What do Diana monkeys know about the focus of attention of a conspecific?

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ABSTRACT

Converging experimental and observational evidence suggests that some non-human primates are able to co-orient with shifts in visual attention, both of conspecifics and humans. However, the underlying cognitive mechanisms involved are unclear. To investigate attention-following in Diana monkeys (Cercopithecus diana diana), we used photographs of familiar conspecifics orienting towards one of two locations. A subject monkey was shown a photograph, and shortly afterwards a toy appeared at one location or the other. The toy's position therefore either matched the location signalled by the head and body orientation of the photographed monkey (compatible), or was opposite to that location (incompatible). Overall, monkeys' first inspections, total duration of looking, and number of looks were more likely to be directed to the compatible location, i.e. towards the direction of attention shown in the photograph. Furthermore, when a photograph of an adult monkey signalled attention to one location, but the toy appeared at the opposite (incompatible) location, subjects re-inspected the monkey photographs more often than when the toy appeared at the compatible location, suggesting a violation of expectancy. This effect was not the case if the photograph was of an immature animal. Our results show that attention-following was not limited to simple reflexive orienting by the monkeys, and that monkeys perceived a relationship existing between agent and object of attention.

The attentional states of other individuals are characterised by overt signals, including facial expressions and cues to attention direction, whereas this is not the case for all mental states, e.g. beliefs (Gomez, 1996). Thus, co-orienting one's own line of sight with another's direction of attention could be an important precursor to understanding their attentional focus towards an object. Indeed, recent theories propose detection of eye direction as a crucial phylogenetic and ontogenetic precursor to understanding shared attention (Baron-Cohen 1995). The present study is predicated on the distinction between attention-following behaviour in itself, and the understanding of attention as a relationship between the agent and object of attention.

Following the Direction of Attention

Attention-following behaviour refers to "looking where someone else is looking" (Butterworth 1991, p. 223). It is generally accepted that chimpanzees (Pan troglodytes) can co-orient in gaze, head and body direction with humans (Povinelli & Eddy 1996) and with conspecifics (Itakura et al. 1999). However, evidence for attention-following in monkeys is more controversial, with discrepant results across different studies and species (e.g., cf. Itakura 1996; Anderson & Mitchell 1999; Ferrari et al 2000; Tomasello et al. 2001). These discrepancies may stem from varying requirements to achieve correct visual co-orientation: for example, stump-tailed macaques (Macaca arctoides) fail to turn to a location outside their own visual field (Itakura 1996), whereas they achieve smaller turns to the left or right of the midline (Anderson & Mitchell 1999; the precise location of the attention target affects co-orientation abilities even in human infants, Butterworth & Jarrett 1991). A second reason for discrepant findings could be that subjects may not be either as motivated or as adept in following human attention cues as monkey ones. Success with conspecific models support this interpretation: white-collared mangabeys (Cercocebus torquatus), rhesus (Macaca mulatta), pigtail (Macaca nemestrina) and stump-tailed macaques spontaneously co-oriented with a conspecific that had been shown a desirable fruit from afar (Tomasello et al. 1998); adult rhesus macaques also co-oriented with videotapes of macaques directing attention towards the attended of two identical objects (Emery et al. 1997) and with static pictures of macaques directing attention towards different locations in space (Lorincz et al. 1999). Thirdly, monkeys may require additional cues to attention and this may change through development. Monkeys fail most often when human gaze alone is used as a cue to visual orientation (Itakura 1996) and, in contrast with adult pig-tailed macaques, juveniles can follow human attention when this is signalled by head and eye cues, but not eyes alone (Ferrari et al. 2000). Therefore, when attempting to test attention-following abilities for the first time with a particular species, a focus on eye gaze alone may increase the probability of false negatives.

Indeed, Lorincz et al. (1999) found that both gaze and head direction of monkey models modulated macaques' visual co-orientation. Further neurophysiological evidence and theoretical proposals (Perrett et al. 1992, Perrett & Emery 1994, Langton et al. 2000) suggested that for humans, as well as for non-human primates, gaze, head, pointing and body cues are all important in affecting the accuracy of directional judgements. Computations of attention direction may be based on the most prominent cue available, with eyes playing a more prominent role than head and body (Perrett & Emery 1994). Since the starting point of the current study was to establish whether Diana monkeys show any ability to follow attention, we used conspecifics as models and their focus of attention was signalled by multiple redundant cues (gaze, head, and body posture).

"Understanding" Attention Direction

Attention-following behaviour may be a necessary but not a sufficient prerequisite for an understanding of others' attention, both for human (Butterworth 1991) and non-human primates (Povinelli & Eddy 1996). Langton et al. (2000) propose that automatic processing of social directional signals has been selected as a beneficial trait because attentional cues are reliable indicators of the presence and location of a third party or object of interest. If this suggestion is correct, we may be able to find evidence of such 'reflexive' orienting in non-human primates, but this behaviour might not entail an understanding of attention. Indeed, tests of attention understanding using the classical object-choice paradigm have yielded negative or mixed results, even for primate species that have previously shown to follow attentional cues (cf. the positive findings with chimpanzees by Itakura et al. 1999 and the negative findings by Povinelli et al. 1999). On these grounds, some researchers have suggested that non-human primates detect attention direction through low-level rules, rather than through an understanding of attention as a mental state and a referential act (Povinelli et al. 1999).

However, theoretical and methodological considerations should warn against accepting these failures as definitive evidence of a lack of attentional understanding. From a theoretical point of view, a dichotomy between low-level, rule-based behaviour reading (used to compute attention direction despite a poor understanding of visual attention) and high-level attributions of attentional states, may be too simplistic. Attention-following could reflect an understanding of attention as an external state that is implicit in the orienting behaviour (Gomez 1996; Byrne 2003). This representation may not be available to make correct choices in the paradigms discussed above, as has been argued for children's behavioural performance on various tasks (Karmiloff-Smith 1992). Methodologically, most current paradigms used to test attention understanding may not be appropriate because they are not naturalistic. For example, when a dominant chimpanzee and a subordinate compete for food, subordinates attempt to retrieve the food to which they (and not the dominants) had good visual access, suggesting that they can use knowledge about what others can and cannot see to guide their behaviour in naturalistic situations (Hare et al. 2000; 2001; but cf. contrasting evidence from Karin-D'Arcy & Povinelli 2002 for chimpanzees and Hare et al. 2003 for capuchin monkeys). Finally, many paradigms require intensive training that could favour cue discrimination rather than social interpretation of the experimenter's cues (Gomez 1998). To avoid this problem, Santos & Hauser (1999) measured spontaneous variations in looking time in response to violation of expectancy. They found that cotton-top tamarins (Sanguinus oedipus) look for a shorter time at displays in which visual attention towards an object is followed by an action on it rather than on an unattended object. Similarly, Call et al. (1999) found that chimpanzees often checked back to the experimenter when she suddenly shifted attention to an empty location in space rather than to a real object. This checking behaviour suggests that some kind of understanding of a relation between agent and the object of attention had been violated.

Therefore, our second aim was to investigate whether Diana monkeys would give indication of "understanding" others' attention, by testing their reactions when the expectations that would be predicted by potential underlying representations were violated.

Attention Detection in Diana monkeys

Diana monkeys' head position is unambiguous from all viewpoints, and visible body and limb patterns are particularly appropriate for long-range signalling by means of body-postures (Kingdon 1980). It is unknown whether wild Diana monkeys use this information to interpret conspecifics' attention. Detecting a conspecifics' orientation towards a predator would be extremely useful when the predator was a pursuit hunter (e.g. chimpanzees and humans), who use prey vocalisations to guide hunts. In those instances, Diana monkeys adopt a strategy of crypsis, suppressing vocalisations and retreating to the high canopy (Zuberbuehler et al. 1999), during which visual signals of attention may become very important. Although the use of predator-specific vocalizations by Diana monkeys has been extensively studied (Zuberbuehler et al. 1997, 1999), it is unknown whether they also use conspecifics' attention direction as a visual signal for the presence or the location of a predator.

We investigated, first, Diana monkeys' ability to visually co-orient with attention signalled by the body direction of conspecifics, and second, their reactions to violations of the relation between attention direction and location of a target object. An absence of visual co-orientation would suggest an inability to follow attention. Attention-following prior to the appearance of a target, but no evidence of detection of a violation in situations when the target appears at an unattended location, would suggest automatic reflexive orienting. Both co-orientation and surprise reactions in violation trials would suggest that the monkeys have at least some understanding of a relation between the agent and the object of attention. Furthermore, if successful this method could be adapted for use on other species and aid in developing a comparative study of attention-following, even for species that are not commonly found in the laboratory.

METHODS

Subjects

Diana monkeys are diurnal guenons inhabiting the West African forest between Gambia and Ghana. They live in uni-male polygamous groups, in which individuals entertain complex relationships both in the wild (Hill 1994) and in captivity (Byrne et al. 1983). The wild population is now highly vulnerable to extinction due to hunting by humans (IUCN 1988).

Subjects were six Diana monkeys housed at the Scottish Zoological Park (Edinburgh Zoo); age and gender are indicated in Table 1.The Director of Research at Edinburgh Zoo provided authorisation for the project on the grounds that it would not involve entering the subjects' enclosures and it would not change their feeding habits. Monkeys were housed in two separate enclosures, each with an indoor section (where testing took place, see below for further details on the experimental set-up) and an outdoor section. The monkeys were free to move from one section to the other. The indoor sections varied in size: the largest enclosure measured approximately 12 x 3 x 3 m; the smaller measured 3 x 3 x 3 m. Both were enriched with fixed and mobile springing platforms, tree-trunks, climbing frames, ropes and foraging boards. Monkeys were fed independently by staff at the Zoo and their diet was enriched daily with fruits, vegetables and seeds. Morning and afternoon testing sessions followed feeds. Furthermore, monkeys were free to join or leave the experiment at any time: their participation was voluntary, and their feeding habits were not modified to encourage participation.

Experimental Set-up

The testing apparatus was presented to the monkeys through the glass dividing their indoor enclosure from the public area (Fig. 1a). It consisted of a platform on top of which the stimuli sheets were vertically placed. These sheets each displayed a monkey photograph, with a photograph of a toy situated below the monkey photograph and to either the right or the left of it. The toy's photograph was initially covered by a long cardboard strip extending to both sides of the monkey photograph, so that during the first phase of the trials only the monkey photograph was visible (see Fig. 1b). As illustrated in Figure 1a, the experimenter placed herself as far away from the apparatus as possible while operating the video-cameras. Before the beginning of each session all stimulus sheets to be used were pre-arranged in a pile, so that as the session progressed the used sheets were manually flipped forward uncovering the new sheets. Stimulus sheets were separated by blank cardboard sheets that were flipped forward when the trial began. The experimenter was blind to the photograph presented during each test trial, to avoid providing visual cues to the monkeys that might allow attention following (although it should be noted that the monkeys did not pay attention to the experimenter's direction of attention: Scerif, unpublished dissertation).

Subjects were filmed by two video cameras, one recording their upper body alone (used for all blind coding), and one recording the experimental set-up and surrounding parts of the enclosure (to monitor for distractions etc.). The experimenter sat beside the apparatus to operate the video cameras and to present stimuli. Test stimuli were four photographs of two current members of the group directing attention towards two peripheral locations in space (right down, left down). Two photographs were selected from amongst a number taken while showing the monkeys various objects of interest: they depicted an adult male and a 9-month-old female, respectively. The other two pictures were obtained by reversing the negatives of these originals, to maintain all characteristics of the photos identically except for the monkeys' attention direction. Test stimuli were interspersed amongst non-test photographs (plants, familiar animals and monkeys) to avoid habituation to the test photographs.

Procedure

Subjects were tested in their Zoo enclosures. Testing started with a period of familiarisation that lasted from 5 to 10 minutes, to ensure that all individuals had observed the experimental apparatus through the glass partition dividing the enclosure from the public.

Testing sessions were distributed across a period of six months. Each took place early, before the arrival of visitors to the Zoo, or shortly before closing time. Because subjects were free to join the experiment, trials per subject varied from one to six per session and were separated by variable inter-trial intervals. Subjects were tested only when alone or distant from other potential subjects. Each trial lasted for 10 seconds or until the subject either left or stopped facing the display for more than three seconds. The experimenter monitored the subject's position with respect to the display using peripheral vision, trying to avoid facing the monkeys and keeping as far away as possible from the display. Trials interrupted or disturbed by other members of the group, etc., were discarded from later analyses. The experimenter attracted a subject into a position in front of the apparatus by showing them various objects (toys, fruit and mirrors) and quickly hiding these objects outside the monkey's field of vision. Then she uncovered the photograph of a conspecific directing gaze, head and body to the right or left (this was termed the Monkey photograph-Alone phase, Fig. 1b). Three seconds after the beginning of each trial the experimenter manually removed the long cardboard strip so that the toy photograph was now visible at a location either compatible or incompatible with the direction of the photographed monkey's attention (Monkey photograph-and-Toy phase, Fig. 1c). Precise timing of the toy photograph's appearance was recorded visually and vocally on the second camera.

Evaluation of Performance and Inter-observer Reliability

When transferring video-material from the video-camera to standard video-tapes, a time and frame code was added to the images from the first video camera (VITC time-code generator and frame counter – Horita VG50). The screen was divided into four exclusive areas: right down, left down, middle, and elsewhere, a procedure adapted from Lorincz et al. 1999. They had divided the screen into right, left, middle, and elsewhere; however, testing conditions at the zoo were much noisier than in laboratory conditions because the background to the display contained other enclosures and plants. Therefore, it was decided to adopt a more stringent criterion for the target position, limiting it to right down or left down which were more clearly in the direction of the toy and were not backed by distracting stimuli (the floor). This is also a more stringent criterion than the ones used with human infants in the standard attention-following paradigm (e.g., Butterworth & Jarrett 1991). In each trial, inspections were defined as glances to one position of the screen, with the eyes and head remaining static for at least two frames (80 ms). Directions of looks during saccades or full head movements were not scored. The duration of each inspection was defined as the number of video frames the subject spent inspecting one area without intervening moving frames. The number of inspections and the cumulative duration of inspections at the four positions were recorded for each trial by a scorer who was blind to the photographed monkey's attention direction and to trial types. Subsequently these were re-coded according to the relative positions of the elements in the stimulus display in each trial (recorded vocally on the original videotapes and on paper). The "Target" area was defined as the position to which the photographed monkey's head pointed (right down or left down); the "Anti-target" area was defined as an area of equivalent size in a position laterally opposite the target area. The area including the monkey photograph was coded as "Monkey photograph" and all other areas of the screen (right up, left up, up, middle down) were defined as "Elsewhere". Inter-observer reliability was assessed on 10% of the trials with a second scorer who was also blind to the trial type. The two scorers exhibited a high level of agreement (Cohen's K=0.75, p<0.001) on their ratings of inspections assigned to the four positions.

Design and Data Analysis

The order of presentation was constrained to avoid more than three consecutive trials with the photographed monkey directing attention either to the left or right, and more than three consecutive compatible or incompatible trials. Eighty trials were initiated altogether with the 6 subjects; of these 63 Monkey photograph-Alone phases were completed, 28 when the young female was the model and 35 for the adult male. The Monkey photograph-and-Toy phase was completed in 28 Compatible (young female =12, adult male =16) and 25 Incompatible trials (young female =10, adult male =15). A number of further trials were lost because of filming errors (one incompatible, one compatible), movement of the subject out of the camera field (two incompatible), interruptions by other monkeys (four compatible, six incompatible) or no initial inspection of the photograph (three compatible, five incompatible). Data were analysed separately for the Monkey photograph-Alone phase (i.e. before the toy's appearance) and for the Monkey photograph-and-Toy phase.

To rule out differential responses to the original monkey photographs versus the negatives, we compared results in trials during which the monkeys on the photographs directed attention to their left (originals) to those during which they directed attention to the right (negatives). We report the results of these preliminary analyses separately at the beginning of the section dedicated to attention-following during the Monkey-Alone phase and at the beginning of the section dedicated to the monkeys reactions during the Monkey-and-Toy phase. As discussed for each phase below, we analysed three variables: first inspections in each phase, average number, and duration of inspections across the whole phase. This allowed us to obtain evidence that was not limited to first fixations after inspecting the toy, but extended to the whole experimental phase. First fixations could have potentially been influenced by social factors (e.g., perceived dominance of the model, which in naturalistic conditions affects chimpanzees' tendency to inspect a desirable target, Hare et al. 2000). In some cases, t-tests could not be used, as the distributions of these proportions of inspections and durations at each position were not normal (and transformations did not succeed in normalising the data). In those cases, significance levels were obtained with the equivalent non-parametric statistics (Siegel & Castellan 1988). Separate analyses were run for trials with the adult male and young female as models, and order effects were tested across the first and last trials on the Compatible and Incompatible conditions (paired t-tests). For analyses of looks towards the target vs. anti-target location, and monkey photograph vs. elsewhere, we used a 1-tailed level of significance. This choice was justified by the clear direction of our predictions. We predicted that monkeys would direct more first looks, look more often and for longer at the target location than at the anti-target (Monkey photograph-alone) and at the monkey photograph more than elsewhere (Monkey photograph-and-Toy phase). The statistical tests assess these specific predictions against random distribution, and should therefore be 1-tailed. Furthermore, we accompany these group statistics with tables of individual monkeys' data to support our statistical inferences, a procedure that is not always used in studies using the violation of expectancy paradigm (e.g., Hespos & Baillargeon 2001).

Monkey photograph-Alone Phase (to investigate attention-following).

First inspections towards the target and the anti-target location before the appearance of the toy were compared for each monkey using the binomial test. For reasons explained above, we adopted a 1-tailed level of significance in these tests. If the monkey did not look at either the target or the anti-target position (e.g., looking only at the monkey photograph and/or elsewhere), the trial was discounted from the analysis of first inspections, because looks elsewhere could have been a consequence of distraction, and prolonged looking to the photographed monkey alone could have depended on its salience as a social stimulus. Individual monkeys completed a variable number of trials. Therefore, the proportions of trials in which the first inspection was made on the target and on the anti-target position were calculated for each monkey. The mean number of inspections of the target and anti-target position and their duration across the whole Monkey photograph-Alone phase were also calculated for each monkey. These variables were compared using the appropriate parametric or non-parametric test (paired t-tests, Wilcoxon Matched Pairs Signed-Rank test, calculating exact probabilities to account for small sample sizes).

Monkey photograph-and-Toy Phase (to investigate attention understanding).

Call et al. (1999) found that chimpanzees often checked back to the experimenter when she suddenly shifted attention to an empty location in space rather than to a real object. They argued that this checking behaviour suggested that some kind of understanding of a relation between agent and the object of attention had been violated. To assess whether our subjects showed checking behaviour in the incompatible trials (i.e., trials where the direction of gaze of the photographed monkey was inconsistent with the position of the toy) we coded only their inspections after they had first discovered the toy in the incompatible location. This conservative criterion was chosen to avoid an artifactual result: assuming that the monkeys followed the photographed monkey's direction of attention, in incompatible trials they would find an empty space and this might make them look anywhere else, including towards the monkey photograph which happens to be a nearby target; in compatible trials, however, the presence of the toy could prevent further looks elsewhere. Such a contrast could cause the misleading impression that the monkey is inspecting the monkey photograph because it has detected the anomalous Attention-Target connection, when in fact it was simply looking at it because it happened to be close to the empty location. This possible bias was avoided by scoring only the looks that occurred after the toy had been discovered in the incompatible position. For example, if in an incompatible condition a monkey followed the gaze of the photographed monkey to the empty location and then looked at the monkey photograph, this was not scored as checking back; however, if then it looked at the toy (which was situated in the counter target location), and then at the monkey photograph, this look was scored.

Thus we classified the first inspections after the first inspection of the toy as either "Monkey photograph" (location of the monkey photograph or empty location followed by location of the monkey photograph), or "Elsewhere" (empty location alone or elsewhere location).

The proportion of first inspections, total number, and duration of inspections to the monkey photograph in compatible and incompatible trials were calculated for each monkey. These variables were compared using the appropriate parametric or non-parametric test (paired t-tests, Wilcoxon Matched-Pairs Signed-Rank test, calculating exact probabilities to account for the small sample size).

RESULTS

Monkey photograph-Alone Phase

Preliminary analyses showed that there was no statistically significant difference between mean number ($p = .352$ and .269, n.s.) and duration of inspections ($p = .265$ and .981, n.s.) to the target and anti-target locations for trials in which the monkey in the photograph oriented attention to the left (original photographs) vs. the right (reversed negatives). This suggested that monkeys did not react differentially to reversal of any of the characteristic markings of the models. Therefore, this variable was dropped from the analyses detailed below.

Analysis of individual monkeys' first fixations (see Table 2) showed that four subjects were significantly more likely to inspect the target than the anti-target position, despite the limited number of trials per individual and the known stringency of the binomial test for small numbers of observations (Siegel & Castellan, 1988). Even in the case of the two monkeys whose data only approached significance, 7 out of 8 first looks were directed to the target. Overall, first inspections suggested a strong tendency for subjects to look in the target direction (45/58 first fixations). When we examine the monkeys' proportion of first looks to the target and to the antitarget, thus adjusting for the variable number of trials, monkeys directed significantly more first fixations towards the target than the anti-target, Wilcoxon Signed-Rank test, 1 null difference, $T = 0$, $p < 0.031$, 1-tailed exact significance. This was the case for both the adult (Wilcoxon, $T = 0$, $p = 0.016$, 1-tailed exact) and the young monkey photograph (Wilcoxon, $T = 1$, $p = 0.031$, 1-tailed exact).

Furthermore, monkeys tended to inspect the target more often than the anti-target (Wilcoxon Signed-Rank test, 1 null difference, $T = 1$, $p = 0.062$, 1-tailed exact), and spent significantly longer inspecting the target position (Wilcoxon Signed-Rank test, $T = 1$, $p = 0.031$, 1-tailed exact). There were no significant differences in number or duration of inspections to the target across trials with either the young and the adult as models (Wilcoxon, inspections: $T = 9$, $p = 0.406$, n.s.; duration: 1 null difference, $T = 5$, $p = 0.313$, n.s.). Duration and number of inspections to the target location did not differ across first and last trials (paired t-test, inspections: $t(5) = 0.0$, $p = 1.0$, n.s.; duration: $t(5) = 0.653$, $p = 0.543$, n.s.).

Monkey photograph-and-Toy phase

Preliminary analyses showed that there was no statistically significant difference between mean number ($p = .386$) and duration of the looks ($p = .775$) towards the monkey photograph for trials in which the monkey in the photograph oriented attention to the left (original photos) vs. the right (reversed negatives). Therefore this variable was dropped from the analyses detailed below.

Table 3 shows the individual monkeys' proportions of first inspections towards the monkey photograph after the toy had appeared in compatible and incompatible conditions when the photographed model was the young female or the adult male. When the model was the young female, monkeys did not inspect the model after looking at the target more often in Incompatible than in Compatible trials; however, when the model was the adult male, there was a trend in this direction (Wilcoxon, 3 null differences, $T = 3$, $p = .625$, n.s., and 1 null difference, $T = 1$, $p = 0.063$, respectively; both 1-tailed exact probabilities). More qualitatively, inspecting Table 3 shows that four monkeys out of six directed first fixations at the adult monkey photograph more often on incompatible than compatible trials. In contrast, only one monkey did so with the juvenile monkey photograph. As shown in Fig. 2, with the young female as a model the mean number of inspections of the model position and their duration did not differ across conditions throughout the whole Monkey photograph-and-Toy phase (Wilcoxon Signed-Rank tests, inspections: 2 null differences, $T = 3.5$, $p = 0.375$, n.s.; duration: 1 null difference, $T = 6$, $p = 0.406$, n.s.). In contrast, the monkeys tended to inspect the adult male more often in the incompatible than in the compatible condition (Wilcoxon, 1 null difference, $T = 0$, $p = 0.031$, 1-tailed exact), but not for longer ($T = 5$, $p = 0.156$, n.s.). The overall amount of looking at the monkey photograph did not differ from first to last trials (paired t-tests, $t(5)$ = from 2.233 to 0.255, p = from 0.077 to 0.809, n.s.).

DISCUSSION

Following the Direction of Attention in Diana Monkeys

The behaviour of our Diana monkeys suggested that at least some of them engaged in visual co-orientation in response to photographs of conspecifics, before the appearance of a target. Co-orientation abilities were apparent in monkeys' first fixations, with some individuals first inspecting the target location more often than the opposite location. Monkeys also looked at the target location more often and for a longer period of time than at the opposite location, providing converging evidence for attention-following abilities. Furthermore, this behaviour did not vary across trials. Lack of variation across trials implies that attention-following did not depend on learning an association between the model's attention direction and the target, which would have been signalled by a general increase in looking to the toy across trials.

Despite the limited number of individuals and trials per individual, our findings resemble those obtained with rhesus monkeys using photographs and videos under laboratory conditions (Emery et al. 1997; Lorincz et al. 1999). This convergence of data implies the gaze-following adaptation was present in ancestors we share with Cercopithecinae, and by implication all Old World monkeys. Our study further suggests that this paradigm can be used successfully with monkeys in less restrained and more naturalistic conditions than in the laboratory. It could therefore be extended to test a number of primate and non-primate species that are not commonly found in the laboratory, to aid in developing a comparative study of attention-following. It would be interesting to use this same paradigm in future experiments to address systematically the question of whether there are real differences in following attention cues from models of different species; photographs of other monkey species with which the subjects have visual contacts, either in the wild or in captivity, could be employed in addition to contrasting monkey and human models (Lorincz, Perrett & Gomez in prep.). This would allow separation of species- and experience-dependent determination of attention following behaviour. Is visual experience with a certain species necessary to visually co-orient with individuals from that species?

Deliberately, our stimuli conflated congruent gaze, head and body attention cues. In the future, research should focus on determining the relative importance of the different potential cues in determining an orienting response in Diana monkeys, as has been done for rhesus monkeys by Lorincz et al. (1999). This could clarify whether possible interspecific differences lie not in the ability to visually co-orient, but in the type of cues modulating this behaviour. Furthermore, our results suggested that adult individuals might be more likely to follow attention, a developmental trend that has been previously found for following of human attention cues in rhesus macaques (Tomasello et al. 2001) and pig-tailed macaques (Ferrari et al. 2000). However, our current low number of subjects and trials limit this conclusion. Rigorously investigating changes across different age groups may reveal the extent to which behaviour reported in this investigation is the product of a developmental process.

"Understanding" Attention Direction in Diana Monkeys

Monkeys tended to direct their inspections towards the adult monkey photograph more often and for longer after noticing the toy at a location incompatible with the model's attention direction than when the toy was at a compatible location. Despite the limited statistical power afforded by our small group of monkeys, this finding provides suggestive evidence that the appearance of the toy at the unattended location violated a relation between the agent and the object of attention. The monkeys appeared to be "checking" what was going on, as if surprised. Moreover, this checking behaviour occurred when the model was an adult male but not a young female, despite the fact that, before the appearance of the toy, monkeys followed equally attention indicated by the adult and the yearling monkey photograph. We will first discuss these results in terms of the implications for our original question: do Diana monkeys "understand" the relation between an agent and her object of attention? We will then address alternative interpretations of the difference in behaviour for the adult and the young models.

Do our findings contrast with the negative results obtained using the object-choice paradigm (e.g., Anderson et al. 1995), and with the interpretation of primates' performance in terms of low-level rule based behaviour proposed by Povinelli et al. (1999)? Certainly, our data imply that Diana monkeys' responses to expectancy violations cannot be reduced to a simple reflex orientation, at least in the case of pictures depicting adult conspecifics, but imply a psychological mechanism capable of computing attentional cues as directed to targets. However, it is important to stress that these results do not yet warrant attributions of mentalistic understanding. More simply, attention can be understood as a state characterised by explicit physical cues that indicate a relation between the agent and the object of attention, a relation implicit in the orienting behaviour, without the need to understand attention as an internal mental state (Gomez 1996, in press; see also Byrne 2003). This representation may not be available to make correct choices in object-choice paradigms, but it may be revealed in competitive settings and/or in responses to violation of expectancy, as in the current study. A dichotomy between low-level, rule-based behaviour reading (used to compute attention direction despite a poor understanding of visual attention) and high-level attributions of attentional states, may be too simplistic, and it may be more fruitful to reason about the specific demands of failed and passed tasks.

Despite the fact that monkeys followed equally the attention of the adult and young monkey photograph, they reacted differently to adult and young models in trials during which the position of the target object violated the agent-object relation: they displayed "checking behaviour" for violations only when the model was the adult. The fact that initially monkeys fixated the target location as often and for as long with both models suggests that the monkeys did not find attention direction perceptually less discriminable in the young female. Later disparities specific to the violations of the relation between the model and the target of attention may depend on allocation of social attention according to rank for primates and Cercopithecinae in particular. Chance (1967) showed how dominant animals in any primate group are particularly monitored in ambiguous situations, when appropriate behaviour on the part of subordinates could be crucial to respect dominance hierarchies. An earlier investigation of captive Diana social relations also established that the Diana male and dominant females tend to receive most visual attention and approaches for grooming, in contrast with the youngest in the group (Byrne et al. 1983). The hypothesis that monitoring in ambiguous situations is related to social hierarchy or physical dominance, while simple visual co-orientation is not, could be studied by contrasting attention-following behaviour and reactions to violations with photographs of different ranking individuals within the group.

Moreover, our data converge with recent studies of Diana monkeys' vocalisations that provide further evidence of a social understanding going beyond perceptual discrimination. Zuberbuehler (2000) investigated the responses of Diana monkeys to chimpanzee social calls, signalling their presence, and compared them with responses to chimpanzees alarm calls to the presence of leopards. He found that a high proportion of Diana groups responded to the latter as they would to a real leopard, showing that calling behaviour is modified according to whether chimpanzees' calls announce the presence of another predator or the threat of a chimpanzee hunt itself. While these findings need not warrant claims of intentionality and mentalistic attributions to the caller or the signaller, they certainly speak for a sophisticated causal understanding. The convergence between results in the vocal modality and our findings perhaps suggest a generalised ability to "understand" orientation of attention in Diana monkeys, but in a statistical rather than a mentalistic sense (see Byrne 2003).

In conclusion, we have provided a new experimental tool for the study of attention in animals. This methodology could aid in developing a comparative picture of both attention following and understanding, which is currently lacking. We presented evidence suggesting that, (1) attention-following occurs in Diana monkeys; (2), this attention-following may occur in a relatively automatic way; but, (3) monkeys seem to expect the presence of a target to be linked to the model's attention. We have interpreted this as implying an understanding of attention, different both from the learning of simple contingencies and from an understanding based upon explicit representations or concepts.

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TABLES

Table 1. Subjects' identity, age and gender.

Monkey identity	***Age (years:months)***	***Gender***
Kefi	0:9	Female
Kasai	2:5	Female
Loko	3:7	Female
Bo	5:4	Female
Karina*	7:11	Female
Robbie	9:11	Male

* **housed in a separate enclosure**.

Table 2. Monkey photograph-Alone phase. Total number of trials, discarded trials (looks coded as "elsewhere" throughout the Monkey photograph-Alone phase) and scored trials. For individual monkeys, trials during which first fixations were directed to the target or anti-target respectively were compared using the binomial test, 1-tailed.

Monkey	*Trials*	*Elsewhere*	*Target*	*Antitarget*	*p level*
Kefi	15	1	7	7	n.s.
Kasai	8	0	5	3	n.s.
Loko	11	1	9	1	0.011
Bo	9	1	7	1	0.035
Karina	11	1	10	0	0.001
Robbie	9	1	7	1	0.035
GROUP	**63**	**5**	**45**	**13**	

Table 3. Monkey photograph-and-Toy phase. For individual monkeys, we represent the percentage of trials during which first fixations after inspecting the toy were directed to monkey photograph (as opposed to elsewhere) in Compatible and Incompatible trials when the monkey on the photograph was (a) the female juvenile, (b) the adult male. Proportions for monkeys that directed first inspections towards the monkey photograph more often in incompatible vs. compatible trials, suggesting a violation of expectancy, are shown in bold italics.

Monkey Photograph	***Monkey***	***Compatible Trials***	***Incompatible Trials***
(a) Female Juvenile	**Kefi**	0	0
	Kasai	0	0
	Loko	100	67
	Bo	33	0
	Karina	***0***	***100***
	Robbie	0	0
	GROUP	**26.6**	**33.4**
(b) Adult Male	**Kefi**	***0***	***67***
	Kasai	33	0
	Loko	0	0
	Bo	***50***	***100***
	Karina	***50***	***100***
	Robbie	***0***	***67***
	GROUP	**22.2**	**55.7**

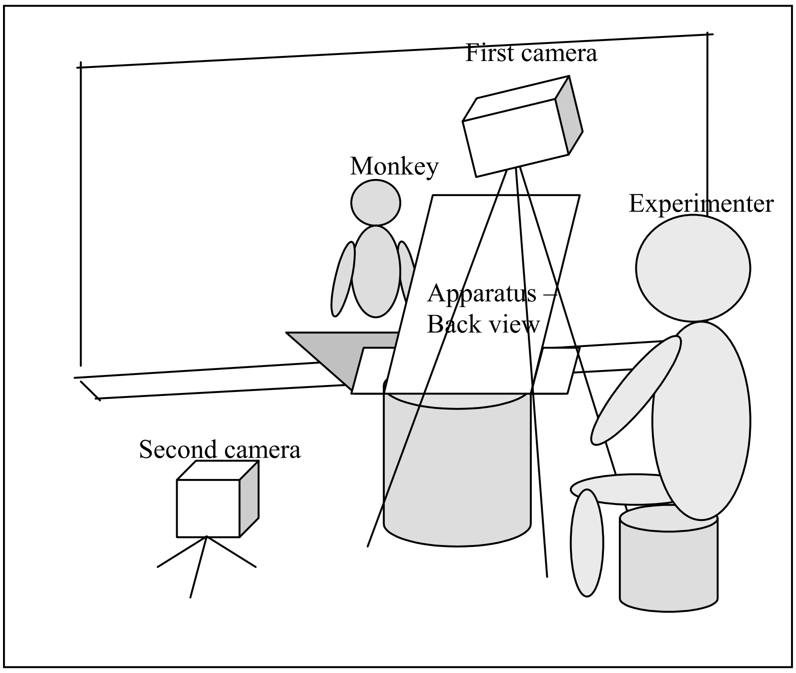
FIGURE CAPTIONS

Figure 1. a) Experimental set-up. Across trials, the experimenter sat randomly at either side of the apparatus. **b)** Monkeys' view of the experimental display in the Monkey photograph-Alone phase (adult male model). Notice the long cardboard strip covering the lower part of the apparatus, where the Toy is hidden. **c)** Monkey-photograph-and-Toy phase (young female, Compatible condition). The experimenter removed the long cardboard strip covering the toy. In Incompatible conditions the toy would appear on the opposite side to the line of regard of the monkey on the photograph. Across conditions, the toy appeared randomly to the left or right of the monkey photograph.

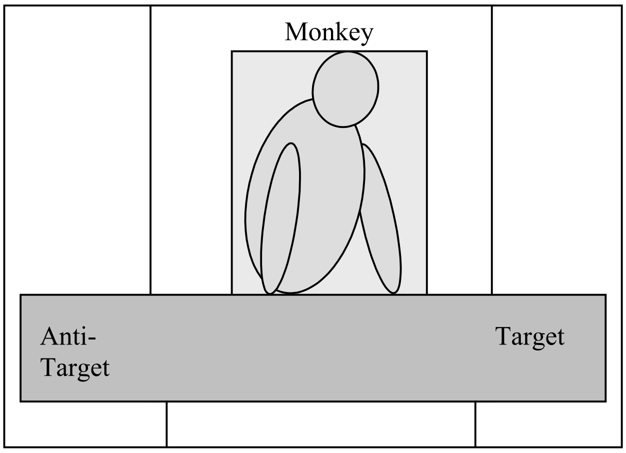
Figure 2. Monkey photograph-and-Toy phase – Monkeys produced more inspections of the adult Monkey photograph in the incompatible than the compatible condition, but not of the young female (mean inspections +/- SEM). Mean number of frames spent inspecting the Monkey photograph for the group and individuals did not vary across conditions and models (see text).

Figure 1

1a)



1b)



1c)

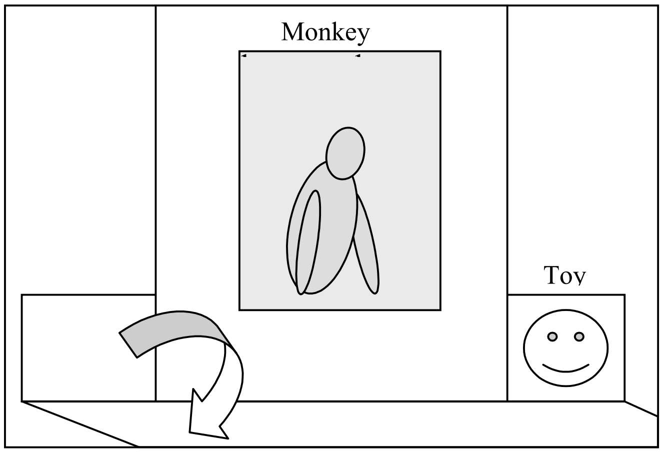
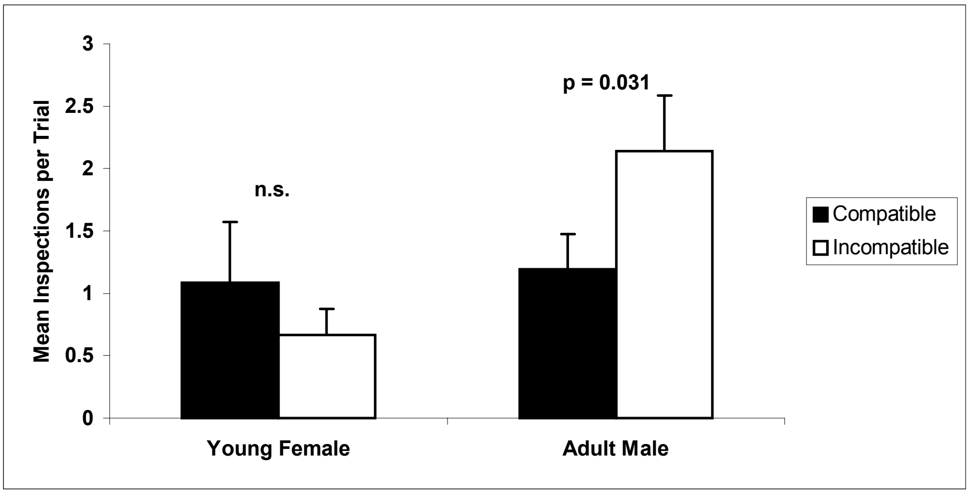


Figure 2


3
2.5
2
1.5
1
0.5
0
Mean Inspections per Trial
n.s.
p = 0.031
Young Female
Adult Male
Compatible
Incompatible