

Sarah-Jane Vick · Dalila Bovet · James R. Anderson

Gaze discrimination learning in olive baboons (*Papio anubis*)

Received: 27 May 2000 / Accepted after revision: 5 February 2001 / Published online: 21 April 2001

© Springer-Verlag 2001

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

Keywords Baboon · Experimenter-given cues · Gaze · Object-choice task · Picture discrimination

Introduction

Anthropoid primates are extremely sensitive to eye gaze, or at least to one particular form of eye gaze: direct eye contact. From early infancy, humans and monkeys respond differentially to images or observers displaying eye contact or averted gaze (Mendelson et al. 1982; Kalin et al. 1991; Vecera and Johnson 1995; Hains and Muir 1996). There is considerable sensitivity to small deviations in eye gaze from a central position: for example,

Symons et al. (1998) reported that 5-month-old human infants displayed less attention and smiling to adults who averted their gaze by 5° horizontally (but not vertically). Similarly, infant rhesus monkeys discriminated direct from averted gaze (Mendelson et al. 1982) and adult rhesus monkeys discriminated between photographs depicting direct gaze and gaze averted by 5° (Campbell et al. 1990). At the neurophysiological level there is evidence that specific areas of the brain are specialised for the processing of gaze information; single cell recordings in the superior temporal sulcus have identified cells that are sensitive to eyes directed towards the viewer and to averted gaze (Perret et al. 1985). Further, monkeys with lesions in this area fail to discriminate efficiently between gaze aversion and eye contact (Campbell et al. 1990).

However, it is not clear whether the distinctiveness of direct gaze as a percept reflects a more general capacity for discriminating gaze direction; that is, determining whether or not another individual is looking at you does not necessarily imply an ability to distinguish whether the individual is attending to an object based on eye direction, for example. It has been suggested that direct gaze may be a special form of stimulus that receives rapid processing due to its social salience (von Grunau and Anston 1995; Kummer et al. 1996). In nonhuman primates, direct or averted gaze is a critical element in many social situations; for example, maintained stare is a component of threatening facial gestures in many monkeys, while averted gaze can be a sign of submission (Chance 1967; Perret and Mistlin 1991). Moreover, neurophysiological research has thus far only demonstrated sensitivity to direct and averted gaze (in terms of head and eye orientation) and has not revealed sensitivity to gaze in relation to the object of attention (Perret et al. 1985, 1988; Emery 2000). Thus, the function of gaze monitoring in nonhuman primates may serve primarily to detect whether or not another individual is looking at you.

On the other hand, where another individual looks may signal important objects or events, so gaze monitoring could also enable nonhuman primates access to a wealth of information about their physical and social environment

S.-J. Vick (✉) · J.R. Anderson
Department of Psychology, University of Stirling,
Stirling FK9 4LA, Scotland, UK
e-mail: sarah-jane.vick@stir.ac.uk,
Tel.: +44-1786-466839, Fax: +44-1786-467641

D. Bovet
Language Research Center, Department of Psychology,
Georgia State University, Atlanta, Georgia, USA

(Kummer 1967). As stated by Tomasello et al. (1998, p. 1063) “the ability to follow the direction of conspecifics’ visual gaze would seem to be a social skill with immediate adaptive benefits. Following the gaze of others might help individuals perceive important entities in the environment such as food, predators, and certain kinds of social interactions among group mates.” However, a distinction has been made between an ability to follow another’s attention to a location in space and to follow attention to a fixated object. That is, simply co-orienting in the same direction may lead an individual to fortuitously perceive an object, but this is not the same phenomenon as following the direction of gaze in order to mutually fixate an object (Emery et al. 1997; Emery 2000). Simple co-orientation to a spatial location may be a learned or reflexive behavioural response rather than reflecting any appreciation of seeing as a mental state (Tomasello et al. 1998).

Whatever the underlying mechanism, nonhuman primates do co-orient with conspecifics and humans; apes and monkeys but not prosimians have been shown to visually co-orient with another individual (e.g. Emery et al. 1997; Tomasello et al. 1998; Anderson and Mitchell 1999). While studies with chimpanzees have demonstrated an ability to co-orient to changes in another individual’s eye direction alone (Povinelli and Eddy 1997), most studies with monkeys have not attempted to determine whether body posture, head or eye direction cues underlie co-orientation. However, Lorincz et al. (1999) recently used photographic stimuli in order to separate the cues available and reported that rhesus monkeys also co-orient with eye direction alone.

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

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

Study 1

Methods

Subjects

Four olive baboons (*Papio anubis*) were studied, two males (Kiki and Gaspard) and two females (Esmeralda

and Domi) housed at the CNRS Centre de Primatologie, Rousset-sur-Arc, France. Their ages ranged from 3.5 to 10 years and they had either been born at the centre or were transferred there from a safari park approximately 2 years before the study was conducted. All baboons were housed in spacious indoor/outdoor enclosures in small social groups. For the purposes of testing, the baboons were restricted to the outside area; dominant baboons were tested in the presence of other group members, while for testing subordinate baboons more dominant members were closed indoors. The monkeys were fed a diet of commercial monkey pellets, fruit and vegetables, with feeding being postponed until the daily testing sessions were completed. Standard food items were used as reinforcers (small pieces of fruit and vegetables or grains of maize).

Apparatus

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

Materials

Condition 1: Direct Gaze. The stimuli were ten pairs of colour photographs (15 cm×22.5 cm) which had been enlarged using a colour photocopier. Each picture consisted of a face-on head-and-shoulder view of one adult person (viewer) in the centre (face approximately 8 cm×6 cm), the identity of the viewer changed with each new pairing presented. In each pair, one photograph depicted direct gaze, that is towards the observer, while the other depicted

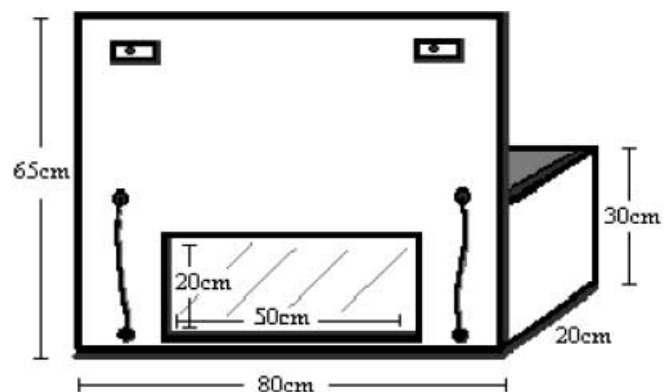


Fig. 1 The apparatus as seen by the baboon

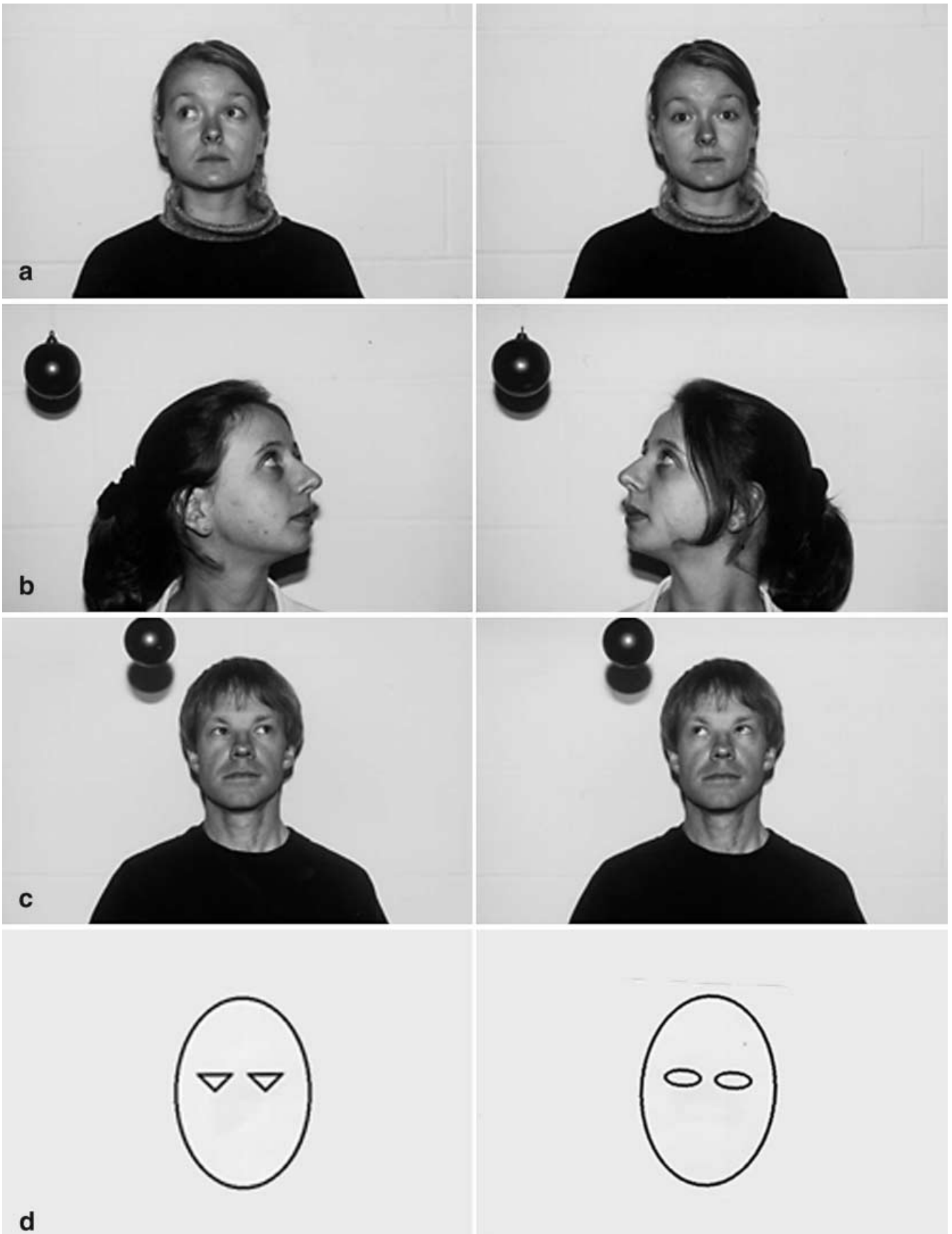


Fig. 2a–d Examples of the stimulus pairs presented. **a** Direct Gaze, **b** Head Orientation, **c** Eye-Gaze Fixation, **d** Geometrics. The images on the *right-hand side* were the correct choices

averted gaze (eyes 25° to one side). The positive stimulus was the direct gaze image (Fig. 2).

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

Condition 3: Eye-Gaze Fixation. Ten pairs of photographs again depicted a central viewer and the target object (located as in condition two). However, in the photographs used in this condition the viewer was always face-on, and one of the pair showed the viewer's eyes fixated on the target while the second showed eye gaze averted from the target (both with 25° deviation from centre; Fig. 2).

Condition 4: Geometrics. Ten pairs of simple line drawings, the same size as the photographic stimuli, were used in this condition. The drawings consisted of a central geometric shape (e.g. ellipse, rectangle) which were approximately the same size as the average faces in the photographic conditions (8 cm×6 cm). Two smaller symbols (e.g. diamonds or parallel lines, 1.5 cm by 7.5 cm, i.e. approximately the same size as the eyes in the photographs) were placed in what would be the eye positions of a human face. Within each pair, the large shape was constant but the small symbols were different; one member of each pair was selected as the correct choice and was always rewarded (Fig. 2).

Design

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

Procedure

Training. Before commencing with the experimental conditions the baboons were trained to meet the response de-

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

Testing. Testing was carried out at approximately the same time each day for each subject but test sessions varied in length depending on the baboons' motivation to perform the task. Basic sessions consisted of 30-trial blocks with the correct stimuli being pseudo-randomly presented to the left or right, with no more than three consecutive baitings to either side. For each trial, an opaque card screen was placed in the window and the pictures were put in place side by side behind this screen; the screen was then removed and the baboon responded by pulling one of the cords. Pulling on the cord next to the correct stimulus was rewarded by the experimenter who delivered a food item directly beneath the centre of the apparatus. The stimuli were then concealed and arranged for presentation on the next trial. An incorrect response was followed by the immediate replacement of the card screen and a short delay (approximately 10 s). Responses were recorded on a score sheet. A problem was considered mastered when the subject performed at 80% or above over two consecutive blocks; attainment of this criterion resulted in the next stimulus pair of the set being presented in the next session. A condition was considered completed if a baboon reached criterion within two blocks of the problem, that is, 80% correct responses for the first 60 trials presented, for two consecutive stimulus pairs.

Results and discussion

All four baboons reached criterion in at least one of the photographic or line drawing discriminations. In each case the first condition was mastered only after many trials and with marked individual differences in performance. However, two baboons then required only between 2 and 11 sessions to learn subsequent problems. Thus, olive ba-

Table 1 Subject characteristics and the experimental conditions encountered by each baboon in study 1

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

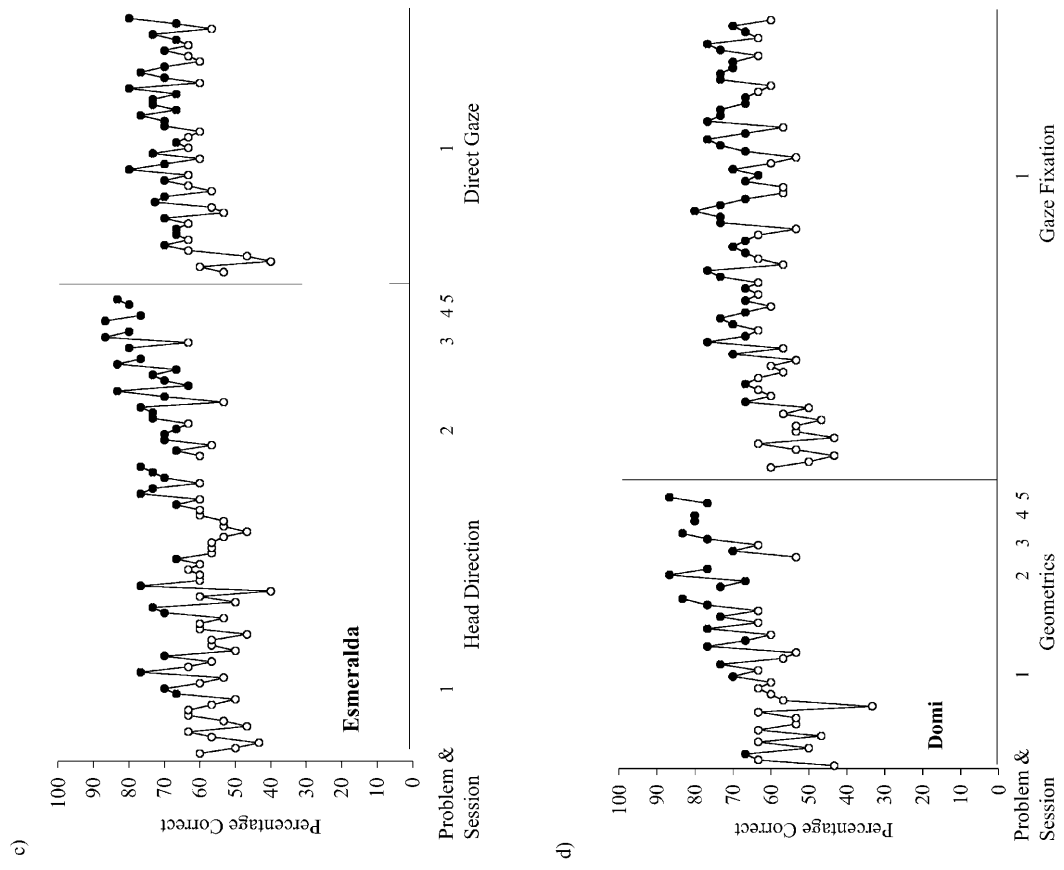
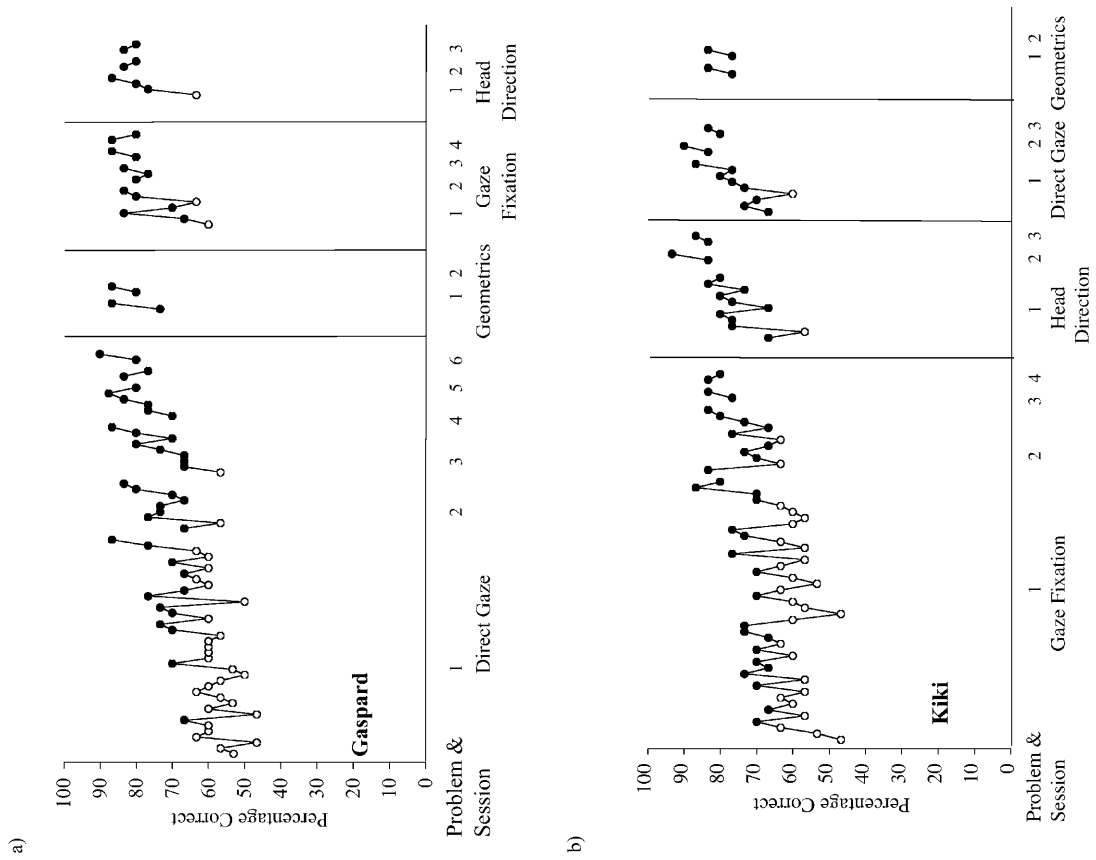


Fig.3 Individual performance on the picture discrimination task for **a** Gaspard **b** Kiki **c** Esmeralda **d** Domi. *Solid data points* represent above-chance performance (binomial tests $P < 0.05$) and *open data points* represent chance-level performance

boons were able to learn to respond selectively to photographs according to the eye and head orientations depicted and showed some evidence of limited transference of this discrimination to novel stimuli. Figure 3 shows development of the baboons' performances across sessions in the conditions presented.

Only two baboons (Gaspard and Kiki) completed all four conditions. They both quickly mastered all three conditions presented after the first condition. For Gaspard the first condition was Direct Gaze, which he mastered in 67 sessions; for Kiki the first condition was Eye-Gaze Fixation, mastered in 59 sessions. In contrast, Esmeralda and Domi both completed their first conditions but failed to complete the subsequent conditions presented even after 48 sessions and 76 sessions respectively. Thus, while able to master the Geometric (Domi) and Head Orientation (Esmeralda) conditions, respectively, these baboons did not reach criterion in a condition requiring that the direction of gaze as indicated by eyes alone be discriminated. This suggests that eye-gaze discrimination tasks may have been more demanding, or at least that previous learning during Head Orientation and Geometric conditions did not readily transfer to eye direction discriminations (whereas mastering eye direction problems did appear to facilitate performance on subsequent tasks). Both Gaspard and Kiki showed fastest learning in the Geometric condition, which, in addition to Domi's ability to perform this discrimination, is suggestive of lesser cognitive demand in this task, perhaps because the stimuli were simpler; for example, there was no need to consider any target objects for successful responding and the physical differences between the images may have been more salient.

It is difficult to determine exactly how the baboons solved the problems presented. Gaspard and Kiki both showed gradual improvement across successive conditions. While their results could indicate that a concept of "visual attention" had been learned, they could also reflect simple improvement at discriminating complex visual images rather than responding to the photographs as meaningful images. That is, rather than learning to respond to photographs depicting visual attention, the baboons may have been responding according to more simple rules. For example, the photographic problems could be solved using physical cues such as absolute head or eye orientation, or, for the Direct Gaze condition, the detection of a highly salient image; namely direct gaze (e.g. Mendelson et al. 1982; von Grunau and Anston 1995). However, the fact that even this image was not readily discriminated, requiring 67 sessions for Gaspard and 13 sessions for Kiki, might suggest the absence of any attribution of social meaning to the photographs.

Studies of face processing in nonhuman primates have suggested that face discrimination can be processed in two distinct ways: either holistically or in a piecemeal or feature based manner (Perret et al. 1988). Task demands have been identified as determining to some extent the method of processing engaged; for example, some face recognition tasks simply do not require any configurational processing and are easily performed on the basis of

specific feature discriminations (Keating and Keating 1993). It has been proposed that when monkeys are tested on categorisation tasks, larger stimulus sets preclude piecemeal strategies; the individual characteristics of images are not learned but rather a more general categorisation (e.g. Schrier and Brady 1987). The present study used a limited stimulus set for each condition, and only two images within any given problem, which leaves open the possibility that successful baboons may have learned to discriminate key features of the photographs presented, rather than requiring a concept of visual attention to guide their responses..

Study 2

Does gaze discrimination transfer from photographic stimuli to a live model?

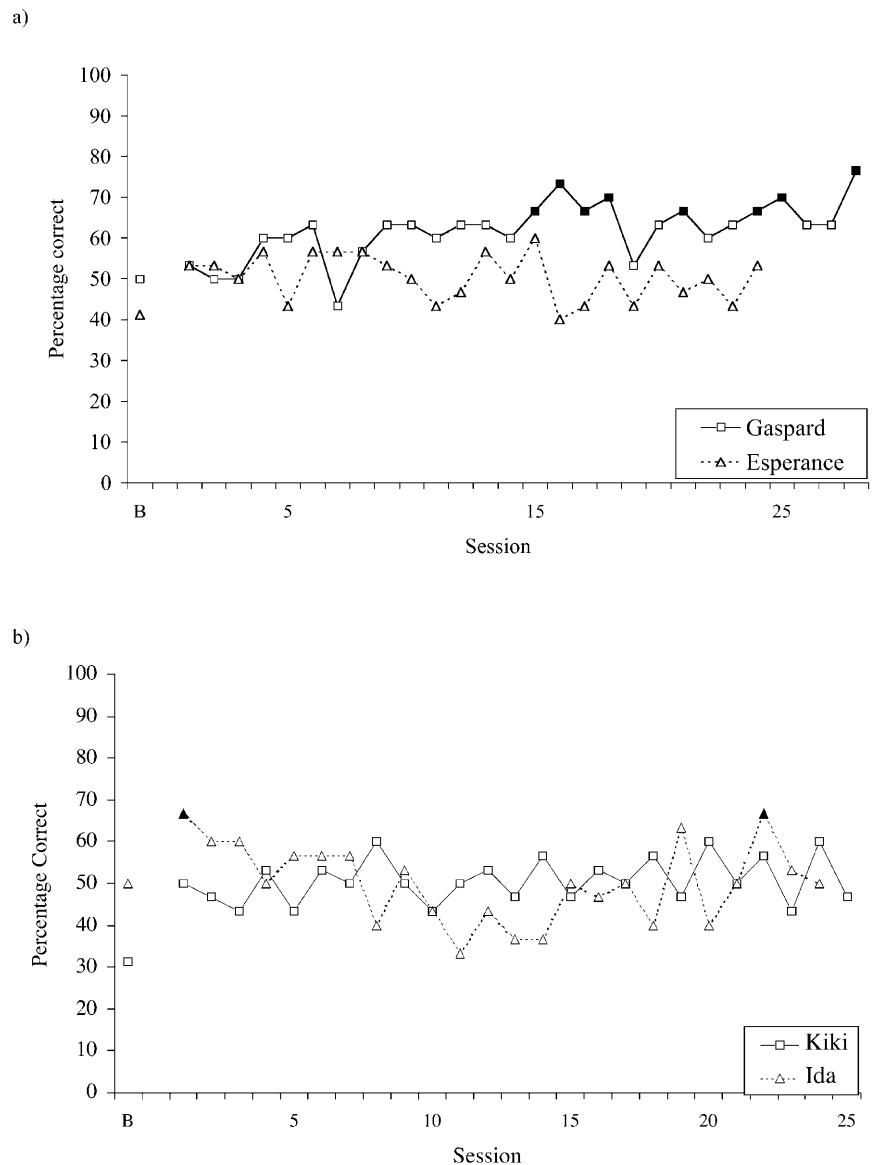
Study 2 was designed to investigate further the possible strategies used by baboons showing gaze discrimination in study 1. If the baboons perceived the photographs as socially salient and encoded something about the looking behaviour (at any level) of the model, then this experience might facilitate subsequent performance on a related task using a real model. A task was presented so that a simple discrimination, such as consistently responding to the absolute orientation of the head or eyes (that would have sufficed for an individual problem in the first study) would not lead to mastering the new experimental conditions. The only way in which such simple rule learning could facilitate performance on the new task would be if it were based on the relationship between a cue and the location of the target object in the photographs, (e.g., visible sclera away from target object). While this would also be simple visual discrimination, it is indistinguishable from identifying "looking" at the object and indeed such a simple mechanism may not be any different from how non-human primates perceive visual attention. For example, a "low-level" account of gaze following simply requires co-orientation until something of interest is encountered; eye direction may be a simple discriminative cue to look in a given direction (Tomasello et al. 1998). Thus, visual attention in others could be encoded by the direction of gaze as an arbitrary discriminative cue and the presence of an object or event in the congruent direction.

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

Subjects

Four olive baboons (*Papio anubis*) were studied. Two males, Gaspard and Kiki, had learned to discriminate gaze

Fig. 4 Individual performance in the object-choice task for **a** head orientation **b** eye-gaze. *Solid data points* represent above-chance performance (binomial tests $P < 0.05$) and *open data points* represent chance-level performance



direction in photographs in study 1. Two females, Esperance (9 years old) and Ida (5 years old), had no experience of tasks involving facial stimuli but had extensive experience in an unrelated object and picture categorisation task using the same apparatus (Bovet and Vauclair 1998). None of the baboons had any prior experience of tests in which the experimenter communicated cues. Housing and feeding were as described for study 1. Dietary treats (raisins) were used as reinforcers.

Apparatus

The apparatus was a wooden rectangular box (80 cm×20 cm×20 cm) which could be hooked onto the outside wall of the cage approximately 50 cm above ground level. Two shallow food-wells (3 cm diameter) were set 60 cm apart in the top of the box; these were each covered by a square piece of wood (5 cm×5 cm) which were secured in

one corner and could be rotated to reveal the wells. A large, hand held screen (50 cm×90 cm) was used to conceal the baiting procedure.

Procedure

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

Testing. During testing, the baiting procedure was concealed from the baboons by the screen; experimenters always rotated the covers of both wells in the same order so

that sound cues were not available. The location of the treat was pseudo-randomised between the left and right food-wells with no more than three consecutive baitings on one side. After baiting was completed, the screen was lowered so that the experimenter could be clearly seen by the baboon, while the two food wells remained concealed. The experimenter was already in a static posture according to the cue condition for that trial. Baseline trials showed the experimenter fixated on the centre point between the two food wells and therefore supplying no cue, while in cue conditions the experimenter had either head and eyes or eyes only oriented towards the correct side, according to condition. There was a minimum 5-s (extendable up to 10 s) observation period to ensure the baboon looked at the experimenter. The screen was then fully removed to allow the baboon to respond; a correct choice revealed a food item which they could retrieve and consume, while an incorrect response was immediately followed by the screen being reinstated and hence the end of the trial. A 10-s time-out followed an incorrect response and a correction procedure was used with the treat remaining in the same location on correction trials until found. Responses were noted on a record sheet. Sessions consisted of 30-trial blocks and the baboons completed one to four sessions a day.

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

Results and discussion

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

In the eye direction cue condition, neither subject learned to use this cue in order to locate the food. For Kiki this suggests an absence of positive transfer of any comprehension of attention or gaze direction from his experi-

ence with photographic stimuli. Both Kiki and Ida failed to learn the task even after more than 700 trials (excluding correction trials). Although Ida was above chance during her very first session, her subsequent performance suggests that this was not indicative of a cue-reading ability but rather that it was a spurious effect.

The results of study 2 make it difficult to draw any strong conclusions regarding the salience of head and eye direction as experimenter-given cues for baboons; the failure of the baboons to master their initial cue conditions prevented any comparison of the baboons across conditions and therefore individual differences cannot be excluded. It is noteworthy that the only baboon to show signs of learning was tested in the head orientation condition; findings to date suggest that head orientation, rather than eye direction alone, is a more salient attentional cue for nonhuman primates in object-choice tasks (Itakura and Anderson 1996; Povinelli et al. 1999; Vick and Anderson 2000). However, while head turns by a model may spontaneously produce visual re-orienting in monkeys (Tomassello et al. 1998; Anderson and Mitchell 1999), when it comes to object discrimination even this cue may not be readily used without explicit training (Anderson et al. 1995, 1996; Itakura and Anderson 1996; Vick and Anderson 2000). While one baboon did learn to exploit head orientation as a cue this required a considerable number of sessions, suggesting that the cue was learned and that the task was not tapping an underlying visual co-orientation mechanism.

General discussion

A potential problem in integrating the results of studies 1 and 2 concerns the use of different tasks to assess the discrimination of visual attention versus not attending. For example, the target items were visually very different. However, it seems reasonable to expect that any natural ability to discriminate the object of another individual's attention would be generalisable to a range of contexts, objects and even events, as long as the cues remained explicit. In other words, it could be argued that if the baboons in study 1 had learned or used a strategy based upon "visual attention" at any level, they should have subsequently exploited the corresponding type of information presented in study 2 to master the object-choice task.

However, the results of these studies can be interpreted in several ways. Firstly, although nonhuman primates are adept at monitoring the behaviours of others (Cheney and Seyfarth 1991), this sensitivity to behavioural cues might not reflect an ability to attribute attentional states to others. Thus, the baboons solved the problems on a cue-learning basis as this was the only means available to them. Alternatively, it may be that nonhuman primates are able to attribute attentional states to others but that the methods used in these studies did not invoke the use of this ability. For example, the relatively slow rates of acquisition and lack of transfer may have been due to motivational problems; basic procedural flaws such as too

short a time-out period may have led to less than optimal performances. Moreover, it may be that the use of a small stimulus set in study 1 favoured the use of a piecemeal processing strategy (Schrier and Brady 1987; Perret et al. 1988). Although the signs of positive transfer displayed by two baboons within study 1 could be seen as contrasting with such a position, it may be that they had simply started to form learning sets (Harlow 1949; Schrier and Brady 1987).

Further, it is possible that the baboons did not perceive the photographs as representations of real objects and could have processed them independently of their representational content. Whether, and at what level, animals perceive a correspondence between objects and their pictorial representations is currently being debated (Bovet and Vauclair 2000; Fagot et al. 1999). It is also conceivable that during the object-choice task, the baboons did not consider the experimenter as a social interactant. However, nonhuman primates readily respond to humans with appropriate social gestures (Exline 1971; Kummer et al. 1996), so it is unlikely that the central problem was due to the inter-species nature of the interaction or the stimuli used.

A third explanation for the results obtained is that the baboons did use information concerning attending versus not attending at some level (rather than simple physical cues) during study 1 but failed to make explicit use of the related information in study 2. The object-choice task has produced equivocal results concerning nonhuman primates' abilities in using attentional cues. While many species of primates have been shown to respond by visually co-orienting to the changes in head and/or eye direction of another individual (Anderson and Mitchell 1999; Tomasello et al. 1998), performance in the object-choice task often fails to reflect these abilities. For example, chimpanzees that demonstrated gaze following in response to shifts in eye direction alone were subsequently unable to use this same information to solve an object-choice task (Povinelli et al. 1999). Nonhuman primates show at best inconsistent responses across variants of the object-choice task (Call and Tomasello 1994; Anderson et al. 1995, 1996; Call et al. 1998, 2000; Itakura et al. 1999; Vick and Anderson 2000). However, a recent paper (Hare et al. 2000) has highlighted a central problem with much of the research into nonhuman primates' responses to gaze, particularly the object-choice paradigm: for nonhuman primates, access to resources is usually more a matter of competition than co-operation (Kummer et al. 1996). In contrast to the inconsistent performances found with traditional paradigms, chimpanzee performance within a competitive paradigm showed that the apes were capable of taking another individual's perspective into account when choosing between food items (Hare et al. 2000). Thus, it may be that the object-choice task was an inappropriate transfer task.

Baboons are able to learn gaze discrimination using photographic stimuli, but it is difficult to ascertain whether this reflects an underlying concept of "attending to" as they did not demonstrate any positive transfer from pic-

ture discrimination to an analogous problem presented by a real model. However, several methodological problems with the present studies have been identified which may account for this failure. In spite of evidence suggesting that baboons are sensitive to the attentional status of others (e.g. in "tactical deception", Byrne and Whiten 1988), it remains to be demonstrated that such behaviours are based upon an ability to attribute the mental state of "seeing" to others.

Acknowledgements This study was conducted at the CNRS Station de Primatologie, Rousset-sur-Arc, France. We thank Jacques Vauclair, Eric Damerose and the technicians for their assistance and hospitality, and Aurelie Van Der Meiren for help with testing. This research conforms to French guidelines for the use of animals in research.

References

- Anderson JR, Doherty MJ (1997) Preschoolers' perception of other people's looking: photographs and drawings. *Perception* 26:333–343
- Anderson JR, Mitchell RW (1999) Macaques but not lemurs co-orient visually with humans. *Folia Primatol* 70:17–22
- Anderson JR, Sallaberry P, Barbier H (1995) Use of experimenter-given cues during object-choice tasks by capuchin monkeys. *Anim Behav* 49:201–208
- Anderson JR, Montant M, Schmitt D (1996) Rhesus monkeys fail to use gaze direction as an experimenter-given cue in an object-choice task. *Behav Proc* 37:47–55
- Bovet D, Vauclair J (1998) Functional categorization of objects and their pictures in baboons (*Papio anubis*). *Learning Motivation* 29:309–322
- Bovet D, Vauclair J (2000) Picture recognition in animals and humans. *Behav Brain Res* 109:143–165
- Byrne R, Whiten A (1988) Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes and humans. Clarendon, Oxford
- Call J, Tomasello M (1994). The production and comprehension of referential pointing by orangutans. *J Comp Psychol* 108:307–317
- Call J, Hare B, Tomasello M (1998) Chimpanzee gaze following in an object-choice task. *Anim Cogn* 1:89–99
- Call J, Agnetta B, Tomasello M (2000) Cues that chimpanzees do and do not use to find hidden objects. *Anim Cogn* 3:23–34
- Campbell R, Heywood CA, Cowey A, Regard M, Landis T (1990) Sensitivity to eye gaze in prosopagnosic patients and monkeys with superior temporal sulcus ablation. *Neuropsychologia* 28:1123–1142
- Chance MRA (1967) Attention structure as the basis of primate rank orders. *Man* 2:503–518
- Cheney DL, Seyfarth RM (1991) Reading minds or reading behaviour? Tests for a theory of mind in monkeys. In: Whiten A (ed) *Natural theories of mind: evolution, development and simulation of everyday mindreading*. Blackwell, Oxford, pp 175–194
- Emery NJ (2000) The eyes have it: the neuroethology, function and evolution of social gaze. *Neurosci Biobehav Rev* 24:581–604
- Emery NJ, Lorincz EN, Perret DI, Oram MW, Baker CI (1997) Gaze following and joint attention in rhesus monkeys (*Macaca mulatta*). *J Comp Psychol* 111:286–93
- Exline RV (1971) Visual interaction: the glances of power and preference. *Nebraska Symp Motiv* 19:163–206
- Fagot J, Martin-Malivel J, Dépy D (1999) What is the evidence for an equivalence between objects and pictures in birds and non-human primates? *Curr Psychol Cogn* 18:923–949

- Grunau M von, Anston C (1995) The detection of gaze direction: a stare in the crowd effect. *Perception* 24:1297–1313
- Harlow HF (1949) The formation of learning sets. *Psychol Rev* 56:51–65
- Hains SMJ, Muir DW (1996) Infant sensitivity to adult eye direction. *Child Dev* 67:1940–1951
- Hare B, Call J, Agnetta B, Tomasello M (2000) Do chimpanzees know what conspecifics can and cannot see? *Anim Behav* 59:771–785
- Itakura S, Anderson JR (1996) Learning to use experimenter-given cues during an object-choice task by a capuchin monkey. *Curr Psychol Cogn* 15:103–112
- Itakura S, Agnetta B, Hare B, Tomasello M (1999) Chimpanzee use of human and conspecific social cues to locate hidden food. *Dev Sci* 2:448–456
- Kalin NH, Shelton SE, Takahashi LK (1991) Defensive behaviors in infant rhesus monkeys: ontogeny and context-dependent selective expression. *Child Dev* 62:1175–1183
- Keating CF, Keating EG (1993) Monkeys and mug shots: cues used by rhesus monkeys (*Macaca mulatta*) to recognize a human face. *J Comp Psychol* 107:131–139
- Kummer H (1967) Tripartite relations in hamadryas baboons. In: Altmann SA (ed) *Social communication among primates*. Chicago University Press, Chicago, pp 63–72
- Kummer H, Anzenberger G, Hemelrijk CK (1996) Hiding and perspective taking in long-tailed macaques. *J Comp Psychol* 110:97–102
- Lorincz EN, Baker CI, Perret DI (1999) Visual cues for attention following in rhesus monkeys. *Curr Psychol Cogn* 18:973–1003
- Mendelson MJ, Haith MM, Golman-Rakic PS (1982) Face scanning and responsiveness to social cues in infant rhesus monkeys. *Dev Psychol* 18:222–228
- Perret DI, Mistlin AJ (1991) Perception of facial characteristics by monkeys. In: Stebbins WC, Berkley MA (eds) *Comparative perception*. Wiley, New York, pp 187–215
- Perret DI, Smith PAJ, Potter DD, Mistlin AJ, Head AS, Milner AD, Jeeves MA (1985) Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proc R Soc Lond* 223:293–317
- Perret DI, Mistlin AJ, Chitty AJ, Smith AJ, Potter DD, Broenniman R, Harries M (1988) Specialized face processing and hemispheric asymmetry in man and monkey: evidence from single unit and reaction time studies. *Behav Brain Res* 29:245–258
- Povinelli DJ, Eddy TJ (1997) Specificity of gaze following in young chimpanzees. *Br J Dev Psychol* 15:213–222
- Povinelli DJ, Biershwale DT, Cech CG (1999) Comprehension of seeing as a referential act in young children, but not juvenile chimpanzees. *Br J Dev Psychol* 17:37–60
- Schrier AM, Brady PM (1987) Categorization of natural stimuli by monkeys (*Macaca mulatta*): effects of stimulus set size and modification of exemplars. *Anim Behav Proc* 13:136–143
- Symons LA, Hains SMJ, Muir DW (1998) Look at me: five-month-old infants' sensitivity to very small deviations in eye gaze during social interactions. *Infant Behav Dev* 21:531–536
- Tomasello M, Call J, Hare B (1998) Five primate species follow the visual gaze of conspecifics. *Anim Behav* 55:1063–1069
- Tomasello M, Hare B, Agnetta B (1999) Chimpanzees (*Pan troglodytes*) follow gaze direction geometrically. *Anim Behav* 58:769–777
- Vecera SP, Johnson MH (1995) Gaze direction and the cortical processing of faces: evidence from infants and adults. *Visual Percept* 2:101–129
- Vick SJ, Anderson JR (2000) Learning and limitations of eye gaze an experimenter-given cue in an object choice task by capuchin monkeys (*Cebus apella*). *J Comp Psychol* 114:200–207