do this task successfully (i.e. over 80% of trials correct) within the 30-trial session.

Testing. The baiting method for test sessions was identical to that used in training trials. For the testing sessions two identical brown containers (hereafter called ‘objects’) were presented; the location of the food item was pseudo-randomised between sides so that there were equal baitings of the right and left object up to a maximum of three consecutive trials on either side. Each experimental condition was preceded by a baseline session. During baseline trials the experimenter removed the screen then pushed the tray towards the monkey while maintaining a neutral posture, head facing forward and fixating midway between the objects. During experimental trials, the experimenter removed the screen to reveal the appropriate cue condition, then pushed the tray toward the monkey following the observation period. Again, the monkey had to choose the baited object in order to obtain the food item; an incorrect choice led to a time out and a correction trial (see Appendix B). Table 1 describes the cue conditions.

The monkeys were tested in a given cue condition until a criterion of 80% correct choices on two consecutive sessions was reached or for ten sessions. However, flexibility was allowed to the extent that if a monkey appeared to be improving and was approaching criterion the condition continued for up to five extra sessions. If a monkey failed to reach criterion with a cue presented near to the correct object (15cm) she was not tested in the far condition (60cm). Each session consisted of 30 trials (plus correction trials), with a maximum of two sessions each day.

Table 1: Cue conditions used in Study 5.

-
1. **Tap:** The experimenter's head and eyes oriented towards the correct container; experimenter taps the top of the container with the index finger during the 5 second observation period.
 2. **Point:** The experimenter looks towards (head and eyes) and points to the correct container; the index finger being approximately 15cm away from the object.
 3. **Head and Eyes Near:** Head and eyes oriented towards the correct container at a distance of about 15cm.
 4. **Head and Eyes Far:** As in Condition 3, but at a greater distance (approximately 60cm)
 5. **Eyes Near^a:** The experimenter faces the experimental cage at a distance of about 15cm, with eyes only oriented towards the correct container.
 6. **Eyes Far:** As Condition 5 but at a distance of about 60cm.
 7. **Glance Near^a:** The experimenter's head oriented towards the test cage at a distance of approximately 15cm, eyes fixated centrally between the two containers.. During the observation period the experimenter makes three to-and-fro eye movements between the correct container and the centre point, before presenting the stimuli.
 8. **Glance Far^a:** The experimenter follows the same procedure as in Condition 7 but at a distance of approximately 60cm.
-

^aThese conditions are additions to the Itakura and Anderson (1996) procedure.

Results and Discussion

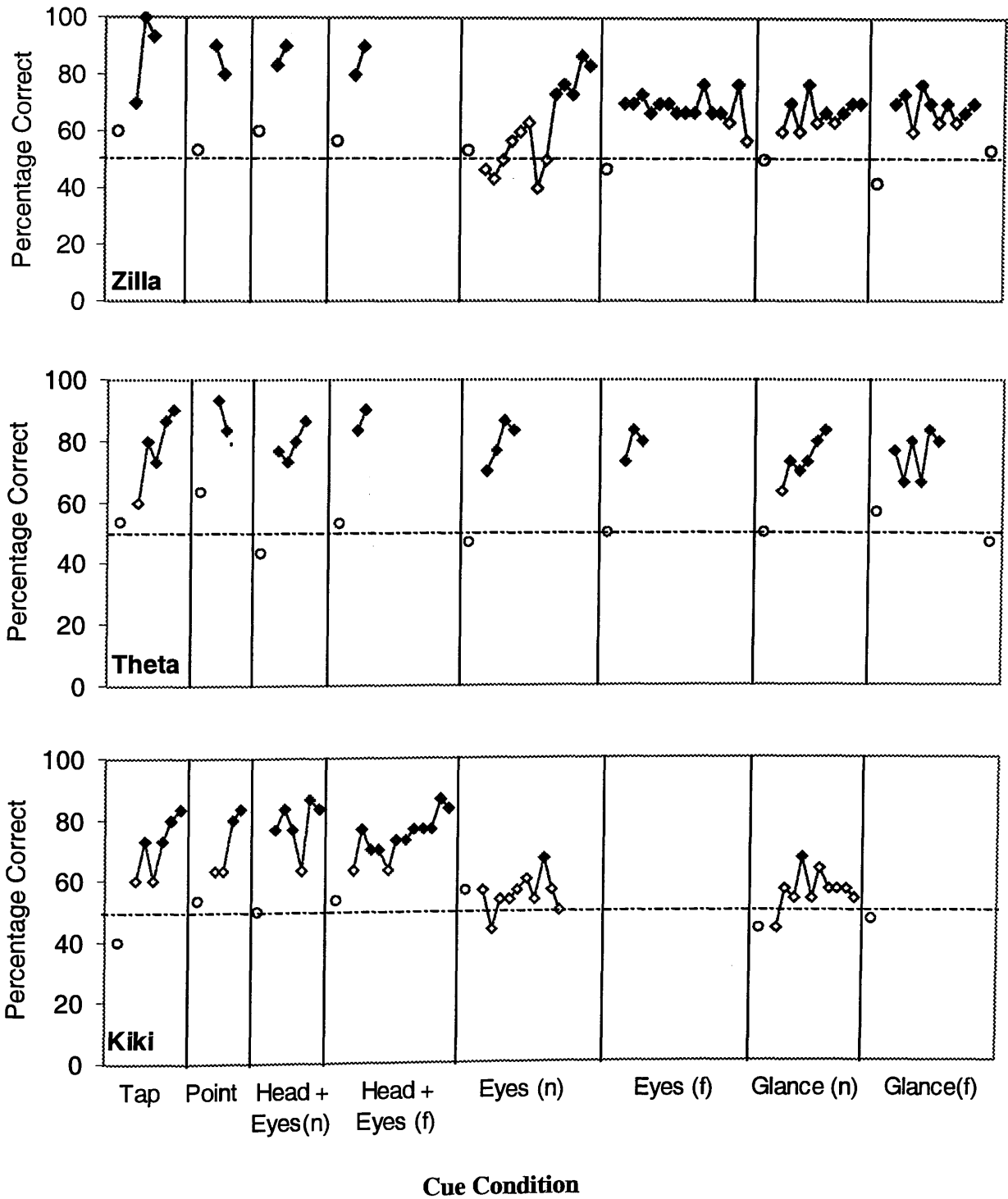
As can be seen in Figure 1, all three monkeys scored at around chance levels in all baseline sessions, when no explicit cue was displayed by the experimenter. Figure 1 also shows that all three monkeys successfully mastered conditions 1 – 4 (Tap, Point, Head and Eyes Near, and Head and Eyes Far), and met the criterion of 80% on two consecutive sessions. This required the minimum of two sessions (Theta: conditions Point and Head and Eyes Far; Zilla: three of the four conditions) and a maximum of twelve (Kiki: condition Head and Eyes Far). When eye direction became the only cue available, Theta continued to show consistently high levels of performance. She met the criterion of two consecutive sessions with 80% of trials correct in all conditions involving only the eyes, although she took longer to do so in the Glance conditions. Zilla showed an initial decrease in performance in the Eyes Near condition. She performed at chance levels for eight consecutive sessions, before finally reaching criterion in this condition after 13 sessions. Her subsequent performance in Eyes Far and Glance conditions, while significantly above chance (binomial tests, $p < 0.05$), did not reach 80% correct for two consecutive sessions. Kiki's performance also diminished markedly in the eyes-only cue conditions; her performance did not rise consistently above chance levels in either of the two conditions in which she was tested (Eyes Near and Glance Near).

These results indicate that, allowing for individual differences, capuchin monkeys are capable of learning to use eye direction alone as an experimenter-given cue. Although this result contrasts with that reported by Itakura and Anderson (1996), the results of the earlier study (a single capuchin unable to master an 'eyes only far' condition within a block of eight 30-trial sessions) are comparable to the performance of two monkeys in the present study tested on their first eyes only condition (Eyes Near). In the present study, the diminished performance of one monkey and the inability of another to use eye direction as a cue at all, suggests that while the eye-direction of a human experimenter may

become an effective cue, it may not be very salient for capuchin monkeys even after successful training with other cues, including head and eye direction together.

Figure 1: Individual performances across cue conditions 1-8.

Circles represent baseline sessions and filled data points represent above chance performance.



One monkey showed above chance performance in the Eye Far and Glance conditions but she failed to reach 80% correct for two consecutive sessions, suggesting that despite some exploitation of eye orientation she had not truly mastered the association between this cue and the stimulus. Conceivably, some degree of automatic orientation in response to the cue occurred (see Lorincz, Baker & Perrett, 1999) which then increased the probability of a response to the cued side. However, her performance is more indicative of cue learning than of some untrained orienting mechanism as her performance improved over sessions. In contrast, Theta's consistently higher performance suggests that she was better able to exploit eye direction as a cue in a manner comparable to the earlier, more gross cues.

Zilla's diminished performance in the Eyes Far condition relative to the Eyes Near condition, and Kiki's similar decline in performance from Head and Eyes Near to Head and Eyes Far, indicates that reducing the cue-stimulus distance may facilitate the use of experimenter-given cues. The addition of movement to the eye cue in the Glance conditions seems to have been detrimental to performance for Zilla and, initially, for Theta (see Figure 1). This corresponds with Povinelli and Eddy's (1997) finding that movement did not improve gaze following to eye direction alone in chimpanzees or performance on an object-choice task with experimenter-given cues (Povinelli & Eddy, 1997; Povinelli, Bierschwale & Čech, 1999). In the present study, performance may have decreased in Glance conditions because the eye direction cue was available for a shorter overall duration within the observation period, thus making it potentially easier for the monkeys to miss the cue. In addition, the monkeys often continued to look at the experimenter while the tray was pushed forward; in all previous condition this would have revealed the cue condition but in Glance conditions the experimenter had returned their fixation to the centre of the tray and subsequently offered no cue immediately prior to the monkeys' response.

Study 6: Extents and limits of gaze reading

In view of the varying levels of performance attained by the three monkeys in Study 5, additional procedures were conducted in order to clarify the extent and limits of the monkeys' use of eye-direction as a cue.

As monkey Theta successfully mastered all the cue conditions up to and including Glance Far in the previous experiment, further sessions were conducted in order to assess whether she would transfer use of this cue to a novel experimenter. As Kiki did not master any of the conditions involving eye direction as the only cue, she was tested again in the Eyes Near condition, but the experimenter wore a hood in order to remove facial features other than the eye region. The reasoning behind this modification was as follows: research with human infants has shown that removing the face may facilitate gaze following and while the authors suggest that it is specifically fixation on the eyes which prevents visual co-orientation occurring, the possibility that the face itself is distracting cannot be discounted (Hood, Willen & Driver, 1998). Furthermore, Povinelli and Eddy (1996a) found that chimpanzees discriminated more easily between two trainers' eyes (open versus closed) when faces were obscured using screens than when full faces were visible. However, another study reported that wearing a hood to obscure the face led to reduced responses from monkeys; suggesting that eyes need to be presented within the context of a face (Exline, 1972). Thus, it was not entirely clear whether concealing all facial features except the eyes would have a beneficial or detrimental effect on performance. Finally, Theta and Zilla, who had both demonstrated the ability to use eye direction alone as a cue in Study 5, were tested in a "mixed cues" condition for two sessions each (Corkum & Moore, 1995). In these sessions head and eye cues were varied in order to try and identify the relative salience of these cues (Emery et al, 1997; Langton, 2000; Lorincz, Baker & Perrett, 1999).

Methods

Procedure

For the transfer sessions conducted with Theta, the experimenter was an adult female highly familiar to the monkey; the procedure was the same as for condition 6 in Study 5 (Eyes Far) and ten sessions were conducted. The procedure for the hood experiment with Kiki was the same as for the Eyes Near condition in the previous experiment except that the experimenter (the same as previously) wore a hood so that only the eye region of the face was visible.

For the mixed cues condition presented to Zilla and Theta, four types of trial were presented within each session, 10 each of two new cue conditions and five of two previous conditions. The order of these trials was pseudo-randomised with an equal number of baitings to either side. The conditions were as follows:

- A) Head only: As Condition 4 above but with the experimenter's eyes closed.
- B) Head and eyes: As Condition 4 above; head and eyes both oriented towards the correct object.
- C) Eyes only: As in Condition 6 above; head oriented forward with only eyes directed towards the correct object.
- D) Head versus eyes: The experimenter's head oriented towards one object but her eyes fixated on the other. For these trials both objects were baited as both were effectively being cued.

Results and Discussion

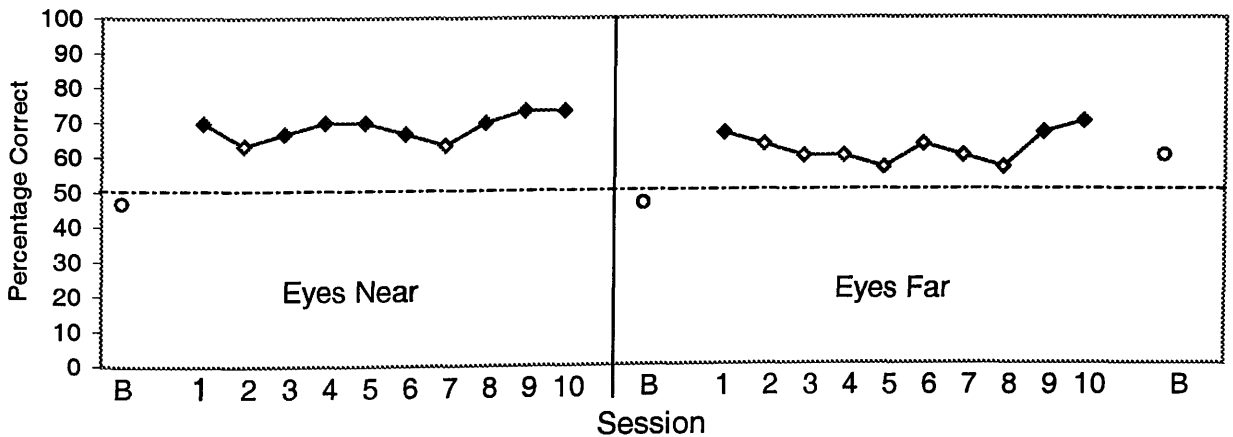
Theta's performance on the sessions with a new experimenter was considerably lower than in previous conditions. She scored significantly above chance on six of the ten sessions, but her performance on the final two sessions (68.3%), although significantly above chance

(binomial test $p < 0.049$), was well below the 80% which she had achieved in the same condition in the previous experiment.

Figure 2 shows Kiki's performance when presented with the Eyes Near and Eyes Far conditions by the hooded experimenter. Kiki showed a considerable improvement in performance during the Eyes Near condition compared to her performance in the corresponding condition presented without the hood in the previous study. She was significantly above chance in eight out of the ten sessions (binomial tests, $p < 0.05$) although she did not reach 80% correct. Nevertheless, in view of the fact that she showed improvement, the experimenter proceeded to the Eyes Far condition again with the hood. When the cue-stimulus distance was increased her performance initially diminished and she performed at chance levels on seven of the ten sessions, however, in the two final sessions she was significantly above chance (binomial tests, $p < 0.05$).

Figure 2: Kiki's performance in the 'hood' conditions.

B represents baseline sessions and filled data points represent above chance performance.



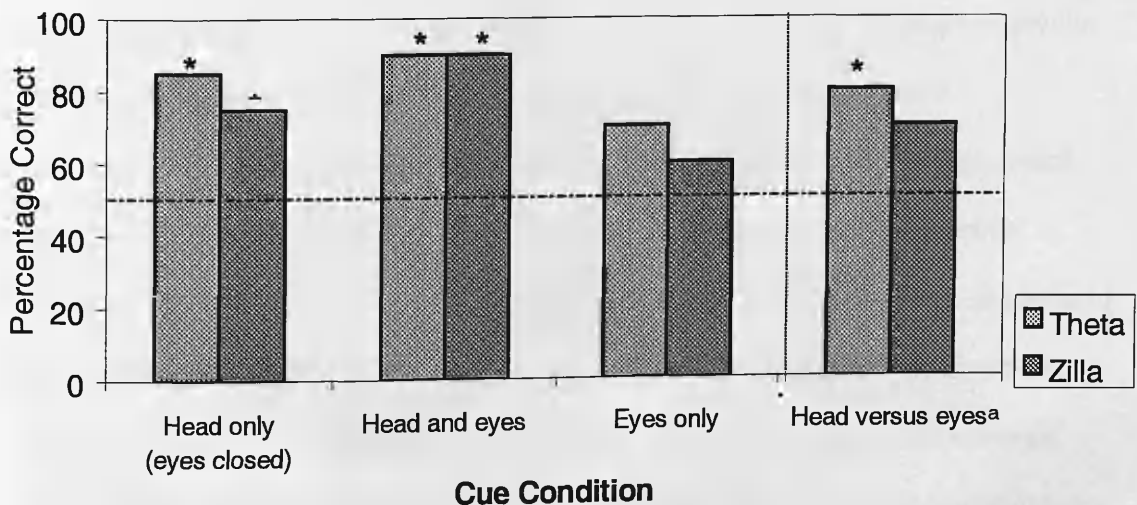
Kiki's results are difficult to interpret; while the removal of facial features except for the eyes might have facilitated performance, order effects cannot be ruled out, as these hood sessions directly followed 20 sessions in which eye direction was the only cue

available. It would have been interesting to return to the non-hood eye direction conditions in order to see whether the improved performance levels were maintained, but unfortunately time constraints precluded this.

As shown in Figure 3, Theta and Zilla both readily used head direction as a cue in the absence of any eye cue (Condition A, Theta was correct on 17/20 trials $p < 0.01$, Zilla on 15/20 trials, $p < 0.05$). When head direction was presented in conflict with eye direction the results were less clear; both monkeys showed a preference for the object cued by head (rather than eye) direction although both objects were baited (Condition B, Theta 16/20, $p < 0.01$, Zilla 14/20, $p = 0.058$), but at a lower level than in Condition C when head and eyes were oriented in a congruent manner (Theta 9/10, $p < 0.05$, Zilla 9/10, $p < 0.05$).

Figure 3: Performance in the mixed cues condition.

^a Percentage of trials on which the object indicated by head rather than eye direction was chosen.



Performance on trials in which only eye direction was presented as a cue (Condition D) were not significantly above chance for either Theta or Zilla (7/10, $p = 0.2$, 6/10, $p = 0.3$, respectively). As highlighted in Chapter Two, this reflects findings with human infants which led Moore (1999) to suggest that this type of mixed-cues presentation may lead to diminished responses to eye-gaze. These results suggest that head orientation is more salient than eye direction as a cue; however, performance was best when head and eye cues were congruent. The apparent bias towards responding to head direction over eye direction, despite the fact that monkeys' most recent experience was with eye cue conditions, suggests that head direction may be the cue most readily used by capuchin monkeys. This finding is corroborated by the results of Study 5, in which eye direction was again a relatively difficult cue condition to master.

General Discussion

The main finding of these two studies is that capuchin monkeys are able to follow eye direction alone as an experimenter-given cue, but responding based on eye direction appears more fragile than that based on other cues, such as pointing or head orientation. It may be that the monkeys are simply learning associations between the cues given and the location of the food; head orientation is a more explicit cue and therefore the discrimination is more easily learned. Alternatively, the results may reflect a behavioural disposition for responding to head direction rather than eye direction; conceivably monkeys learn that head orientation in conspecifics is an adequate and reliable predictor of environmental events (Tomasello, Call & Hare, 1998). For one monkey, eye direction discrimination was observed only after the model's other facial features were removed, suggesting that eye direction may be confounded by the processing of other facial features (Hood, Willen & Driver, 1998; Povinelli & Eddy, 1996a).

The monkeys predominantly followed head orientation when it conflicted with eye direction, although performance was best when the two cues were presented congruently. The former finding conflicts somewhat with those of Lorincz et al (1999) who reported that rhesus monkeys showed diminished levels of co-orientation to head orientation when this cue conflicted with eye direction. However, both studies indicate that head and eyes that are congruent is the most effective form of cue. Comparisons are difficult because in Lorincz et al's (1999) study the stimuli were photographs, and the conflicting eye direction was directed towards the monkey; it is a more appropriate comparison to have neither head nor eyes directed at the monkey but oriented in different directions. In addition, they recorded eye-movements as a dependent measure and their procedure did not involve explicit responses to objects; these measures may yield very different results (e.g. Clements & Perner, 1994). Furthermore, the finding that congruent head and eye direction facilitates performance, complements neurophysiological evidence of cells which are sensitive to a particular head orientation also often being sensitive to congruent eye direction (although cells may also respond independently to head and eye orientations, Perrett et al, 1985).

The reduction of cue-stimulus distance generally enhanced performance in this study although the Far conditions still presented the cues within quite close range (less than 100cm). It is worth noting that the change in distance had a considerable impact on the angular deviation of the eyes relative to the central position, and hence ratio of sclera to iris; the angle being greater when the cue is presented in Near conditions. Rhesus macaques discriminating direct from averted gaze have been shown to be sensitive to angular deviations; performance decreasing as the deviation is reduced (Campbell et al, 1990). It has been suggested that variability in this ratio has been selected for in humans; it allows more eye movement and therefore increases the visual range which can be scanned by eye movement alone, and also renders such movements more salient (Kobayashi & Koshima, 1997; 2001). Primate species that rely predominantly on head movements for

visual scanning also display less visible sclera; as suggested above, in such species head movements may be a better indicator of attention. Whatever the precise reasons, the fact that monkeys' performance decreased over small changes in cue-object distance reinforces the view that monkeys were learning to discriminate cues rather exploiting an pre-existing ability in order to solve the problem. Moreover, while the ability to use eye direction alone showed some degree of transfer to a novel experimenter in one monkey, the diminished performance during these transfer trials is again suggestive of a fairly specific cue discrimination as opposed to a general ability to exploit gaze.

It might be argued that the task demands in these experiments simply favoured cue discrimination, and that perhaps monkeys did not see the experimenter as an interactant and therefore attached no meaning to their behaviour. However, previous research suggests that this is not the case as monkeys do respond to human experimenters, by responding to an experimenter with appropriate threat and appeasement behaviours, for example (Kummer, Anzenberger & Hemelrijk, 1996). Additionally, the task may have been somewhat unusual in that if the monkey followed the experimenter's gaze all she encountered was an uninteresting object, that is, the gaze did not identify a food item as such but rather a location. This line of argument was proposed by Call, Hare and Tomasello (1998) to account for chimpanzees' initial failure to use an experimenter's gaze direction as a cue, but as an objection it is weakened by the fact that the monkeys clearly learned an association between the object and a food reward, responding appropriately by pushing the container aside.

The monkeys in this study did not use the experimenter-given gaze cues as readily as chimpanzees, an orangutan or human infants tested with a similar methodology by Itakura and Tanaka (1998). While this discrepancy may reflect a socio-cognitive divide between the great apes and other primates (e.g. Byrne, 1995), Peignot and Anderson (1999) report that gorillas also failed eye orientation cue conditions; the gorillas would not even

respond to eye-gaze cues, let alone exploit these to locate the baited object. However, the amount of interaction the gorillas had with humans was far less than the apes in the Itakura and Tanaka (1998) study, and it may be that extensive human interaction is an important factor in whether nonhuman primates learn to use gaze cues, at least when presented by a human experimenter (contrast Gomez, 1991, with Peignot & Anderson, 1999, and Itakura & Tanaka, 1998, with Call et al, 1998).

As highlighted earlier, eye contact in nonhuman primates often has considerable emotional salience, which may mean that eye direction it is not readily monitored during interactions with a human experimenter. While the monkeys in this study did learn to use eye direction cues it was not a spontaneous event and seemed to require training. Therefore, it would be interesting to examine the ability of relatively 'enculturated' (Call & Tomasello, 1996) monkeys (such as 'helping hands' capuchin monkeys) to use human gaze cues (see Herve & Deputte, 1993; Custance, Whiten and Fredman, 1999). It may be that rather than indicating a divide between great apes and other primates, the schism may be between primates habituated to humans and with extensive exposure to their non-verbal communication patterns and primates lacking such experience (Tomasello & Call, 1997).

In this study, as in Povinelli and Eddy's (1996b) study with chimpanzees, closing the eyes was not detrimental to the monkeys' performance, that is, monkeys were not deterred by the fact that the experimenter was not actually perceiving any object. This suggests that the monkeys did not appreciate the role of the eyes in visual perception. The capuchins may assess another's visual orientation but without using eye direction to do so, possibly using grosser postural cues instead, such as head direction. Thus, monkeys may not attribute seeing or states of mind at all but instead monitor contingencies between looking behaviours and the locations of important events or objects. Another possibility is that co-orientation reflects a reflexive visuospatial orienting mechanism whereby social cues, such as head direction, exert a reflexive influence over the observer's visual

orientation without any recourse to representations (see Chapter Six). Reflexive orienting and gaze following may produce the same result in that once the observer's orientation is congruent with the other individual's it is simply more likely that the target of the latter's gaze will be perceived (Povinelli & Eddy, 1996b). A simple behavioural mechanism which leads to co-orientation could allow for the development of more sophisticated appreciation of others' looking behaviours. For example, visual co-orientation could facilitate learning to accurately detect the object of another's gaze, for example, ignoring distractors and accounting for occluders (Povinelli & Eddy, 1996c; Tomasello et al, 1999).

However, it may be that the object-choice task demands some further processing beyond the processing of gaze. Chimpanzees which have been found to visually co-orient with a human experimenter's eye movements did not successfully use eye direction, but did use head orientation as an experimenter-given cue (Povinelli, Bierschwale & Čech, 1999). Call et al (2000) suggest that exploiting gaze direction within the object-choice paradigm may require an appreciation of the communicative intentions implicit in the task. For nonhuman primates, this aspect of the object-choice may explain their failure to exploit gaze cues in this context but not others, (i.e. visual co-orientation). Moreover, such an explanation allows for the discrepant findings of so-called enculturated apes and other primates as enculturation exposes primates to patterns of human behaviour including their communication strategies. Recent research that has circumvented this feature of communicative intent or co-operation (by using a competitive task) seem to be yielding more positive results regarding nonhuman primates' abilities to use another individual's visual orientation in a problem-solving task (Hare, 2001).

Chapter summary

The abilities of three capuchin monkeys to use experimenter-given cues were investigated using an object-choice task. While the monkeys were able to use the eye direction of an experimenter to solve an object-choice task, the results suggest that the monkeys learned to use eye gaze as a simple discriminative cue. Reducing cue-stimulus distance and obscuring facial features other than the eyes were both conducive to eye-gaze use, while movement reduced the use of eye direction as a cue. One individual's ability to exploit eye direction did show some transfer to a novel experimenter although performance levels were reduced. Monkeys responded more readily to gestural cues (tapping and pointing) and head orientation. When the relative salience of head and eye direction cues were examined, the monkeys showed highest levels of performance in response to head orientation cues.

These present findings converge with other studies which indicate that nonhuman primates may be more adept at using more gross postural cues, such as head orientation or manual gestures (e.g. Itakura & Anderson, 1996), but also that they are able to learn to exploit subtler behavioural cues. The evidence that monkeys will spontaneously visually co-orient with another individual's eye direction (Lorincz, Baker & Perrett, 1999; Ferrari et al, 2000) and yet are initially unable to exploit eye direction as an experimenter-given cue in an object-choice task, supports the view that these two tasks do not tap the same underlying processing mechanism. However, visual co-orientation has not yet been studied in New World monkeys, making drawing comparisons between these tasks difficult, and perhaps premature. Further research should aim to clarify why these two superficially related tasks reveal discrepant results (e.g. Hare, 2001).

Chapter Five

Use of Gaze Cues in a Competitive Task by Olive Baboons

Research has shown that animals are sensitive to human visual co-orientation, in as much as behavioural phenomena such as tonic immobility (Gallup, 1972), injury feigning (Ristau, 1998) and flight responses (Hampton, 1994) are influenced by whether or not a nearby human is looking at the animal. However, research on animal's abilities to co-orient to changes in non-self-directed gaze and to exploit the informational value of another individual's visual orientation has been limited to a few species: primarily primates, but also domestic dogs and horses (Hare & Tomasello, 1999; McKinley & Sambrook, 2000; Miklosi, Polgárdi, Topál & Csanyi, 1998).

The study of nonhuman primates' abilities to monitor and exploit the visual orientation of others is almost exclusively restricted to two experimental paradigms: gaze following and object-choice tasks. However, these paradigms have produced divergent results (see Chapter One, Section 3). Visual co-orientation with humans or conspecifics has been demonstrated in great apes and several species of monkeys; these primates are sensitive to variations in both head and eye orientation in terms of visually inspecting locations congruent with another's gaze (Anderson & Mitchell 1999; Call, Hare & Tomasello, 1998; Emery et al, 1997; Ferrari et al, 2000; Lorincz, Baker & Perrett, 1999; Povinelli & Eddy, 1996b; Tomasello, Hare & Fogleman, 2001). Nonetheless, the second main experimental paradigm, the object-choice task, has revealed some unexpected limitations of gaze following by primates; in spite of their ability to track gaze, most primates tested have serious difficulties in mastering the object-choice task.

While some great apes and monkeys tested on object-choice are able to use experimenter-given cues up to and including eye direction alone (Itakura & Tanaka 1998; see Chapter Four), there are some complicating factors, including the type of objects utilised (Call, Hare & Tomasello, 1998) the identity of the cue-giver (Itakura et al, 1999), and the extent of early social experience with humans (Call, Hare & Tomasello, 1998; Itakura & Tanaka 1998; Peignot & Anderson, 1999; Povinelli, Bierschwale & Cech, 1999). Moreover, for monkeys, explicit training in object-choice gaze exploitation may be required; monkeys are usually given prior experience with manual gestures such as pointing before gaze orientation cues are introduced (Anderson, Montant & Schmitt, 1996; Anderson, Sallaberry & Barbier, 1995; Itakura & Anderson, 1996).

It is conceivable that the apparent difficulty of the object-choice task is due to the fact that it is based on co-operation between the experimenter and subject; primates (or at least those with limited human contact) may be less likely to demonstrate their gaze monitoring abilities in such a context (Call et al, 2000). That is not to say that nonhuman primates fail to see human experimenters as interactants; they readily demonstrate appropriate behavioural responses to humans (Kummer, Anzenberger & Hemelrijk, 1996; Thomsen 1974). However, the object-choice task may neglect an important point: For nonhuman primates, access to resources is usually more a matter of competition than co-operation (Byrne & Whiten, 1988; Coussi-Korbel, 1994; Peláez, Gil-Burmann & Sánchez, 2000; Schaub, 2000). Viewed from this perspective, the interaction with a human experimenter sitting behind (and effectively controlling access to) food is intrinsically a competitive one (Hare, 2001; Ristau, 1998)

Thus, an alternative means to studying gaze monitoring is to adopt a competitive approach (see Chapter One for studies investigating hiding and competitive cue-reading in nonhuman primates). Nonhuman primates may display their abilities to monitor the visual orientation of others more readily in other situations characterised by competition over

resources, as suggested in reports of tactical deception (Byrne & Whiten, 1988), and in patterns of social monitoring (Blois-Heulin & Girona, 1999) and behaviour (Hare et al, 2000; Hare, Call & Tomasello, 2001) during food competition. As Hare (2001) states: ‘the lives of all primates are dominated by intense competition with conspecifics. All environments have finite supplies of resources on which survival and reproduction are dependent.... In species as diverse as ring-tailed lemurs, squirrel monkeys, and chimpanzees the majority of the day is spent in the company of one’s most intense competitors: conspecifics.’

Study 7: Can olive baboons use gaze cues to solve a competitive task?

The present study was derived from the object-choice approach, but the task was modified to become competitive rather than co-operative in nature. Instead of being required to follow the experimenter’s gaze in order to locate and select a baited object, the baboons needed to monitor the experimenter’s visual orientation in order to take the one of two visible food items presented that the experimenter was *not* looking at. Note that this also means that the task could not be performed on the basis of simple gaze following as this would lead to an incorrect response. As this experiment aimed to approximate naturalistic competition over food, the baboons were not explicitly trained to monitor the experimenter’s gestures as in previous object-choice studies with monkeys, instead they were simply presented with gaze behaviours: either head and/or eye directions. In Study 4, baboons were presented with these same cues in a standard object-choice task without any scaffolding with manual cues. The baboons did not exploit either head or eye gaze, although one baboon showed signs of learning to respond to head direction as an information source. Thus, this present study allows a comparison on the two tasks with the same study species; will a competitive context be conducive to using another’s gaze?

Methods

Subjects

The monkeys were four adult olive baboons: two captive born males, Sylvestre (18 years old), and Balthazar (15 years old), and two females, Green (7 years old, wild born), and Ida, (6 years old). The baboons were housed in 2 groups (one with 9 members and the other with 7 members) in indoor/outdoor quarters (35 m² each) at the CNRS Station de Primatologie in Rousset-sur-arc, France. They received their daily food ration (fruit, dried pellets and vegetables) at the end of daily training and testing. Standard food items (pieces of fruit) and treats (nuts, raisins, cereals) were used during test sessions.

Apparatus

The apparatus consisted of a wooden tray (60cm x 40cm) which rested upon a wooden base (50cm x 30cm x 40cm). The tray's midline was marked from front to back and a small square (2cm x 2cm and 10cm in from the front and side of the tray) was marked on either side of the midline. A chronometer was used to signal 5-second intervals.

Procedure

The tray was placed about 50cm away from the enclosure for baiting. The experimenter (SJV) sat in a neutral posture behind the tray, and while fixating on the centre of the tray, placed a food item on each of the two squares simultaneously (the food items were the same type and size within each trial). The experimenter's head and eyes were approximately 50cm from the food items. The experimenter then presented the cue condition for 5-seconds and then, maintaining the cue, pushed the tray against the mesh wall of the enclosure to allow the baboon to respond (see Appendix C).

Baboons were tested in the presence of other group members, with any individuals of higher dominance rank being restricted to the indoor area during the testing sessions.

Each baboon was presented with 30-trial sessions with a baseline session preceding each block of five cue-condition sessions. For baseline sessions, the experimenter looked down at the midline at the near-side of the tray, while for cue conditions she oriented head and/or eyes towards one of the food items. The ‘correct’ side was the side that the experimenter was *not* oriented and/or looking towards. The baboons responded by reaching towards one of the food items. If they reached towards the non-fixated side they were permitted to take the food item and consume it. However, if they reached for the side that was oriented towards, the tray was quickly pulled away so that they could not take the food item and the experimenter then pretended to consume the food item.

The inter-trial interval was approximately 30 seconds. Both sides were oriented towards an equal number of times, with the constraint that no more than three consecutive trials were allowed in which the cue was presented to the same side. Two baboons commenced with a head and eye cue condition (Balthazar and Ida) while the other two (Sylvestre and Green) were first presented with eye gaze alone as the cue. Each baboon continued in a given condition until they reached a ‘mastery’ criterion of 80% correct for two consecutive sessions within a 5-session block (which they then completed) or until they had completed 25 sessions; the baboons were then presented with the alternative cue condition. One to three sessions were conducted daily with a minimum of 15 minutes interval between sessions.

Results and Discussion

Individual performances are illustrated in Figures 1a-b and 2a-b. The baboons reached for one of the two food items on every trial, showing their full participation in the competition for food. Only one baboon (Ida) reached the mastery criterion of 80% correct in the first cue condition presented; in the head and eyes condition she was above chance performance in four of the five initial sessions (binomial tests, $p < 0.05$) and at 80% or

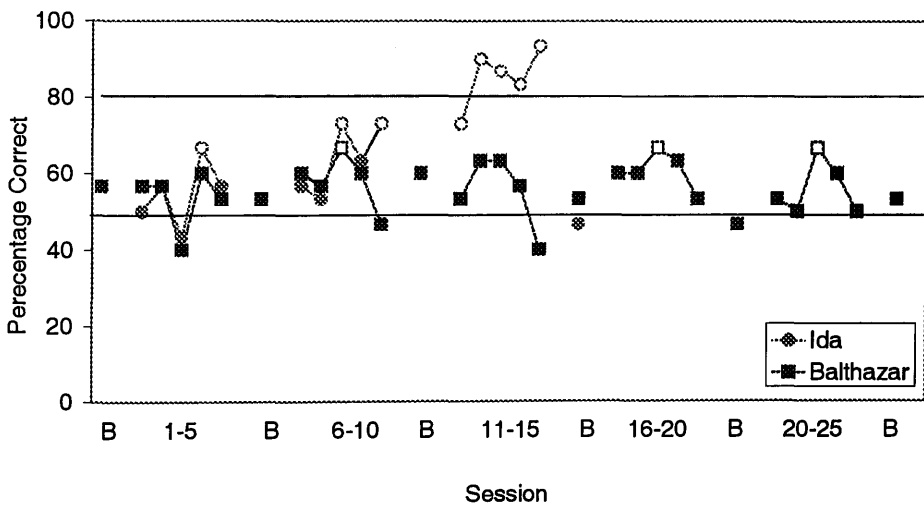
above for all of sessions 6-10 (all $p < 0.01$, see Figure 1a). Balthazar, presented with the same cue condition, performed consistently above chance (with the exception of one of the fifteen sessions) from session 11 onwards (binomial tests, $p < 0.05$) but he failed to meet the mastery criterion of 80% correct (see Figure 1a). In contrast, both subjects presented with eye direction alone as a cue were at chance levels throughout the 25 sessions (with the exceptions of one cue and one baseline session for Sylvestre, see Figure 1b).

In their second conditions two of the four baboons reached mastery criterion. Ida successfully mastered the eye direction only condition after 11 sessions (see Figure 2a), while Green reached criterion in the head and eye orientation condition after 7 sessions, though she performed significantly better than chance from session 3 onwards (with the exception of session 6, binomial tests, $p < 0.05$, see Figure 2b). Balthazar and Sylvestre failed to reach criterion in the eye direction only and head and eyes orientation condition, respectively. Although Sylvestre did perform at above chance levels (binomial tests, $p < 0.05$) in eight out of ten sessions from session 6 onwards, he did not maintain a consistent level of performance thereafter (see Figure 2b). These results establish that the competitive approach is an appropriate method for studying gaze monitoring; this is the first evidence of baboons demonstrating an ability to master gaze cues in a problem-solving interaction.

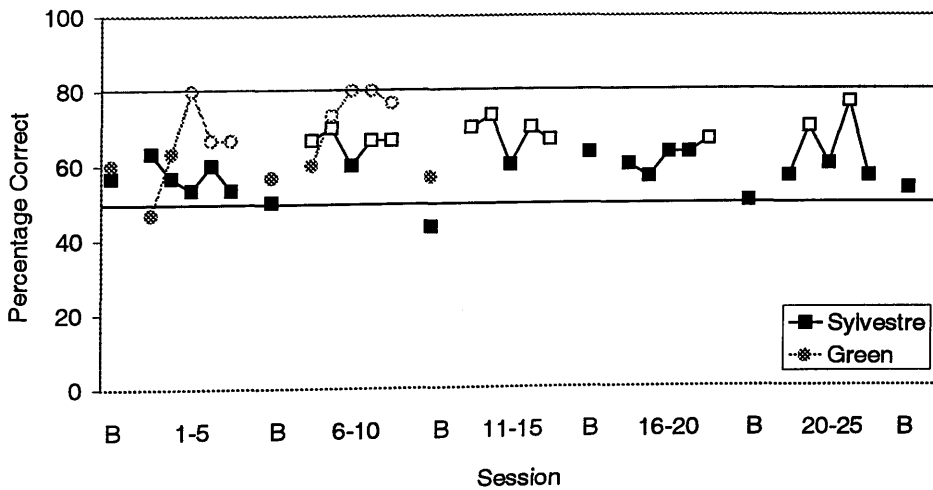
Figure 2: a) Performance of Ida and Balthazar in their second cue condition: eye direction. b) Performance of Green and Sylvestre in their second cue condition: head orientation.

B represents a baseline session. Open data points represent above chance performance ($p < 0.05$). The solid horizontal line represents chance performance; the dotted horizontal line represents the 80% correct level.

a)



b)



To summarise: one baboon mastered both the eye direction alone and head and eye orientation cues, one mastered head orientation but not eye direction and two failed to reach mastery criterion levels of performance in both conditions, although one of these did perform consistently above chance levels when presented with head and eye orientation as a cue. Combined head and eye orientation appears to be a more effective cue than eye direction alone; two baboons reached the mastery criterion and a third performed consistently above chance when head orientation was a component of the cue, while only one baboon mastered the eyes only cue condition. Moreover, although Ida mastered both conditions, she did so more rapidly in the head and eyes orientation condition even though this was the first condition she encountered (in session 6 compared to session 12 for eye direction alone). These results converge with other evidence that monkeys more readily use head direction than eye direction alone as experimenter-given cues in object-choice tasks (e.g. Itakura & Anderson 1996) and perhaps also within a gaze following paradigm (see Study 1).

The results of the Study 7 demonstrate that olive baboons are able to learn to use the gaze cues of a human experimenter without requiring prior training with more explicit gestural cues. While this could suggest that baboons are more adroit at reading gaze than other species, for which manual cues appear to be facilitating (Itakura & Anderson 1996), this seems an unlikely explanation. A previous object-choice study with olive baboons, which did not incorporate scaffolding in the form of manual cues, resulted in only one of four baboons learning to use (but not master) an experimenter-given cue (head orientation) after 700 trials (see Study 4). Table 1 presents details of previous object-choice tasks to allow for a better comparison between that task and this competitive task.

Table 1: Object-Choice studies. + indicates successful use of cue, - indicates failure to exploit cue given. Numbers beneath give number of sessions (or trials – see notes) presented.

Authors	Species	Number	Gesture	Head & eyes near	Head & eyes far	Eye gaze Alone	Note
Anderson et al, 1995	Capuchins	3	+ + + 18 9 18	- - - 10 10 10	+ + - 26 26 35	- - - 10 10 10	H&E reported as non-significant as not different from baseline performance
Anderson et al, 1996	Rhesus macaques	3	+ + - 5 23 25	- - - 10 10 10	- - - 21 20 20	- - - 10 10 10	Cues were presented as far before near, eyes were presented as near only.
Call et al, 1998	Chimpanzees	6			+ + + + + - 24 trials		Results vary according to objects (most positive results given).
Call, Agnetta & Tomasello, 2000	Chimpanzees	15		7+ 8- 24 24		4+ 11- 24 24	TRIAL numbers given not session. Cues accompanied by vocalisations except eyes only cue.
Itakura & Anderson, 1996	Capuchin	1	+ 4	+ 6	+ 3	- 8	Trained with time-outs and correction procedure.
Itakura & Tanaka, 1998	Chimpanzees	2	+ + 4 4	+ + 4 4	+ + 4 4	+ + 4 4	Correction procedure used.
	Orangutan	1	+ 2	+ 2	+ 2	+ 2	Orang-utan and children tested in single sessions.
	Human infants (22 months)	10 (group)	+ 2	+ 2	+ 2	+ 2	

Criterion = 2 sessions above chance response levels (30 trials = 66.7%) NB, many had considerably more sessions with cues due to stricter criterion level e.g. 2 sessions at above 80% correct. Some studies presented only 1 session in a given cue.

Table 1 (cont.): Object-Choice studies. + indicates successful use of cue, - indicates failure to exploit cue given. Numbers beneath give number of sessions (or trials - see notes) presented.

Authors	Species	Number	Gesture	Head & eyes near	Head & eyes far	Eye gaze Alone	Note
Itakura et al, 1999	Chimpanzees	4	3- 1+		2+ 9- 1+		TRIAL data. With sounds added increased 9+ (after 48 trials) 20 trials per session.
		12	24	+ + + +	24 24 48		
Peignot & Anderson, 1999	Gorillas	4	+ + + +	+ + + +	+ + + +	- - - -	
			4 4 5 4	4 7 5 9	2 3 3 1	- - - -	
Povinelli et al, 1997	Chimpanzees	7	6+ 1+		7+		TRIAL data. Previous training with pointing. Pointing not always combined with gaze cues. Cue distance manipulated: success with near pointing.
			12 24		8		
	Children (38 months)	24	+		+		
		(group)	1		1		
Povinelli et al, 1999	Chimpanzees	7	5+ + +		2+ 2+		TRIAL data, trials were probes within near point sessions, only the 'looking at' condition considered. Prior training with point. No gaze cue when pointing.
			40 160 170		8 6		
	Children (49 months)	24	+		+		
		(group)	5		2		
Study 5	Capuchins	3	+ + +	+ + +	+ + +	+ + -	Near cues presented before far conditions.
Study 4	Olive baboons	2	5 4 7	2 2 2	2 2 3	4 12 10	Two subjects tested in each cue condition
		2			19 24	25 25	
Study 7	Olive baboons	4	+ + + -	+ + + -	2 14 4 25	12 25 25 25	Competitive task with no objects concealing food items.

Criterion = 2 sessions above chance response levels (30 trials = 66.7%) NB, many had considerably more sessions with cues due to stricter criterion level e.g. 2 sessions at above 80% correct. Some studies presented only 1 session in a given cue.

Study 8: Further exploration of abilities

Study 7 showed that baboons are able to use indicators of looking behaviours in the context of a competitive task. However, given the individual variability in performances of the baboons, further conditions were proposed in order to assess the extent and limitations of these monkeys' abilities to exploit experimenter-given cues in a competitive task.

As Sylvestre had failed to master either experimental condition, he was presented with a pointing condition in an attempt to exclude any problems with motivation and to assess his sensitivity to a more explicit cue. Previous studies using the object-choice paradigm have repeatedly shown that monkeys are more readily able to use manual gestures such as pointing or tapping, than non-manual cues such as gaze (Anderson, Montant & Schmitt, 1996; Anderson, Sallaberry & Barbier, 1995; Itakura & Anderson, 1996). If Sylvestre were to learn to exploit the pointing cue, this would suggest that his performance in Study 7 reflected an inability to exploit the gaze cues presented rather than a lack of motivation.

Green's high level of performance in the second condition presented (head orientation) following chance performance during the eye direction condition could be due to order effects rather than indicating head orientation as a more effective cue. In order to assess this possibility, Green was presented with a further 25 sessions in which eye direction was the only cue given. Balthazar was not tested in Study 8 as during the eye gaze sessions in Study 7 he became increasingly difficult to work with (threatening the experimenter and attempting to monopolise the apparatus, similar to the responses of gorillas reported by Peignot & Anderson, 1999).

Ida's ability to use eye direction alone as a cue was explored using supplementary conditions used in previous studies with the object-choice paradigm. Both a novel experimenter condition and a glance (repeated short fixations) condition were presented;

the former addressing the ability to transfer the use of the cue to a novel interactant and the latter to investigating how the addition of eye movement might affect performance. In addition, a mixed cues condition (Corkum & Moore, 1995) presenting a variety of head and eye cue combinations was included in order to examine the relative salience of these cues. In an object-choice study with capuchins (Study 6), limited transfer to a novel experimenter occurred, eye movements proved to be slightly detrimental to eye gaze reading, and in the mixed cues condition head orientation was found to be the more salient feature.

Methods

Procedure

The same apparatus and general procedure as in Study 7 were used. For the pointing condition (with Sylvestre), the experimenter oriented her head towards one item and also placed her left hand centrally on the nearside of the tray with the index finger extended towards the item. For the eye gaze condition (with Green), the procedure was identical to that used in Study 7 for the same condition. For Ida, in the novel experimenter condition, the eye gaze condition was conducted as above by a female experimenter who was unfamiliar to the baboon (CB). In the glance condition, the same experimenter as in Study 7 conducted sessions which were as in the eyes only condition but with the experimenter alternating fixation between a point in the centre of the tray's nearside and the food item being looked at. In the mixed cues condition, Ida was presented with four combinations of head and eye orientations within each of four 30-trial sessions.

Within each session were five trials each of two previously encountered trial types in addition to ten trials of two new cue conditions, with the order of trials randomised.

Thus, the four conditions presented were as follows:

- A) Head and eyes: head and eyes both oriented towards the food item (as in Study 7).
- B) Eyes only: head in a central position with eyes oriented towards the food item (as in Study 7).
- C) Head only: head oriented towards the food item with eyes closed (the eyes were always closed before the head was turned). Obviously, responses could not be directly observed in this cue condition; after 5 seconds the experimenter opened her eyes and the item removed by the subject was noted.
- D) Head versus eyes: head oriented towards one food item but eyes oriented towards the other item. For these trials, as both sides were effectively being cued, the baboon was permitted to take either food item and her choice was noted. In alternate sessions, the head or eyes were directed first followed by the remaining cue. For example, in session 1 the eyes were oriented to one side and then the head turned to the other while in session 2 the head was turned first.

Baseline sessions were conducted between the novel experimenter, glance and mixed conditions.

Results and Discussion

In the pointing condition, Sylvestre avoided the indicated food item with significant regularity from the second session (binomial tests, $p < 0.05$), reaching an 80% avoidance level by session 7. As he reached mastery criterion with pointing as a cue, he was again presented with only the experimenter's head and eyes oriented towards the food item for 10 sessions, in order to see if he would show transfer from pointing to head direction. Sylvestre's performance immediately fell to chance levels (mean 60.3%) when the pointing cue was removed; even after 300 trials he was unable to respond on the basis of head and eye orientation.

Green's performance in the second eyes only condition also remained at chance levels (mean 55.9%). That is, despite mastering the head orientation cue condition in Study

7, she was unable to exploit eye direction alone as a cue after a further 25 sessions (750 trials) in which only this cue was presented. This result rules out order effects as an explanation for her ability to read head orientation but not eye gaze as a cue in the previous study.

Ida continued to demonstrate mastery of the cues in all new conditions presented. In the session with a novel experimenter, she successfully transferred her performance with eye direction as the only cue (binomial test, $p < 0.01$), avoiding the fixated item in 25 of the 30 trials presented. In the glance condition, Ida's performance was above 80% correct in the first two sessions; testing with the glance cue was therefore discontinued. In the mixed cues condition, Ida again performed at mastery criterion levels in the head and/or eyes control condition. More interestingly, however, she continued to respond to head orientation even when the eyes were closed or in a incongruent direction, whether eye direction was presented before head orientation or vice versa (eyes before head, 16/20, $p < 0.06$; head before eyes, 19/20, $p < 0.001$). Thus, even though Ida's more recently successful strategy was to avoid the food item being fixated with only eye direction as a cue, head orientation was a more salient attentional cue than eye gaze.

The results of Study 8 confirm those of Study 7: head orientation is the more salient cue to monkeys when performing a competitive food acquisition task. A similar predominance of head orientation over eye direction in the object-choice task has been reported in Chapter Four. Despite receiving a total of 1500 trials (combining Studies 7 and 8), one baboon was still unable to master the eye gaze only cue and the individual who did exploit eye direction was shown to respond preferentially to head direction when the two sources of information conflicted.

Study 9: Influences of motion, objects and cue-type in a competitive task

Given that three baboons demonstrated an ability to use head and eye orientation as cue in Study 7 (two meeting the mastery criterion of 80% and a third performing consistently above chance levels), a final set of manipulations set out to further explore this ability. The first concerned the role of motion in head orientation as a cue. Object-choice tasks have typically presented static gaze cues (Anderson, Montant & Schmitt, 1996; Anderson, Sallaberry & Barbier, 1995; Itakura & Anderson 1996) and it could be that the presence of movement facilitated the exploitation of cues in the competitive situation used in Study 7. Call et al (2000) have proposed that motion may enhance performance by acting both as an 'attention getter', emphasizing the experimenter's actions, and providing directionality. However, the addition of movement to head and/or eye orientation cues in an object-choice task with chimpanzees did not improve performance (Povinelli, Bierschwale & Čech, 1999; but see Povinelli & Eddy, 1996b, for contrasting evidence using a trainer-choice task); thus, it remains unclear whether motion is conducive to the reading of visual orientation cues.

The second manipulation attempted to determine the baboons' level of understanding of looking behaviour; although only one baboon used eye direction explicitly, was there any evidence of a more implicit influence of the eyes (Moore, 1999), and also, how accurate were the baboons in discerning the focus of gaze? While all but one of the baboons were unable to compete effectively on the basis of eye gaze direction alone, it may be that the baboons would be sensitive to a grosser cue concerning the role of eyes in visual orientation, that is, whether or not the eyes were open or closed (Corkum & Moore, 1995; Povinelli and Eddy, 1996b). In terms of actual focus of gaze, it has been proposed that a 'high level' understanding of gaze predicts that subjects should respond differentially according to whether an experimenter is looking at or above an object. A 'low

level' model, based on more general co-orienting responses to grosser behavioural indices, would not predict such accuracy in identifying the target of another's gaze (Povinelli, Bierschwale & Čech, 1999).

The third manipulation was aimed at identifying possible sources of monkeys' difficulty with the typical object-choice task. Is competition conducive to cue-reading or is the difficulty in object-choice at least partially due to other features of the procedure? For example, might the use of objects and a screen somehow distract the baboons from the task of monitoring experimenter-given cues? There are several ways in which the introduction of screen and objects could change the task for the baboons. For example, concealing the food items might alter the motivational salience of the situation. In addition, previous studies have found that introducing a screen during delays diminishes performance on delayed-response tasks (Fletcher, 1965); the screen and objects might simply increase the complexity of the task and distract from cue-reading.

Methods

Subjects and Apparatus

Three of the baboons tested in Study 7 were tested: Balthazar, Green and Ida. The basic apparatus was the same as that used in Study 7. Additional items were: a cardboard screen (100 x 80cm) and two identical yellow plastic cups (6cm diameter x 6cm high).

Procedure

Four consecutive sessions were conducted with each of the three new manipulations (Movement, Cue and Objects), with baseline sessions separating each of these blocks. In all sessions, subjects were presented with ten trials of the previously mastered head and eye condition, pseudo-randomly mixed with ten each of two new trial types; that is, there were 30 trials a session with the three conditions presented in a randomised order. However,

because Ida had mastered use of eye gaze alone, in half of her sessions the control trials consisted of the eye direction only cue, and with the exception of the eyes closed condition described below, during these sessions the new conditions were also eye direction only conditions.

In the Movement sessions, in addition to control trials the baboons were presented with a static cue; following the usual baiting procedure, a hand-held screen (100cm x 80cm) was interposed between the experimenter and the baboon to conceal the movement of the experimenter's head or eyes towards one of the items; the screen was then removed and the trial proceeded as previously. To control for any effects of simple introduction of the screen, a third trial type (movement and screen) was included which incorporated the screen as above but the experimenter did not move her head or eyes until after the screen was removed, producing a standard trial in which the screen was irrelevant.

In the Cue sessions, two novel types of trial were presented; an eyes closed condition, with the head oriented as in control trials but with the eyes closed before the head was turned, and a 'general direction' condition in which the experimenter oriented her head and eyes to the side but upwards (about 30 degrees from the neutral head position) instead of down towards the food item. As the experimenter was not looking at the food item in either of these new trial types, she maintained the cue position for 5 seconds after presenting the tray and the baboon's choice of food item was noted. Thus, the baboons received a reward regardless of their choice of food item.

In the Objects condition, two identical containers were used to conceal the food items; baiting was done as in standard trials and then the two cups were placed over the food items. For half the trials, the trial then proceeded as in control trials with the baboon simply having to move the object in order to retrieve the food item (which they readily did), while for the remaining trials (objects and screen) a screen was introduced once the

cups had been put in place, held in place for 5 seconds and then removed before the trial continued.

Results and Discussion

As Ida's performance was significantly above chance in all conditions, whether head orientation or only eye direction was the cue, her data for the two session types were combined to give a mean score according to condition type and comparable with that of the other two baboons.

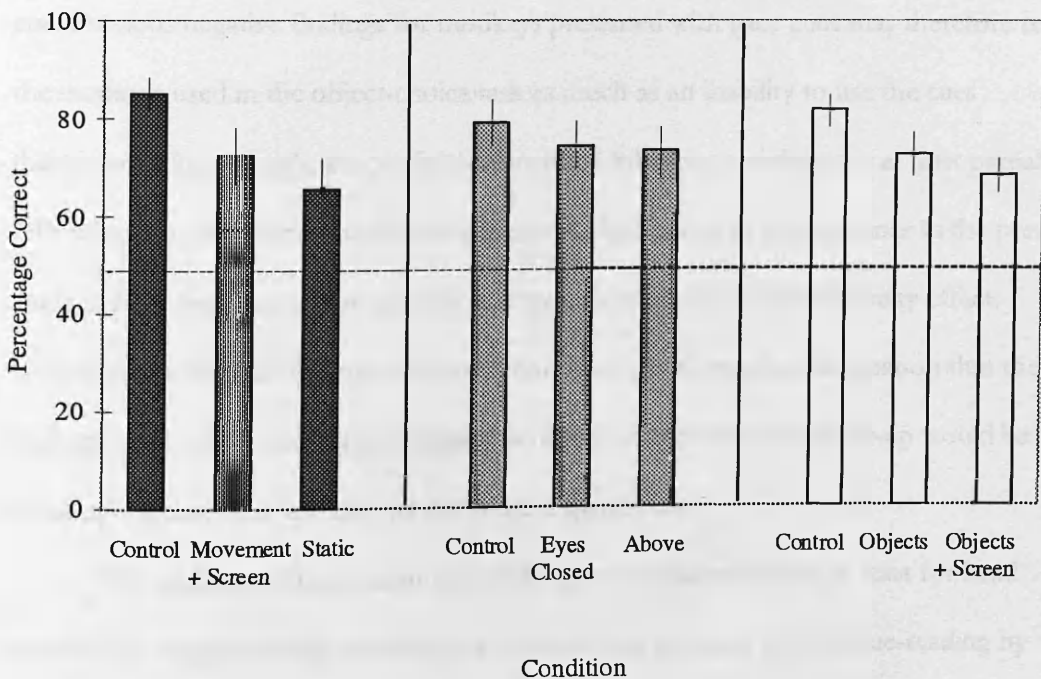
Movement. As can be seen in Figure 3, overall performance remained high in the control condition (mean 85%; all individuals $p < 0.05$), but deteriorated in both the static cue and movement plus screen conditions (means 65.8% and 72.5%, respectively). A Friedman's test indicated a marginally non-significant effect of condition ($\chi^2 = 5.64$, $p = 0.06$). Consideration of individual scores revealed that while performance deteriorated when the cue was static (to chance levels for two of the three baboons, 22/40 and 21/40 for Balthazar and Green, respectively; Ida, 36/40, $p < 0.01$), there was also a decrease in response to the introduction of the screen even if movement was retained, although performance did remain above chance levels for two baboons and approached significance for the third (Balthazar, $p < 0.05$, Green, $p = 0.078$, Ida, $p < 0.01$). That is, although the screen influenced performance levels whether the cue was static or dynamic, the absence of motion led to a greater deterioration in performance.

Cue-type. Overall, the baboons performed significantly above chance in the control condition (mean of 79%, all three individuals were above chance performance, $p < 0.05$) as well as in both of the new conditions: eyes closed (mean 74.2%, individuals: $p < 0.05$, $p = 0.078$ and $p < 0.01$ for Balthazar, Green and Ida, respectively) and looking above (mean 73.3%, individuals: $p < 0.01$, $p = 0.078$ and $p < 0.01$, for Balthazar, Green and Ida, respectively). A Friedman test showed no significant effect of condition: the baboons

continued to respond to the head orientation cue regardless of whether the eyes were open or closed and also when the experimenter was not directly looking at the food item ($\chi^2 = 0.055$, $p = 0.76$). As the baboons were able to take either of the food items on the tray, a Friedman's test was used to assess whether the baboons learned across sessions that the experimenter was not monitoring the food items. The results showed no effect of session on performance in these conditions (eyes closed: $\chi^2 = 3.96$, ns; looking above: $\chi^2 = 3.0$, ns).

Figure 3: Means (and SEM bars) for performance in Movement, Cue-type and Objects conditions.

The dotted horizontal line represents chance performance (50%).



Objects. Performance in the control condition was above chance for all three baboons (mean 81.6%; for all individuals binomial tests, $p < 0.05$) but overall performance showed a considerable decrease in both the objects and objects plus screen conditions (means 72.5% and 68.3%, respectively). A Friedman's test showed a near-significant effect of condition ($\chi^2 = 5.64$, $p = 0.06$). Analysis of individual performances revealed that with

both the introduction of the objects and the objects plus screen, performance remained above chance levels for both Green and Ida (both at $p < 0.01$) but only approached significance for Balthazar (both conditions, $p = 0.078$). An analysis of performance across sessions addressed possible novelty effects, but the baboons showed no significant change across the four sessions (objects: $t_F = 2.78$, $p = 0.43$; objects and screen: $t_F = 2.52$, $p = 0.47$).

The results of Study 9 suggest that although the baboons had learned to take the experimenter's head orientation into account when performing the competitive task, their performance was diminished by procedural modifications including concealing the food items with objects and a screen, and, to a lesser extent, by omitting movement from the cue. Previous negative findings for monkeys presented with gaze cues may therefore reflect the methods used in the object-choice task as much as an inability to use the cues themselves. For example, successful performance following training may at least partially reflect habituation to the objects and screens used, although as performance in the present study did not improve across sessions this appears more than a mere novelty effect. However, it is difficult to separate habituation from the alternative explanation that the task is simply made more complex with these additions; habituation to the set-up would be indistinguishable from learning a new, more difficult task.

The addition of movement may make gaze cues more salient, at least for head orientation, suggesting that presentation of static cues may also impede cue-reading by nonhuman primates. It has been proposed that changes in head direction may be a more effective cue (than eye gaze) because they provide a stronger motion transient (Hood, Willen & Driver, 1998). Interestingly, the addition of movement within this competitive paradigm could not enhance performance merely by eliciting visual co-orientation with the experimenter (as might be the case in an object-choice task). Instead, head movement

simply made the direction of the head more salient for the baboons (see also Call, Agnetta & Tomasello, 2000).

The results of the cue manipulations are noteworthy: the baboons continued to respond according to previously learned rules when the experimenter could not see the food item, that is, when the eyes were closed and even the orientation of the head itself (or eyes in Ida's case) was not aligned with one of the food items. It is conceivable that the baboons simply continued to respond in a manner that they knew to be successful. Even if they were aware of the experimenter's eyes being closed or that the head was oriented above rather than towards the food, they knew from past experience that choosing the food item not aligned with the experimenter's head orientation was a guaranteed strategy for success. However, the baboons also failed to learn from their occasional 'errors' that food items could also be removed from the side congruent with head orientation in over half the trials presented. Overall, it appears that the baboons were responding on the basis of past experience and not making any relevant assessment of the experimenter's visual orientation (as also suggested by Povinelli & Eddy, 1996a). Alternatively, the lack of sensitivity to eyes could also be due to the availability of head direction cues (see Chapter Two for discussion). That is, baboons may be sensitive to whether the eyes are open or closed, but not within a context where head direction is providing directional information (Moore, 1999). However, two of the three baboons also failed to respond to eye gaze when this was the only cue presented, suggesting that head orientation might simply be a more salient cue than eye direction.

General Discussion

The results of these studies suggest that while primates may co-orient with others as a means of locating important events or objects, they are also sensitive to the gaze cues of others on another level, namely, that they can exploit this information competitively in

certain circumstances (see also Byrne & Whiten, 1988; Hare, 2001). As with visual co-orientation, such a skill may be the result of simple associative learning; for example, primates may learn that head orientation is a good signal of whether or not a dominant individual is likely to become aggressive over access to food or mating opportunities. As Cheney & Seyfarth (1991, p 193) state, modifying behaviour in response to other individuals' orientation and direction of gaze 'certainly demands that monkeys recognise that attentiveness can strongly affect actions,' but it does not require any appreciation of the underlying mental states of attention.

The two baboons who quickly learned to exploit the experimenter's visual orientation, at least as indicated by head orientation, were females. Possibly, the males acted less upon gaze cues because they were less accustomed to losing competitions for resources; in this captive environment a single adult male can enforce exclusive access to receptive females and priority of access to food. Alternatively, it has been suggested that females perform better on delayed-response problems because they are less distractable than males, and this may offer some explanation for the gender differences observed (Fletcher, 1965). It would be interesting to consider responsiveness to gaze cues as a function of social status in other contexts. While previous research has underlined the importance of the 'attentional structure' of groups (Chance, 1967; Watts, 1998), there may also be some relationship between gaze monitoring and social hierarchy (see Blois-Heulin & Girona, 1999, for patterns and targets of looking relative to rank in a species of Old World monkeys). Lower ranking individuals may gauge the visual orientation of dominants and thus assess the risk of approaching desirable social partners or food items, for example (Hare, Agnetta & Tomasello, 2000).

The results of this study converge with those obtained using a standard object-choice approach in that the baboons responded more readily to head orientation than to eye direction alone (Anderson, Montant & Schmitt, 1996; Itakura & Anderson, 1996;

Peignot & Anderson, 1999). Furthermore, during supplementary testing with Ida using a combination of head and eye cues, she preferentially responded to head direction when this conflicted with eye gaze, as also demonstrated in capuchin monkeys performing the object-choice task (see Study 6). It is possible that monkeys simply learn to respond to arbitrary cues in order to solve the problem presented (Povinelli & Giambrone, 2000). That is, they learn head or eye direction as a cue to respond to the appropriate side without any appreciation that these are indicators of another's visual orientation (Tomasello, Call & Hare, 1998); as head direction is a more obvious cue, this association may be more readily learned. Alternatively, the advantage for head over eye direction cues may reflect an underlying tendency to attend to this form of cue; for many of species of nonhuman primates, head orientation may be a reliable signal of another individual's visual orientation (see Kobayashi & Koshima, 1997; 2001). Whatever the reason underlying the greater salience of head orientation as a cue, it is important to note that the baboons were not sensitive to the actual focus of the experimenter's gaze; a similar finding has been reported in chimpanzees (Povinelli, Bierschwale & Čech, 1999). While these results may offer little to support the view that the baboons were accurately adopting the visual perspective of the experimenter in the competitive task, it is also possible that their responses were simply tempered by their experimental experience. A different experimental design, with 'looking above' and 'eyes closed' trials integrated from the onset of testing might be illuminating (e.g. Povinelli Bierschwale & Čech, 1999).

Although the baboons learned to use gaze cues to perform the competitive task without explicit training, it is difficult to ascertain which features of these experiments were conducive to effective cue exploitation. Possibly, the competitive paradigm is more suited to revealing gaze reading than the more frequently used object-choice paradigm (Hare, 2001), but the results of Study 9 suggest that the use of screens and containers, both integral aspects in the object-choice task, may also hinder cue reading. Thus, while the

relative speed of acquisition (compared to the object-choice task) by the baboons could be seen as contradicting the learning of an arbitrary cue (as this would presumably apply equally to a co-operative task) and support the view that the competitive task was somehow more meaningful, it could be that the modified task simply had fewer sources of information (such as objects) to be processed in order to solve a discrimination task (see Hare, Agnetta & Tomasello, 2000; Povinelli & Giambrone, 2000). Counterbalancing the order of presentation of an objects and no objects condition within the competitive paradigm might help clarify this issue.

In conclusion, the object-choice paradigm may not be the most appropriate means of assessing nonhuman primates' abilities to assess the visual co-orientation of other individuals. Performance on the object-choice task does not stem directly from a tendency to co-orient with others; although monkeys readily co-orient with other individuals (Anderson & Mitchell, 1998; Emery et al, 1997; Ferrari, Kohler, Fogassi & Gallese, 2000; Tomasello, Hare and Fogleman, 2001) they may require explicit training to master tasks which could be performed on the basis of co-orientation. The present study has identified features of the object-choice task that may hinder effective cue reading: the use of objects and a screen disrupted the performance of baboons already experienced at using experimenter-given cues to solve a task, and the presentation of static cues may also impede performance. While it is difficult to draw conclusions regarding the importance of the competitive rather than co-operative nature of the task used here, the baboons learned to make use of experimenter-given cues in competition without the need for explicit training, and one individual did so fairly quickly. Finally, unlike the object-choice task, the competitive task could not be solved on the basis of a direct co-orienting response, that is, any learned or reflexive tendency to co-orient with other individuals could not have directly facilitated performance in this competitive task. Thus, complementary approaches to

studying gaze monitoring abilities in nonhuman primates are required before strong conclusions regarding comparative abilities are reached.

Chapter summary

The ability of four olive baboons to use human gaze cues during a competitive task were investigated; the baboons were allowed to remove only the non-fixated one of two simultaneously presented food items. Three baboons successfully learned to exploit the human's head orientation as a cue to obtain a food item, and one also learned to use eye direction alone as a cue. However, the baboons were insensitive to whether the experimenter could actually perceive the food item and therefore use of visual orientation cues may not be indicative of visual perspective-taking abilities in baboons. Performance was disrupted by the introduction of a screen and objects to conceal the food items, but not by the absence of movement in cues presented. As the baboons did not receive prior training with gross gestural cues, their performance suggests that the competitive paradigm may be more conducive to gaze monitoring in nonhuman primates than the standard object-choice paradigm.

Chapter Six

Do Java Monkeys Reflexively Orient in Response to Gaze Cues?

Studies of nonhuman primates' abilities to use or understand gaze have been conducted using a number of methods including object-choice (Anderson, Sallaberry & Barbier, 1995), trainer-choice (Povinelli & Eddy, 1996a) and simple gaze following (Itakura, 1996; Tomasello, Call & Hare, 1998). A fundamental problem with the former two paradigms is that of the primate learning to respond on the basis of simple associations during the course of training. Povinelli and Eddy (1996a) in a series of studies to investigate young chimpanzees' knowledge about seeing, suggested that these apes were responding on the basis of learned associations, for example, between choosing a trainer whose face is visible and obtaining a reward. While such response strategies can be successful and may give the chimpanzees the appearance of being able to read another's gaze (by choosing between a trainer with a bucket over their head as opposed to one holding the bucket, for example), there are much simpler associative learning explanations for the responses observed.

For example, within the object-choice paradigm, some studies have used scaffolding training with grosser gestural cues before exploring nonhuman primates' abilities to respond on the basis of gaze information (head and eye direction or eye direction alone). While several species of nonhuman primates have succeeded in exploiting experimenter-given cues to locate hidden food items, some of these have taken a considerable number of trials to do so (Itakura & Anderson, 1996; Peignot & Anderson, 1999; Itakura & Tanaka, 1998). Consequently, when a nonhuman primate responds to gaze cues it is unclear whether this ability is the result of learning of associative rules during training and testing, or rather that the training has simply been in terms of the task

demands themselves and the sensitivity to the significance of gaze is a pre-existing ability (Povinelli and Eddy, 1996a). Thus, responses may be confounded by within-study learning of which response strategies are successful. As Povinelli and Giambrone (2000, p 44) suggest, nonhuman primates may simply be responding on the basis of ‘arbitrary social stimuli with nothing more concrete than our reinforcement procedures unifying them.’

Evidence from studies of spontaneous gaze following suggests that the problem may lie with the methods employed rather than the ability to respond to another’s gaze. Several species of nonhuman primates have been shown to change their visual orientation and track the gaze of another individual; to human or conspecific models and to head and eye direction or eye gaze alone (Anderson & Mitchell, 1999; Emery et al, 1997; Ferrari et al, 2000; Lorincz, Baker & Perrett, 1999; Tomasello, Call & Hare, 1997; Tomasello, Hare & Agnetta, 1999). Thus, some of the other approaches used to date may have underestimated gaze-reading abilities in nonhuman primates (see also Hare, 2001).

A recent integration of methods used to investigate spatial orienting within the visual cueing paradigm with research into social cognition, such as gaze following, has produced some interesting results concerning human adults’ processing of social information. Studies employing a modified Posner cueing paradigm¹ (Posner, 1980) with a central stimulus face looking to a peripheral location have demonstrated that participants are faster to respond to a location cued by the central face than to an incongruent location. This effect is found with both schematic and photographic stimuli and with both head and eye direction as the central cue (Driver, Davis, Ricciardelli, Kidd, Maxwell & Baron-Cohen, 1999; Friesen & Kingstone, 1998; Langton & Bruce, 1999; Kingstone, Friesen & Gazzaniga, 2000).

¹ In this paradigm, a peripheral location cue precedes a peripheral target. The cue may be valid, appearing in the same location as the target; invalid, appearing in another spatial location to the target; or neutral, providing no information about the target’s spatial location. Response times are typically faster when the target is preceded by a valid cue (benefits) and slower following invalid cues (costs).

The phenomenon has been interpreted as reflecting ‘an exogenous orienting mechanism which is engaged reflexively’ by social attention cues (Langton & Bruce, 1999). It is termed exogenous because it seems to be due to properties of the cue itself rather than voluntary (endogenous) processing of cue information (Driver et al, 1999). It is considered reflexive because it is unaffected by whether or not the cue is predictive (Jonides, 1981). Manipulating cue-target contingencies has demonstrated that even if the target is four times more likely to appear on the side which is incongruent with the gaze cue (and participants are explicitly informed of these contingencies), participants still respond faster to congruent targets (Driver et al, 1999). In addition, this response has a time course that is seen as reflecting reflexive responses, peaking when cues precede targets by 100-150msecs, while endogenous or voluntary responses occur from around 300-400 msecs (Cheal & Lyon, 1991).

However, there are some differences between studies in relation to time-course; while Langton & Bruce (1999) found an effect at a cue-target stimulus onset asynchrony (SOA) of 100ms but not at 300 or 1000msec, Friesen & Kingstone (1998) report an effect from 105msec up to 600msecs and dissipating by 1005msec. Driver et al (1999) report that the effect was greatest at 700msec and absent before 300msecs, although decreasing the contingency between cue and target locations did result in the effect disappearing by 700msec, suggesting that at this longer SOA the orienting may have been endogenous. Although it is unclear precisely what time-course this reflexive orienting has, it clearly emerges rapidly and dissipates at longer SOAs. The suggestion that cueing is exogenous rather than endogenous is of importance; previous research had suggested that only peripheral cues which drew the participant’s attention to a location could exert an exogenous shift in attention. The central face cues used are more akin to symbolic central cues, such as arrows, which are thought to engage the endogenous mechanism (Langton & Bruce, 1999).

Thus, social attention cues may be a unique form of stimuli that are processed separately from other information sources.

Although termed exogenous, the response patterns obtained within his paradigm do not fit entirely with standard exogenous orienting. Reflexive orienting is normally characterised by a biphasic effect whereby at cue-target SOA's of 300msecs and longer, responses to congruent targets are actually inhibited and reaction times (RTs) become longer to congruent than incongruent locations. This inhibition of return (IOR, for a recent review see Klein, 2000) phenomenon has not been found using central facial stimuli as cues (Friesen & Kingstone, 1998; Langton & Bruce, 1999; Driver et al 1999). Therefore, reflexive orienting to central, unpredictable social cues exhibits a unique combination of features:

- a) Time course similar to standard exogenous pattern (emerges at very short SOA latencies, dissipates at longer SOAs).
- b) No IOR effect (unlike standard exogenous responses).
- c) Effects not tied to cue location, that is, cue is not at target location (unlike standard exogenous orienting responses).
- d) Unaffected by predictive value of cues (unlike standard endogenous responses).
- e) Central cue influences responses to peripheral targets (like standard endogenous responses).
- f) Benefits at congruent locations (compared to neutral and incongruent cues) but no attentional cost (RT at incongruent location is the same as RT to a neutral cue location).

Although gaze cues may be a unique form of stimuli, as Driver et al (1999, p 534) identify, 'our gaze-cues differed in so many respects from standard central or peripheral cues (e.g. not only in their physical size and eccentricity, but also in the information that must be encoded to determine which side they should benefit), that further work would be

needed for any full understanding of the basis for these similarities and dissimilarities.' For example, there is some uncertainty as to whether the orienting is overt or covert in nature (see Langton & Bruce, 1999); while traditional gaze following requires an overt response (change in gaze direction) this paradigm does not preclude covert shifts in attention. To date, eye movements during task performance have not been monitored and conclusions cannot therefore be made regarding the nature of participants' orienting. It may be that covert shifts in attention occur; this would be extremely interesting as initial covert shifts would allow an individual to monitor their environment without signalling this fact to conspecifics by making overt gaze shifts (Driver et al, 1999). Such a mechanism would concur with recent hypotheses that nonhuman primate eye morphology may serve to camouflage gaze behaviours (e.g., Kobayashi & Koshima, 2001). However, this issue is of peripheral interest here as it does not undermine the claims of automaticity that are presently the central focus of this research. That is, despite such concerns, these studies have revealed a robust phenomenon using a variety of stimuli (photographs and simple schematic faces) and methods (identifying, locating or detecting target stimuli), identifying some form of automatic orienting in response to uninformative social cues.

The present study explored whether depicted gaze directions would induce attention shifts in Java monkeys. This method allows a number of issues to be addressed. This paradigm does not encourage the learning of simple associations; the cues are *nonpredictive* so that the monkeys are not rewarded according to whether or not they follow the gaze information (as in the object-choice task, for example). This does not necessarily mean that gaze-following responses are not based upon previously learned associations between others' gaze direction and interesting events, for example, but any phenomenon observed is unlikely to be an artefact of the study itself (Langton & Bruce, 1999). The nonpredictive nature of the cues would suggest that any tendency to orient in response to gaze cues is reflexive in nature, as identified in humans. Furthermore, reflexive orienting

within this paradigm might indicate that gaze following in a natural context is also automatic and this could suggest different underlying mechanisms. Orienting in response to gaze shifts may be a special kind of orienting response, maybe innate, or perhaps an over-learned response which it is difficult to suppress (Langton & Bruce, 1999), rather than being based on a more cognitive evaluation of another's shift in gaze (e.g., Baron-Cohen, 1995).

A recent study (Fagot & Duruelle, submitted) used a paradigm similar to Friesen and Kingstone (1998) to examine reflexive orienting in baboons (*Papio papio*). The study used a go no-go procedure and presented both schematic and photographic faces in addition to a pair of schematic eyes alone and scrambled-face controls; eyes oriented to either the left or right appeared either 300ms before a target letter appeared either to the congruent or incongruent side. This study found that the baboons did not demonstrate any reflexive orienting in response to the central images; both accuracy of target identification and response times failed to distinguish congruent trials from incongruent trials.

Several modifications were made in order to explore the baboons' responses more fully; the SOA was increased to 800ms, the cue-target distance was reduced, and the baboons were trained to attend to the central area of the monitor. While none of these changes had any impact on the results obtained, a final procedural modification did produce some interesting results. The predictive value of the central cue was altered so that the direction of the eyes reliably indicated target location. After over 1000 trials with this new cue-target contingency, incongruent probe trials were reintroduced to the testing schedule; response times (but not accuracy) differentiated cued from uncued trials, that is, RTs were shorter when targets were cued. Thus, Fagot & Duruelle (submitted) conclude that for baboons, eye gaze may not be the most salient indicator of visual orientation and that visual co-orientation may not be an automatic response but rather a learned response.

However, although the authors suggest that a learning mechanism may also underlie the development of human infants' visual co-orientation responses (e.g., Moore, 1999), the baboons were adults and therefore had extensive experience with others' gaze behaviours.

While Fagot & Duruelle's study is the first to report the use of this paradigm with nonhumans, the study has several limitations. For example, the study uses a single SOA of 300ms (though 800ms is used in one experiment) and this may not be the most appropriate choice. This SOA is considered to signal the shift from exogenous to endogenous orienting; that is, after 300ms responses may be based upon voluntary shifts in attention (Cheal & Lyon, 1991). As the exact time-course for the responses is not yet known for humans, it may be that in order to explore this phenomena in nonhuman primates a range of SOAs should be used. Moreover, the only cue presented is eye gaze, and it would be interesting to consider a variety of cues and their interactions (e.g. Langton, 2000; Perrett & Emery, 1994). That is, what features of social cues are critical for triggering the attention shifts observed (Driver et al, 1999)?

It may be that the baboons tested previously were over-trained with the go no-go task. The study demonstrated that initially they were not attending to the central region of the screen, and even though the task was modified to encourage them to monitor the whole screen, it may be that they were not processing the central stimuli. However, the fact that they did learn the contingency between eye direction and target in the final experiment, suggests that they were not impervious to the central image. Another potential problem is that they are so experienced with responding to images presented out of any context, that they have ceased to see the images as meaningful (e.g. Vauclair & Zayan, 1998). While it may simply be that baboons (and other nonhuman primates) do not exhibit the sensitivity to gaze that has been demonstrated in humans using this paradigm (Fagot & Duruelle, submitted), further studies are merited before strong conclusions are drawn.

This computer-based paradigm allows the ability to respond to head and eyes or eye gaze alone to be studied using a central schematic or photographic face and peripheral target, somewhat similar to Emery et al (1997). However, the present study examines whether such responses are reflexive. Human interactants have presented gaze cues in almost all research into nonhuman primates' tendencies to visually co-orient (exceptions being Emery et al, 1997; Lorincz, Baker & Perrett, 1999; Tomasello, Call & Hare, 1998); the computer based presentation removes the necessity to interact with a human experimenter. It is unclear how this might affect results because while inter-species interactions may not be the most conducive context for nonhuman primates to express their socio-cognitive abilities, the relatively context-free computer paradigm may also hinder such expression. However, as noted by Fagot & Duruelle (submitted), the computer paradigm eliminates the possibility of the human interactant giving unintentional cues. For example, the experimenter may give additional cues such as inadvertently making slight head movements when presenting an eye gaze only cue. While it may be assumed that all the human participants were both familiar with computer interactions and pictorial representations of social stimuli, these factors may influence the monkeys' performances. Although the monkeys tested are familiar with using a computer set-up, picture perception in primates remains a moot issue (for recent reviews see Bovet & Vauclair, 2000 & Fagot, Martin-Malivel and Dépy, 1999).

In the present study, one departure from the procedure used in previous studies is the temporal separation of the central face cue and peripheral target. In most studies the central facial stimuli remain on the monitor when the target appears, the exception being Langton and Bruce's (1999) procedure (Driver et al, 1999; Fagot & Duruelle, submitted; Friesen & Kingstone, 1998; Kingstone, Friesen & Gazzaniga, 2000). This procedural modification may be important: Hood et al (1998) reported that human infants responded more readily to gaze shifts when the central face was removed before the peripheral target

appeared. It may be that the face is such an engaging feature that human infants are unable to shift their attention in another direction; removing the facial stimuli allows infants to express their sensitivity to eye direction. Monkeys may have similar difficulty 'disengaging fixation from a salient central stimuli' (Hood, Willen & Driver, 1998, p 131); thus, in the present studies the central cue is always removed prior to target presentation.

Study 10: Responses to schematic faces

Study 10 examines whether Java monkeys demonstrate reflexive orienting in response to gaze cues depicted in schematic drawings. Human adults respond to schematic faces depicting eye direction, and this form of stimuli has certain advantages over more naturalistic stimuli; extraneous complexities such as facial asymmetries and hair are eliminated (Friesen & Kingstone, 1998). In addition, this study also employed a control condition which presented scrambled faces; this was aimed at determining whether responses were made on the basis of social information presented or on the basis of perceptual asymmetries in the stimuli (Langton & Bruce, 1999; Fagot & Duruelle, in press).

Methods

Subjects

The monkeys were 9 Java macaques housed in a large social group (46 individuals) at the Ethology Station, University of Utrecht, The Netherlands (see Table 1). The group had access to a large indoor enclosure (80m²) and in good weather conditions, to an outdoor enclosure (200m²). The monkeys also had access to an observation room (16m²) in which the apparatus could be set up and individuals could be separated in a smaller experimental area (0.5m x 1.2m) for testing purposes, while maintaining auditory and limited visual contact with their group. The monkeys were fed twice daily with commercial monkey

pellets and twice a week this was supplemented with fruit or vegetables and grain. Grain and dietary treats such as nuts, raisins and cereal were used as reinforcers during testing.

Table 1: Details of monkeys studied: name, age and gender.

Name	Age	Gender
Alfa	12	Female
Felix	26	Female
Freya	9	Female
Hoeba	11	Female
Kraa	9	Female
Milva	10	Female
Roza	17	Female
Vip	25	Male
Yudea	13	Female

Apparatus

A 14 inch Apple Macintosh monitor was secured in front of an opening in the mesh of the test area. The monitor was fitted with a Micro-Touch touch-screen and was connected to an Apple Macintosh computer which presented the trials and recorded responses using Authorware Professional software. Correct responses were rewarded by food items delivered by a Universal Feeder that was connected to the computer. A video camera was secured above the test area so that the experimenter could monitor the monkeys as they performed the task.

Procedure

Training. Although the monkeys had previously been trained and tested using this experimental set up (Veenema, 1998), the present study was conducted after approximately 3 years in which no testing was undertaken with any members of the group. Therefore, the

monkeys were re-habituated firstly to the experimental room and subsequently to the apparatus. The monkeys were encouraged into the testing area with food items and the amount of time spent alone in the test area was increased gradually over a period of a month. Most monkeys readily used the touch-screen to respond to a simple task (touching a geometric shape which appeared on the monitor) and obtain a reward.

Testing. Once the monkeys had demonstrated an ability to use the touch-screen and could be reliably separated from the group for a reasonable duration (at least 10 minutes), testing commenced. Once a monkey had entered the test area, the area was partitioned from the rest of the enclosure using sliding doors. The computer program was then initiated and the experimenter observed the session from an adjacent room via the video link. Each monkey remained in the test area until a maximum of 50 trials had been presented or 25 minutes had elapsed. If a monkey ceased responding for over 3 minutes or was clearly distressed (for example, when group fights broke out in the adjacent enclosure), the testing session was terminated and the monkey was released.

The task. Following a 30-second delay during which the monitor was uniformly black, the monkey was presented with a schematic face or control (scrambled face) stimulus; and touching this central face initiated the trial. After a 500msec delay, pupils then appeared in the face or control image, positioned in one of five locations: up, down, left, right or central (a neutral condition which offered no directional cue towards peripheral locations). Following another delay of 100ms, 300ms or 1000ms, the central image was removed and a target square appeared in one of the four locations (up, down, left, right). See Figures 1 and 2 for stimuli and sequence of presentation. The monkey responded by touching the target, which then disappeared, and a reward was then delivered by the automatic feeder. The next trial commenced after a 30-second inter-trial interval. If the monkey failed to touch the initial image within 30 seconds, the image was erased and re-appeared after a 10-second time-out. If the monkey touched the first image presented

and initiated a trial but subsequently failed to touch the target within 30 seconds, the target was deleted and a new trial was presented without any reward being delivered.

The trials varied according to four factors: whether the image was a schematic face or a control drawing, the stimulus onset asynchrony (SOA), location of the target (up, down, left, right) and whether or not the depicted gaze direction predicted the location of the target. This resulted in 12 experimental conditions: Face (Face and Control), SOA (100ms, 300ms and 1000ms), and Cue condition (Congruent, Incongruent and Neutral); the four target locations were used to ensure that cues were uninformative and target location was not considered in subsequent analyses. Trials were pseudo-randomly presented with no more than three consecutive trials with the same stimuli type, SOA, target location or predictive value. The program allowed for the sequence to be initiated at four different points within the schedule so that the trials presented varied daily. Responses to each trial were recorded in terms of the time and the co-ordinates of each touch to the screen; response time (RT) was measured in milliseconds and timed from the target onset.

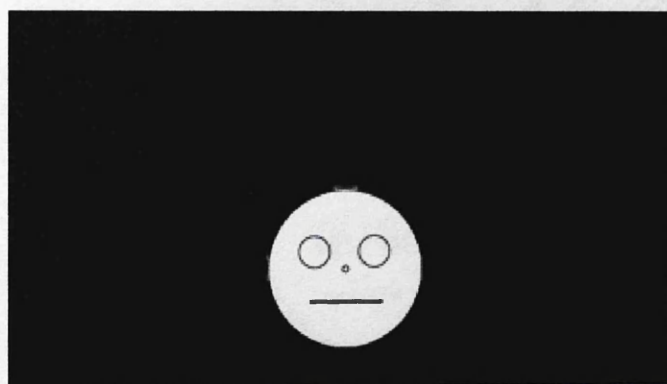
Data Analysis

Reaction times of less than 100msec (anticipations) or greater than 3000msec (time outs) were excluded from the analysis. The percentage of trials eliminated by this procedure was 11.6% (347/3003). Incorrect responses (touches to areas of the screen other than to the target area) were also excluded from analysis, removing a further 281 trials (9.4%, only 16 of these trials were responses to locations 'cued' on incongruent trials). Mean RTs were calculated for each individual in each condition; means were used instead of medians as trial numbers were unequal (Miller, 1998). Repeated measures Anovas were conducted on the mean RT data. A repeated measures analysis of variance was percentage errors was conducted in order to examine whether error rates varied systematically (Friesen & Kingstone, 1998); there were no significant effects or interactions (p 's > 0.1).

Figure 1: Sequence presented on each trial.

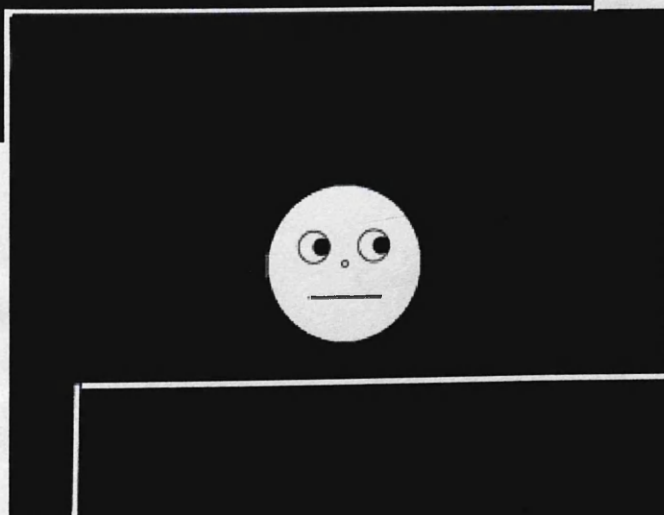
An example of a congruent Face trial.

An example of a congruent Face trial.



Touch face to start trial

**500ms delay before
pupils appear in face**



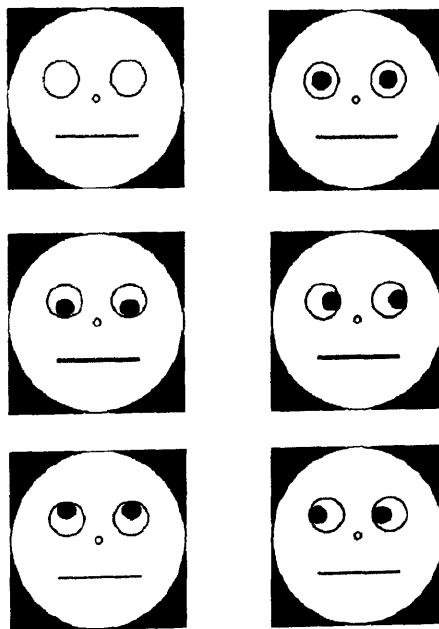
**100ms, 300ms or
1000ms delay
before target
appears**



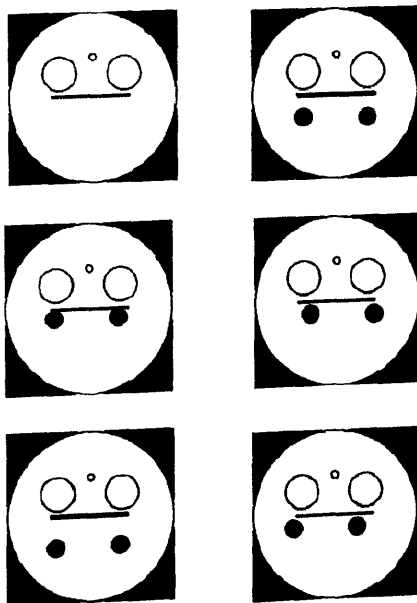
**Touch target
to obtain
reward.**

Figure 2: All central stimuli, faces and control images

Faces



Controls



Results

Excluding, time-outs, anticipations and errors, the individual mean reaction times (RTs) and standard deviations are summarised in Appendix D. A 2 (Face) x 3 (Cue condition) x 3 (SOA) repeated measures analysis of variance was conducted on mean RTs. There were no significant main effects, that is, response times did not differ according to whether or not a face or control image was presented, the timing of the cue or by the cue's predictive value (see Table 2). Comparable studies with human subjects have not incorporated a control condition (e.g. Friesen & Kingstone, 1998), and as a means of both increasing power and attempting a comparable analysis, face and control data were analysed separately in two 3 (Cue condition) x 3 (SOA) analyses of variance. When considered separately, neither the Control data nor Face data showed significant effects or interactions (see Table 2 & Figures 3a & 3b).

Figure 3a: Mean response times to congruent, incongruent and neutral Control stimuli at 100ms, 300ms and 1000ms SOAs.

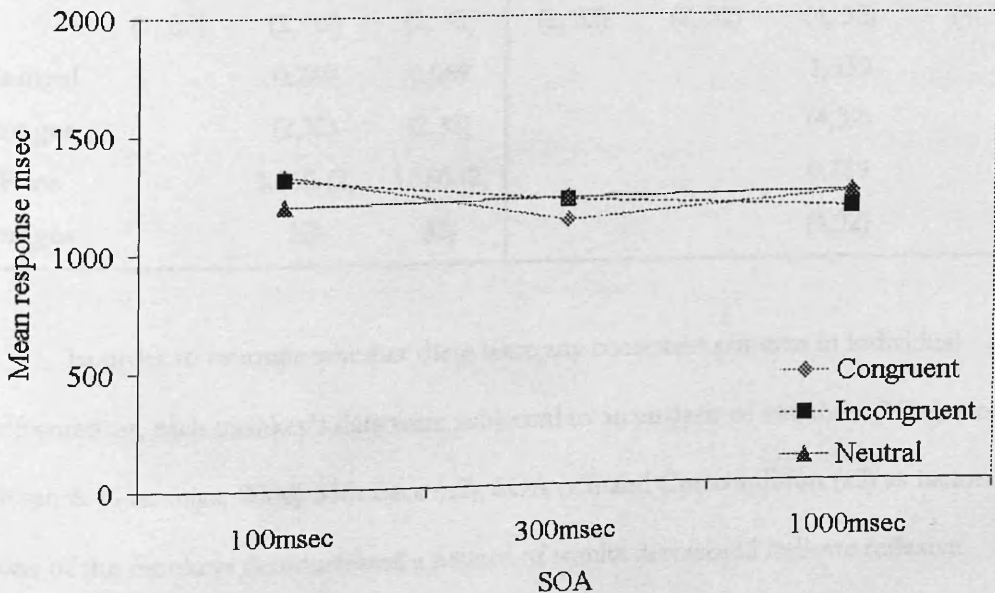


Figure 3b: Mean response times to congruent, incongruent and neutral Face stimuli at 100ms, 300ms and 1000ms SOAs.

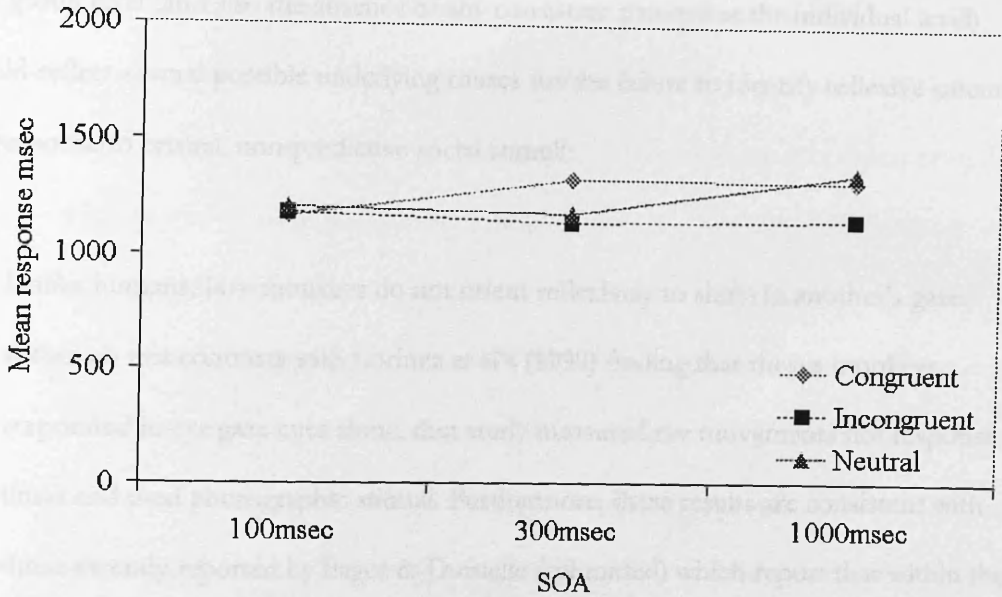


Table 2: Anova table for analyses of overall, Control and Face data.

F values with df given in brackets. F = Face, C = Cue, S = SOA.

	Face	SOA	Cue	F x S	F x C	S x C	F x S x C
Overall	0.001 (1, 32)	0.770 (2, 32)	2.765 (2, 32)	1.515 (2, 32)	1.830 (2, 32)	0.888 (4, 32)	1.119 (4, 32)
Control		0.749 (2,32)	0.069 (2,32)			1.539 (4,32)	
images							
Face		3.060 (2, 32)	3.386 (2, 32)			0.789 (4,32)	
images							

In order to examine whether there were any consistent patterns in individual performances, each monkey's data were subjected to an analysis of variance (Kingstone, Friesen & Gazzaniga, 2000) with Face (x2), SOA (x3) and Cue condition (x3) as factors. None of the monkeys demonstrated a pattern of results that would indicate reflexive orienting and the results are summarised in Appendix E.

Discussion

Overall, the results are very difficult to interpret. The absence of any significant effects at the group level (and also the absence of any consistent patterns at the individual level) could reflect several possible underlying causes for the failure to identify reflexive orienting in response to central, non-predictive social stimuli:

- a) Unlike humans, Java monkeys do not orient reflexively to shifts in another's gaze. Although this contrasts with Lorincz et al's (1999) finding that rhesus monkeys responded to eye gaze cues alone, that study measured eye movements not response times and used photographic stimuli. Furthermore, these results are consistent with those recently reported by Fagot & Duruelle (submitted) which report that within the same paradigm, baboons do not demonstrate reflexive orienting in response to eye direction in schematic faces.
- b) Alternatively, it might be that they do reflexively orient, but not in response to eye gaze information alone (the only cue information available in this study). Previous research has suggested that for nonhuman primates head orientation might be a more salient social cue than eye gaze alone. The salience of head and eye direction as indicators of another individual's visual co-orientation is still under debate (Emery, 2000; Langton, 2000), but head orientation certainly does play a role in determining another's gaze direction. Thus, Java monkeys might demonstrate reflexive orienting in response to grosser directional cues, such as head or bodily orientation.
- c) Although nonhuman primates may reflexively orient in response to gaze cues (possibly even eye gaze), the Java monkeys tested in this study did not demonstrate the behaviour due to methodological factors.

While the present data do not allow any conclusive stance on these three alternative possibilities, there are aspects of the present study that may have impeded reflexive orientation. One potential problem with the study was the nature of the stimuli used; while humans have demonstrated reflexive orienting in response to schematic faces (Friesen & Kingstone, 1998; Kingstone, Friesen & Gazzaniga, 2000) nonhuman primates may not always interpret pictorial stimuli as meaningful (e.g., Perrett et al, 1998). Furthermore, even if they are able to interpret two-dimensional images in a representational manner, or as equivalent to real stimuli, it may be that for the monkeys these simplistic line-drawings were insufficiently salient to produce any social responses (including reflexive orienting).

The failure to demonstrate any overall significant differences in RTs to the face and control images could indicate that the monkeys did not discriminate between the images, perhaps suggesting that the stimuli lacked social salience for the monkeys. Study 11 addresses the issues of stimuli type and also cue presented; using the same paradigm to investigate responses to more socially salient photographic images and to both head and eye direction. While Fagot & Duruelle (submitted) also used photographs and failed to report any differences between the findings with schematic and photographic images, there are procedural differences between that study and the current one which make the use of different image types an interesting modification nonetheless.

Study 11: Responses to photographic stimuli

Study 11 attempted to address (at least partially) two of the issues raised by the results of Study 10. The first concerns the nature of stimuli used; in an attempt to make the stimuli more socially meaningful photographed human faces were used. While there are undoubtedly still potential problems with using this type of stimuli, it seems reasonable to

suggest that these more realistic images would be more effective than schematic drawings in eliciting social responses (see Chapter One, section 1.2). The second examines the nature of the cue presented; the absence of reflexive orienting in response to eye-direction alone need not mean that the monkeys do not demonstrate such a phenomenon in response to other socially relevant information such as head orientation, for example. Thus, the present study used photographed faces and presented visual orientation using combination of head and eye directions.

While Perrett & Emery (1994) have proposed a Direction of Attention Detector (DAD) hierarchy (whereby gaze information takes precedence over head orientation and head orientation takes precedence over postural cues), the relationship between these information sources need not be asymmetrical. It may be that these cues are used in a more integrated manner, that is, that they may be 'mutually influential in the computation of social attention' (Langton, 2000, p 834). Langton (2000) used a Stroop-type interference task (with adult humans) to explore the role of head and eye direction in determining another's gaze. The results demonstrate that head and eye direction both influence the perception of visual orientation. For example, when head and eye direction were both congruent with each other and a verbally given direction, responses were faster, however, this benefit was eliminated by presenting conflicting head and eye cues. Langton's results suggest that information regarding another's direction of gaze may be better envisaged as channels processing various different signals (which all exert an influence on the judgement reached), rather than as a hierarchical structure. The present study therefore explores reflexive orientation in response to a variety of head and eye direction cues in order to examine the influence of these information sources on nonhuman primates' perception of another's visual orientation (Driver et al, 1999).

Methods

Subjects and Apparatus

The same monkeys as in Study 10 were tested using the same apparatus.

Procedure

Study 11 commenced a few days after the completion of Study 10. The general procedure was the same as that of Study 10. However, the task was modified slightly to accommodate the presentation of a new type of stimuli.

The task: The overall task was very similar to that used in Study 10 with a few notable changes. Instead of a schematic face or control image being presented before the subject started a new trial, the pre-trial stimulus was a white square that appeared in the centre of the screen. Once the monkey touched this square, the square disappeared and the trial commenced after a 500ms delay with the stimulus appearing in the centre of the screen (see Figures 4 and 5). The SOAs and target were as described for Study 10. The trials were again pseudo-randomised and could be initiated at different points within the schedule.

The stimuli were a set of photographic images of a female human with her head and eyes oriented according to the cue condition (see below). The faces cued only along the horizontal axis, e.g. head and/or eyes to the right/left. However, there were still some incongruent targets on the vertical axis (in order to maintain the nonpredictive nature of the social cues presented and to deter any side preferences in responding). Each cue was presented as congruent and incongruent with the subsequent target at each of the three SOAs. In addition, there was a neutral condition, with a straight-on face displaying direct gaze and a half-neutral condition with the head in half-profile and the eyes again showing direct gaze. Thus, the cues presented were as follows:

- a) Head and eyes: head turned in profile to left or right.
- b) Eyes only: eyes directed to either the left or right, or displaying direct gaze.

- c) Half-profile: head turned 30 degrees from centre with eyes either congruent with head turn or fixated centrally (direct gaze).

As in Study 10, sessions consisted of 50 test trials or continued until 25 minutes had elapsed and all touches to the screen were recorded in terms of time and location.

Data Analysis

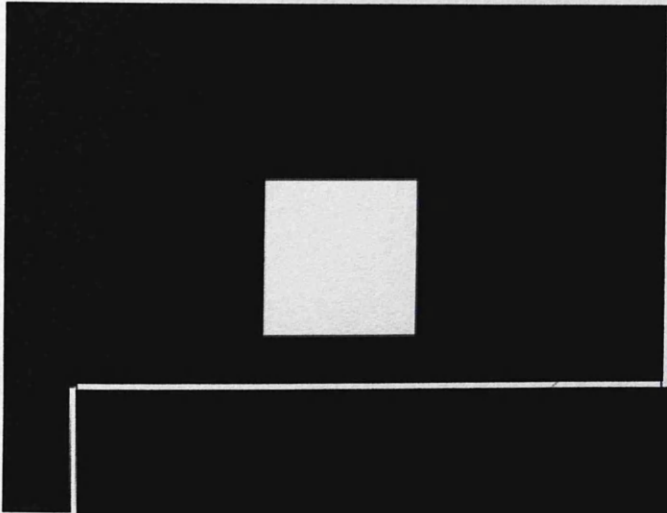
Reaction times of less than 100msec or greater than 3000msec were excluded from the subsequent analysis. The percentage of trials eliminated by this procedure was 7% (226/3226). Incorrect responses (touches to areas of the screen other than to the target area) were also excluded from analysis, removing a further 368 trials (11.4%, only 14 of which were responses to a location cued by incongruent cue condition). Repeated measures analyses of variance were conducted with the percentage errors and there were no significant effects or interactions (p 's > 0.05); errors did not vary according to experimental condition.

Results

Excluding time-outs, anticipations and errors, the individual mean RTs and standard deviations are summarised in Appendix F. Mean RTs were analysed using a repeated measures analysis of variance. In order to compare face type as a condition, an overall analysis was conducted with face type as a factor and with only congruent and incongruent trials considered as a cue factor (as these were the only cue conditions common to all face conditions). Subsequent analysis examined each face type separately in order to allow all cue combinations to be more fully analysed. Individual responses were also examined; however, there were no consistent patterns and the results are therefore not presented here (see Appendix G for individual analyses).

Figure 4: Sequence presented on each trial.

An example of a incongruent Head trial.



**Touch square to
start trial**

**500ms delay before
face appears**



**100ms, 300ms
or 1000ms delay
before target
appears**



**Touch target
to obtain
reward.**

Figure 5: All central photographic stimuli.

a) Head in profile, b) head half turned and c) eye direction.

a) Head in profile:
looking left or right



b) Half turned head: looking to left
and right, with eyes either congruent
or displaying direct gaze



c) Eyes: displaying
direct gaze or looking
to left or right



Overall

A 3 (Face) x 3 (SOA) x 2 (Cue: congruent versus incongruent) repeated measures Anova was conducted on mean RTs (see Table 3). There was a significant Face by SOA interaction; responses were fastest to Head and Eye images at the shortest SOA but fastest to half-profile images at 300ms. There was also a significant Face x SOA x Cue interaction ($p = 0.018$). Figure 6 presents overall RT Costs (uncued RT minus cued RT) for each face type and SOA. Targets cued by a congruent head direction were located faster than incongruent targets at 300ms SOA, while they were located more slowly at 100ms and 1000ms SOAs. Targets congruent with the direction of a face in half-profile were responded to significantly more slowly than incongruent targets at the 300ms SOA, at 100ms there was also a tendency for less efficient responding to congruent targets, but at the shortest SOA congruent targets were detected more rapidly than incongruent. In the eye gaze only condition, congruent targets were located faster than incongruent at 300ms and 1000ms SOAs, but slower than incongruent targets at the fastest SOA (100ms). Overall, the interaction effect is not indicative of a reflexive orienting response.

Figure 6: RT costs for each condition and each SOA. Bars to the right indicate a positive RT value (RT cost = RT incongruent - RT congruent).

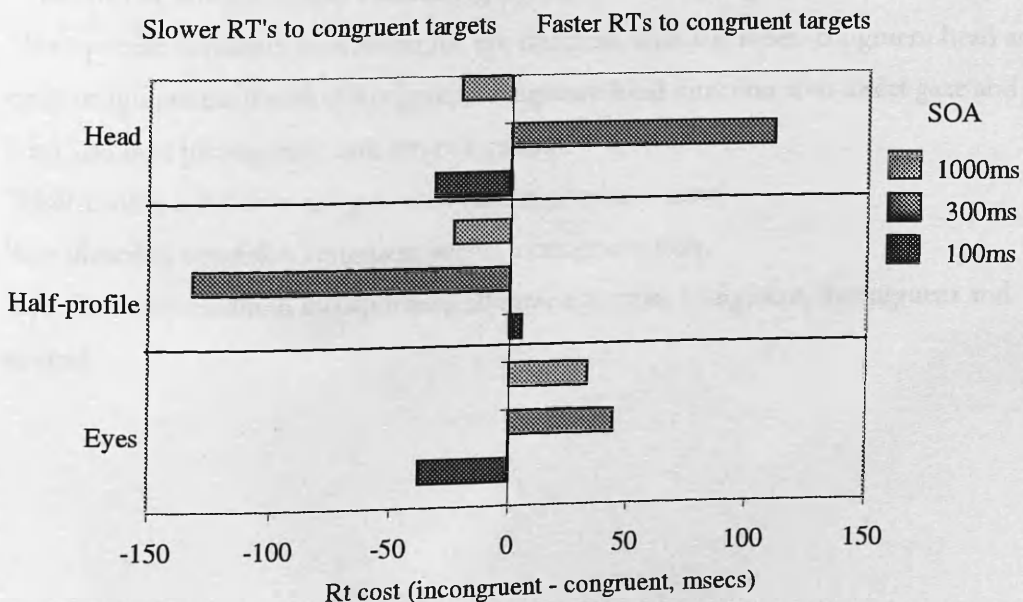


Table 3: Anova table for overall analysis of all conditions and separate analyses according to face type presented.

F values with df given in brackets. F = Face (Head, Half-profile or Eyes), SOA = Stimulus Onset Asynchrony (100ms, 300ms or 1000ms), Cue condition (congruent or incongruent).

	Face	SOA	Cue	F x S	F x C	S x C	F x S x C
Overall^a	0.347 (1,16)	2.256 (2,16)	0.003 (1,16)	3.547 * (4,16)	0.894 (2,16)	0.028 (2,16)	3.495 * (4,16)
Head direction		3.106 (2,16)	0.316 (1,16)			2.317 (2,16)	
Half-profile^b		0.615 (2,16)	1.511 (1,16)			0.7089 (2,16)	
Half-profile^c		1.203 (2, 48)	0.835 (3, 48)			1.019 (4, 48)	
Half-profile^d		1.399 (2,16)	0.105 (1,16)			1.040 (2,16)	
Eye direction^e		4.190 * (2,16)	0.0209 (1,16)			0.460 (2,16)	
Eye direction^f		3.1401 (2, 32)	3.859 * (2, 32)			1.317 (4,32)	

*= $p < 0.05$.

^a Head, Half-profile and Eyes: congruent versus incongruent only. Anova table for 3 (Face) x 3 (SOA) x 2 (Cue condition)

^b Half-profile condition only considering head orientation (congruent versus incongruent)

^c Half-profile condition accounting for eye direction: four cue types (congruent head and eyes, congruent head with direct gaze, incongruent head direction with direct gaze and both head and eyes incongruent with target location).

^d Half-profile condition: eye gaze only (direct or averted gaze)

^e Eye direction condition congruent versus incongruent only.

^f Eye direction condition incorporating all three cue types (congruent, incongruent and neutral).

Head direction

As head direction either cued or did not cue the target location, a 3 (SOA) x 2 (Cue) a repeated measures Anova was conducted on group data. There were no significant results at group level; RTs did not differ according to SOA or whether the target was congruent or incongruent (see Table 3 for Anova results and Table 4 for mean RTs).

Table 4: Mean reaction times and standard deviations (msec) for detecting targets cued by congruent and incongruent head direction.

SOA	Cue Condition	
	Congruent	Incongruent
100ms	959 (128)	928 (159)
300ms	988 (132)	1099 (145)
1000ms	1049 (201)	1028 (186)

Half-profile

As head and eye direction could either be congruent or incongruent, the data were analysed on the basis of head orientation alone (i.e. ignoring eye direction) and also taking account of whether or not eye gaze was compatible. When the data were analysed on the basis of head direction alone in a 3 (SOA) x 2 (cue condition) repeated measures Anova, there were still no significant effects or interactions (p 's >0.05). In order to examine whether head and eye direction interacted, a 3 (SOA) x 4 (Cue condition: head and eye directions) repeated measures Anova was conducted on group data (see Table 3 for Anova summaries and Table 5 for mean RTs). There were no significant main effects or interactions; RTs did not differ according to SOA or cue type (p 's >0.05).

Table 5: Mean reaction times and standard deviations (msec) for detecting targets cued by congruent and incongruent half-profile direction.

SOA	Cue Condition	
	Congruent	Incongruent
100ms	991 (184)	1041 (145)
300ms	1012 (101)	880 (76)
1000ms	1021 (103)	997 (224)

These results suggest that a face turned in half-profile is not able to exert a reflexive influence over the monkeys' orienting. Furthermore, unlike direct gaze within a frontal face (see eyes section below) direct gaze as depicted within a half-turned face did not influence RTs even when data were analysed simply on the basis of whether the eyes were engaging in direct gaze or were averted (see Table 3). These results suggest that a half-turned face does not elicit orienting in Java monkeys and, further, that systematically varying the eye direction with the half-profile face does not influence response patterns.

Eyes

Eye direction was first analysed on the basis of cued versus uncued trials; a 3 (SOA) x 2 (Cue: congruent or incongruent) repeated measures Anova was conducted on the mean RT's. There was a significant main effect of SOA; the monkeys responded more quickly at the shortest SOA (mean response time 100ms SOA = 938ms, 300ms SOA = 1011ms, 1000ms SOA = 1008ms).

As eye direction could either be congruent, incongruent or neutral regarding the target location, a 3 (SOA) x 3 (Cue) repeated measures Anova was conducted on group data (see Table 3 for Anova results and Table 6 for mean RTs). There was a significant main effect for cue condition; RTs did not differ according to SOA but did vary according to whether the target was congruent or incongruent or neutral ($p = 0.043$). Fisher's tests revealed that responses were faster to neutral compared with incongruent targets ($p = 0.03$;

neutral mean RT = 946ms, incongruent = 1012) while responses to congruent targets were not significantly different from either (999ms). Overall, the data from the eye-direction conditions fail to replicate the evidence for reflexive orienting previously found with adult human subjects.

Table 6: Mean reaction times and standard deviations (msec) for detecting targets cued by congruent, incongruent and neutral eye direction.

SOA	Cue Condition		
	Congruent	Incongruent	Neutral
100ms	954 (125)	916 (132)	944 (109)
300ms	1033 (117)	1078 (95)	923 (100)
1000ms	1010 (121)	1043 (159)	971 (130)

Discussion

The results of Study 11 demonstrate that photographic images were no more effective than schematic drawings in terms of invoking a response to depicted gaze. This finding reflects those reported for baboons (Fagot & Duruelle, submitted). In addition, head orientation was no more salient than eye direction within this paradigm. Thus, Java monkeys did not demonstrate a reflexive response to gaze in response to photographic images depicting various gaze cues.

There are methodological issues that should also be considered. For example, it may be that introducing a neutral face (as used in the schematic faces study) before presenting the cue would have improved the procedure; Driver et al (1999) suggest that allowing for face-processing time, rather than suddenly flashing up a facial image, enhances performance. Furthermore, if done appropriately, this could lead to the appearance of movement in the images (Hood, Willen & Driver, 1998); it might be that a motion transient would invoke a reflexive response when a static image failed to do so.

General Discussion

The findings of Studies 10 and 11 corroborate those of baboons tested with a similar methodology (Fagot & Duruelle, submitted), but contrast with the results found with human participants who have demonstrated reflexive gaze to both schematic and photographed faces (Friesen & Kingstone, 1998; Langton & Bruce, 1999; Driver et al 1999). While a reflexive orienting mechanism would presumably be adaptive for any social primate, it may be that only humans reflexively orient to gaze. However, it may be that the methodologies used to date are unsuitable for nonhuman primate research.

There are various procedural modifications that could be made to these studies that could have implications for the results obtained. Firstly, the high percentage of time-outs and errors might suggest that the monkeys were not fully attending to the task. In order to reduce these numbers it might be adroit to introduce catch-trials (when no target appears) and time-outs for errors and failures to respond, that is, leave the monkeys with a shorter window in which to respond as this would encourage them to respond rapidly and accurately. Increased on-task attention would be more conducive to observing a phenomenon such as reflexive orienting (Fagot & Duruelle, submitted). Further issues which might be considered include the use of pictorial stimuli (however, this is necessary for this paradigm), allospecific stimuli (but see Chapter One for discussion) and the absence of a meaningful context. Perhaps the use of familiar conspecifics would be a means of addressing these latter concerns, though of course, this could lead to subsequent complications concerning individual responses to significant others (see Chapter One, Section 2).

The present studies required that the monkeys make a preliminary response to the screen in order to initiate a trial; while this was included in order to try and ascertain that the monkeys were attending to the trial, it may have actually hindered performance. For example, a monkey may have still been completing a movement when the stimulus image

appeared and their actions may have obscured the cue, or their posture may have influenced their response time to the subsequent target. It is difficult to think of an appropriate means of avoiding this problem. Manual initiation of a trial by the experimenter when the monkey is suitably attentive to the screen would be one rather cumbersome means, but a more practical solution might be to have each trial flash up for a very short duration so that a distracted monkey would miss the trial altogether unless they were attending. Within the present set-up the monkeys were free to move around the test area and it was therefore impossible to ensure that they remained centrally fixated. An alternative set-up whereby the monkey's head is positioned upon a chin-rest to ensure that the head remains static and oriented forwards during testing might be a more appropriate means of testing within this paradigm. However, this is the method used in a recent study with baboons that yielded the same results as the present studies (Fagot & Duruelle, submitted). Another possible modification would be to change the task requirements; for example, the localisation task used here would have been subject to any idiosyncrasies in a monkey's position, posture or response action, while an identification or detection task which required a response to a central location would avoid this problem. However, this may not be the cause of the results obtained as the findings coincide with those of Fagot and Duruelle (submitted) who used a joystick and therefore did not have problems due to the baboons' positions.

An alternative task could involve the introduction of a central facial stimuli on random trials within an ongoing discrimination task: would cue condition effect accuracy rates or response times on an already mastered discrimination task? Or could monkeys learn a complex discrimination task if the relevant factor were a short social cue (e.g., Lambert & Sumich, 1996), that is, would implicit learning occur more rapidly in response to such a condition than during a more abstract cue condition? In addition, studies using eye movement recording techniques could be used to investigate orienting response times

to central social stimuli; response latencies to peripheral targets following a central facial cue could be explored in nonhuman primates (Hood, Willen & Driver, 1998). That is, rather than recording a manual response, a more sensitive measure such as latency to saccade might be informative. Thus, this general approach may prove to be a general basis for future research. In addition, social cues could be incorporated into a change-blindness paradigm (Langton & O'Donnell, submitted); the presence of social cues has been found to lead to more rapid detection of congruent changes in stimuli (such as the removal of objects from scenes). This method has the advantage of presenting more naturalistic images; instead of an artificial, isolated face appearing on a screen, visual orientation cues are depicted within a more meaningful context. This approach could certainly be adapted for use with nonhuman primates.

Chapter summary

The perception of pictorial gaze cues was examined in Java monkeys. More specifically, a cueing paradigm was used to explore whether or not monkeys would exhibit an orienting reflex in response to the presentation of eye and head direction cues. Although this automatic gaze following has proven to be a robust phenomenon in humans, the present study did not provide evidence of an analogous behaviour in monkeys. Despite several methodological limitations, the findings coincide with those reported using a similar paradigm with baboons (Fagot & Duruelle, submitted). Thus, it may be that reflexive orienting is specific to humans or apes (who have not been tested using this paradigm), or that further methodological innovations may be needed to better examine this phenomenon in nonhumans. That is, although the results of the present study and that of Fagot and Duruelle (submitted) do not indicate any form of reflexive orienting in nonhuman primates, this paradigm may provide the general basis of further exploration of gaze monitoring in nonhuman primates.

Chapter Seven

Overview, Discussion and Future Directions

Chapter one: Literature review

This chapter outlined previous research findings and stated the aims of the present study. Nonhuman primates extract information from faces: they recognise conspecifics, individual identity and facial expressions. Primates are particularly sensitive to the presence of eye-like stimuli; responding to direct and averted gaze with spontaneous and trained behavioural responses and at the neurophysiological level. Research into non-self directed gaze has produced less consistent results; nonhuman primates may respond to another's change in direction (visual co-orientation), but seem limited in their ability to use this same information within alternative paradigms, such as the object-choice task. This thesis set out to further explore monkeys' responses to gaze and to examine whether varying methodologies have contributed to inconsistent findings regarding their abilities.

Chapter two: Spontaneous responses to gaze

Study 1 examined whether baboons would visually co-orient with a human experimenter's shift in head and/or eye gaze direction. Baboons did change their visual orientation in response to a shift in head direction (even when the eyes were closed) and also demonstrated, albeit less reliably, a tendency to follow a shift in eye gaze only.

Study 2 presented various novel objects and explored whether varying perceptual contact would influence baboons' and capuchin monkeys' subsequent exploration of these objects. Results were inconsistent, although the monkeys did seem to prefer an object that had

most recently been the focus of the more salient cue presented. Methodological concerns were discussed and refinement of the method was considered to be desirable before drawing strong conclusions.

Chapter three: Gaze discrimination in baboons

In Study 3, baboons were presented with a pictorial discrimination task, which required the categorisation of whether depicted models were looking at or looking away from a target. The results of this study were ambiguous; baboons required extensive trials in order to categorise the stimuli successfully and furthermore, the baboons did not transfer the ability to a human model (Study 4). This suggested that either that baboons do not form such categories or that the approach was not tapping the ability which it had aimed to; it seemed that the baboons were responding according to simple perceptual rules and not processing the looking behaviour per se.

Chapter Four: An object-choice task with capuchins

It seemed that the object-choice task might offer a means of assessing the abilities of nonhuman primates to read gaze cues. Although capuchin monkeys were able to use cues up to and including eye direction alone (Study 5), further investigations suggested that they had simply learned rules in order to respond successfully (Study 6); a view also taken by Povinelli & Eddy (1996a) following extensive research with chimpanzees. In addition, head orientation was found to be more salient than eye gaze when these two cues were incongruent.

Chapter Five: A Competitive task with baboons

The results from studies 5 and 6 (in addition to inconsistencies reported by others using the object choice task) led to a consideration of what features of the object-choice task

might be problematic for nonhuman primates. The idea that nonhuman primates are naturally competitive over resources and not co-operative, led to a modified task whereby baboons had to exploit a human experimenter's visual orientation in order to remove food items that were *not* fixated. The results of this study suggested that a competitive approach might be a more fruitful one when investigating the gaze reading abilities of nonhuman primates; the baboons used cues fairly quickly and without explicit scaffolding training (Study 7). These abilities were explored further in Study 8; manual gestures were found to be more salient than head direction, and head direction was more effective than eye gaze (and was the preferred cue when conflicting head and eye directions were presented). The findings also suggested that the procedural details of the object-choice task adversely influence cue reading (Study 9).

Chapter Six: Reflexive orienting in Java monkeys

Chapter 6 described a computer-based approach to investigate processing of gaze information. A modified cueing paradigm was presented in which central gaze cues were presented immediately before the appearance of a target. Although cues were non-predictive of the target's location, research has shown that humans detect cued targets more rapidly than uncued targets. Study 10, using simple schematic drawings, found no differences in response times to cued and uncued stimuli. Study 11 used photographic stimuli but also failed to produce a response pattern characteristic of reflexive orientation. However, this paradigm could be modified in order to examine nonhuman primates' responses to gaze more fully.

1) How do findings fit in with previous findings and theories?

It appears clear that different approaches to studying nonhuman primates' responses to gaze may produce divergent findings, despite the fact that they are all purportedly aim to explore the same abilities. Nonetheless, consistencies are emerging from the plethora of studies published to date:

- A) Many species of nonhuman primates reliably and spontaneously demonstrate visual co-orientation in response to changes of both head and eye direction (see Chapter One, Section 3.4a and Study 1).
- B) Nonhuman primates do not readily demonstrate gaze reading abilities within other contexts, such as object-choice tasks. Nevertheless, they are able to learn contingencies between gaze information and outcomes, allowing them to solve the problems presented (see Studies 3, 5 and 7).
- C) Competitive paradigms may be more conducive to gaze monitoring in nonhuman primates (Study 7).
- D) Although nonhuman primates may respond to eye gaze alone, like young human infants, they respond more readily to head orientation (Studies 1, 4, 5, 6 7 & 8).

The results reported in the above chapters confirm previous findings that performances in a simple visual co-orientation task diverge considerably from those obtained in all other paradigms (see Chapter One, Section 3). Baboons demonstrated spontaneous visual co-orientation but within other paradigms they did not demonstrate any immediate response to gaze. For example, the object-choice task could be successfully performed on the basis of simple co-orientation; being oriented to the correct side makes a correct choice more likely. However, it has been shown that the gaze following response does not facilitate performance on this task. There are two aspects that should be

considered: What features of simple visual co-orientation situations elicit a gaze following response in nonhuman primates? What features of the other tasks presented are detrimental to gaze following?

Simple gaze following may be effective because, as Povinelli and Eddy (1996a) identify, this situation most resembles the 'normal day to day interactions' of nonhuman primates. The gaze following scenario often presents a human interactor in a fairly naturalistic context (e.g., Anderson & Mitchell, 1999); the experimenter typically engages in a contingent interaction with the subject, and trials are presented infrequently within each session. The other tasks presented were far more rigid and 'unnatural' and this may be a significant difference between the studies and their outcomes. The reliability of the gaze following response could mean that it is some form of hard-wired response, or that it is the result of considerable experience and learning of the contingencies between others' visual co-orientation and the detection of objects and events. The failure to detect a reflexive orienting response in Studies 10 and 11 may favour the latter as a more appropriate explanation. However, Langton and Bruce (1999) proposed that an over-learned response could also produce a reflexive orienting response. It may be that methodological weaknesses underlie the discrepant findings in between gaze following studies and the computer-based approaches tested to date.

When tested using paradigms other than simple gaze following, nonhuman primates do not seem to have an appreciation of the informative value of head and eye direction. The repeated failures to spontaneously respond to gaze in the other tasks presented are difficult to explain; null findings 'seldom lend themselves to diagnosis' (Premack, 1988; Heyes, 1998; Zentall, 1998). However, it may be that the methods used to date have simply failed to reveal such an ability. Nonhuman primates are usually tested with human interactants (Povinelli & Eddy, 1996a) and in rather contrived experimental designs devoid of any wider context (Hare, 2001; Matheson, Cooper, Weeks, Thompson &

Fragaszy, 1998). Thus, nonhuman primates' apparent reliance on simple procedural rules may be an outcome of the experiments themselves which may encourage such response strategies (Povinelli & Giambone, 2000). Although comparative psychologists may consider the task demands to be fairly obvious, in the object-choice task for example, nonhuman primates are presented with a plethora of information and they are expected to extract the relevant information from the situation.

Perhaps the tasks presented lack ecological validity; many cues are presented in quick succession and the experimenter's behaviour lacks contingency (with the animal's own behaviours). Repetitive trials may lead to habituation to otherwise salient gaze behaviours (Povinelli & Eddy, 1996a; Tomasello, Hare & Fogleman, 2001). However, this seems improbable, as initial trials would be successful and the association between gaze and consequent location of food would presumably reinforce the response (Corkum & Moore, 1995). An example of noncontingency is found in the observation period in an object-choice task; although the monkeys may initially co-orient with a gaze cue, the delay between their co-orientation and object presentation may be too long (see Study 1).

Conceivably, human interactants may be unsuitable models, as nonhuman primates may only be sensitive to the behaviour of conspecifics (Goméz, 1998; Povinelli & Eddy, 1996a; Tomasello, Call & Hare, 1998). This argument is weakened by the fact that nonhuman primates respond to human gaze shifts within the gaze following (Study 1; Anderson & Mitchell, 1999; Ferrari et al, 2000; Povinelli and Eddy, 1996b; Tomasello, Hare & Fogleman, 2001). They also respond to human gaze behaviour in and other paradigms (Exline & Yellin, 1969; Kummer, Anzenberger & Hemelrijk, 1996; Thomsen, 1974).

Another possible explanation for the relatively poor performance of nonhuman primates in many gaze paradigms is that studies have focused upon using gaze to locate food items (Studies 4-9) and perhaps nonhuman primates do not naturally use gaze information in this context (Itakura et al, 1999; Povinelli & Eddy, 1996a). Gaze monitoring

may be important for monitoring social events and for predator detection (Povinelli & Giambrone, 2000), but perhaps location and direction of conspecifics is a sufficient cue for identifying food sources. The location of group members and their direction is probably a very reliable indicator of food sources (Menzel, 1974). However, the gaze following response presumably occurs regardless of what the actual target of gaze might be; that is, the target is not known until after co-orienting! Moreover, recent research using a competitive paradigm, suggests that chimpanzees do readily use another's visual orientation to obtain food items; this has led to the suggestion that it is the co-operative nature of object-choice tasks, rather than the foraging context, that is important in interpreting negative results (Hare et al, 2000; Hare, Call & Tomasello, 2001; Hare, 2001).

A potential fundamental flaw with most paradigms is that they do not reflect the competitive nature of nonhuman primate interactions (Byrne & Whiten, 1988; Coussi-Korbel, 1994; Schaub, 2000). In addition to recent findings with chimpanzees (Hare, 2001), the competitive alternative to the object-choice task (Chapter 5) suggests that a competitive approach may indeed be more conducive than the object-choice task to gaze monitoring in nonhuman primates. However in addition to the co-operative context, there are other features of the object-choice task, such as the presence of screens and objects, that may be detrimental to performance (see Study 9). Moreover, Hare and colleagues' approach benefits from being more ecologically valid in terms of using conspecific interactants, and from presenting a more naturalistic task than most previous studies. Studying nonhuman primates in such controlled but 'naturalistic' interactions with conspecifics, whether competitive or not, may be a more valuable approach than experiments which involve interactions with human experimenters (see Section 3.3; Blois-Heulin & Girona, 1999; Hare, 2001; Tomasello, Hare & Call, 1998; Johnson, 2001).

Of particular theoretical interest are the findings that eye gaze does not appear to take precedence over other cues for nonhuman primates (Studies 1, 4, 5, 6, 7 & 9). These

data correspond with previous research suggesting that head direction is the more readily used cue (Anderson, Montant & Schmitt, 1996; Itakura & Anderson, 1996; Itakura & Tanaka, 1998). This conflicts not only with Baron-Cohen's (1994) original concept of the EDD and its functions, but also with Perrett and Emery's (1994) modified DAD (which although incorporating alternative information sources, still proposes that the eyes take precedence when determining visual orientation). That is not to say that the eyes are not an important component of nonhuman primate interactions (see Chapter One, Section 3). It is clear that direct gaze is a highly salient signal for primates (and many other animals) and that Baron-Cohen's (1994) model may be correct in identifying an EDD that detects eye-like stimuli. However, accurately detecting direct gaze and using another's gaze as an information source regarding non-self directed targets, also requires that head orientation be taken into account. Thus, it would seem that Perrett and Emery's (1994) DAD is a more appropriate model, although recent research has suggested that various information sources may be processed in parallel rather than in the hierarchical manner proposed (Langton, 2000).

The finding that head orientation takes precedence over eye direction, and an insensitivity as to whether eyes are open or closed, may indicate that Baron-Cohen's (1994) model is also incorrect in proposing that EDD incorporates an appreciation of 'seeing'. Nonhuman primate data are not accommodated by the model in this respect and, furthermore, young human infants may also fail to respond to non-self-directed eye direction until around the age of 18 months (Corkum & Moore, 1995; Moore, 1999; but see Hood, Willen & Driver, 1998). Nonhuman primates do not seem to show any appreciation of 'seeing' per se, unless this is amodal and it is simply that the role of the eyes is not critical (Povinelli & Eddy, 1996a). To date, there is no compelling evidence that nonhuman primates' responses to gaze are based upon an appreciation of the 'connectedness' of perception (Flavell, 1999). Moreover, an appreciation of 'seeing' would

have to be deduced from differential responses to the status of another's eyes (such as open, closed, occluded or looking away); such responses could only identify a sensitivity to another's looking behaviours and would not conclusively identify whether or not 'seeing' was understood (see Chapter One, Section 4). Even an appreciation of the seeing/knowing relationship would only identify an awareness of the association between looking behaviours and subsequent actions. However, sensitivity to eye gaze would at least indicate a possibility that nonhuman primates understand that visual perception somehow connects the perceiver to what is seen.

Research to date does not indicate that nonhuman primates proceed to the shared attention (SAM), let alone Theory of Mind (TOM), level of Baron-Cohen's (1994) model. While gaze is undoubtedly a highly salient feature of nonhuman primate interactions, and they may be capable of sophisticated geometric gaze following, these could all be processed by a Direction of Attention (DAD) mechanism (Perrett & Emery, 1994). If Tomasello's (1995) hypothesis is correct, then the absence of an appreciation of intentionality would preclude any recognition of 'attention'. That is, nonhuman primates may lack an Intentionality Detector (ID). However, nonhuman primates certainly see others as both animate and directed (Jellema et al, 2000; Tomasello & Call, 1997). Baron-Cohen's model is not particularly precise regarding the nature of the putative ID mechanism; he attributes it with identifying self-propulsion and direction, but this does not necessarily mean it identifies 'intention'. Tomasello (1995) suggests that both nonhuman primates and children younger than one-year old, do not see others as intentional agents; that is, even the gaze following of infants should not be interpreted in a mentalistic manner (Butterworth & Jarret, 1991). As Povinelli and Giambrone (2000, p 25) suggest, for young infants and nonhuman primates, gaze following may be understood 'not as a projection of an internal psychological state of attention, but as a directional cue (i.e. a vector leading away from the eyes and face).' Tomasello (1995) suggests that during their second year, human infants

begin to appreciate intentionality and subsequently start to appreciate looking behaviour as intentional attentional states; if nonhuman primates do not develop this understanding of intentionality then they cannot progress beyond a geometric appreciation of gaze.

Although nonhuman primates have yet to demonstrate any mentalistic appreciation of others' looking behaviours, this is not to say that their responses to gaze must be simple learned associations. Johnson (2001) has suggested that viewing nonhuman primate social cognition as either mentalistic or based on simple rule learning may not be constructive, as it ignores many possibilities in between; behaviour may be complex without the capacity for mental state attribution (Povinelli & Giambrone, 2000). Whiten (1997, p 144) favours an interpretation based on mental state attribution, which he considers to be highly advantageous for social primates; 'one of the most powerful ways to succeed in a complex social world is to read the very minds of one's companions, and get one step ahead in whatever competitive or co-operative games are at stake.' In contrast, Povinelli and Giambrone (2000) propose a reinterpretation hypothesis whereby linguistic abilities allow humans to label behaviours in terms of mental state attribution although the behaviour itself preceded such labelling and need not be seen in such terms. That is, gaze following and other social behaviours are simply behavioural responses and do not need recourse to internal mental states: reading behaviour is sufficient even for sophisticated social behaviours. Povinelli and Giambrone (2000) draw support for such a position from findings of computer simulations of chimpanzee social groups; these virtual chimpanzees behave in behaviourally sophisticated manners and inhabit a socially complex environment, but they do not reason about other individuals' mental states, responding instead to behavioural contingencies alone.

An example of a complex but non-mentalsitic interpretation of nonhuman primate social cognition is given for recent findings regarding the gaze following abilities of chimpanzees (the species studied most extensively). Tomasello, Hare and Agnetta (1999, p

776) conclude that ‘chimpanzees do not follow the gaze direction of others generically, and they do not just learn gaze direction as a simple discriminative (arbitrary) cue; they actually understand something about the visual activities of other animate beings.’ Thus, chimpanzees (and some other nonhuman primates) may have a tendency to gaze follow, but experience allows them to develop an understanding of other’s gaze across a wide variety of situations (for example, how perception is affected by barriers) and how gaze relates to subsequent behaviours. As Heyes (1998, p 112) proposes, ‘it should be recognized that alternatives to theory of mind hypotheses are not necessarily ‘behaviorist’ or derived from learning theory. The social behavior of primates may be based on abstract, symbolic representations of nonmental categories.’

2) Methodological issues

Hare (2001) highlights three general methodological issues that affect research with captive nonhuman primates in general, and all of these are directly relevant to the studies reported in the preceding chapters. Firstly, sample sizes are usually small; consequently, subjects are often tested in several experimental conditions in repeated-measures designs. Even if counterbalanced designs are used, there are still problems relating to order effects so that learning effects become an important consideration when interpreting results. Secondly, not only are sample sizes small but as a direct result, individual variations may have a disproportionate influence on outcomes and therefore interpretation (Boysen, 1994). For example, in Study 4, only one baboon was tested in each experimental condition; thus, each baboon’s performance had implications for how each condition was evaluated.

Many factors may influence a nonhuman primate’s motivation to perform a task. As most tasks use food as reinforcers, the most obvious is how hungry an animal is; fortunately, maintaining a regular feeding routine is a fairly straightforward matter. However, even small disruption in husbandry routines (delayed feeding, cleaning and

temporary removal of animals from groups) can affect nonhuman primate behaviour (Waitt & Buchanan-Smith, in press; Weinberg & Levine, 1980). In addition, social dynamics, such as agonism within groups, undoubtedly influence performance. For example, male baboons can be impossible to test when females in adjacent enclosures are visibly in oestrus (personal observation). Larger sample sizes would allow more freedom in experimental design and render the results more resistant to individual idiosyncrasies.

Thirdly, experimental design is tightly limited by logistical constraints. Researchers usually cannot physically interact with their study animals, it is often impractical to manipulate interactions between conspecifics (for example, most gaze following studies have used human interactants), and enclosure design largely determines what experiments can be conducted (Hare, 2001). For example, Hare et al's (2000; 2001) studies with chimpanzees required very specific enclosure arrangements; conspecifics needed to see each other from either side of a communal test area, to which both had access during testing. Any replication of this study with monkeys would require similar facilities.

The studies reported in this thesis also had some more specific methodological problems. One potential criticism concerns baseline trials in which the experimenter maintained a neutral posture (Studies 5 – 9); perhaps these trials resulted in the monkeys initially learning that the experimenter provided no information about the location of the food. This could be a serious design flaw as during the initial session when the monkeys were attempting to solve the problems, no relevant gaze information was available. The experimenter's non-contingent behaviour might have reduced the clarity of the task demands. However, any such effect was clearly limited to the earliest conditions presented; the monkeys did learn that the experimenter could provide effective cues and they used this information whenever possible, within their limits. The removal of initial baseline sessions might allow a better understanding of the nonhuman primates' spontaneous responses when presented with these tasks.

As already mentioned, perhaps the tasks presented were too contrived for the nonhuman primates to make sense of. For example, in addition to the often non-contingent behaviour of the experimenter, there were also arbitrary rules such as limiting choices to one per trial (Hare et al, 2000). This clearly does not reflect any natural foraging tendencies of nonhuman primates, who would presumably continue looking for food items. The constantly changing location of the hidden food in the object-choice task might be problematic; nonhuman primate search patterns are based upon location (e.g. Ristau, 1998; Tomasello & Call, 1997). In addition, the presence of food may in itself be detrimental to performance. For example, in a study of self-control, chimpanzees were unable to respond appropriately (they had to indicate the smaller quantity) when presented with food items, but were successful when food was replaced by symbolic representations of quantities (Boysen & Bernston, 1995). The presence of food and the fact that the task requires a suppression of natural search preferences may both be problematic; these factors may help to account for the divergence between simple visual co-orientation studies and other tasks assessing nonhuman primate responses to gaze.

A serious issue for most of the studies reported in this thesis is that of differential reinforcement; the monkeys received feedback on each trial and this contributed to the learning of gaze cues, but the monkeys' responses may not have corresponded to behavioural predispositions (Hare, 2001; Heyes, 1998; Povinelli & Eddy, 1996a; Povinelli & Giambrone, 2000). It is unclear whether the monkeys needed to learn more about the task demands or the cues themselves; but the latter seems unlikely as monkeys readily respond to gaze cues in the visual co-orientation paradigm. What the results do demonstrate is that despite the methodological problems highlighted, and a lack of ecological validity for many of the situations presented, monkeys are able to learn to exploit the behaviours of a human interactant to good effect, showing that they are flexible learners. However, although performances were often indicative of learning strategies rather than some sort of general

gaze appreciation, this does not necessarily mean that nonhuman primates do not have such an ability: the methodologies employed may have been inadequate (Hare, 2001).

3) Future directions

Despite the plethora of studies in recent years, further research of nonhuman primates' responses to gaze is indicated; some directions for future research are proposed in the following sections. Although these may appear contradictory, for example, suggesting both greater ecological validity and the use of computer-based paradigms, these directions would serve distinct purposes. More naturalistic studies allow the exploration of sensitivity to gaze in relation to the nonhuman primates' natural environment. At the same time, the use of controlled experimental paradigms, such as computer-based approaches, allows extremely sensitive measures of nonhuman primates' gaze processing to be made. It is through such research that the psychophysics and neurocognitive processing of gaze can be explored.

3.1) Study species

Tomasello and Call (1997) highlighted the lack of data on the cognitive abilities of most primate species and their comments are still pertinent a few further years on. Concerning research on gaze perception, the only species that has been extensively studied is the chimpanzee; even other ape species have received far less attention. Monkeys have been neglected, with most research being conducted on macaques; little is known about New World monkeys and nothing is known about colobines. In addition, prosimians have been the focus of only two studies (Itakura, 1996; Anderson & Mitchell, 1999). Thus, there is a paucity of data concerning the responses of most nonhuman primates to gaze. For example, only chimpanzees have been tested on their understanding of their own looking behaviour (Call & Carpenter, 2001). Comparative data on a wider range of species would be informative for constructing a phylogenetic picture of these skills (Byrne, 1995; Povinelli

& Eddy, 1996a; Tomasello & Call, 1997). They would also be useful for determining how and in what circumstances the various species respond to gaze.

Some authors have advocated a division between the great apes and other species of primates in terms of their social cognitive abilities (e.g. Anderson, 1996; Byrne, 1995); however, the data from gaze studies do not yet support such a position (Tomasello & Call, 1997). Chimpanzees have certainly demonstrated sophisticated responses to gaze, but the abilities of other species have not been tested in comparable studies. Where comparable data is available, there is no evidence that the responses of apes differ from those of monkeys (further research is necessary for an evaluation of prosimian abilities). For example, both apes and monkeys readily gaze follow but have difficulties within other paradigms, such as object-choice tasks. Where differences are found these may be due to what Tomasello and Call (1996) term 'enculturation'; as highlighted in Chapter One, nonhuman primates with extensive interaction with humans usually out-perform conspecifics without such experience. As yet it is unclear whether extensive exposure to human interactants results in 'species-atypical competencies' (Tomasello & Call, 1997) or individuals who will more readily interact with a human experimenter and have a better appreciation of human behaviours in general. Cross-species comparison of this issue is impossible at this time, as monkeys have not been raised within a human environment in a manner comparable to the so-called 'enculturated' apes. However, as noted in Chapter Four, studying 'helping hands' capuchins' responses to human looking behaviours might be informative (Custance, Whiten and Fredman, 1999; Herve & Deputte, 1993;).

Kobayashi and Koshima's (1997; 2001) recent work indicates that eye morphology is directly related to the amount of visual scanning with eye movements alone. This leads to testable hypotheses regarding gaze following in nonhuman primates. For example, do species vary in their sensitivity to eye gaze according to the external morphology of the eyes? That is, if elongation of the eyes increases the visual field with eye movements alone,

does sensitivity to eye movements increase accordingly? Furthermore, if coloration (especially of the sclera) serves to camouflage eye position and direction, does this correlate with abilities of different species to detect eye movements?

Moreover, while gaze following has been recorded in several primate species (e.g. Tomasello et al, 1998) the phenomenon has only been well studied in two primate species, namely humans and chimpanzees (Butterworth & Jarret, 1991; Moore, 1999; Povinelli & Eddy, 1996b, 1997; Scaife & Bruner, 1975; Tomasello, Hare & Agnetta, 1999). Both human infants and chimpanzees have demonstrated sophisticated abilities when responding to another individual's visual orientation (Povinelli & Giambrone, 2000). In humans, although there is some disagreement regarding the precise time course of the development of gaze following, it emerges early in infancy and is well consolidated by 18 months (Moore, 1999). The only study of the ontogeny of gaze following in chimpanzees indicates that they reliably follow gaze from late infancy (3-4 years old). Like human infants, chimpanzees are able to:

- 1) Follow another's gaze to targets outside their own visual field (Povinelli & Eddy, 1996b).
- 2) Accurately locate the target of gaze, for example, scanning past distractors (Tomasello et al, 1999).
- 3) Respond to changes in another's eye gaze only (Povinelli & Eddy, 1996b).

In addition, chimpanzees also show an appreciation of opaque barriers when following gaze (Povinelli & Eddy, 1996b; Tomasello et al, 1999).

It is noteworthy that, with the exception of responses to eye gaze (Study 1; Emery et al, 1997; Ferrari et al, 2000; Sato & Nakamura, 2001), this type of research into gaze following abilities has yet to be conducted other primate species; the abilities listed above need to be explored in a wider range of species. For example, are non-ape species able to

follow gaze geometrically, that is, beyond their own peripheral vision and past distractor objects to locate the target of another's gaze? Until research has been broadened, conclusions regarding the evolutionary origins and phylogenetic distribution of gaze following may be premature.

3.2) Developmental studies

Another area that has been largely neglected is ontogeny. Although the emergence of spontaneous gaze following has recently been explored in pigtailed and rhesus macaques and chimpanzees (Ferrari et al, 2000; Tomasello, Hare & Fogleman, 2001), it would be valuable to have further information on more species. In addition, it would be interesting to further explore the emergence of some of the forms of visual co-orientation recorded in human infants and chimpanzees. For example, human infants respond to head orientation rather than eye gaze until they reach around 18 months (Moore, 1999). The results with nonhuman primates are as yet unclear. Pig-tailed macaques tested as juveniles (2-6 years old) and rhesus monkeys tested in infancy (5.5 months onwards) were shown to respond to head and eye orientation, but only the pigtailed macaques were tested with eye gaze alone; while adults responded to shifts in eye directions, juveniles did not (Ferrari et al, 2000). However, the broad age-range of the monkeys studied (2-6 years) does not give much indication of when this ability emerges.

It remains to be determined whether the emergence of various gaze following abilities in nonhuman primates follows a comparable time course to that observed in human infants. Tomasello et al (2001) suggest that once chimpanzee gaze following emerges as a reliable response, it may already be at a sophisticated level; those chimpanzees who reliably visually co-oriented had also performed well in an earlier study which examined their abilities to accurately locate the target of another's gaze (Tomasello, Hare & Agnetta, 1999). However, these conclusions are based on the performance of only four

chimpanzees. Studies into human infants' visual co-orientation abilities offer a plethora of methods that could be adapted for nonhuman primate studies (see Moore & Dunham, 1995, & Moore, 1999).

3.3) Ecological validity

A recent paper by Johnson (2001) suggests that research into primate social cognition has been too constrained by the concept of mental representations and associated experimental paradigms. She proposes that rather than hypothesising about the complexity of the mental state underlying behaviour, the complexity of the behaviours themselves may be more informative. This alternative, distributed-cognition model (e.g. Fogel, 1993) bases analysis on the complexity of ongoing observable behavioural contingencies; as Johnson (2001) puts it, it focuses upon 'micro-level dynamics of particular interactions within that situation'. For example, research into gaze could be conducted using a micro-analysis of where and when an individual looks, and how this related to the ongoing situation, such as when and where other individuals look. Some studies with nonhuman primates have already considered some aspects of gaze behaviour within ongoing social interactions (Carpenter, Tomasello & Savage-Rumbaugh, 1995; Russell, Bard & Adamson, 1997), but further research in this area is desirable. These types of studies benefit from the fact that these interactions are occurring naturally, that is, results would not be unduly influenced by the methods imposed (Hare, 2001; Povinelli & Eddy, 1996a). That is not to say that the context could not be controlled experimentally, for example, competitive contexts could be created and interactions then recorded (e.g. Blois-Heulin & Girona, 1999). Focusing upon behaviour rather than representations need not result in a reduced richness of interpretation. Indeed, even for those who focus upon mental state attribution, their methods depend on observable behaviours on which their interpretations are based: as

mental states can only be inferred from behaviours; perhaps behaviour is both necessary and sufficient for an analysis of even complex social interactions.

The divergence between nonhuman primates' spontaneous gaze following and their responses in alternative experimental paradigms suggests that the latter may lack external validity. Surprisingly, gaze research with nonhuman primates is only now undergoing a paradigm shift from co-operative to more competitive contexts (Hare, 2001). Theories to explain primate behaviour have for some time focused on the social environment and the need to compete with conspecifics (e.g. Byrne & Whiten, 1988; Dawkins & Krebs, 1978). As Whiten (1997, p 162) states, 'to a Machiavellian primate, an entry level approach to mindreading through sensitivity to attention makes sense, insofar as reading the attention of others affords information of those aspects of the environment that will most probably affect their decision-making and thence determine future behaviour.' Preliminary evidence indicates that competitive contexts may be conducive to exploring gaze perception in nonhuman primates (Study 7; Blois-Heulin & Girona 1999; Hare et al, 2000; Hare, Call & Tomasello, 2001; Hare, 2001). To date, only chimpanzees have been tested in direct competition with conspecifics with the focus on sensitivity to visual co-orientation.

Nevertheless, further exploration of co-operative contexts may also prove valuable. Although co-operative situations with human experimenters do not appear to be conducive to gaze monitoring in nonhuman primates (or at least those with limited experience with humans), it would be interesting to study gaze patterns within co-operative situations involving conspecifics. For example, nonhuman primates reportedly use gaze when soliciting support from conspecifics by alternating their gaze between their potential ally and antagonist (Cheney & Seyfarth, 1990a; Kummer, 1967; de Waal, 1989). This form of gaze alternation should be studied in finer detail as it involves a sophisticated visual co-orientation interaction. Other co-operative situations, including social learning, food sharing, or studies employing tasks designed to elicit co-operation, may reveal insights into

nonhuman primates' use and appreciation of gaze cues. In a co-operative task, do individuals simply focus upon the task, or do gaze patterns alter as the individual becomes aware that assistance from others is required for successful performance? Gaze may be an important component of all of these interactions, and fine-grained analysis of interactions may reveal complex and sophisticated gaze behaviours (Johnson, 2001).

Direct comparisons of performance in co-operative and competitive situations might lead to a better understanding of how and when nonhuman primates use information from others' gaze. For example, Blois-Heulin & Girona (1999) examined mangabeys' social looking patterns in competitive and non-competitive contexts; non-food-related attentional structures were compared with patterns of gaze monitoring within a competitive situation. Introducing a co-operative dimension to this paradigm would allow a comparison of gaze patterns in the two contexts.

Another area that has been neglected is the role of rank on gaze monitoring behaviours. While rank is known to influence visual monitoring within social groups (Chance, 1967), does it also influence their sensitivity to other individuals' visual orientation? One approach might be to present group-living primates with both competitive and co-operative situations in order to assess whether the monkeys reveal different levels of sensitivity to the visual orientation of others. Previous research suggests that subordinate individuals spend more time monitoring others than dominant group members do (e.g. Blois-Heulin & Girona, 1999; Watts, 1998). It may be that gaze monitoring has emerged as a response to social competition within groups. For example, when approaching a valuable resource, it would be adaptive for a lower-ranked individual to be aware of the location and also the visual orientation of dominant group members.

It may also be asked whether general vigilance also varies with rank; that is, are subordinates simply more vigilant in general or do they just spend more time monitoring their social environment (i.e., Chance's attention structure, 1967)? Does it matter whether

an event is intra-group or external, for example, a copulation as opposed to a predator? This could be explored using playbacks of vocalisations related to predators and social events, which could then be matched with control non-playback data collection (e.g. Cheney & Seyfarth, 1990a). This might offer some insight into the function of visual attention within group-living primates, that is, is it primarily due to pressures to deal with the intra-group or external environment, or both (Povinelli & Giambrone, 2000)

With regard to context, it could be argued that subordinates should display similar patterns of gaze monitoring even when they (as opposed to dominant individuals) have access to food items, for example. If a subordinate individual is fortunate enough to locate a desirable food source, it would still be important to monitor other group members, in order to assess whether a dominant is visually oriented in their direction (and potentially aggressive). Alternatively, it may be that the location of other individuals and not their visual orientation is important. For example, subordinates may respond similarly when a dominant individual is in close proximity, even if they are oriented in another direction and therefore not looking. Measures of visual monitoring could take into account the location and orientation of other individuals, amount of time spent looking at other individuals, and the type of look (for example, scanning, glancing or visual tracking; Blois-Heulin and Girona, 1999).

3.4) Alternative methods

Further research into the psychophysics of gaze monitoring is desirable. Many species are extremely sensitive to direct gaze, but it is not yet clear what features determine this detection. For humans, it has been suggested that ratio of sclera to iris is crucial (Baron-Cohen, 1994) and that this may be a robust cue, even though head direction may influence perception of gaze direction (Langton, Watt & Bruce, 2000). In other words, computations based on scleral contrast might be inaccurate when the face is not centrally oriented, but

this would only lead to small errors in judgements about direct versus averted gaze (Anstis, Mayhew & Morley, 1969; Thayer, 1977). However, at more extreme angles of head directions, scleral contrast may not be sufficient; a head turned in profile but with direct eye gaze has a contrast pattern that is similar to that of averted gaze in a frontal-face. Thus, detecting direct gaze presumably requires information regarding eye direction to be processed within a framework that also processes head orientation (Emery, 2000; Langton, 2000; Perrett & Emery, 1994).

Moreover, scleral contrast might be a less appropriate measure in nonhuman primates, due to eye morphology and coloration (Kobayashi & Koshima, 2001). Nonetheless, eye direction is perceptible in nonhuman-primates (see Chapter One, Section 3.2), and an exploration of the features underlying this process is lacking. For example, is the iris/sclera relationship crucial (albeit less apparent), or perhaps the position of the pupils? Do eye-like stimuli (regardless of gaze direction) produce a ‘pop-out’ effect in nonhuman primates or is it only direct gaze that shows this pattern (von Grünau & Anston, 1995)?

More sensitive measures could be informative regarding nonhuman primates’ responses to gaze. For example, response times and eye movements might be more effective than using grosser behavioural or manual responses. Although studies reported above (Studies 10 & 11) used response times (but did not identify reflexive orienting to gaze), there were methodological problems with these and Fagot and Duruelle’s (submitted) studies. This paradigm is a likely direction for future research as it allows the detection of spontaneous and subtle behavioural responses to gaze. Although it is conceivable that reflexive orienting may be a consequence of a mentalistic appreciation of gaze (Driver et al, 1999), it may instead be foundational to future developments of visual co-orientation; research with nonhuman primates could help to clarify what underlies reflexive orienting responses in humans.

Moreover, Fagot and Duruelle (submitted) reported that baboons learned to use the eye-direction information to predict target location; it would be interesting to explore these trained abilities further. For example, how would such predictive cues influence the learning of a discrimination task? Within an implicit learning paradigm (e.g. Lambert & Sumich, 1996), would 'social' cues such as eye and head direction be any more effective or readily learned than equivalent non-social stimuli? Another possible approach for use with nonhuman primates is a 'flicker' paradigm used to examine change blindness (for a recent review see Simons, 2000); this is the phenomenon whereby changes to visual scenes (or even real interactions) go unnoticed. The flicker paradigm presents two almost identical images in very quick succession; in one an object may be missing or have changed colour; these images can be repeatedly presented until the subject eventually 'spots the difference'. A change blindness paradigm incorporating social cues as to the location of change led to adult humans detecting changes more rapidly; the disappearance of an object was detected more quickly if an individual was oriented towards that object in the preceding scene (Langton & O'Donnell, submitted). For nonhuman primates, images could be manipulated to show a stimulus monkey oriented towards or away from the location of the changed item in the image; in addition, variables such as cue type (head, eyes or posture), cue-stimulus distance and identity of the model could be manipulated. This would allow exploration of critical features; would mere proximity of a conspecific be an effective cue, or is visual orientation (head and/or eyes) also important?

Eye movements are a sensitive dependent measure. Research with human children has revealed that implicit behaviours, such as gaze, are sometimes dissociable from explicit verbal responses; in fact, gaze identifies the correct response on a false-belief task despite the children giving erroneous answers (Clements & Perner, 1994). Nonhuman primates could be tested with the methods used by Hood, Willen and Driver (1998); the gaze of a central face presented immediately prior to a peripheral target influenced the latency of 10-

week-old infants' orientation to the target. This method may be more effective than the cueing paradigms used with nonhuman primates to date because it does not require a manual response (such as joystick or touch-screen responses). In addition, the images used by Hood et al (1998) appeared to have motion, perhaps making them more realistic than the static images presented in the computer-based studies with monkeys.

A few studies have recorded frequency and duration of monkeys' visual inspection of scenes depicting gaze (Emery et al, 1997; Lorincz, Baker & Perrett, 1999; Santos & Hauser, 1999), but latency to respond to gaze information has yet to be explored. Emery (2000) has highlighted how different eye movement measures, such as duration and frequency of fixations, can lead to different results and interpretations (see also Mitchell, 1972). Detailed data on visual scan patterns would allow saccade latency and duration and frequency of fixations to be analysed. Hood et al (1998) suggest that traditional gaze following methodologies (e.g. Scaife & Bruner, 1975) may have underestimated infants' perception of gaze behaviours because of infants' tendency to fixate on facial stimuli; perhaps nonhuman primates are similarly constrained by 'sticky fixation'. Thus, although several species have been shown to follow gaze, in response to both head and eye direction, applications of Hood et al's paradigm with nonhuman primates would allow increased sensitivity of the dependent measure (saccade latency) and potentially conducive conditions (removal of central face).

It would also be interesting to attempt to distinguish between location-based responding, such as gaze following to a location in space, and some form of object-based responding which would indicate that the target of the gaze had also been noted in some way. One approach might be to move previously fixated objects to a new location prior to the animal's response on a modified object-choice task. I attempted to conduct such a study with baboons but did not proceed beyond the training phase. Nonhuman primates exhibit a strong position preference and did not master the task of choosing an object that

they had seen baited when its position was swapped with a non-baited object. Rather than using visual cues to guide their searches, nonhuman primates often exhibit a strong position preference (Ristau, 1998; Tomasello & Call, 1997). Study 2, which looked at levels of interest in previously fixated items, could also be taken further by adapting the procedure so that nonhuman primates watched conspecifics attending to various objects in qualitatively and quantitatively different manners (using video, for example) prior to introducing various novel objects. This would allow a fuller exploration of how another's visual orientation to an object might influence behaviours.

Even a simpler exploration of how visual orientation influences subsequent responses to objects would be informative. For example, visual orientation could be explored using a similar paradigm to that used in Cook & Mineka's (1989) study of social referencing. Although this study has been cited as identifying the role of gaze in social learning (Emery, 2000); it is not clear what role visual orientation plays in nonhuman primates' social referencing. Would visual co-orientation influence which objects nonhuman primates linked the emotional signals with (Baldwin, 1995)? That is, would they specifically identify the object of another's emotional response, or display a more general response to any nearby objects? Young children show specificity in their social referencing; rather than displaying a simple mood-contagion response, children (12 months old) showed differential responses according to which objects and adult had been oriented towards (Hornik, Risenhoover & Gunnar, 1987; Walden & Ogan, 1988). Such paradigms could be readily adapted for use with nonhuman primates (Russell, Bard & Adamson, 1997). In addition, the social relationships of the demonstrator and observer could be taken into account (e.g., Coussi-Korbel & Fragaszy, 1995).

Study 3 attempted to examine whether baboons could form a concept of 'looking at' using a simple discrimination task. A better alternative might be to use a habituation/dishabituation paradigm, asking whether nonhuman primates perceive changes

in depicted visual orientation. Human neonates are sensitive to direct gaze within a habituation paradigm, and this paradigm could be readily adapted for nonhumans (Batki, Baron-Cohen, Wheelwright, Connellan & Ahluwalia, 2000). Moreover, using paired images, this paradigm would also allow investigation of whether nonhuman primates perceive the relationship between models and the focus of their gaze. Pairs of images that are the same in terms of visual orientation in relation to target objects, for example, both depicting individuals looking toward an object (AA) or both showing models looking away from objects (BB), could be presented in sequence with pairs of images depicting different visual orientations (e.g. AA > AB or BB > AB). If subjects are sensitive to differing relationships between visual orientation and targets, then their interest should increase when a sequence of pairs of 'same' images is interrupted by a pair of 'different' images (and vice versa). Premack and Dasser (1991) recommend this paradigm for exploring cognitive abilities, as they draw a distinction between performing at a perceptual and a conceptual level. For example, relational matching to sample requires responses at a conceptual level, while a habituation/dishabituation paradigm simply requires recognition of perceptual changes.

Chapter summary

The data reported in this thesis are consistent with previous research in this field.

Nonhuman primates spontaneously follow gaze within a simple visual co-orientation paradigm, but they do not readily use gaze as an informational cue within other paradigms, such as the object-choice task. Explanations of this pattern of results have been suggested, mainly focusing on the ecological validity of the tasks and general procedural issues. In addition, nonhuman primates do not demonstrate preferential responding to eye gaze, in fact, head orientation seems to be a more salient cue. These findings are not readily accommodated by Baron-Cohen's (1994) model in which the eyes are the pre-eminent source of information regarding another individual's gaze direction. Directions for future research are identified. There is considerable scope for further research on a wider range of primate species, and for a greater consideration of ontogenetic aspects. A more detailed analysis of the role of gaze in nonhuman primates' natural interactions is desirable, but experimental paradigms are also worth pursuing.

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Appendix A:

Testing Olive baboons with an object-choice task.

Figures show experimenter (AV) oriented to the left (head and eyes) and the baboon (Gaspard) making a correct response.



Appendix B:

Testing capuchins with an object-choice task.

Figures show experimenter (SJV) oriented to the left (head and eyes) and the capuchin (Theta) making a correct response.



Appendix C:

Testing baboons with a competitive task.

Figures show experimenter (SJV) oriented to the right (head and eyes) and the baboon (Sylvestre) making a correct response.



Appendix D

Table A: Reaction times (msecs) for locating target cued by a central CONTROL stimulus (mean, standard deviation)

	Stimulus Onset Asynchrony								
	100msec			300msec			1000msec		
	Valid	Invalid	Neutral	Valid	Invalid	Neutral	Valid	Invalid	Neutral
Alfa	1180 (300)	1280 (840)	1230 (340)	1080 (120)	1270 (290)	1470 (430)	1320 (430)	1400 (500)	940 (290)
Felix	1110 (460)	1240 (440)	1330 (530)	1180 (390)	1330 (690)	990 (480)	980 (400)	980 (340)	1050 (390)
Freya	1320 (490)	1320 (570)	1390 (700)	1070 (450)	830(180)	1100 (450)	1330 (390)	1280 (610)	1640 (590)
Hoeba	1190 (410)	1170 (480)	1060 (420)	1080 (400)	1110 (540)	1090 (370)	1130 (460)	1190 (460)	1050 (310)
Kraa	1300 (370)	1110 (430)	950 (170)	1340 (740)	1570 (730)	1230 (590)	1050 (150)	1210 (570)	1180 (250)
Milva	1510 (580)	1570 (460)	1140 (490)	1270 (620)	1310 (650)	1790 (710)	1400 (720)	760 (220)	1210 (340)
Roza	1680 (850)	1590 (720)	1240 (750)	820 (290)	1050 (290)	920 (380)	1560 (680)	1370 (100)	1610 (610)
Vip	1520 (660)	1370 (440)	1490 (440)	1370 (420)	1510 (550)	1490 (520)	1350 (500)	1360 (580)	1390 (480)
Yudea	1150 (480)	1160 (420)	980 (360)	920 (360)	950 (540)	920 (280)	1030 (380)	1010 (390)	1090 (460)

Appendix D cont.

Table B: Reaction times (msecs) for locating target cued by a central FACE stimulus (mean, standard deviation)

	100msec			300msec			1000msec		
	Valid	Invalid	Neutral	Valid	Invalid	Neutral	Valid	Invalid	Neutral
Alfa	1170 (430)	1180 (580)	1370 (350)	1370 (580)	1060 (540)	1110 (270)	1520 (630)	1030 (330)	1080 (430)
Felix	1110 (510)	1020 (300)	1140 (490)	1230 (530)	1310 (610)	1000 (560)	1130 (400)	920 (300)	1480 (650)
Freya	920 (310)	1170 (630)	1350 (670)	1500 (670)	1060 (500)	1300 (460)	1410 (700)	1250 (580)	1250 (630)
Hoeba	1200 (450)	1050 (260)	1130 (380)	1100 (380)	1300 (430)	1030 (260)	1020 (260)	1010 (320)	1180 (380)
Kraa	1640 (670)	1400 (760)	850 (390)	1270 (530)	1030 (380)	1710 (500)	1440 (640)	1190 (500)	1520 (380)
Milva	1460 (640)	1090 (650)	1350 (510)	1300 (490)	1350 (190)	920 (270)	1350 (440)	1630 (890)	1430 (410)
Roza	610 (140)	1300 (780)	1130 (610)	1680 (840)	690 (120)	1420 (930)	1460 (1000)	1000 (180)	1780 (930)
Vip	1350 (460)	1460 (440)	1570 (510)	1500 (620)	1660 (670)	1170 (390)	1470 (670)	1440 (530)	1530 (550)
Yudea	1060 (390)	970 (330)	960 (530)	1010 (420)	820 (230)	960 (290)	1130 (480)	960 (340)	990 (510)

Appendix E:

Individual Analyses for Schematic Images.

In order to examine individual performances, each monkey's data were subjected to an analysis of variance (Kingstone, Friesen & Gazzaniga, 2000) with Face (x2), SOA (x3) and cue condition (x3) as factors, the results are given in Table A. One monkey showed a main effect of SOA; Yudea was significantly faster to respond at the 300ms SOA (100ms SOA mean RT = 1050ms, 300ms = 930ms, 1000ms mean = 1040ms, $p = 0.043$). There were no other significant main effects.

Table A: Overall Anova table for individuals with schematic images.

Face (Control ad Face) x Soa (100ms, 300ms, 1000ms) x Cue condition (Congruent and Incongruent). F values with df given in brackets.

Subject	Face	SOA	Cue	F x S	F x C	S x C	F x S x C
Alfa	0.158	0.027	0.254	0.145	1.870	1.740	0.968
	(1, 130)	(2, 130)	(2, 130)	(2, 130)	(2, 130)	(4, 130)	(4, 130)
Felix	0.079	0.654	0.195	2.146	0.862	2.980*	0.708
	(1, 241)	(2, 241)	(2, 241)	(2, 241)	(2, 241)	(4, 241)	(4, 241)
Freya	0.012	1.974	1.411	2.896	0.163	0.992	0.874
	(1, 178)	(2, 178)	(2, 178)	(2, 178)	(2, 178)	(4, 178)	(4, 178)
Hoeba	0.021	0.420	0.712	0.770	0.704	1.624	2.191
	(1, 575)	(2, 575)	(2, 575)	(2, 575)	(2, 575)	(4, 575)	(4, 575)
Kraa	1.819	0.871	0.501	0.798	1.267	2.330	1.561
	(1, 124)	(2, 124)	(2, 124)	(2, 124)	(2, 124)	(4, 124)	(4, 124)
Milva	0.009	0.136	0.488	3.556*	0.669	0.497	3.481*
	(1, 155)	(2, 155)	(2, 155)	(2, 155)	(2, 155)	(4, 155)	(4, 155)
Roza	0.313	1.938	0.440	2.441	0.954	0.882	1.168
	(1, 78)	(2, 78)	(2, 78)	(2, 78)	(2, 78)	(4, 78)	(4, 78)
Vip	0.373	0.167	0.178	0.498	0.518	1.290	1.463
	(1, 356)	(2, 356)	(2, 356)	(2, 356)	(2, 356)	(4, 356)	(4, 356)
Yudea	0.918	3.165*	1.249	0.538	1.210	0.479	0.373
	(1, 376)	(2, 376)	(2, 376)	(2, 376)	(2, 376)	(4, 376)	(4, 376)

* = $p < 0.05$.

Two monkeys showed significant interactions. Felix showed an SOA x cue condition interaction ($p = 0.02$); at the 1000ms SOA there were significant differences in RT according to cue condition with neutral (direct gaze) targets being responded to significantly slower than incongruent targets ($p = 0.019$, congruent mean RT = 1046ms, incongruent = 952ms, neutral = 1254ms, and showing a trend in the same direction compared with congruent trials, $p = 0.074$). In other words, she was significantly slower to respond to neutral stimuli but only at the longest SOA.

Milva's results indicate significant interactions between stimulus type and SOA ($p = 0.031$); she responded more slowly to the schematic face than to the control, but only at the 1000ms SOA, at shorter SOAs the face condition produced faster RTs (100ms SOA face mean RT = 1340ms, control = 1410ms; 300ms SOA face = 1180ms, control = 1430ms; 1000ms SOA face = 1420, control = 1250ms). Milva also showed an interaction between stimulus type, SOA and cue condition ($p = 0.009$); she responded more quickly when presented with a neutral schematic face at 300ms SOA, than to a neutral control image at the same SOA, was faster to respond to an incongruent target than to a congruent or neutral target with the control stimuli at 300ms SOA, but was slower to locate a incongruent target than a congruent or neutral target with a schematic face presented at 1000ms.

Appendix F

Table A: Reaction times (msec) for locating target cued by a central HEAD stimulus (mean, standard deviation).

	Stimulus Onset Asynchrony					
	100msec		300msec		1000msec	
	Valid	Invalid	Valid	Invalid	Valid	Invalid
Alfa	1040 (320)	890 (320)	1160 (590)	1210 (610)	990 (220)	1000 (240)
Felix	1070 (400)	980 (450)	1010 (520)	1170 (740)	960 (520)	1200 (650)
Freya	650 (150)	800 (310)	780 (200)	990 (440)	860 (230)	860 (300)
Hoeba	960 (390)	860 (190)	940 (300)	810 (210)	950 (220)	750 (210)
Kraa	940 (340)	1250 (590)	990 (290)	1030 (450)	1410 (530)	1280 (640)
Milva	910 (400)	770 (280)	1000 (460)	1120 (420)	1330 (540)	970 (240)
Roza	990 (670)	750 (370)	840 (420)	1100 (520)	810 (300)	900 (410)
Vip	1020 (230)	1040 (390)	980 (190)	1140 (410)	1040 (300)	1270 (450)
Yudea	1050 (620)	1000 (330)	1190 (610)	1320 (500)	1090 (290)	1020 (420)

Appendix F cont.

Table B: Reaction times (msec) for locating target cued by a central EYES stimulus (mean, standard deviation)

	Stimulus Onset Asynchrony											
	100msec				300msec				1000msec			
	Valid	Invalid	Neutral		Valid	Invalid	Neutral		Valid	Invalid	Neutral	
Alfa	1100 (400)	870 (170)	890 (320)		1100 (600)	1100 (570)	870 (340)		1020 (240)	1180 (720)	940 (220)	
Felix	1000 (380)	680 (210)	1010 (320)		1230 (640)	1140 (510)	740 (100)		670 (110)	960 (520)	760 (210)	
Freya	770 (330)	870 (270)	830 (350)		890 (290)	1010 (370)	860 (370)		880 (310)	1000 (590)	920 (490)	
Hoeba	980 (470)	880 (220)	910 (210)		870 (290)	910 (310)	880 (230)		850 (110)	960 (380)	880 (160)	
Kraa	950 (320)	800 (200)	1060 (360)		1160 (520)	1070 (580)	1030 (480)		1250 (410)	1270 (600)	1120 (450)	
Milva	1030 (560)	1080 (490)	810 (280)		1010 (530)	1170 (390)	980 (470)		1340 (620)	890 (220)	1140 (400)	
Roza	750 (90)	980 (700)	850 (440)		1000 (550)	990 (430)	900 (410)		910 (430)	860 (420)	870 (450)	
Vip	920 (100)	1080 (410)	1100 (270)		1030 (310)	1080 (210)	1060 (300)		1010 (150)	1280 (440)	1100 (340)	
Yudea	1090 (440)	1000 (210)	1040 (360)		1010 (340)	1220 (510)	990 (380)		1160 (620)	990 (410)	1010 (350)	

Table C: Reaction times (msec) for locating target cued by a central HALF-PROFILE stimulus (mean, standard deviation)

	Stimulus Onset Asynchrony											
	100msec				300msec				1000msec			
	Valid	Invalid	Neutral	Half-cued	Valid	Invalid	Neutral	Half-cued	Valid	Invalid	Neutral	Half-cued
Alfa	870 (280)	1220 (580)	1260 (930)	980 (390)	1050 (290)	940 (580)	970 (290)	900 (280)	990 (310)	1420 (730)	930 (250)	970 (210)
Felix	1240 (750)	960 (390)	990 (430)	840 (210)	920 (290)	760 (280)	820 (300)	900 (590)	870 (320)	770 (280)	890 (500)	670 (110)
Freya	1010 (620)	890 (470)	990 (590)	810 (380)	870 (340)	920 (460)	1030 (500)	790 (360)	1050 (540)	1100 (430)	930 (330)	1080 (800)
Hoeba	930 (260)	860 (240)	760 (170)	1020 (360)	960 (310)	950 (290)	820 (170)	900 (220)	920 (190)	880 (100)	1080 (480)	870 (250)
Kraa	1150 (500)	1060 (470)	960 (470)	800 (260)	1140 (700)	800 (340)	1040 (710)	1120 (450)	1190 (480)	1160 (390)	1420 (520)	1650 (850)
Milva	800 (140)	1160 (440)	1730 (970)	1020 (500)	980 (570)	780 (160)	1190 (480)	1010 (480)	1120 (580)	830 (390)	1200 (560)	1180 (630)
Roza	700 (360)	890 (510)	630 (120)	860 (300)	940 (410)	930 (330)	760 (350)	990 (460)	1000 (470)	810 (190)	900 (390)	950 (380)
Vip	1020 (150)	1110 (370)	1130 (200)	1120 (510)	1120 (230)	930 (120)	1140 (440)	1010 (260)	950 (130)	1170 (280)	1110 (420)	960 (300)
Yudea	1200 (500)	1120 (360)	1220 (480)	1140 (370)	1130 (630)	910 (470)	1190 (350)	1020 (420)	110 (510)	830 (290)	1040 (300)	1080 (470)

Appendix G:

Individual Analyses for Photographic Stimuli

All face types: congruent versus incongruent:

Supplementary individual Anovas were conducted. Three monkeys showed significant main effects and two others demonstrated interactions. Freya's results indicate a significant effect of face type ($p = 0.035$); she was significantly faster to respond to the head than half-profile condition ($p = 0.01$, mean RT head = 823ms, half-profile = 975ms, eyes = 903ms). Kraa showed a significant main effect for SOA ($p = 0.016$), responses in the 1000ms SOA condition were significantly slower than in the two shorter SOA conditions (100ms mean = 981, 300ms mean 1024, 1000ms mean 1166, both $p < 0.05$). There was an effect of cue condition for one monkey; Vip was significantly faster to locate congruent targets compared with incongruent targets ($p = 0.012$, mean congruent = 1012ms, incongruent = 1123ms).

Felix demonstrated a face type by SOA interaction ($p = 0.044$); she was faster to respond to eye stimuli at 100ms and to the half-profile at 300ms, but was slower to head stimuli at 1000ms (see Appendix F for mean RTs). Milva showed a SOA by cue condition interaction ($p = 0.008$), she was faster to respond to a congruent location at 100ms SOA (mean congruent = 910, incongruent = 1060) and at 300ms SOA (mean congruent = 1000ms, incongruent = 1040) but she was slower to respond to congruent than incongruent targets at the longest SOA (mean congruent = 1220ms, incongruent = 910ms).

Table A: All cues (head, eyes and half-profile) congruent versus incongruent.

Anova table for Soa (100ms, 300ms, 1000ms) x Cue condition (Congruent and Incongruent). F values with df given in brackets.

Subject	Face	SOA	Cue	F x S	F x C	S x C	F x S x C
Alfa	0.090	1.163	0.748	1.033	1.621	1.155	1.188
	(1, 193)	(2, 193)	(2, 193)	(4, 193)	(2, 193)	(4, 193)	(4, 193)
Felix	1.482	1.118	0.314	2.510*	2.028	2.028	0.293
	(1, 179)	(2, 179)	(2, 179)	(4, 179)	(2, 179)	(4, 179)	(4, 179)
Freya	3.386*	2.294	2.560	0.943	0.718	0.332	0.355
	(1, 296)	(2, 296)	(2, 296)	(4, 296)	(2, 296)	(4, 296)	(4, 296)
Hoeba	0.443	0.223	2.751	0.447	2.044	0.265	0.683
	(1, 315)	(2, 315)	(2, 315)	(4, 315)	(2, 315)	(4, 315)	(4, 315)
Kraa	0.454	4.204*	0.505	1.104	0.895	0.428	0.669
	(1, 82)	(2, 82)	(2, 82)	(4, 82)	(2, 82)	(4, 82)	(4, 82)
Milva	1.702	1.205	1.867	1.100	0.143	4.997*	1.629
	(1, 213)	(2, 213)	(2, 213)	(4, 213)	(2, 213)	(4, 213)	(4, 213)
Roza	0.125	1.337	0.265	0.132	0.082	0.475	1.721
	(1, 224)	(2, 224)	(2, 224)	(4, 224)	(2, 224)	(4, 224)	(4, 224)
Vip	0.203	1.638	6.390*	0.377	0.699	2.609	0.771
	(1, 194)	(2, 194)	(2, 194)	(4, 194)	(2, 194)	(4, 194)	(4, 194)
Yudea	0.228	1.027	0.937	1.826	0.753	1.177	0.805
	(1, 290)	(2, 290)	(2, 290)	(4, 290)	(2, 290)	(4, 290)	(4, 290)

* = $p < 0.05$.

Stimulus Type:

a) Head

As head direction either cued or did not cue the target location, a 3 (SOA) x 2

(Cue) Anova was conducted on the individual data (see Table B).

Table B: Head: congruent versus incongruent.

Anova table for SOA x Cue condition. F values with df given in brackets.

Subject	SOA	Cue	SOA x Cue
Alfa	1.840	0.098	0.359
	(2,64)	(1,64)	(2, 64)
Felix	0.080	0.523	0.433
	(2,59)	(1,59)	(2, 59)
Freya	3.165*	4.154*	1.100
	(2,98)	(1,98)	(2, 98)
Hoeba	0.499	7.451*	0.399
	(2,105)	(1,105)	(2, 105)
Kraa	2.997	0.425	1.206
	(2,65)	(1,65)	(2, 65)
Milva	3.400*	1.739	2.323
	(2,69)	(1,69)	(2, 69)
Roza	0.457	0.112	2.007
	(2,74)	(1,74)	(2, 74)
Vip	0.755	2.253	0.433
	(2,66)	(1,66)	(2, 66)
Yudea	2.123	0.001	4.14
	(2,89)	(1,89)	(2, 89)

* = $p < 0.05$.

At the individual level, Freya showed significant main effects for both SOA ($p = 0.047$) and cue ($p = 0.044$). Her responses were faster at the shortest SOA (720ms) and increased with longer SOAs (300ms SOA mean RT = 890ms; 1000ms SOA = 860ms). Freya showed a cueing benefit, being faster to locate a target congruent with the head cue (mean RT = 760ms) than to detect an incongruent target (mean RT = 890ms). Hoeba showed a significant main effect of cue condition ($p = 0.007$), being faster to detect targets at locations incongruent with head direction (congruent mean RT = 950ms, incongruent = 810ms). Milva's data reveal an effect of SOA ($p = 0.039$); like Freya, her RTs increased as SOA increased (mean RTs = 860ms, 1050ms, 1140ms for 100ms,

300ms and 1000ms SOAs, respectively). Thus, two monkeys showed slower response times to longer SOAs, one monkey showed signs of a cueing benefit for head direction but another showed a cost of cueing. Overall, there is little evidence that head direction cues were inducing reflexive orienting responses in the monkeys; while one monkey showed both an SOA and cue condition effect, there was no interaction: she did not demonstrate the characteristic response pattern for reflexive orienting. There was no significant overall benefit (in terms of RT) for targets that were preceded by a congruent rather than incongruent head, nor was there any significant interaction between the SOA and cue condition.

b) Half-profile

As the half-profile face could either be congruent or incongruent and congruent or incongruent with neutral eyes (direct gaze), a 3 (SOA) x 4 (Cue) Anova was conducted on the individual data (see Table C). At the individual level, two monkeys showed significant main effects and a third showed an interaction. Kraa's responses were influenced by the SOA; she was significantly slower to respond at the longest SOA ($p = 0.014$: mean RT 100ms SOA = 1020ms, 300ms = 1040ms, 1000ms = 1350ms). Milva showed a significant effect of cue ($p = 0.004$); she was slower to respond a incongruent half-profile with direct gaze (mean RT = 1270ms) than in either the congruent or incongruent condition (congruent = 1000ms, $p = 0.018$, incongruent = 1020ms $p = 0.034$), but not significantly so in relation to the other direct-gaze cue condition (half-cueing = 1070ms, $p = 0.086$). Hoeba showed an SOA by cue interaction ($p = 0.021$); she was slower to respond to the neutral condition at 1000ms (mean = 1080ms) than at 100ms (760ms) or 300ms SOA (820ms).

Table C: Half profile: Anova table.

SOA (100ms, 300ms, 1000ms) x Cue condition (congruent head and eyes, incongruent head and eyes, congruent head, neutral eyes, incongruent head, neutral eyes). F values with df given in brackets.

Subject	SOA	Cue	SOA x Cue
Alfa	1.039	1.936	1.256
	(2,123)	(3,123)	(4, 123)
Felix	2.012	1.462	0.494
	(2, 110)	(3, 110)	(4, 110)
Freya	1.135	0.338	0.609
	(2, 191)	(3,191)	(4, 191)
Hoeba	0.355	0.364	2.546*
	(2, 203)	(3, 203)	(4, 203)
Kraa	4.387*	0.545	1.436
	(2, 121)	(3, 121)	(4, 121)
Milva	1.567	4.581*	1.918
	(2, 146)	(3, 146)	(4, 146)
Roza	1.621	0.874	0.659
	(2, 139)	(3, 129)	(4, 129)
Vip	0.332	0.696	0.839
	(2, 123)	(3, 123)	(4, 123)
Yudea	2.386	1.100	0.604
	(2, 190)	(3,190)	(4, 190)

* = $p < 0.05$.

c) Eyes

As eye direction could either be congruent, incongruent or neutral regarding the target location, a 3 (SOA) x 3 (Cue) Anova was conducted individual data (see Table D). At the individual level of analysis, only one monkey demonstrated any significant effect; Felix showed an SOA x cue interaction ($p = 0.018$). At the 100ms SOA she was faster to locate an incongruent target than those preceded by congruent or neutral faces (mean RT incongruent = 679ms, congruent = 1003ms, neutral = 1011ms), at 300ms SOA she was

considerably faster when presented with a neutral face (congruent = 1232ms, incongruent = 1136ms, neutral = 741ms) and at the longest SOA she was faster to locate congruent targets than during incongruent or neutral trials (congruent = 673ms, incongruent = 957ms, neutral 765). The pattern of responses demonstrated are not typical of those of reflexive orienting, however, her responses at 1000ms SOA could suggest that she was endogenously orienting in line with the eye-gaze cues and was thus faster to congruent locations and slower when targets were incongruent with eye direction.

Table D: Anova results for individuals in eye direction conditions.

SOA (100ms, 300ms, 1000ms) x Cue condition (Congruent and Incongruent and Neutral). F values with df given in brackets.

Subject	SOA	Cue	SOA x Cue
Alfa	0.421	0.098	0.359
	(2,90)	(2,90)	(4, 90)
Felix	2.713	0.774	3.167*
	(2,82)	(2,82)	(4, 82)
Freya	1.169	1.230	0.103
	(2,139)	(2,139)	(4, 139)
Hoeba	0.190	0.097	0.539
	(2,157)	(2,157)	(4, 157)
Kraa	2.656	0.193	0.558
	(2, 89)	(2,89)	(4, 89)
Milva	0.831	0.950	1.912
	(2,97)	(2,97)	(4, 97)
Roza	0.530	0.269	0.293
	(2,105)	(2,105)	(4, 105)
Vip	0.955	2.127	0.582
	(2, 92)	(2, 92)	(4, 92)
Yudea	0.070	0.426	1.159
	(2,146)	(2,146)	(4, 146)

* = $p < 0.05$.