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The eyes have it: the neuroethology, function and evolution of social gaze

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Abstract

Gaze is an important component of social interaction. The function, evolution and neurobiology of gaze processing are therefore of interest to a number of researchers. This review discusses the evolutionary role of social gaze in vertebrates (focusing on primates), and a hypothesis that this role has changed substantially for primates compared to other animals. This change may have been driven by morphological changes to the face and eyes of primates, limitations in the facial anatomy of other vertebrates, changes in the ecology of the environment in which primates live, and a necessity to communicate information about the environment, emotional and mental states. The eyes represent different levels of signal value depending on the status, disposition and emotional state of the sender and receiver of such signals. There are regions in the monkey and human brain which contain neurons that respond selectively to faces, bodies and eye gaze. The ability to follow another individual's gaze direction is affected in individuals with autism and other psychopathological disorders, and after particular localized brain lesions. The hypothesis that gaze following is "hard-wired" in the brain, and may be localized within a circuit linking the superior temporal sulcus, amygdala and orbitofrontal cortex is discussed. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Social living confers a number of costs and benefits to the members of a group. Larger social groups provide increased opportunities for mating, and therefore increased genetic diversity of potential offspring, as well as a reduction in potential inbreeding. They also provide protection from predators, and provide opportunities for learning strategies for coping with the environment, i.e. increasing group size leads to an increasing probability of learning from others. Animals living in smaller groups, however, do not experience competition for valuable resources, such as food and mates. Living in a large group may require different cognitive abilities from those required for living in smaller groups. For example, a hierarchical system of dominance, by its very nature, requires that individuals have access to information about other hierarchy members, know their position within the hierarchy, and have the means to predict other individual's behavior and emotional disposition. The increased reliance on visual signals in some primate species may have been driven by the increased sophistication of social interactions. Coalition formation, tactical deception, reciprocity and knowledge of third

party relationships would be very difficult without such an elaborate system of visual signaling [38,51,142]. Most of the studies on sophisticated social cognition have been carried out in human and non-human primates.

The primate brain contains over 30 regions dedicated to visual processing, including areas which contain neurons responsive to visual social signals (Ref. [55]; see Section 7.1). These signals can be directed to specific individuals, they are less ambiguous than auditory and olfactory signals, and they may be used to communicate emotional and mental states; and as such may be used to predict another individual's behavior. Visual social signals, which contain such a potential range of complexity, may not be present in other vertebrates.

Visual signals in some birds, for example, provide information about the sexual status of a male, through the use of bright coloration, sexual displays and elaborate tails and head crests [19]. Some species of birds, such as parrots and corvids (crows, ravens and jays), which do appear to live in sophisticated social systems, do rely to some extent on visual signals; but the information contained within these signals may be restricted to one form of information (such as sexual status). This pattern is also seen in other social and non-social species, such as some species of mammal. What may be unique to primates is their ability to use intricate visual social signals that appear to have multiple meanings (such as emotional expression and indicator of interest).

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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. The eyes are very important components of the face that can provide this information, especially information about emotional and mental states. This review will focus on the evolution, function and neuroethology of social gaze in a number of vertebrates. The main focus, however, will be gaze perception in human and non-human primates for a number of reasons. First, as described above, primates have sophisticated social systems that rely on visual behavior and visual signals. Second, as mentioned above, the primate brain contains neurons that respond to eye gaze and head orientation. Third, there has been a bias in testing non-human primates, rather than other vertebrates with gaze perception tasks. This has been due to the following: a) monkeys and apes are closely related to humans, b) other vertebrates are not as visually oriented as primates (however see birds), c) non-human primates utilize faces as a means of primary communication, and d) what has been termed mental state attribution (also known as theory of mind) or the ability to infer the psychological states; intentions, beliefs, desires, etc. of other individuals from non-verbal cues (see Section 6; see also Ref. [10] for a review).

Gaze provides other animals (specifically conspecifics) with a means for evaluating an individual's interest in their internal and external environments. The eyes provide very subtle signals to other individuals, and information transferred by this manner is dependent largely on the ability to understand that the eyes capture information about the world. This level of processing may not be available to non-primate animals (however, non-primates have not been evaluated for these abilities).

The review begins by proposing that many primates rely on gaze perception and this is related to a) the ecological constraints of the environments in which they reside, and b) the morphological constraints of the face and body. Next, there is a discussion of the evolution of gaze perception in many vertebrates, and the possible function of gaze detection in these species. The ability to use the information provided by the gaze of others is discussed in the next section on gaze following and joint attention. The following section describes studies, primarily in Old World monkeys and apes, which have attempted to evaluate the contribution of eye gaze perception to attributing mental states in non-human primates. Many of the reports in this section are anecdotal due to a lack of strict testing in any non-human species, however, the anecdotal evidence is intriguing and interesting in relation to the few laboratory studies that are described. The next section discusses the presence of specialized regions of the primate (specifically monkey and human) brain which either respond to gaze stimuli, or fail to discriminate gaze stimuli when lesioned or when compromised in psychopathological disorders, such as autism. The final section of the review evaluates a theory

of eye gaze, autism and a specific brain region implicated in gaze processing called the amygdala (which is located within the medial temporal lobe).

2. Social gaze is more than just the eyes

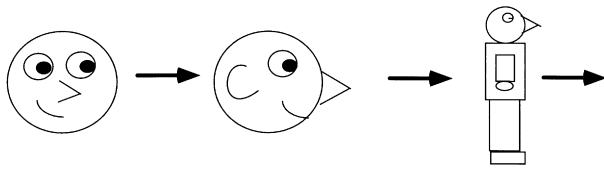
Throughout this review, gaze is not limited to information from the eyes (although this is the primary source). Gaze is not the only cue that is used to determine the focus of another individual's direction of attention, and is not the only component of facial expressions. The whole head, in particular the orientation in which it is directed (using the nose, for example) is a sufficient indicator of attention direction (and therefore interest). In some instances, the eyes are not visible and the only cue available for processing is the head direction (see physiological discussion later). By the same reasoning, if the head is occluded or in shadow, the orientation of the body (determined from the direction of the feet in an upright individual, or the posture of an animal in a quadrupedal stance) provides a sufficient cue for communication (see Fig. 1). This proposition is discussed in greater detail in later sections and in a recent review by Langton and colleagues [90].

3. Morphological & environmental constraints on social gaze

This section will discuss the morphological and environmental changes which may have necessitated a shift in the primary methods of social perception employed by primates. Within the primate order, there is a diverse range of species differences in facial anatomy. Examples include the small face of the loris with the proportionally large forward facing eyes, the long snout of the ring-tailed lemur, the dog-like face of the hamadryas baboon, the prominent nasal features of the proboscis monkey, the malleable lips of the chimpanzee and the large cheek pouches of the adult male orangutan [78].

One clear difference in the facial morphology of prosimians and monkeys compared to the apes is the reduction in the protrusion of the face, in particular, the reduction in jaw size and length of the snout or nose. The hominoid species (orangutans, gorillas, chimpanzees and humans) have relatively flat faces whilst retaining some prominent features. For example, the human face has high cheekbones, a conspicuous nose and eyebrows framing the eyes. Such features may highlight the region around the eyes (the eyebrows), or are used to move the eyes (the cheekbones and related musculature) or may signal direction of attention (the nose). These anatomical changes (a reduction in facial protrusion) may have forced a shift in salience from the shape of the face (and its orientation) to the eyes, as sources of information about attention direction (as a function of gaze). (These anatomical changes may also have emphasized the eyes as an important component of facial

ATTENTION TO THE RIGHT



Eye Gaze Direction > Head Direction > Body Orientation

Q. 1. ARE THE EYES VISIBLE?	Y. DIRECTION OF GAZE N. GO TO Q. 2.	➔	RIGHT
Q. 2. IS THE HEAD VISIBLE?	Y. DIRECTION OF HEAD N. GO TO Q. 3.	➔	RIGHT
Q. 3. IS THE BODY VISIBLE?	Y. DIRECTION OF BODY N. NO CUES AVAILABLE!!!	➔	RIGHT

Fig. 1. Cues to attention or social gaze, are not only provided by the eyes. The direction of the head and orientation of the body may also provide important indicators of attention, when the eyes are obscured or not clear, or if the eyes are used for other purposes, such as the primary component of threatening facial gestures. If all cues are available for processing, a hierarchy of importance exists whereby the eyes provide more important cues than the head, and the head is a more important cue than the body [114].

expressions.) Determining the direction of another individual's attention is easier to establish from larger visual cues, such as the head. Flattening the face of the great apes (for example, as a result of a reduction in olfactory processing and an increased reliance on binocular vision) could have reduced the amount of information that could be transmitted by the head alone. The eyes are much smaller than the head, but they present a more precise indicator of where another is looking [112,114].

The primate face has also evolved an elaborate system of facial musculature that aids in producing expressive facial movements [73,74]. For example, in the rhesus monkey, the muscles surrounding the eyes (*Muscularis orbicularis oculi*) enable the gross movement of the eyes and with the *Muscularis frontalis* (the muscle controlling the eyebrow ridge) the monkey can produce threatening stares. The *Zygomaticus* muscle mass and the *Muscularis triangularis* provide the jaw with the maneuverability to masticate, but would also function in lip smacking and teeth chattering [73]. The *Muscularis obliqui et transversi*, and the *Muscularis auricularis* posterior connected to the back of the ears, may also function in threat sequences and submissive behavior.

In non-primate animals, the facial musculature is undeveloped or non-existent [6,7,73] and therefore, whenever they direct their gaze, they have to move their entire head. Other parts of the body, such as the tail and the extremities, may be important indicators for determining attention direction [18,71,160] when the eyes are unavailable for evaluation. The California quail (*Callipepla californica*), for example, has a large crest on the top of its head (which looks like a question mark) that may function to indicate its direction of attention when its head and body are hidden

in the undergrowth [160]. When the quail is looking ahead, the crest shape is indistinguishable, so the bird must either be looking away from or towards the viewer. If the bird is looking perpendicular to the viewer, the crest either appears as a question mark (if facing to the left), or the mirror image of a question mark (if facing to the right). The small horns of antelope, giraffe, rhinoceros, etc., may also provide indicators as to the direction of their attention, when their heads are occluded [160].

Non-ape species not so reliant on head or gaze direction as cues to attention direction may use the orientation of another's body to decipher where they are attending. Apes may also become reliant on such cues if a second individual's head and eyes were occluded from view, were too small to distinguish with any degree of accuracy, or were hidden in shade or darkness. It would appear to be relatively simple to determine the direction in which a body is pointed if a quadrupedal stance is adopted. Humans rarely adopt this posture, remaining in a more upright bipedal stance. Monkeys and apes, being characteristically quadrupedal in posture, may not require a more accurate method for interpreting direction of attention than head direction or body posture, because the information provided from posture may be sufficient. Orientation of the body, head and eye gaze are in congruent directions for the majority of time spent foraging, grooming, eating, playing and fighting, therefore attention direction can usually be extrapolated from the direction of the body alone.

Body size would also appear to be a constraint on what information is gained from the eyes, head and body. Bigger eyes (or head, or body) are easier to see, and therefore easier to gain information from. It would therefore seem reasonable to suggest from other allometric measures (such as brain size) that as body size increases, so does the size of the head. This is, however, not necessarily true for eye size. Solitary prosimian species without a substantial need for social communication via the visual channel have small bodies and heads, but very large eyes (relative to the size of the face).

The eyes do not appear to have paralleled the changes in facial and body anatomy. Although size differences are apparent, the actual morphology of the eyes themselves does not appear to differ markedly between the many species of primate. The most obvious contrast between species is the relationship between the dark iris/pupil and the white or light brown sclera. A high level of dark iris compared to sclera has been reported for many primates [85]. The major extent of the visible eye is taken up by the dark iris, and a very small part by the white sclera. Humans, in contrast, have a large extent of white sclera either side of the dark central iris (when looking forward, Ref. [115]). This ratio may be one of the factors which has allowed humans to use the orientation of other individual's eyes for learning about objects in the environment (referential active communication), whereas non-human primates may be unable to use such cues (see later discussions).

The morphology of the body, face and eyes provides a set of constraints for primates' use of gaze in a communicative capacity. A further set of constraints is provided by the ecology of the environment in which the primates reside. Those species living in an arboreal (tree-living) environment have a different sensory emphasis of perception and communication from those species living in a terrestrial (ground-dwelling) environment. A forest or jungle environment is perpetually dark; therefore vision would be an inefficient means of communication. Species who live in this environment therefore have to rely on other sensations as their primary method of communication, such as olfactory or auditory. Both auditory and olfactory communication have two distinct disadvantages from visual communication: they are indirectly focused (anyone within range can hear a call, or smell an odor, including predators), and are limited to projecting simple information (such as mating signals, "I'm ready to mate" or spatial position, "I'm over here"), and are less appropriate for projecting information about objects in the environment (unless used in conjunction with visual behavior, "Look at that fruit tree").

4. Phylogenic aspects of gaze perception

The eyes have long held special interest to humans; they are said to be the *window to the soul* [10], they are often used as symbols of a curse (*evil eye*) or as warning signals, but are also one of the first points of contact between infants and their mothers [64]. Non-human vertebrates are also attracted to the eyes, gather information from the eyes and appear to use their own eyes for communication, such as warning others of their emotional disposition (threatening or submissive). This section discusses how a number of different non-human vertebrate species utilize information contained within the eyes (such as for defense against predators), and how this specialized form of visual social perception may have become utilized in non-human and human primates for more complex communicative functions.

Simple schematic representations of the eyes (two black or colored circles) are perceived as eyes in a number of species, and appear to form part of a rapid predator detection system. Lesser mouse lemurs (*Microcerbus murinus*), for example, display more gaze aversion when presented with two schematic eyes presented in a horizontal orientation, than when the same stimuli are presented in a vertical orientation, or when more than two circles are presented or when different stimuli which do not have ethological relevance, such as squares, are presented [40]. A similar effect has also been reported for jewelfish [41], various species of birds [79,134] and wild house mice [146] using similar stimuli. Some species of butterflies and moths (*Lepidoptera*) have evolved eye shaped patterns (eye spots) on their wings as an effective method to deter potential predators (such as lemurs and birds), as they resemble the eyes of other predators

(such as felines and birds of prey) that are the natural predators of small mammals and birds [49].

It would appear adaptive for all prey species to have the ability to distinguish forward facing eyes (or simple representations of the eyes) from other similar stimuli, as most predators have eyes facing the front (binocular vision aids in hunting). The view of one eye, or eyes too close together to be facing forward, present information to the prey species that the predator is not attending to them (see later sections) and therefore may be eluded. Therefore, an important further function of recognizing the presence of the eyes is to determine whether they are looking at or away from you. A large number of species appear to perform this discrimination. Black iguanas (*Ctenosaurua similis*), for example, can differentiate the difference between whether an approaching human is looking towards or away from them [24]. Burger et al. suggested that iguanas perceive gaze contact and direct approach as threatening and escape quicker than when the same experimenter is approaching directly, but looking away from them. Iguanas also appear to be sensitive to the size of the approaching eyes, responding quicker when the eyes are larger [23].

Some species of birds can also perform this type of discrimination. Ristau [130] studied plovers' (*Charadrius sp.*) reactions to human experimenters who walked past their nests either looking at the nests in the dunes, or in the opposite direction towards the ocean. Plovers incubating their young remained off the nest longer under threatening situations, such as when an experimenter was gazing towards the plover's nest, compared to when the experimenter was gazing towards the sea. Gallup, Cummings and Nash [59] also looked at birds' responsivity to human gaze. Chickens (*Gallus gallus*) respond to staring humans by becoming rigid (*tonic immobility*). This is said to correlate highly with fear [59]. The length of immobility was greatly reduced when the eyes of an experimenter were directed away from the chickens. The same phenomenon has also been reported in some species of lizards (*Anolis carolinensis*, Ref. [68]).

A related phenomenon to tonic immobility is *death feigning*, as seen in hog-nosed snakes. This occurs in reaction to eyes directed towards the snakes [25,26]. For example, hog-nosed snakes not only react to the presence of a human experimenter (as a predatory threat), but their response is dependent on the orientation of the experimenter's gaze (towards or away from the snake). Whether these actions are innate behaviors or learnt through extensive experience with predators is not known, although from an evolutionary perspective it would be adaptive to possess this ability innately. Scaife [133,134] suggested that the ability to discriminate the eyes as a stimulus, which is part of the face (a more primitive ability than determining whether gaze is directed or averted), is an innate predisposition.

Other avian species have been tested for their responsivity to specific human head orientations and gaze directions. House sparrows (*Passer domesticus*) were found to increase

flight (an escape response) when a face was directed towards them, but were unresponsive to the direction of the eyes, whether pointed away or towards them [65]. The sparrows, however, could determine the line of gaze from the number of eyes visible. Therefore, the sparrows seemed to associate the perception of direct eye gaze and head direction with a subsequent aversive event, such as capture. Hampton did not test the birds with other stimuli containing eyes or eye-like shapes to determine whether the sparrows had learnt that humans (or other animals) which were directed towards them were to be avoided (producing a flee response) or whether this was a trait that was present early in development.

Primates also possess a great interest in the eyes and the region around them. How some primates may use the information transmitted by the eyes will be discussed in the next sections. Experimental studies of face recognition in monkeys have revealed the interest some primate species have in the eyes. Keating and Keating [83] studied the eye movement responses of two rhesus monkeys whilst they viewed different primate faces (rhesus monkey, chimpanzee and human) with neutral expressions, and also to schematic faces. The subjects showed an extreme bias of looking at the eyes and the small region surrounding the eyes compared with the nose and the mouth, for all four neutral face stimuli, regardless of species. Nahm et al. [107] expanded on these studies using implanted eye coils to record precisely the eye movements of head-restrained monkeys when viewing neutral and expressive faces. The subjects displayed a predominant interest in the eyes and the mouth (the primary components of facial expressions, see below). Baboons have also been shown to look at the eye region more than other parts of the face, and the eyes are essential to them for face recognition. Kyes and Candland [89] presented baboon subjects with slides of other baboon faces, and parts of faces. Although the subjects looked longer at the slides of full (complete) faces, they also inspected pictures which contained eyes longer than slides containing just the nose, or the mouth, or the nose and mouth. Therefore, the eyes seem to be the most important components of the face to these species of primates.

What is not known however, is whether this great interest in the eye region is related to the eyes being a major component of facial expressions, or whether the presence of the eyes is essential for the recognition of individual faces. Can non-human primates recognize faces by the eyes alone? There is some evidence that humans can recognize and remember faces when only presented with the eyes [42,97]. Although some non-human primates can recognize different individuals [142], it is not known what features they use to perceive differences between individuals. It is likely to be a multitude of features: eyes, facial configuration, body size, color, behavior, personality, etc., which provide clues to identity in non-human primates.

Color also performs an important function in highlighting the eye region of some primate species. Kingdon [84]

described the facial patterns and coloration of different species of guenon (*Cercopithecus sp.*, an Old World monkey). For example, *C. mona* and *C. cephus cephus* have bright blue coloration around the eyes, but no coloration of the genital area (white instead of the bright red color of the majority of Cercopithecines, Ref. [60]). This may be interpreted as an increased importance of the face and eyes, and therefore used in facial expressions during sexual or social signaling, or further enhancing the differentiation between the face and the genital region. *Cercopithecus neglectus* have a wide orange-colored brow-ridge, which highlights the position of the eyes [84]. Species of guenon, which do not have brightly colored facial features, usually have brightly colored genitals. It may be interesting to note that the brightly colored genitals are blue, and that the color around the eyes of those species without the genital coloration is blue, although the significance of the color blue is not known.

The eyes play a pivotal role in all primate facial expressions [6,7,18,78,129,147]. Table 1 presents descriptions of the role of the eyes, eyelids and eyebrows in each of Van Hoof's thirteen universal facial expressions for catarrhine primates [147]. Any discussion of the role of the eyes in primate emotional communication must, however, mention the role of the whole face. The eyes are not processed separately from the rest of the face, they are analyzed in concert with other features, such as the nose and mouth, and in particular the ocular muscles surrounding and controlling the movements of the eyes. This is not to say that the eyes alone are not important stimuli for the expression of emotion. In some primates, the effect of a stare without the accompanying facial movements is very effective in eliciting fear or flight responses from conspecifics.

The majority of primates have very darkened eyes compared to humans. Kobayashi and Kohshima [85] found that of eighty-eight primate species, only humans had eyes with a white sclera and a dark iris. The sclera of most primate's eyes was found to be brown or light brown, with two species (Old World macaques) having a pale brown sclera and four species (Old and New World monkeys) having a partially white sclera. The sclera of macaque infants is less pigmented than adults. Perrett and Mistlin [115] suggested that the reason why the sclera of adult macaques may become darker compared to infants is that adult monkeys could look out of the corner of their eye without invoking threatening gestures usually associated with eye contact from other conspecifics, whereas infant macaques are less of a threat. Determining the precise direction of another's attention is difficult to assess when there is no differentiation between the sclera and the iris. In humans, interpreting gaze direction is made easier by the morphology of the eyes. Gaze following can be performed using a simple rule (dark in the center of the eye equals eye contact; dark to the left of the eye equals looking left; dark to the right of the eye equals looking right).

Primates have excellent abilities for discriminating

Table 1

Description of the contribution of the eyes, eyelids and eyebrows to different facial expressions in monkeys and apes (taken from Ref. [147])

Facial Expression	Description
Relaxed face	Eyes in a “neutral position”, “upper eyelid is not lifted completely, the iris being only partly exposed”.
Alert face	“fully opened eye”.
Tense-mouth face	“eyes may be opened rather widely and are staring fixedly towards a partner”, “eyebrows are normal or lowered in a frown”.
Staring open-mouth face	“eyes are staring fixedly at the partner”, “eyebrows are lifted in a vary marked way...the skin of the upper eyelid and the region immediately above it...is exposed”, “the eyebrows may be lowered in a frown”.
Staring bared-teeth scream face	“eyes in most cases are staring fixedly at the opponent”, “eyelids are fully apart, so that the eyes are fully open”, “eyebrows are fully lifted and the upper head skin is retracted”.
Frowning bared-teeth scream face	“eyes are closed or opened only to a small degree...when not closed the eyes are never directed straight towards the opponent; the animal looks away”, “eyebrows are lowered in a frown”.
Silent bared-teeth face	“eyes may be staring at the opponent in a fixed way or be evasive (i.e. it may throw short glances towards the partner out of the corners of its eyes”, “eyebrows...may be relaxed or in a lifted position”, “the degree of opening of the eyes varies; it may be maximum, or normal to slightly opened”.
Bared-teeth gecker face	Same use of eyes as the silent bared-teeth face display.
Lip-smacking face	“eyelids are usually fully apart, so the eyes are completely opened”, “eyes are usually staring in a fixed way at the partner. The head may also...be turned sideways a little, so that the animal is looking out of the corner of its eyes”, “eyebrows are often lifted”.
Teeth-chattering face	“eyelids may be fully apart or in the normal position”, “eyes are either staring at the partner in a fixed way or making evasive movements”, “eyebrows...may be retracted”.
Protruded-lips face	“eyelids may be either fully apart or in the normal position”, “eyes may either be staring at a partner in a fixed way or making evasive movements”, “eyebrows...are lifted completely”.
Pout face	“eyelids are either in the normal position or farther apart”, “eyes may be directed towards a partner”, “eyebrows may be lifted...especially when the expression movement is directed towards a partner”, “simultaneous contraction of the <i>m. depressor supercilli</i> and perhaps the <i>m. corrugator supercilli</i> antagonistic to the <i>m. frontalis</i> responsible for the lifting, may result in a curious slanting position of the eyebrows”.
Relaxed open-mouth face	“eyelids are usually in the relaxed position or slightly drawn together”, “outer corners of the eyes are always slightly lifted due to a pressure from the zygomatic muscle, which draws the mouth-corners backwards and upwards”, “eyes may occasionally be directed to the partner...the gaze is...less fixed”, “eyebrows...are usually in the normal position...they may...be lifted when the display is directed to a partner from a distance”.

whether they are being looked at or whether another’s gaze is directed away from them. Keating and Keating [83] also studied monkey subjects’ eye movements in response to viewing slides of rhesus monkeys with gesturing faces. The expressive stimuli included a slide of a threatening rhesus face with a direct stare, a slide of a rhesus grinning with direct gaze, a slide of a rhesus grinning with averted gaze and a slide of a rhesus with a neutral expression with direct gaze. Both subjects looked at the eye region more often than the nose and mouth and looked at the faces with direct gaze (irrespective of facial expression) more than the face with averted gaze. This pattern of results was repeated when the subjects were presented with slides of human faces. Only slides of two human gestures were presented to the subjects, raised eyebrows and lowered eyebrows. The eye region elicited a higher number of fixations than the nose and mouth regions, and there were a higher number of fixations on the human faces with raised eyebrows. (This does not suggest, however, that the monkeys understood the meaning of the human facial expressions.)

Perrett and Mistlin [115] reported the number of submissive gestures (lip smacking and teeth chattering) that macaque subjects give in response to a human head, with the head oriented towards or away from the viewer and the eyes positioned in compatible or incompatible directions to the

head. The largest number of submissive gestures were made by the subjects when the eyes were in contact with the observing monkey, independent of the human’s head position. This experiment was repeated for elevation of the head [102]. The raised head received fewer appeasement (submissive) gestures compared to a level head position or a head averted laterally by 45°. Similar results were found when Mistlin tested the emotional reactions of stumptailed macaques to a life-sized model of an adult male macaque. The model’s head and eyes could be positioned to provide a range of head and eyes orientations or elevation combinations. The lowered head (similar to a threatening gesture) received more appeasement gestures compared to the head raised or level.

A number of different variables can influence a primates’ reaction to eye contact from a human experimenter, and presumably a conspecific. Thomsen [141] measured the mean frequency of eye contact directed towards a human staring at them; in differently reared rhesus monkeys; in different primate species (talapoin, patas, and squirrel monkeys and crab-eating, rhesus and stumptailed macaques); and in rhesus macaques of different ages and sexes, tested at two distances from the human experimenters. Wild-born rhesus displayed more frequent eye contact than the surrogate reared monkeys. Talapoin monkeys displayed more frequent eye contact with the experimenter

than patas, crab-eating, stump-tailed, squirrel and rhesus monkeys. Young rhesus females displayed more frequent eye contact than young males, and adult females and males. In each case, the frequency of eye contact was less at greater distances between the experimenter and monkey subject. Frequency of eye contact, however, has a different meaning to duration of eye contact. More frequent eye contact suggest that the subject is checking the changing state of the eye gaze of the experimenter, whereas a long duration of eye contact would suggest a threat or affiliative gesture (see below). Unfortunately, duration of eye contact was not measured in this study. These results suggest vast species differences in the importance of eye gaze. For example, talapoin monkeys are a highly vigilant species, compared to rhesus monkeys that avoid eye contact in most social situations. Eye contact does not carry the same relevance for young monkeys as adult monkeys, which would suggest that it is a learnt response. Infant monkeys do, however, respond differentially to a face where the gaze is averted compared to a face with eye contact, as early as three weeks of age [99].

Autonomic physiological changes in non-human primates have been reported to accompany the detection of eye contact, suggesting that eye gaze is an emotive stimulus. Wada [149] studied the EEG responses from the brainstem of macaques to electrical stimulation of the cortex. He found that if he looked at the monkey subjects the EEG trace would change dramatically (p. 41).

When the animal discovered it was being watched, the response was depressed as long as the animal could see the experimenter.... Such flattening regularly occurred whenever the animal realized that the experimenter's gaze was fixed on it.... The direct meaning of the experimenter's gaze...suggests concentrated focusing of discriminatory attention of a quality necessary for self-preservation.

This physiological response may form part of a circuit linking eye contact with a hormonal and/or motor response during courtship and sexual behavior between male and female monkeys. Linnankoski et al. [95] found that females presenting their hindquarters to specific males (proceptivity) caused the males to masturbate and ejaculate, but only when eye contact was established between the male and female. Other visual or olfactory cues, such as inspecting the females perineal region, were not as effective initiators of ejaculation as eye contact.

Monkeys do not appear to make the subtle distinctions between direct staring and mutual eye contact that some great apes and humans do. Direct staring is different from mutual gaze or eye contact in a number of ways. Staring involves the eyes, but also the eyebrows and brow ridges being raised to increase the visibility of the eyes, the ears being pulled back and the hair on the head standing up. The timing of a stare may also be shorter than the duration of mutual gaze. Face-to-face sex is an example of the way that

great apes such as bonobos [43], orangutans [58] and humans [104] may use looking into each other's eyes as a method for confirming and strengthening the sexual and affiliative bond [44]. Linnankoski's [95] study discussed above would also suggest that monkeys might occasionally use the eyes for this function.

5. Gaze following and joint attention

Determining the precise direction of another's attention may be an important ability for non-human primates. Gaze cues provide salient information about the location of objects, but may also function in complex forms of social cognition, such as visual perspective-taking, deception, empathy and theory of mind (see Ref. [152,153,154]).

An important use for gaze following may be determining the position of an individual in a dominance hierarchy. Chance [36] called this *social attention*, where "each individual [*in a social group*] accords and receives attention as a function of his or her rank". The most dominant animal in a social hierarchy receives the highest number of glances (attention from less dominant animals), and glances at other animals the least. Chance stated that members of a social group must have the capacity to determine 1) that the dominant individual is the focus of the others' attention, 2) that these glances total more than those directed towards less dominant animals, and 3) that the group members extrapolate the information that the animal is dominant due to the larger number of glances. There is very little quantitative data to confirm Chance's hypothesis, largely due to difficulties in measuring gaze in the animal's natural environment. A recent study by McNelis and Boatright-Horowitz [98], however, found that social gaze could be measured accurately in patas monkeys (*Erythrocebus patas*) and that lower-ranking animals directed their gaze more towards higher-ranking animals than vice versa.

Observational learning about specific objects in the world would be impossible without gaze following (although other forms of social learning may not require an appreciation of gaze; Ref. [31]). In an interesting series of experiments, Mineka et al. [101] attempted to determine whether fear of snakes in rhesus macaques could be induced in young monkeys through observational conditioning (a specific form of social learning). Young laboratory-reared rhesus monkeys (who were not previously fearful of snakes) became fearful when they observed their wild-reared parents showing fearful responses to real, toy and model snakes. For the young monkeys to become fearful of the snakes by observational learning, they must have used the attention direction of their parents, coupled with their parents' fearful facial expressions directed towards the snakes. Individual X is producing a fearful response, and individual X's attention is directed to the object Z on the ground, therefore, they must be fearful of the object Z on the ground. This form of observational learning would appear to

require information about another's direction of attention and also so-called *joint attention* between the individual X following the direction of conspecific Y's attention onto object Z (an object of joint focus; see Fig. 2).

Shared attention differs from joint attention in a subtle way (Ref. [53,112], see also Fig. 2). However, in the literature the two terms are used interchangeably. Joint attention requires that two individuals (X and Y) are attending to the same object (Z), based on one individual using the attention cues of the second individual. Shared attention, however, is a more complex form of communication that requires that individuals X and Y each have knowledge of the directions of the other individual's attention (or a method for checking that what the other individual is looking at is the same as what they are looking at). Baron-Cohen [9] proposed a modular system for theory of mind (see later) that develops in human infants, which contained components of the gaze communication system. The four modules were an Eye Direction Detector (EDD), an Intentionality Detector (ID), a Shared Attention Mechanism (SAM) and a Theory of Mind Mechanism (ToMM). The EDD module would represent gaze following and joint attention. Perrett and Emery [112], in a commentary to Baron-Cohen [9], proposed a Direction of Attention Detector (DAD) module for processing all potential attention cues (eyes, head or body) and a Mutual Attention Mechanism (MAM) used for detecting mutual gaze. Joint attention would only require activation of the EDD or DAD modules, whereas SAM would require activation of the EDD or DAD, and MAM modules.

Laboratory studies of gaze following and joint attention per se are limited to a small number of species. The ability to gaze follow has been demonstrated most successfully in human infants. The age at which an infant first follows another's gaze is controversial, ranging from 6 to 18 months of age [28,30,39,135]. These age differences may be due to differences in methodology (variation in angle of gaze, the use of an experimenter versus the infant's mother as a stimulus) or in the definitions for gaze the experimenters utilized (see above). Before 12 months old, human infants follow their mother's gaze, but do not direct their attention to the object of her attention. At around 12 months old, infants begin to follow their mother's gaze towards particular objects in their visual field, and at around 18 months old they can direct their attention to objects outside of their field of view (e.g. behind them; Ref. [27]).

Joint attention may be important for language learning in human infants [47,106,144], and human enculturated and language-trained bonobos [63] and parrots [111]. An early stage in language development is the process of associating a word (usually a noun) with the physical presence of an object, such as pronouncing "apple" whilst attending to an apple. This stage of language learning is difficult to achieve without the ability to follow gaze onto (or pointing) at specific objects.

The clearest evidence for the ability to follow gaze in non-human primates comes from experimental work on

the great apes, in particular, studies with chimpanzees. Povinelli and Eddy [121,122,123,125] in their experiments concluded that chimpanzees can follow a human experimenter's gaze, but not use that information to learn about objects in the world or the "mental state" of the individual providing the gaze cues (see next section). Povinelli and Eddy trained chimpanzee subjects to enter a room, and respond for food from an experimenter by using a natural begging gesture (placing a hand in front of the experimenter for a food reward, this signified the end of a trial). Once trained to do this, the human experimenters performed specific attention sequences for the subjects. The three conditions were first eyes and head, where the experimenter shifted his head and eye gaze to behind and to the left or right of the subject. The second condition was similar to the first, but the experimenter only shifted the direction of his/her eyes. The final condition was no change in attention. These three conditions were randomly assigned to test sessions and each session was rewarded. In the eyes and head condition, 50% of the trials (10 trials in each of 8 test sessions) elicited a gaze-following response from the subjects to the correct side, and in the eyes-only condition, 30% of the trials elicited a gaze-following response to the correct side. Povinelli and Eddy interpreted this as shared or joint attention on the part of the chimpanzee subjects.

In a further series of experiments, Povinelli and Eddy [123] obstructed the subjects' line of sight with an opaque shield. The experimenters used their head and eyes to look at an object out of sight of the subjects (on the same side as the experimenters behind the shield). Subjects could follow the experimenter's line of sight to the unseen object (i.e. the subjects would look at the point on the opaque barrier where the experimenter's line of sight hit the barrier). This ability may be important when trying to extrapolate information from other's attention, when the focus of attention is out of sight (such as a predator or food hidden in the undergrowth).

Tomasello, Hare and Agnetta [145] replicated Povinelli and Eddy's experiment with different types of barrier (gutter, board, different rooms and a wall). They attempted to determine whether the chimpanzees were using a simple rule to follow gaze (i.e. stop gaze following when an interesting object comes into the line of sight) or whether they could actually use the experimenter's gaze to determine *geometrically* what specific object the experimenter was looking at. They replicated Povinelli and Eddy's results (the subjects looked more around the barrier when the experimenters had done so, than when the experimenters looked in different directions). To further examine whether the chimpanzees' gaze following was at a low or high level, they provided an interesting distracter object for the experimenter to look at. The subjects were presented with three conditions. First, the experimenter looked at a target location on a wall. Second, the experimenter looked at an animate object (distracter) which was located close to him. Third, the experimenter looked at the target location

whilst the distracter was in view. Tomasello et al. found that the subjects looked at the distracter object, but continued to follow the experimenter's gaze onto the target. This suggests that chimpanzees do not just reflexively follow gaze onto the first available object within view, but track another individual's gaze geometrically to specific locations and objects they attended to. Tomasello et al. suggest that this is the first study to show geometric gaze following in a non-human primate, however, see the arguments and similarities to these results below.

Other investigators have replicated the presence of gaze following in chimpanzees and have described an absence in Old and New World monkeys. Itakura [75] recently studied the ability of eleven species of prosimians, monkeys and apes to follow a human experimenter's gaze (eyes, head and pointing in a corresponding direction). Only the orangutan and chimpanzee subjects made greater than 70% correct responses, with the orangutan making 100% correct responses. This may be attributed to enculturation of the orangutan as has been suggested for chimpanzees [35]. The non-ape subjects (brown lemur, black lemur, squirrel monkey, brown capuchin, whiteface capuchin, stump-tailed macaque, rhesus macaque, pig-tailed macaque, and tonkean macaque) did not respond above chance level.

Anderson, Sallaberry, and Barbier [4] investigated the ability of three capuchin monkeys (*Cebus apella*) to utilize human attention cues to gain food rewards in a Wisconsin General Testing Apparatus (WGTA). Anderson, Montant, and Schmitt [3] also used the same paradigm with three rhesus macaques. Both studies used a forced choice scenario in which the monkey was allowed to choose one of two wells in the WGTA, one covering a food reward. A human experimenter would stand between and behind the two covered food wells and demonstrate attention to the baited food well using different cues; "pointing only", "gaze only" (which included both head and eye cues), and "gaze and pointing" (a combination of both these cues). None of the macaque or capuchin subjects could be trained to use the "gaze only" cues to guide choice of food well. Two subjects of each species could be trained to use either "pointing only" or "gaze and pointing". It is likely that the success with the "gaze and pointing" situation can be attributed to cues arising from pointing rather than the monitoring of gaze direction cues (local enhancement; learning the correct location of the food by using the proximity of the hand to the correct well).

Pettigrew, Forsyth, and Perrett [119], using a similar protocol (but without pointing), obtained equivalent results. Despite training (>100 trials) they found that four out of six rhesus monkeys failed to learn the rule that the head and gaze direction of a human experimenter predicted the location of food reward.

In a gaze paradigm similar to that of Anderson and colleagues [3,4], Itakura and Tanaka [77] found that chimpanzees, an enculturated orangutan and human infants (3–4 years old) could all use gaze (head and eyes) cues (near and

close to the baited food wells), pointing and glancing (eyes only directed towards the food wells) to choose the well baited with food. The responses of all subjects appeared to be spontaneous, not requiring learning. Povinelli and colleagues [120] have also used a similar paradigm to test chimpanzees. They found that the chimpanzee subjects could not determine which well was baited with food when using the experimenter's eyes only as a cue. When the experimenter's head and eyes were directed towards the baited well or slightly above the well, the subjects responded well above chance. The subjects could also follow active gaze (head and eyes, not eyes only), i.e. attention initially directed between the two wells then shifting gaze to the baited well. The negative glancing (eyes only) result reported by Povinelli et al. [120] could have differed from the positive glancing result in the Itakura and Tanaka [77] study due to the age, experimental experience and enculturation of the different groups of subjects.

Itakura and Anderson [76] reported successfully training one juvenile capuchin monkey to use the experimenter's head direction to choose between two presented objects. Peignot and Anderson [110] also found positive results when using captive lowland gorillas. All the subjects appeared to be able to use, pointing and/or head plus gaze cues to locate hidden food, but not use the "eyes alone" as a cue.

As an aside to a study of apes' understanding of intentional versus accidental actions, Call and Tomasello [32] described the failure of five chimpanzees and three orangutans to follow a human experimenter's gaze (it is not known whether eyes alone or head plus eyes were provided as cues) onto one of two baited boxes. The subjects did display an appreciation of intentional action versus accidental action, so it is possible that the subjects did not "trust" the gaze cues of certain experimenters. Also, the subjects results were pooled together and included an enculturated orangutan, which may have looked significantly at the box attended by the experimenter. Unfortunately, no individual data was presented.

Call et al. [33] replicated these experiments with chimpanzees, and found that they readily followed the experimenter's gaze to objects and locations out of their view. The subjects were also tested on their levels of gaze following when the type of occluder was manipulated. In the previous experiments, the experimenters *knew* the location of the hidden food, but could not *see* the food. Different abilities may be important for solving these different problems. When a bowl, which completely covered the food, was used, the chimpanzees could not use gaze to locate the food. When tubes or upturned boxes which allowed the experimenter, but not the subject, to see the food were used, the subjects could use gaze cues to locate the food. This suggested that the chimpanzee subjects could understand the physical properties of an occluder and that the experimenter could see the food, but they could not. The chimpanzees therefore appeared to understand that seeing

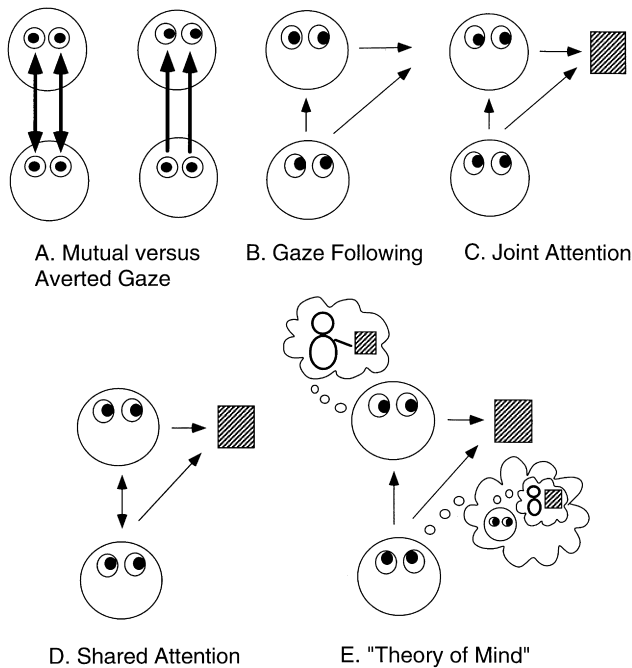


Fig. 2. Gaze direction provides a number of potential *social cues* which may be utilized by an individual to learn about the external (other individuals, objects, events, etc.) or internal (emotional and intentional) states. A. **Mutual gaze** is where the attention of individuals A and B is directed to one another. Averted gaze is where individual A is looking at B, but the focus of their attention is elsewhere. B. **Gaze following** is where individual A detects that B's gaze is not directed towards them, and follows the line of sight of B onto a point in space. C. **Joint Attention** is the same as Gaze Following except that there is a focus of attention (such as an object), so individuals A and B are looking at the same object. D. **Shared Attention** is a combination of Mutual Attention and Joint Attention, where the focus of individual A and B's attention is on the object of joint focus and each other (i.e. "I know you're looking at X, and you know that I'm looking at X"). E. **Mental state attribution or theory of mind**, probably uses a combination of the previous A-D attentional processes, and higher-order cognitive strategies (including experience and empathy) to determine that an individual is attending to a particular stimulus because they intend to do something with the object, or believe something about the object.

leads to knowing, but not that knowledge persists over time (i.e. the experimenter saw where the food was located, but not when it was covered). This result is surprising, as chimpanzees (and a number of other species) have a concept of object permanence [142]. Chimpanzees may have a concept of object permanence, but do not appear to attribute this concept to the minds of other individuals (see next section).

There are a number of potential reasons that New and Old World monkeys may have failed in these tasks. One is the use of human experimenters as demonstrators. In their natural habitat, if non-human primates can utilize others' gaze cues (as is suggested from field research); a more appropriate line of research would be to use conspecifics as stimuli. A second potential reason may be related to the use of operant tasks (using food rewards). Povinelli and Eddy [122,123] suggested that following another individual's gaze might be an automatic response and form part of a primitive orienting reflex (POR). This would be more

adaptive than an evaluation system, especially when confronted with the possibility of attack from predators or losing a food or mating resource. The use of operant tasks to test for gaze following, therefore, would fail to test the presence of a POR compared to a more complex mechanism involved in social cognition (such as theory of mind). Monkeys may follow gaze, but do not learn how to use gaze during an operant task. This can be assessed by recording the natural, automatic behavioral responses of subjects (such as head and body turns, eye movements or facial expressions) in response to conspecific social stimuli.

Emery et al. [53] utilized both of these techniques (conspecifics as stimuli and eye movement recording) in an attempt to evaluate the naturalistic-type responses of rhesus monkey subjects to gaze stimuli. Briefly, the subjects were head restrained and presented with videotaped sequences of conspecific monkeys looking at a point in space, monkeys looking at two identical moving objects (created using video mirroring technology) or the two objects with no conspecific monkey present. The subjects consistently looked more at the region in space and the object attended to by the conspecific. In the trials where the conspecific was absent, the subjects looked equally at the two identical objects. The subjects were also utilizing the gaze cues from the conspecific and not making a random response, as the largest amount of time (and number of fixations) was directed towards the conspecific. These results suggest that rhesus monkeys can follow the gaze cues of other monkeys, and that this is an automatic POR which is unrelated to the attribution of mental state (X is looking at Y because of Z). If the subjects had continued looking at the previously attended object after the conspecific disappeared from the video display, this would have suggested that the subjects learned that one object was inherently more important than the other based on the behavior of the previously viewed conspecific. This may have been used to argue for a more complex role in mental state attribution.

It is unclear which cues the observer monkeys were using to direct their own attention, as body orientation, head direction and eye gaze direction were all available and all presented in congruent directions. Lorincz, Baker and Perrett [96] recorded the eye movements of monkeys to the presentation of slides of head and body cues in either comparable or conflicting directions (i.e. head left, body oriented right) to determine which cues the monkeys used to orient their own attention. They also presented the subjects with slides of heads only, with the head and eyes in either comparable or conflicting directions. They found that the observing subjects used the information from the head more readily than the body, and they also appeared to follow eye gaze cues when the demonstrator's head was oriented towards the observer monkey. This is therefore the first evidence for eye gaze following in a non-ape species. Although it is possible that that observers were

averting their gaze from the demonstrator monkey, the direction in which they orient their own gaze is consistent with the gaze direction of the demonstrator. When the head and eye gaze were conflicting, however, the observers tended to follow head direction only.

In a study cited above [145], Tomasello and colleagues suggested that they had found the first evidence for geometric gaze following in a non-human primate. However, in the Emery et al. study [53], the monkeys observing the gaze cues of the monkeys on the video directed their own gaze to very specific locations on the video screen. When the demonstrator monkey only was present the subjects looked significantly more at the location in space in which the demonstrator was attending than elsewhere on screen (apart from the demonstrator monkey itself). A similar result was obtained when two objects were presented on screen. This may suggest that the observer monkey was not looking at the first interesting object of attention, as there was not a physical end-point to the demonstrator's gaze (i.e. no object), and was therefore directing its gaze geometrically. It remains to be tested whether monkeys can ignore distracter objects which are located closer to the target object, and not just presented on the opposite side of the screen.

Tomasello, Call and Hare [143] confirmed that some species of primates could follow the gaze of conspecifics. Tomasello et al. found that five species of non-human primate, rhesus, stumptailed and pigtailed macaques, sooty mangabeys and chimpanzees, could follow the gaze cues of conspecifics when semi-free-ranging in a large outdoor enclosure. The experimenter waited for two conspecifics to be proximal to one another, and then the experimenters would attempt to gain the first conspecific's attention by holding up some food. The experimenter would then record the second conspecific's (named the subject) behavior in relation to the gaze behavior of the first conspecific. The experimental trials were analyzed as either questionable or valid. The questionable trials were trials where the conspecific looked at the food, but the subject did not notice the conspecific's attention cue, but did look at the food. The valid trials were designated as trials where the subject looked at the conspecific (and hence gaze cues) and then looked at the food. In the control trials, the food was presented when only the conspecific was present. Tomasello and colleagues found that in all species tested, the subjects looked at the food on a highly significant number of valid trials (79–100%). Interestingly, the stumptailed macaque subjects responded 100% correctly (significantly better than chimpanzees). Stumptails may use gaze cues more often in affiliative gestures than other species. This may be due to the gentle, relaxed manner with which stumptailed macaques interact with conspecifics (such as alerting others to danger, Ref. [44]).

In a recent report, Anderson and Mitchell [5] reported that stumptailed macaques, but not black lemurs, could follow the head turn of a human experimenter from eye contact to a

point in space at an angle 60–90° from center. The authors do not describe how many sessions each subject received (average six trials per session) and present the results as absolute frequencies. The species differences therefore may be due to the number of times in which the subjects participated in the experiment, as there is some evidence that lesser mouse lemurs can respond to low level aspects of gaze (gaze aversion; Ref. [40]).

A sophisticated socio-cognitive ability may not be the exclusive pre-requisite for gaze following, or learning to use another's attention cues to locate a food reward. A number of recent studies have proposed that domestication may also effect gaze following abilities in dogs. Miklosi et al. [100] examined whether assistant dogs (for the blind) could utilize human attention cues (pointing, bowing, nodding, head turning and glancing) to find hidden food. Potential olfactory biases were removed by keeping the food reward wrapped in cloth, which would cover the testing bowls. As with the Anderson [3,4] studies, the experimenter was positioned between the two food receptacles and performed one of the attention cues towards one of the bowls when the subject was paying attention. The subjects responded to the pointing cues immediately, and learnt to utilize the other cues over training. Only one of the assistant dogs learned to use the glancing cue by the end of training.

These results were replicated whilst pet dogs were tested in their owners' homes with their owners providing the cues. The performance was slightly better than the assistant dogs for all the cues. When the experiment was replicated with the experimenter providing the cues, the dogs showed the same level of performance. Dogs can also appear to utilize conspecific cues to locate food. Hare and Tomasello [66] studied the response of dogs to either local enhancement cues (i.e. proximity to the food as a cue) or gaze, body orientation and pointing cues simultaneously, provided by either humans or conspecifics. For the ten subjects tested, 8/10 made the correct food choice when provided with human-local enhancement cues; 5/10 made the correct choice when provided with human-gaze and point cues; 6/10 made the correct choice when provided with dog-local enhancement cues and 4/10 made the correct choice when provided with dog-gaze and point cues. Dogs may be able to use conspecific cues as a throwback to their evolutionary history as pack hunters. Hunting as part of a group requires a degree of cooperation, which may rely on gaze or body orientation monitoring [66].

It appears therefore that monkeys, apes (chimpanzees, orangutans and gorillas) and dogs can follow another individual's gaze, and that this ability is enhanced when the gaze demonstrator is a conspecific. There is also evidence that apes, and to a lesser extent monkeys, can follow gaze to specific locations and objects in space and that gaze following may be more than reflexive and provide information about an animal's behavioral (and possibly mental) intentions. This is discussed in the following section.

6. Gaze and social attention as indicators of mental state

This section evaluates the role that analyzing another's gaze (eye position, or head and body view) may play in assessing what their intentions; dispositions and beliefs are (see Fig. 2). Non-human primates, however, may not be able to infer another's intentions from the presence or direction of their eyes. The eyes may only be used to communicate another's emotional state (such as anger displayed as a threat; Section 4), or to communicate the presence of objects within the immediate environment (Section 5).

There are many instances in the primate literature which suggest that some primates may use gaze to convey information about their intentions, not just of emotions or referring to objects, events or individuals in the environment. Primates may utilize gaze following for soliciting help from conspecifics when challenged by or challenging other group members. Soliciting for assistance or an invitation to co-operate against a third party has been described for baboons [87,109,150] and vervets [38]. Vervet monkeys use quick, furtive glances between an aggressor and a potential helper to gain support from the potential helper. The aggressive monkey needs to be attended to, both by the monkey soliciting help and the potential helper. The helper may then determine the intentions of the soliciting monkey. The object of attention needs to be known to a high degree of accuracy in possibly volatile situations. Soliciting has been described for *Papio anubis* (olive baboons) as (Ref. [109], p. 441):

A triadic interaction in which one individual, the enlisting animal, repeatedly and rapidly turns his head from a second individual, the solicited animal, towards a third individual (opponent), while continuously threatening the third.

Some individuals, during complex behavioral interactions, may utilize the knowledge that other monkeys and apes automatically follow gaze (see previous section). In a database of naturally occurring instances of primate tactical deception, Whiten and Byrne [155] describe an anecdote where they observed a young baboon apparently using gaze direction cues in a possibly deceptive communicative role. Baboons and vervets usually stare and make calls at predators in the distance [38,155]. In the following anecdote, the subadult male, ME, appeared to use this information to his advantage (Ref. [155], p. 237).

Subadult male ME attacks one of the young juveniles who screams. Adult male HL and several other adults run over the hill into view, giving aggressive pant-grunt calls; ME seeing them coming, stands on hind-legs and stares into the distance across the valley. HL and the other newcomers stop and look in this direction; they do not threaten or attack ME.

Whiten and Byrne suggested that subadult male ME

learned that his own attention was a salient cue, which could be used to deter others from chasing him. In this example, a predator (or other interesting object) was not within the field of view (or the object of ME's attention). Attention appeared to be an automatically interesting cue, which was distinguishable enough to disrupt the actions of the pursuing animals. Whiten and Byrne [155,156] discuss many instances where an individual manipulates another's use of attention cues, as a form of deception.

How non-human primates use gaze in intentional communication, and understand the meaning behind this volitional use, has only started to be tested experimentally. One recent study has highlighted one aspect of this use. One gorilla has been shown to successfully use her gaze to refer to objects and to direct humans' attention to objects and the gorilla's behavior [61,62]. Gomez tested an infant gorilla with a problem (similar to one of Kohler's problem-solving experiments with chimpanzees; Ref. [86]) in which it had to get out of a locked room using particular tools. Gomez found that the gorilla not only used conventional objects to solve the problem, but also used the experimenter as a *social object or agent*.

An infant gorilla was placed into a locked room with a latch to lock the door (out of reach of the gorilla), a box high enough to reach the latch and a human experimenter. The infant gorilla used four different strategies to attempt to reach the latch. First, the gorilla dragged the box under the latch and climbed onto the box. Second, the subject dragged the experimenter under the latch, to climb on the experimenter and reach the latch. Third, the gorilla gently led the human experimenter to the door while looking between the experimenter's eyes and the latch (the goal, or object of attention). Finally, the gorilla would look between the experimenter's eyes and the latch without leading the experimenter [61]. By looking at the eyes and face of the experimenter, the gorilla could be said to be directing the attention of the experimenter to the focus of the gorilla's own attention, namely the latch. This may be similar to the baboons described earlier that solicited help by looking continuously between the goal of their attention (an opponent) and a solicited helper [109]. The gorilla may have been checking to see that the experimenter was still attending to the latch and to their actions. The gorilla also appeared to use eye contact to monitor if the human was attending to the gorilla's request which the experimenter acted upon [61].

Chimpanzees have also been described as attempting to influence the behavior of a human caregiver using their eyes (i.e. providing evidence they understand that mental states can be communicated between individuals using gaze). Leavens et al. [91] evaluated the responses of a captive male chimpanzee who alternated his gaze between dropped food (during a matching-to-sample experiment; MTS) and an experimenter. An initial observation of this behavior led the experimenters to videotape the face and body gestures of the chimpanzee during each MTS experiment to determine

whether the chimpanzee was using gaze alternation and/or pointing to direct the experimenters attention to the dropped food. The chimpanzee's behavior was recorded when the experimenter was either present or not present in the room. Analysis of the videotapes over many years showed that the subject appeared to use gaze alternation during 76% of instances in which food was dropped.

Both the Gomez [61] and Leavens [91] studies can be interpreted in ways that do not rely on mental state attribution. Many pet owners discuss the ability of cats and dogs to look at the location of a food source or the door to outside, then back to the pet owner, then back to the food or the door (Emery, personal observations). This behavior is usually associated with vocalizations. Although this behavior is identical to that described above for chimpanzees and gorillas, the domesticated pets would not be described as intentionally communicating with their owners. The pets are likely to have been looking at the location of the food or outside at an earlier occasion, and vocalizing because of motivation to gain the food or entry to outside. The pet owner happened to initiate the required action (get food or open the door) independent of the intentions of the cat or dog. The pet, therefore, learnt through association that looking and vocalizing at an object of interest leads to access to that resource by the actions of the owner.

Distinguishing another individual's visual perspective from one's own is thought to be an important step in interpreting their intentions and thoughts about the world. Kummer et al. [88] attempted to train long-tailed macaques (*Macaca fascicularis*) to take a juice reward, only if a human experimenter was not in a position to observe them taking the reward. The experimenters threatened the monkeys if the monkeys took the reward whilst in their view. The subjects, however, behaved equivalently, drinking juice reward out of sight of the experimenter (hidden behind an occluder), or in front of the experimenter in view. Kummer and colleagues interpreted this as a lack of perspective taking or a lack of "experiencing" another's visual perception.

In an extensive series of experiments, Povinelli & Eddy [124] tested chimpanzees' abilities to choose between an experimenter who can see (and therefore has some knowledge of an event) and an experimenter who cannot see (and therefore does not have the same knowledge). The chimpanzees were trained to make a begging gesture to receive a food reward. The subjects were then presented with a choice of two experimenters: one for whom the eyes were open or free from occlusion, and a second experimenter for whom the eyes were covered with different objects, such as blindfolds, buckets, tinted goggles. The subjects could not differentiate between the experimenters when their eyes were covered (i.e. did not consistently make begging gestures towards the experimenter with the uncovered eyes). When the whole head was covered, however, the subjects made the correct discrimination. The chimpanzee subjects (all juveniles) could not make the inference that seeing (when using

the eyes) leads to knowing about an event (begging gesture), but could when using the head as a cue. This series of experiments has lead Povinelli and Eddy to state that chimpanzees may use a sophisticated level of gaze following (that is probably more sophisticated than that used by macaques; Ref. [53]), but that their use of gaze is not within a mentalistic framework (i.e. they do not have a concept of another individual's mind from gaze cues).

Povinelli and colleagues have recently replicated and expanded these experiments [128] to determine whether the chimpanzee subjects' lack of sophisticated visual perspective-taking in the Povinelli and Eddy [124] study was due to developmental time-course (i.e. the subjects were not old enough to appreciate gaze as a mental event, "seeing"). They found that there was no difference in performance between five and nine years of age, suggesting that chimpanzees do not process another individual's gaze within a mentalistic framework (or at least with respects to this experimental design). Theall and Povinelli [140] also provided evidence that the chimpanzees did not respond preferentially to the experimenter who could see them gesturing, which was not because of the artificial begging response used to evaluate their performance. This was achieved by recording the vocalizations and tactile gestures directed towards each of the experimenters. There was no difference in the number of non-begging gestures directed to the experimenters independent of whether the experimenter was attentive (eyes open and head directed towards the subject) or inattentive (eyes closed or above the subjects).

Santos and Hauser [132] recently utilized a technique often employed in studies of pre-linguistic infants (the expectancy violation paradigm) to determine whether a New World monkey, cotton-top tamarins (*Saguinus oedipus oedipus*), could predict the behavior of a human experimenter based on their gaze cues (head plus eyes or eyes alone). Santos and Hauser presented the tamarins with either an expected or an unexpected event, based on the intention to act related to gaze experience (i.e. an individual gazes at an object he/she intends to interact with, and subsequent actions will be with the attended object, not an unattended object). In the expected trials, the experimenter looked (either with the head plus eyes or the eyes alone) at one of two novel, interesting objects (children's toys), then they reached for the same toy that they were attending to. In the unexpected trials, the experimenter looked at the previously unattended toy, and then reached for the unattended toy. Santos and Hauser reasoned that if the subjects were linking seeing with intentional action, a violation of this expectation (i.e. reaching for the unattended object) would produce longer looking times. They found that this was true when the experimenter looked at the object using head plus eyes, but not the eyes alone. This result may suggest that tamarins can predict another individual's behavior based on their attention, however, there are some difficulties with this technique.

Looking time does not always correlate with interest in an object. Emery et al. [53] found that duration of looking in their study was not significant, however number of inspections (fixations) was significant. A highly vigilant species may be more likely to change their gaze than direct their gaze for long lengths of time onto one area or object. It is also possible that the tamarins were using a simple rule, and that this rule was violated in the unexpected trials (direct gaze at object A → reach [use of specific motor pattern] for object A). This was indeed possible, as the subjects received three identical familiarization trials (expected sequence of behavior) with one of the objects before the test trials. As there was no evidence that the subjects used the experimenter's eyes as a cue, this would also suggest that the tamarins were not attributing mental states to the experimenter (intention to reach for a specific object).

The experiments described above suggest that some apes (and possibly some monkeys) may process another's gaze within a behaviorist framework, but not within a framework which requires a more cognitively based system of mental state attribution (which probably requires some rudimentary language skills). A behaviorist interpretation would state that non-human primates respond to attention cues in terms of reward, and learning about stimulus-response relationships [151]. For example, "X follows the gaze of Y as X has learnt that nutritious fruit attracts Y's gaze". X will be rewarded (i.e. will have access to fruit) if X responds appropriately after observing Y's gaze. This does suggest a level of explicit knowledge of the outcome of another individual's actions and behavioral responses.

Purposive behavior interpretations of the above experiments require that the monkeys and apes understand that other individuals of their own or other species perform acts within an intentional framework (or with a final goal in mind). A leopard hunts monkeys because it has to eat; a chimpanzee looks at a patch of fruit because he intends to eat the fruit, etc. Difficulties in interpretation arise, not just when suggesting that others have purpose in their behavior, but also when suggesting those individuals can interpret and understand another's purpose from individual behavior patterns.

The anecdotal and observational studies described above of monkeys in their natural habitat, and experimental studies of apes in the laboratory, suggest that they may understand the social significance of gaze and social attention cues of other individuals. Studies of monkeys performed in the laboratory, however, suggest a potential dichotomy between the abilities of monkeys and apes in utilizing gaze cues as a means for interpreting another individual's future behavior, in relation to objects. Although the evidence is not entirely convincing, chimpanzees, orangutans and to a lesser extent, gorillas, appear to use direction of attention cues to interpret something about another individual's intentions (as related to objects in the world). There is no evidence that monkeys in the laboratory use gaze cues for this purpose (and the positive evidence provided by anecdotes could be inter-

preted in other ways). This dichotomy may have arisen because the gaze cues presented in the monkey's natural environment would have been provided by conspecifics, and particularly by familiar or related conspecifics (see arguments for monkey gaze following in previous section). In the ape experiments, familiar human experimenters provided the attention cues. (This also explains the positive results for enculturated apes, Ref. [142].) Apes with experience of human experimenters (and particularly enculturated apes [142]), but not wild apes, may have the ability to use non-ape gaze cues (such as provided by humans). Wild monkeys and apes may only utilize conspecific attention direction cues. One potential experiment to test this would be to provide laboratory apes with gaze cues from other primate species (either other apes or monkeys) and test their ability to utilize these cues within a mentalistic framework.

There is very little evidence that any non-human primate can use another individual's gaze cues to evaluate and predict their intentions within a more complex mentalistic framework. This lack of a theory of mind may be due to an absence of language, consciousness or a sense of self in non-human primates [69]. The evidence for the use of gaze cues in humans is much stronger, and will be discussed in Section 7.3.

7. Neurobiology and psychopathology of social gaze

7.1. Neurons responsive to head and gaze direction

The rhesus monkey brain contains neurons that respond preferentially to the sight of human or monkey faces [22,46,117]. An important first step in social interaction is recognizing a conspecific. Cells with responses selective for faces over other objects have been found in the upper and lower banks and the fundus of the anterior superior temporal sulcus (STS, see Fig. 3). This region contains cells that respond to polymodal stimuli (visual, auditory and tactile, Ref. [22]). Perrett et al. [117] recorded from cells in the fundus of the STS (Fig. 3) and found that the responses of face selective neurons were not affected by transformations of the face (changing color, size, vertical orientation). Scrambling the features of the face, however, did reduce the cells' responses, suggesting specificity in the cells' response to facial stimuli. Dividing the face into its component parts (eyes, nose, mouth, etc.) and presenting the separate parts alone also reduced the response of some cells from the initially strong response to the whole face. Some cells, however, responded equally well when the eyes or the mouth region were presented alone.

Rotating the face horizontally away from the front view changes the response of a number of cells. Therefore, the presence of the eyes and a specific head view are important for the responses of a number of cells. For example, one cell displayed an increased response when a face was presented

in profile. Perrett et al. [118] found that changing head view (horizontal orientation) had a dramatic effect on the responses of face responsive neurons. Some cells were tuned to the face, with a gradual decline in neural response with increasing horizontal rotation from the front view of the face (example of a narrow tuning curve). Other cells produced opposite responses, where the cell was preferentially responsive to a profile (e.g. left profile) with a decline in response as the head was rotated towards the face view.

Perrett et al. [114,116] found that neurons responding to all views of the head (broad-tuned, object-centered neurons) were rare, whereas cells responding to specific views of the head (narrow-tuned, viewer-centered cells) were numerous in the anterior STS. A number of viewer-centered cells were responsive to specific views which were not one of the four characteristic views (face, back, left and right profiles). This suggested to Perrett et al. [116] that the function of these neurons (and neurons with responses selective for one of the four characteristic views) may be to determine the direction of another's attention, as these cells were superfluous to requirements for recognizing faces as a distinct class of objects, or for recognizing individual faces.

The breadth of tuning exhibited by some viewer-centered neurons would not explain cell responses to vertical head elevation. Perrett et al. [118] found that a number of cells were unresponsive to changes in horizontal orientations of the head (rotation), but were affected by vertical elevation. For example, a cell responded to all frontal horizontal views, but only when the head was directed upwards. The cell had the same response to front head view directed upwards, as it did to head right profile directed upwards [54]. Other cells were dependent on the view and elevation of the head. For example, a cell responded more strongly when the front head view was directed upwards, compared to the front head view directed downwards [54].

Perrett et al. [114] reported the activity of a cell responsive to attention down. The cell was responsive when the head was directed down, the eyes were directed down or the head and body posture (quadrupedal) was directed downwards. Changing the elevation of the eyes in relation to the head (e.g. eyes directed towards the viewer, head downwards) and the head in relation to the body (e.g. head directed at the viewer, but body posture downwards) changed the direction of attention. Head elevation, therefore, is also an important indicator of attention direction. For example, attention to the left (horizontal, level head) is different to attention up and left or attention down and left.

Eye gaze was also found to be important. Sixty-four percent of cells selective for the face and profile were also dependent on the position of the eyes [113,118]. The majority of cells preferred that the head and eyes were presented in compatible directions with respect to the viewer, such as head left with eyes left. Some cells were selective for eye position independent of the head view. For example, the response to head left and eyes facing viewer would be the same as head and eyes facing the viewer, or head right and

eyes facing the viewer. Eye gaze dependent cells often do not require the presence of the rest of the head to respond [158]. Other cells were only responsive when the eyes were averted from the viewer. As discussed earlier, direct eye contact is a threatening gesture for some non-human primates. These selectively responsive neurons may form part of a dedicated neural system for distinguishing threats from non-threats. Some cells responsive to the face, however, were insensitive to the position of the eyes; i.e. there was no difference in response between eye contact and eyes averted.

It is possible that if the eyes become occluded from view (for example, under poor lighting conditions or occlusion), information from the head becomes more important. In a similar manner, cells responsive to information provided by the body become important if the head is occluded from view. Body orientation is used as a cue for spatial direction (the direction another individual is moving to), especially by hamadryas baboons during their daily marches in search for food and water [136]. A quadrupedal stance is less ambiguous in providing information of attention direction than an upright posture, and may negate the need to use subtler forms of attention cues, such as eye gaze in some animals (see earlier). Neurons in anterior STS have been found which respond to specific views of bodies and body parts in isolation [148]. Perrett et al. [114] proposed that the information provided by eyes/face/body sensitive neurons was part of a processing hierarchy (for attention direction or *social attention*).

Emery [51] recorded from single units in the anterior STS (STPa) and tested the response of head direction specific neurons (such as responsive only to left profile) when an object of focus was also present (see Fig. 4). The cells were tested in response to the head alone, the head looking at the object, the head looking away from the object, the head looking at the object, but with a different, non-selective orientation (such as right profile), and the object alone. None of the cells tested ($n = 4$) were responsive selectively to the head looking at the object (i.e. the cells responded equally to the head alone, and the head looking at the object). This suggests that either the number of cells tested was insufficient or that a different brain region may code for this sophisticated level of gaze processing (joint attention), such as the amygdala. A number of neurons within this brain area respond to another's body movements (walking or reaching) in relation to objects [51,113]. 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).

Neurophysiological responses to eye gaze have also been found in other regions of the macaque brain. Brothers [20,21] recorded from single cells in the amygdala (accessory basal, lateral basal, medial basal, cortical and central nuclei) and the perirhinal/entorhinal cortex. Brothers found two cells which were responsive when a videotaped stimulus of a stump-tailed macaque looked directly into the

camera (i.e. eyes directed towards the viewer), but not when the stimulus monkey averted gaze away from the viewer. The response of these neurons was not analyzed further, but may function in emotive responses to eye contact, as suggested earlier.

Electrophysiological methods have also been employed in humans to determine responses to eye gaze. Bentin et al. [17] recorded event related brain potential (ERP) responses from the lateral temporal scalp of normal subjects and found larger responses to isolated eyes compared to full faces. This contrasts to ERP recordings made directly from electrodes over the fusiform gyrus (ventral temporal lobe) which displayed larger responses to full faces, compared to isolated eyes [2]. The face-specific N170 component of an ERP is larger to the eyes presented alone than to the entire face [17]. Eimer [50], however, tested whether the N170 was dependent on the presence of the eyes in faces, and found no effect on the amplitude of the N170 component; but there was a delay in response to faces without the eyes present. The eyes therefore appear to be as salient a cue for humans as monkeys; however the specific electrophysiological base for these responses requires further investigation.

Neuroimaging studies in normal human subjects have also highlighted a role for the STS and amygdala in gaze processing. Puce and colleagues [127], using functional magnetic resonance imaging (fMRI), found significant activation in the posterior STS to faces in which the eyes or mouths were moving, but not to other moving facial parts (such as facial muscles in the cheeks) and not to other moving stimuli. Wicker and colleagues [157], using an alternative neuroimaging technique (positron emission tomography; PET), found significant activation to mutual and averted gaze in the fusiform gyrus (which also is activated in response to the whole faces; Ref. [126]), right parietal lobe, right inferior temporal gyrus, and the middle temporal gyrus.

Hoffman and Haxby [72] utilized fMRI to determine whether the invariant (permanent and semi-permanent) aspects of a face, such as identity (but this would also include gender, race, age) were processed in different parts of the brain from the changeable (moveable) aspects of a face, such as expression and eye gaze. They found significant activation in the lateral fusiform gyrus to facial identity (see also Ref. [126]), and significant activation in the STS to eye gaze. They also found significant activation in response to eye gaze in the intraparietal sulcus (parietal cortex). Gaze following, rather than detection of the eyes as a facial component, may depend on the connectivity of the STS with the intraparietal sulcus, as the geometric location of objects determined from the direction of eye gaze should require a sophisticated spatial cognition system. There is some evidence for this in the monkey, as neurons responsive to eye gaze in the STS connect reciprocally with neurons in the intraparietal sulcus [67].

The amygdala has also been implicated in gaze processing in humans. Kawashima and colleagues [82] found

significant activation in the amygdala using PET, during a gaze discrimination task (eye contact versus no eye contact). The activation was lateralized to the left amygdala during both the eye contact and no eye-contact conditions, and to the right amygdala during the eye-contact condition. This may not indicate that the amygdala is essential for the discrimination of eye gaze per se, but that eye contact is an emotional stimulus, important enough to activate the amygdala.

7.2. Neuropsychology of gaze perception

Further evidence suggests that the STS, amygdala and possibly orbitofrontal cortex form part of a system coding the direction of another's visual attention (eye gaze direction, not just gaze away or towards a viewer) and the object of another's focus. Campbell et al. [34] and Heywood and Cowey [70] lesioned the STS (specifically the STPa) after testing the limits of eye gaze discrimination in rhesus monkeys. Pre-operatively, the monkeys had to perform a two-choice picture task and to choose the picture with the eyes averted. Differing degrees of eye gaze displacement (head center view), from eye gaze aversion to eye contact, were presented (5, 10 or 20° deviation from center view). The eyes and head were varied independently (e.g. head view 20° from center, eyes 10° from center), to determine whether the monkeys were using eye gaze rather than head position as a discriminative cue. Before surgery, the monkeys were extremely good (75–90% correct) at discriminations of gaze directions, 10 and 20° from center, but poor (chance) at 5° from center. After removal of the STS, the monkeys' performance at discriminations of gaze directions, 10 and 20° from center, was reduced to chance level. It would therefore appear that rhesus monkeys could discriminate gaze averted laterally from eye contact (10 and 20° from center) and that the STS is important for these discriminations.

Eacott et al. [48] also tested the ability of rhesus monkeys with lesions of the STS to discriminate direction of gaze. Pairs of eyes (without the head) were presented towards the viewing monkey subjects (center position) or averted by deviations of 5, 10, 15 or 20° from the viewing monkey. Although the head was occluded, the eyes were presented as part of a head either directed towards the viewer, or averted (20° to the left or right of the viewer). The subjects were presented with a two-choice discrimination, between eyes directed towards the viewer (incorrect stimulus) and eyes averted (correct stimulus), irrespective of the position of the head. The unoperated animals were better (overall) at discriminations of eye gaze deviation greater than 5° (10, 15 and 20°), than the STS lesioned animals, but both groups of subjects were equally impaired at discriminations of 5° from the viewer (however the choices were significantly greater than chance). The percentage number of correct choices increased with increasing deviation from the viewer. Lesioned animals were also impaired on a novel

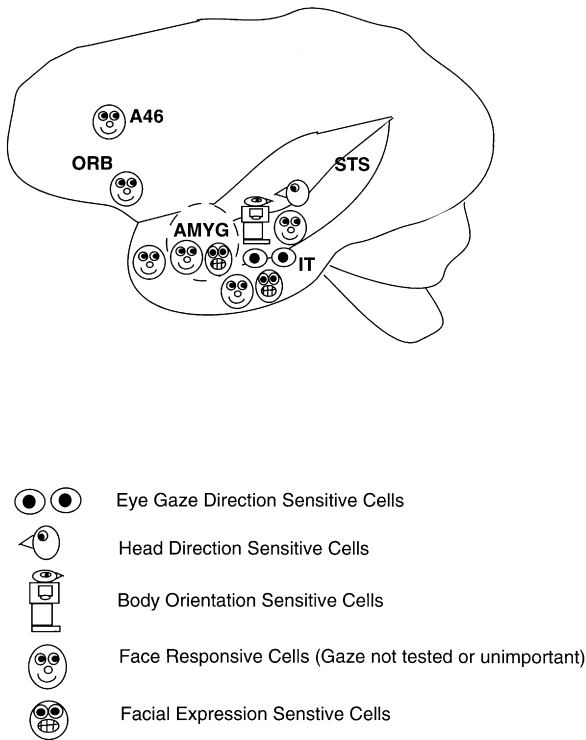


Fig. 3. Schematic representation of a lateral view of the rhesus macaque brain displaying location of cells responsive to faces, eye gaze, head direction, body orientation, and facial expressions. See text for references. Cell types are represented by schematic representations of stimuli, which elicit responses. Left is anterior, right is posterior. Abbreviations: Superior temporal sulcus (STS), amygdala (Amyg), inferotemporal cortex (IT), orbitofrontal cortex (ORB), prefrontal cortex, and principal sulcus (A46).

two-choice discrimination task (between different groups of ASCII characters). Eacott et al. [48] thus concluded that the deficits in processing differences in eye gaze were due to deficits in two-choice discrimination learning. Gaze directed towards the viewer may be an exemplar, which may be compared with other instances of gaze. This may be why there is no difference between operated and unoperated subjects in discriminations of gaze deviations 5° from the viewer. The eye position would not be sufficiently different from the exemplar to aid discrimination. Eacott [48] failed to test the monkey subjects on eye gaze discrimination before STS surgery. It is not known how the operated subjects would have performed pre-operatively in the discrimination task.

Amygdala damage in humans has been shown to cause deficits in processing the direction of another's gaze. Patient DR [159] sustained a bilateral ablation of the amygdaloid complex after surgery for epilepsy, which caused profound disturbances to the patient's processing of faces, such as discrimination of facial identity and expression. DR was also impaired in discriminating between eyes averted and eye contact. A forced-choice paradigm was used where pairs of photographs of faces were presented to the subject. In one-third of the photographs, the head was directed to the viewer, in one-third the head was directed 20° to the left and in one-third the head was directed 20° to the right. Photo-

graphs in which the eyes were directed towards the viewer were target faces. Non-target faces were faces in which the eyes were looking away 5 , 10 or 20° to the right or left. There were therefore six directions of gaze (5 , 10 and 20° left and right) and three head views (0° , 20° left and 20° right), that produced 18 possible trials. Patient DR was deficient in discriminating eye contact (13 out of 18 correct). This was compared to a mean performance of 16.95 (out of 18 correct) for matched control subjects. DR did not make any errors when the faces were deviated by 20° (6 out of 6 correct), but performance was poorer with smaller deviations, 10° (3 out of 6 correct) and 5° (4 out of 6 correct).

The main question that now faces studies of the neurobiology of gaze processing is what are the different contributions of the anterior STS and amygdala. The amygdala has been attributed a role in emotion (particularly fear, Ref. [92]) and social behavior [52]. The STS is likely to be essential for recognizing the eyes, head and body as stimuli used in social communication, whereas the amygdala is likely to be essential for attaching socio-emotional significance to these stimuli, such as a direct stare is a threat, or glancing towards an object may provide information as to its location or valence.

Responses of neurons within the brainstem [149] and changes in the galvanic skin response (GSR, a method to measure changes in the autonomic nervous system in relation to emotive stimuli; Ref. [108]) were dependent on the perception of eye contact. The predominant (and possibly only) route by which visual information about the eyes (and the orientation of the eyes directed towards the viewer; see above) could reach the brainstem, would be via the amygdala. The amygdala may form part of a circuit that attaches emotional significance to the eyes (i.e. threat or embarrassment) and then signals the brainstem to initiate an emotional response (such as an increased GSR or blushing). This could be achieved via a direct projection from the central nucleus of the amygdala to the brainstem [80].

7.3. Psychopathology of gaze perception: autism and schizophrenia

The development of gaze processing in normal human infants follows a specific time course. The age at which an infant first follows another's gaze (usually its mother) is controversial, ranging from 3 to 18 months [28,29,30,39,45,135]. Infants as young as 5 months have been shown to be sensitive to adult gaze shifts as low as 5° (i.e. from the eyes to the ears) when recording changes in the infant's attention and smiling response [139]. During normal development, the ability to focus on the object of another's attention appears between 12 and 18 months of age [103] and the ability to infer mental states from eye gaze appears around 36–48 months [9,10].

Autistic individuals have problems with many forms of social communication. Gaze processing is impaired at many different levels, such as eye contact [81], gaze following

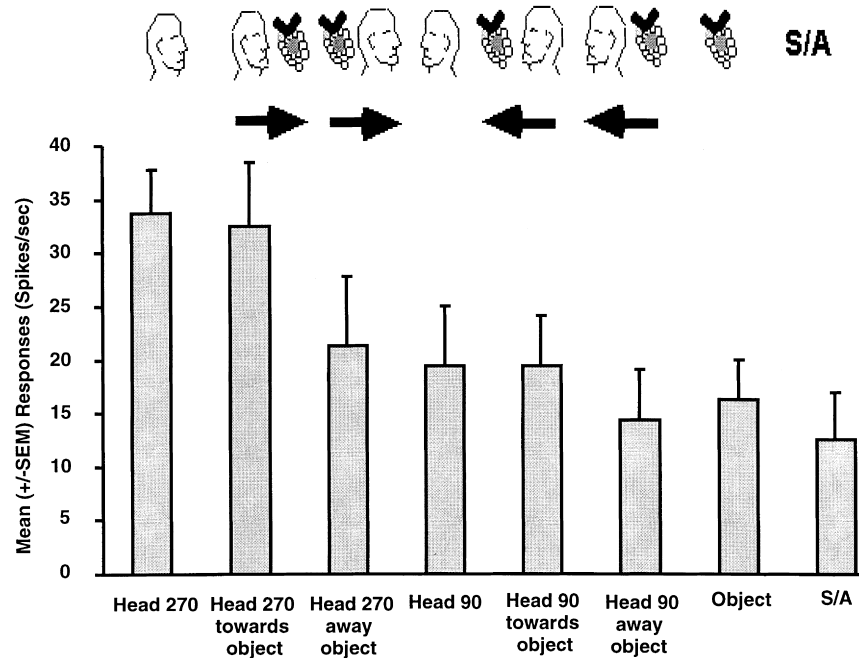


Fig. 4. Neuronal responses of a cell tested for selectivity to head view, and interaction with an object. Mean responses (\pm SEM, $n = 5$ each category) to slides of two different views of a human head (left and right profile), with the head either looking towards and away from an object (hanging fruit), the head without the presence of an object, or the object without the presence of the head, for one cell (S43_2498), located in the STS. There was a significant effect of condition, ANOVA: $F(8, 36) = 3.12$, $p < 0.01$. All views (in all combinations) were significantly different from spontaneous activity; S/A (PLSD, post-hoc comparison, $p < 0.05$). There was a significant main effect of view in a 2-way ANOVA, $F(1, 8) = 9.73$, $p < 0.05$, but no significant effect of object presence, $F(2, 2) = 3.91$, $p = 0.2$. There was also a non-significant interaction between view and object presence, $F(2, 16) = 0.21$, $p = 0.81$. Unpublished data taken from Ref. [51].

[94], joint attention [37], and understanding gaze within a mentalistic framework [11,15,93]. These deficits are not seen in children and adults with Down syndrome [11,15]. A major indication of autism is a lack of joint attention, such as gaze following, protodeclarative pointing (informative pointing), showing or other forms of “referential communication”. Autistic individuals do not direct others attention to objects and events in the environment [105] and they do not use pointing gestures [10].

Two tests of joint attention skills (protodeclarative pointing and gaze monitoring) and a test of pretend play have been used recently as part of a study of 16,000 18-month old normal infants, in an attempt to evaluate the presence of some of the symptoms of autism [12]. The infants were determined to be at risk of being diagnosed as autistic if they failed all three tests. Twelve infants failed all three tests and subsequently ten of them were diagnosed as having autism. After a 3.5-year follow up, all the diagnosed children still displayed the autistic syndrome.

Gaze processing has also been tested in schizophrenics, another syndrome which effects social cognition. The two reported studies found different results. Rosse et al. [131] tested 24 patients with schizophrenia and age-matched controls using similar stimuli to Campbell et al. [34]. The stimuli were slides of a human model with its head and eyes positioned either in the same or incompatible directions at different deviations from view 0° . The subjects were asked

to choose the slides in which the model was looking directly at them. The schizophrenic patients, in particular the paranoid schizophrenics, were more likely to state that the model was looking directly at them than the other subjects. Franck et al. [57], however found that the performance of schizophrenic patients, when presented with a forced choice task of gaze discrimination was no different from control subjects. The task employed was slightly different to that used by Rosse et al. [131] in that the subjects had to state whether the model’s gaze was directed to the left or the right and to respond using a keyboard. This task does not require the subject to use themselves as a reference (mutual gaze), which may be important for emotional processing of gaze, but does require a gaze processing mechanism based on spatial orientation (direction of gaze). The majority of neurons in the macaque STS respond to mutual gaze, or gaze averted, but not to specific directions of gaze. It may be proposed that dysfunction of neurons in the STS responsive to simple gaze (mutual or averted) may play a role in schizophrenia, whereas neurons responsive to specific gaze directions may be unimpaired.

8. Gaze processing, the amygdala and autism: a hypothesis

The potential link between the amygdala and autism has

been suggested from neuropathological analyses of the brains of autistic individuals (the neurons of particular nuclei of the amygdala are more closely packed than in normal brains; Ref. [16]), neuroimaging studies of the living autistic brain [1], and studies of the effects of neonatal lesions in rhesus monkeys [8]. A recent study by Baron-Cohen and colleagues [14] tested normal and high-functioning autistic (Asperger's syndrome, AS) individuals on an eye gaze task, where the subjects had to attribute mental states to photographs containing only the eyes. Performance was measured by the number of correct matches (from two choices) of a mental state term (such as *thoughtful*) to the appropriate picture. The subjects' brains were scanned using fMRI during testing. Both sets of subjects displayed better than chance performance, but the normal subjects were significantly better than the subjects with AS. In normal subjects, the amygdala, prefrontal and superior temporal cortices were activated when making mentalistic judgments about the eyes, but only the prefrontal and superior temporal cortices were activated in AS subjects. This would suggest that the amygdala is important for some aspects of the attribution of mental states to eye stimuli, but not all, as the AS subjects' performance was greater than chance, and they displayed significant activation in fronto-temporal regions. This suggestion has been strengthened by a recent study by Stone et al. [138] who tested patients with amygdala lesions (and patients with orbitofrontal lesions) with the same mental state attribution task using eye stimuli as Baron-Cohen et al. [14]. Both patient groups were significantly impaired on the task (controls 81.2% correct, amygdala-lesioned 66% correct, orbitofrontal-lesioned 67% correct).

It is likely from anatomical and neuropsychological studies in monkeys that the anterior temporal cortex, amygdala and prefrontal cortex (specifically orbitofrontal cortex) are all essential for sophisticated non-human primate social abilities [52]. These regions may also contribute different components to human mental state attribution [54], and would therefore be affected or functionally absent in autistic individuals. Evidence for the role of orbitofrontal cortex in mental state attribution (theory of mind) in humans has been provided by a number of neuroimaging studies. Single photon emission computerized tomography (SPECT) studies during recognition of mental state terms (which autistic individuals fail) revealed significant activation in the right orbitofrontal cortex [13]. PET studies of story comprehension, which also required attribution of mental states, revealed significant activation in the left medial frontal gyrus, area 8 [56]. Finally, Stone et al. [137] tested patients with damage to either the orbitofrontal cortex or dorsolateral prefrontal cortex on theory of mind tasks dependent on processing gaze, and found no deficits in theory of mind tasks in the dorsolateral group. The performance of the orbitofrontal group was comparable to that of patients with Asperger's syndrome. These studies suggest different roles in gaze processing and mental state attribution from gaze cues, for the anterior temporal cortex, amygdala and orbitofrontal cortex, however the different roles are unknown.

dala and orbitofrontal cortex, however the different roles are unknown.

9. Summary and conclusions

A number of different vertebrate species (reptiles, birds, human and non-human mammals) appear to perceive eye gaze and other attention cues in other individuals and use gaze information in their social interactions. The use of eye gaze as a social signal by human and non-human primates may have become necessary due to morphological, environmental and habitat changes throughout primate evolution. This shift to visual processing, and gaze especially, as an important means for signaling, may be related to the development of mental state attribution (theory of mind) in humans (and possibly the great apes).

Although the ability to perceive gaze during various social contexts has been reported (in some form) for monkeys and apes, the use of gaze within a mentalistic context is limited to humans and possibly some of the great apes (although the available evidence is thin and very controversial; Ref. [69,124]). The capacity to follow another individual's gaze onto specific objects, events and individuals in the environment is accomplished by some species of macaques and apes, suggesting that eye gaze may be an important and complex component of learning about the environment from conspecifics, which does not require a more sophisticated 'theory of mind' mechanism. A summary table detailing the presence or absence of gaze processing skills in different animal species, different stages of human development and different pathological states in humans is presented in Table 2.

The ability to learn about the world through another individual's gaze appears to have a dedicated neural basis, and in humans is compromised by a number of psychopathological syndromes, such as autism and schizophrenia and by specific brain lesions. The amygdala has been proposed as an important brain region for processing another's gaze and utilizing these cues as sources of information about the external (objects, events, individuals) and internal (emotions, beliefs, desires, intentions) worlds in human and non-human primates. Future studies will determine the precise role of the amygdala in gaze processing and whether disruption of amygdala function is a major component of autism.

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Table 2

Summary of research on different types of gaze processing in different subject groups (humans at different stages of development; humans with psychopathological or neurological disorders; humans with amygdala lesions; reptiles and birds; monkeys or great apes). ✓ positive evidence, X no evidence, ? not tested or controversial evidence

Subject Group	Eye Presence	Simple Gaze	Gaze Following	Joint Attention	Mental Attribution	References
Fish	✓	?	?	?	?	[41]
Reptiles	✓	✓	?	?	?	[23, 24, 25, 26, 68]
Birds	✓	✓	?	✓ (?)	?	[59, 65, 111, 130, 133, 134]
Rodents	✓	?	?	?	?	[146]
Dogs (domestic)	?	✓	✓	?	?	[66,100]
Prosimians	?	✓	X	?	?	[5, 40, 75]
Monkeys	✓	✓	✓	✓	X	[3, 4, 53, 75, 76, 83, 89, 96, 115, 132, 141, 143]
Great Apes	✓	✓	✓	✓	X (?)	[33, 61, 62, 75, 77, 91, 110, 120, 122–125, 143]
Human						
—3 months	✓	X	X	X	X	[9, 27, 28, 30, 39, 45, 77, 106, 135, 139]
—9 months	✓	✓	X	X	X	[9, 27, 28, 30, 39, 45, 77, 106, 135, 139]
—12 months	✓	✓	X	✓	X	[9, 27, 28, 30, 39, 45, 77, 106, 135, 139]
—18 months	✓	✓	✓	✓	X	[9, 27, 28, 30, 39, 45, 77, 106, 135, 139]
—24 months	✓	✓	✓	✓	X	[9, 27, 28, 30, 39, 45, 77, 106, 135, 139]
—48 months	✓	✓	✓	✓	✓	[9, 27, 28, 30, 39, 45, 77, 106, 135, 139]
—Autism	✓ (?)	✓	?	X	X	[9, 11, 14, 15, 37, 93, 94]
—Down syndrome	✓	✓	✓	✓	✓	[9]
—Schizophrenia	✓	✓	?	?	?	[57, 131]
—Amygdala damage	✓ (?)	X	X (?)	?	X (?)	[138, 159]

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