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An analysis of gaze following to a hidden location in long-tailed macaques (*Macaca fascicularis*)

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Abstract

Gaze following, the ability to track the direction of another's gaze, is thought to be an important component of human and animal social cognition. Several animal species attend to the gaze direction of others, but in Old World monkeys it remains unclear whether this behaviour is based on a simple co-orientation mechanism or on a more sophisticated perception of the other's visual behaviour. The capacity to follow another's gaze to a location hidden behind a physical obstacle has been argued to indicate refined skills in determining the exact direction of the other's gaze ('geometrical gaze following') and a representation of space outside one's own visual field. Human infants, great apes, new world monkeys, wolves (*Canis lupus*) and ravens (*Corvus corax*) have been shown to have this capacity. We investigated whether long-tailed macaques (*Macaca fascicularis*), an Old World monkey, follow conspecific gaze, indicated by head direction and visual orientation, to a hidden location. When a conspecific demonstrator gazed at a mirror hidden behind a barrier, subjects relocated to a position where they could see the mirror location and showed a trend, not statistically significant, to direct more focussed looks behind the barrier than in a situation where there was no conspicuous gaze cue by the demonstrator. The strength of this reaction was greatest in those individuals that looked most frequently at the demonstrator. Thus, long-tailed macaques may follow gaze to a hidden location, suggesting that they possess geometrical gaze following and represent space outside their own visual field. In addition, this capacity may be widespread across the animal kingdom.

Keywords

barrier, cognitive evolution, gaze-following, non-human primates, visual perspective.

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1. Introduction

Gaze following is the capacity to track the looking direction of other individuals to a different location (Scaife & Bruner, 1975). This capacity has received considerable interest, both in animal and human behaviour research (Gomez, 2005), as it is considered to be important in social learning and language acquisition (Baldwin & Moses, 1994). Moreover, the ability to follow another individual's gaze may form the basis of cognitive capacities that relate to mental state understanding (Baron-Cohen, 1995). In human infants, gaze following develops from a general sensitivity to eyes and eye-direction to the cognitively more complex knowledge that the other is seeing something when shifting gaze (e.g., D'Entremont et al., 2007). These latter stages are proposed to be essential in the development of a Theory of Mind (Baron-Cohen, 1995), i.e., the ability to understand that other individuals have emotions, thoughts and intentions different to one's own. In non-human animals, there is growing evidence for gaze following using a variety of task designs in a wide range of species, such as primates, birds, marine mammals and some domesticated species (Itakura, 1996; Miklosi et al., 1998; Emery, 2000; Deaner & Platt, 2003; Bugnyar et al., 2004; Kaminski et al., 2005; Shepherd et al., 2006; Pack & Herman, 2007). In general animal gaze following is studied by investigating whether an individual can track gaze direction, as indicated by cues from a human experimenter or conspecific such as head and/or body direction. Attending to another individual's gazing direction is potentially functionally important for group-living animals, since it can provide information on social events, predators or food locations (e.g., Tomasello et al., 1998). However, for many species little is known about the cognitive mechanisms underlying gaze following.

Butterworth & Jarrett (1991) proposed three mechanisms employed consecutively in the development of gaze following in human infants. First, at the most basic level, the child responds to the approximate direction of the other's look, without tracking the line of sight to a specific target. Second, with a 'geometrical' mechanism the child tracks an imaginary line of sight to a specific object within his/her field of vision, past distracting objects. At the third level, with a 'representational' mechanism the child follows gaze to a location outside his/her field of vision (for instance behind his/herself). Butterworth & Jarrett (1991) use 'representational' in the sense of spatial representations, not in the sense of mentalistic understanding of another's visual behaviour.

A task proposed to indicate the third level 'representational' mechanism tests whether animals can track another individual's looking direction to a location hidden behind a physical obstacle (Tomasello et al., 1999; Bugnyar et al., 2004; Bräuer et al., 2005). In this task an experimenter shifts gaze to a location behind an obstacle that obstructs the subject's view of the location at which the gaze is focussed. If merely responding to the direction of the other's gaze, the observing individual will follow gaze and co-orient in approximately the same direction as the experimenter. Alternatively, the observing animal may recognize that the experimenter's gaze is directed to a location behind the barrier (Tomasello et al., 1999, 2005) and will subsequently attempt to see what the other is looking at. To achieve this, the animal has to extrapolate gaze in a geometrical way. In addition, it must have some representation of the space behind the barrier (sensu Butterworth & Jarrett, 1991) that it cannot visually access from its current perspective.

Human infants (aged 12–18 months), great apes, two new world monkey species, wolves and ravens will respond to an experimenter's gaze to a hidden location behind a barrier by relocating themselves to a position where they can see this location (chimpanzees, *Pan troglodytes*: Tomasello et al., 1999; ravens, *Corvus corax*: Bugnyar et al., 2004; human infants: Moll & Tomasello, 2004; great apes: Bräuer et al., 2005; spider monkeys, *Ateles geoffroyi*, and capuchin monkeys, *Cebus apella*: Amici et al., 2009; wolves, *Canis lupus*: Range & Virányi, 2011), whereas bald ibises failed to look behind a barrier (*Geronticus eremita*: Loretto et al., 2010). If gaze following is a conserved capacity, it is expected that also Old World primates can follow gaze to a hidden location. However, this remains to be established.

We investigated whether long-tailed macaques (*Macaca fascicularis*), an Old World monkey, are able to track a conspecific's looking direction to a hidden location, as this could indicate refined perception of the other's visual behaviour. In the present study, the attention of a conspecific individual (demonstrator) was suddenly drawn to a location not visible to the subject (see Tomasello et al., 1999; Bräuer et al., 2005), by the appearance of a mirror. We reasoned that a conspecific demonstrator would be more salient than a human demonstrator (Tomasello et al., 1998; Itakura et al., 1999; Hare et al., 2001), that mirrors would elicit social responses in the primate demonstrator (Gallup, 1970, 1977) and that social responses would be more salient than neutral looks (Goossens et al., 2008; Teufel et al., 2010). We predicted that if the subject was able to track the conspecific's gaze direction to a location outside its own visual field, hidden behind the barrier, it would move to a suitable viewing area and actively orient to see what the other was looking at.

2. Methods

2.1. Subjects

Subjects were 13 adult long-tailed macaques (6 males, 7 females; mean age: 8.7 years) from a single social group of 27 animals at the macaque colony of Utrecht University. Ten subjects also acted as demonstrators, together with an additional two individuals from the group. Animals were housed in an indoor enclosure (235 m^3) with access to an outdoor compound (800 m^3). Water was available ad libitum throughout. The animals received commercially available monkey chow and grains daily and fruit twice a week. Prior to testing, the dominance hierarchy was determined by analysing submissive and aggressive behaviours that were observed ad libitum (linearity index: $h' = 0.45$, $P < 0.001$). A dominance rank was assigned, the highest ranking individual obtained rank 1, the lowest ranking individual obtained rank 26. The animals did not have previous experience with cognitive tests or other experiments. Only individuals that separated from the group and entered the testing enclosure voluntarily participated in the study.

2.2. Apparatus

A wooden barrier (128 cm × 52 cm h × w) attached vertically to the demonstrator's compartment (Figure 1) created an area that only the demonstrator could see when the demonstrator and subject were at their starting locations. To attract the demonstrator's attention towards this area, we designed an experimental device that could be remotely controlled and would elicit a response from the demonstrator towards the location hidden for the subject. On a tray we fixed a mirror (15 cm × 15 cm) alongside a wood panel of the same size (Figure 1: 'P' and 'M'). The hinged wood panel and mirror could be independently and silently pulled upright by concealed nylon strings from an adjacent room. When flat, both looked similar and did not attract the attention of the animals, since the reflecting side of the mirror was not visible from the demonstrator's start position. However, when pulled up, we expected the mirror to elicit a stronger gazing response from the demonstrator than the wooden panel (e.g., Anderson & Roeder, 1989).

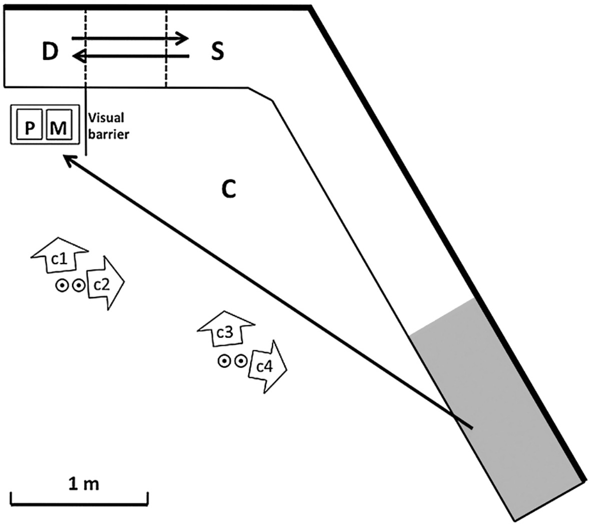

Figure 1. Plan of the experimental enclosure, to scale (bar represents 1 m). In the experimental condition, the demonstrator's (D) attention is drawn towards a mirror (M) pulled to an upright position. In the control condition an unreflective wood panel (P) is raised. At the starting location the demonstrator and the subject (S) can see each other but the subject's view of the area containing the mirror and panel is blocked by a visual barrier. The subject has visual access to the location behind the barrier if it moves to the area shaded in grey, termed the 'viewing location'. The central room is indicated with C. Arrows indicate visual accessibility. The concrete back of the enclosure is indicated in bold; the enclosure's other outer walls consisted of metal bars. The dotted circles represent the 4 video cameras (c1–c4): c1 recorded the demonstrator, c2 recorded an overview of the subject's compartment, c3 recorded the subject at the start position and c4 recorded the viewing location.

2.3. *Experimental procedure*

Animals were tested in subject-demonstrator pairs, with the demonstrator's attention drawn to a hidden area behind a barrier that was visually inaccessible from the starting position of the observing subject (Figure 1). Subsequently it was recorded whether the subject relocated to a designated 'viewing location' by moving away from the demonstrator to the area shaded grey in Figure 1, the only location where the subject could visually access the hidden area. The back of the wooden panel and mirror looked identical from the viewing location. Prior to the experiment, animals were familiarized with and trained to separate from the group voluntarily in the whole test enclosure connected to their home enclosure, where they had no visual access to the group. On test days, selected pairs were directed to the positions from which they could see each other through transparent slides (Figure 1). The demonstrator was restricted to one compartment, whereas the subject was free to move through several compartments of the test enclosure. The demonstrator and the subject were separated by a see-through screen. The subject could not see the reflection of the demonstrator in the mirror from the starting position or the demonstrator from the viewing location. During separation-training we had observed that subjects would move around the test enclosure for a certain amount of time, but would eventually settle down nearby the demonstrator. A trial only began if the subject had settled at this position for at least two minutes. Trials in which subjects did not meet this criterion were terminated and repeated on a different day. Two individuals did not meet this criterion after several testing days and were, thus, excluded from further testing. In addition, we paired one individual (Ge) with a demonstrator that had had this role before (Eu). Therefore, analyses were based on thirteen subject-demonstrator pairs.

After both subject and demonstrator had settled down for two minutes and faced the central room a trial was started (see Figure 1). All animals had experience with the barrier and the inactive experimental device from earlier separation sessions during training, when the experimental device was located near the test enclosure, but never hidden behind the barrier. On test days the experimental device was located behind the barrier before the animals entered. A trial would start by pulling up the piece of wood (Control Condition) or the mirror (Experimental Condition). After five minutes a trial would end by lowering the raised wooden panel or mirror. The demonstrators were not trained with mirrors, yet since their enclosure contained windows and other shiny objects, they most likely had experience with reflections. Pilot tests with other individuals than used in this study had established that the demonstrator responses began after variable time intervals, so we used a five minute trial to encompass this individual variation. After at least 1 min after a trial was finished, and when the subject had moved back to the starting position, the next trial began. Each test consisted of three consecutive trials, with an identical sequence for all subjects (Control–Experimental–Control) and was conducted only once per subject. The use of the wooden panel during the control condition allowed us to control for possible secondary effects of the movement of the mirror on the behaviour of the demonstrator or subject.

Table 1.
Demonstrator, subject, focussed looks of subject behind the barrier and social signals by demonstrator.

Demonstrator (dominance rank)	Subject (sex/age in in years/dominance rank)	Focussed look behind barrier	Social signals by demonstrator during experimental condition
Sq (1)	Eu (♀/6/4)	e	2 × li
Hi (15)	Am (♂/7/23)	e	3 × li, 1 × ls
Mo (25)	Be (♀/3/26)	e, c_2	3 × li
Eu (4)	Ge (♂/26/13)	e	2 × li
Eu (4)	Sq (♂/11/1)	e, c_2	–
Am (23)	Hi (♂/8/15)	c_1	5 × li
St (14)	Xu (♂/4/20)	–	–
Be (26)	Mo (♂/5/25)	–	3 × li
Na (9)	To (♀/9/8)	–	4 × li, 1 × ls
Ch (2)	In (♀/10/10)	–	–
Xu (20)	St (♀/10/14)	–	8 × li, 2 × ls
Va (24)	Ba (♀/5/17)	–	6 × li, 2 × ls
Ba (17)	Va (♀/9/24)	–	8 × li

Individuals that directed focussed looks around the barrier: e, during the experimental condition; $c_{1,2}$, during the first or second control condition. Social signals: li, lifting of the eyebrows; ls, lip-smacking.

Experimental pairs (Table 1) were formed on the basis of individuals' relatedness and their likeliness to associate with each other in the home enclosure. Thereby we attempted to reduce the chance that animals would not pay attention to each other during testing (Watts (1998) describes an association between relationship quality and attention) and to increase the likelihood that they would be at ease near each other during testing. Roles of demonstrator and subject were assigned randomly to the pairs. After having tested all pairs, the roles of subject and demonstrator were reversed in five pairs. We balanced for dominance-direction so that the demonstrator was the more dominant individual on half of the first trials with each pair. Since there was a considerable delay (at least three weeks) between the first and the second test series, we did not expect that experience with the role as either demonstrator or subject would influence responses when tested in the other role (Povinelli et al., 1992). Indeed, test order did not seem to determine behaviour, since of the six individuals that showed the target behaviour (focussed looks), four subjects showed this behaviour before, whereas two subjects showed it after they had been demonstrator.

Some demonstrator animals (Be, Na, Va) showed a startled reaction to the movement of the piece of wood (i.e., they pulled back their head and/or body with a quick movement and/or showed a fearful facial expression) during the first control trial and consequently looked into that direction for a certain period. Although the responses of these demonstrators to the piece of wood were far less obvious than the responses directed at the mirror, we excluded the data collected for both demonstrator and subject during the first controls of these demonstrators from the analyses. The mirror evoked the expected affiliative response in most of the animals (see Results). Trials were recorded simultaneously with four cameras placed at different angles and projected on a split screen.

2.4. Data analysis

An observer, unfamiliar with the theoretical background and blind to the experimental conditions, analysed the videotapes. The observer noted the gazing behaviour of the demonstrators and gazing and body movement of the subjects. Body movement was measured as the movement between different pre-defined compartments (e.g., starting position) within the test-enclosure. A look was defined as change of gazing direction in one of several predefined directions, for a minimum duration of 1 s. We counted demonstrator looks at the wooden panel or mirror. We counted looks in several different directions for both the demonstrators and subjects: Measurement 1: Looks at demonstrator/subject, i.e., the look was directed at the interaction partner. The animals could see each other only when the subject was in the starting position. Measurement 2: Look towards the central room C (Figure 1). Measurement 3: Look up/down, i.e., the demonstrator/subject looked 45° above or below the horizontal. Measurement 4: Look back, i.e., face and/or body oriented towards the back of the enclosure.

The critical behavioural measures were subjects' looks from the viewing location where the hidden area could be seen (shaded in Figure 1). We assumed that subjects that made an attempt at the viewing location to see what was hidden behind the barrier should unmistakably focus on the target location, i.e., should actively position themselves and move to view the location and potential target of the other's gaze. We, thus, distinguished between general looks towards the barrier and focussed looks behind the barrier when the subject was located in the area where the location behind the barrier was visible (see Figure 1, the 'viewing location'): Measurement 5: General looks towards barrier were defined as looks towards the area of the barrier and the back of the barrier from the viewing location, but without focus at a certain location and with subjects passively sitting in one location, and Measurement 6: Focussed looks behind the barrier were scored when the subject showed an active body posture, i.e., standing or holding bars, typically with the face pressed against bars of the enclosure, head and/or body moved while gaze maintained fixed gaze on the target location behind the barrier from the viewing location. Focussed looking resembles to some degree the behaviour 'staring' in this species (Angst, 1974) and is, therefore, thought to be a better indicator for interest and an attempt to see than the more passive general looking behaviour (Measurement 5).

To assess inter-observer-reliability, 25% of the trials were scored by a second coder. Inter-observer reliability based on all measures was good with Cohen's kappa = 0.7 ($p < 0.001$), and inter-observer agreement above 70% for all measures. Data were analysed in SPSS 12.1. Control trials before and after the experimental trial did not significantly differ in any of the recorded variables, so we calculated an average control response, to which the behaviour in the experimental condition was compared, with the exception of those controls in which the demonstrators were startled by the wooden panel's movement and looked multiple times at the panel. In these cases only the other control was used for analysis. The variable 'focussed looks behind barrier' was log-transformed in order to meet normality assumptions for parametric analyses. Tests are two-tailed, with significant effects ($p < 0.05$) and, given this is the first study in this species, non-significant trends approaching the threshold for statistical significance ($0.05 < p < 0.10$) are presented.

3. Results

3.1. Behaviour of demonstrator individuals

We established whether demonstrators reacted differently to the test and the control condition. Demonstrators directed significantly more looks at the raised mirror than at the raised wood (Figure 2; Paired t-test: $t_{11} = 6.35$, $p < 0.001$) and looked longer towards the mirror than the raised wood (Paired t-test: $t_{11} = 5.88$, $p < 0.001$, looking duration (in seconds) wood: $\bar{x} \pm \mathrm{SE} = 28.17 \pm 5.25$, mirror: 75.42 ± 7.92). Most demonstrators (10 out of 13) responded socially with affiliative behaviour to their mirror image,

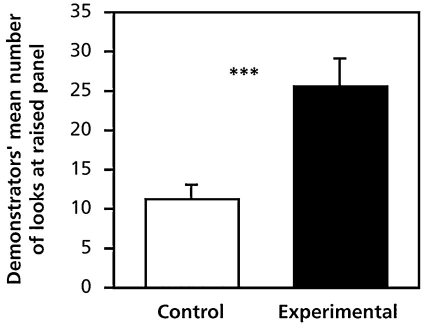

Figure 2. Mean number of looks by the demonstrator directed at the raised mirror or raised wood (± SE). All demonstrators directed more looks at the raised mirror than at the raised wood. Ten demonstrators directed affiliative social signals (lifting and lip-smacking) at the mirror.

the other three demonstrators responded with neutral looks only. All socially responsive animals responded with lifting of the eyebrows and three demonstrators also reacted by lip smacking; both behaviours are commonly shown during friendly interactions (Angst, 1974). The duration of social signalling varied between 8 and 76 s ($\bar{x} \pm \text{SE} = 19.07 \pm 5.72$).

We also analysed gazing behaviours of the demonstrators towards other directions as a measure of their general activity. We found that demonstrators directed more looks down when the mirror was raised compared to the wood (looks down during wood: $\bar{x} \pm \text{SE} = 9.75 \pm 1.53$, mirror: 11.75 ± 1.71, Paired t-test: $t_{11} = 2.37$, $p < 0.04$). Demonstrators also showed a non-significant trend to look more often towards the central room C, the area behind the experimental device, when the mirror was raised compared to when the wooden panel was raised (looks at central room during wood, $\bar{x} \pm \text{SE} = 25.13 \pm 3.19$; mirror, 30.71 ± 2.45; Paired t-test: $t_{11} = 2.15$, $p < 0.06$). Number of looks in other directions (up/down, back, at subject) did not differ significantly between the control and experimental conditions.

3.2. Behaviour of subjects

We determined whether the subjects paid attention to the demonstrator. They looked at the demonstrator in all trials. Subjects looked at the demonstrator more often when the mirror was raised compared to the wooden panel (looks at demonstrator during wood: $\bar{x} \pm \text{SE} = 8.15 \pm 1.55$, mirror: 13.08 ± 2.20, Paired t-test: $t_{12} = 2.56$, $p < 0.03$).

Next, we determined whether their reaction differed between control and test situations. Ten of 13 subjects relocated to the designated 'viewing location' during at least one of the trials (7 subjects relocated in either one of the control trials and 8 during the experimental trial). There was no significant difference in general looks towards the area of the barrier (measure 5) between the averaged control and the experimental condition (general looks during wood: $\bar{x} \pm \mathrm{SE} = 0.50 \pm 0.16$, mirror: 0.31 ± 0.17, Exact Wilcoxon signed-rank test: $T = 5$, $N = 13$, $p > 0.31$). Importantly, five animals directed focussed looks behind the barrier only during the mirror trial or more often during the mirror trial than the control trials, whereas one animal did so only during a control trial (Table 1). Consequently, subjects showed a non-significant trend to direct more focussed looks behind the barrier (Measurement 6) in the mirror than in the averaged control conditions (Figure 3; Paired t-test: $t_{12} = 1.97$, $p = 0.078$). We also compared the total number of changes in looking-direction, i.e., total number of looks (Measurements 1–6) as a measure of general activity and vigilance, but did not find a significant difference in this measure between the averaged controls and the experimental condition (looks during wood: $\bar{x} \pm \mathrm{SE} = 71.85 \pm 7.62$, mirror: 78.92 ± 8.64, Paired t-test: $t_{12} = 0.878$, $p > 0.39$). In addition, when the subject was at its starting position (S, Figure 1), there was no significant difference between the experimental and control conditions in looks towards the central room C (measure 2), which would indicate co-orientation with the demon-

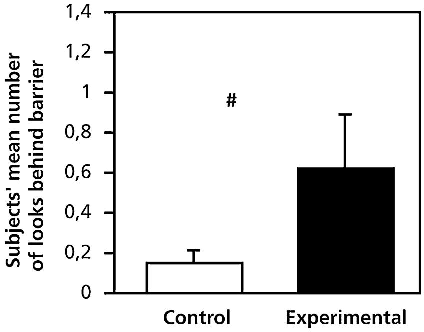

Figure 3. Mean number of focussed looks subjects directed behind the barrier in the averaged control (raised wood) and in the experimental (raised mirror) condition (± SE). Five out of 13 subjects directed focussed looks directed behind the barrier during the mirror condition. Overall, there were more focussed looks to behind the barrier during the mirror condition than during the averaged control condition.

strator (wood, $\bar{x} \pm \mathrm{SE} = 26.53 \pm 2.82$; mirror, 28.15 ± 4.15; Exact Wilcoxon signed-rank test, $T = 27$, $N = 13$, $p > 0.34$).

3.3. Interactions between demonstrator and subject behaviour

We explored whether following gaze or not by a subject depended on its reaction to the demonstrator. The strength of the subject's gaze following reaction was measured as the difference between number of focussed looks behind the barrier (Measurement 6) in the mirror condition minus the averaged control conditions. The strength of the subject's gaze following reaction was significantly and positively correlated with the number of looks at the demonstrator during all conditions (Spearman correlation: $\rho = 0.595$, $N = 13$, $p = 0.03$), suggesting that gaze following individuals paid more attention to the demonstrator than those animals that did not follow the other's gaze. However, the increase in number of looks the subject directed at the demonstrator between the control and experimental conditions was not significantly related to gaze following (Spearman correlation: $\rho = -0.004$, $N = 13$, $p = 0.99$). Neither the number nor the duration of the social displays directed by the demonstrator at the mirror were significantly related to gaze following (mean number of demonstrators' social displays, Spearman correlation: $\rho = -0.336$, $N = 13$, $p = 0.26$; mean duration of social behaviour: Spearman correlation: $\rho = -0.203$, $N = 13$, $p = 0.51$). In addition, there was no significant correlation between gaze following and the change in number of looks from the starting position towards C (Spearman correlation: $\rho = 0.182$, $N = 13$, $p = 0.55$).

4. Discussion

Five long-tailed macaques extrapolated a conspecific demonstrator's gaze direction to behind a physical obstacle, relocated to a predefined position and directed more focussed looks towards the location behind the barrier during the experimental condition, whereas only one did so during a control trial. This suggests the capacity to follow gaze geometrically to a point outside their field of vision. Although the sample size was small and caution is needed in the interpretation of non-significant trends, our results raise the possibility that long-tailed macaques can follow gaze to a location outside their field of vision and employ a third level 'representational' mechanism of gaze following.

From the present results it appears that macaques, when gaze following (as indicated by demonstrators' eye-, head-, body direction and/or facial expression), do not simply move their eyes and turn their head in the same direction another is looking at, since that would result in the animals staying at their starting position and looking straight ahead and slightly downwards, which is the gazing direction of the demonstrator. Instead, they apparently tracked the other's gaze to an out-of-view location, responding by moving and focussed looking towards the appropriate location. The animals employed this ability to follow gaze to a location outside their own visual field, which to some extent requires spatial representational abilities (Butterworth & Jarrett, 1991). We cannot and do not conclude from our results that macaques take the demonstrator's perspective and, thus, understand the other's visual behaviour in a mentalistic sense (i.e., the other is seeing and knowing something else than the subject; Povinelli & Eddy, 1996; Tomasello et al., 1999).

4.1. Alternative explanations

Alternatively, the facial expression that accompanied most demonstrators' gaze during the experimental condition could have enhanced the salience of the gaze cue (Goossens et al., 2008; Teufel et al., 2010) or suggested that another individual was present. Consequently, the emotional expression without a visible object of interest may have prompted a general searching response, resulting in focussed looks to formerly hidden locations. However, we did not detect an increase in looking around in the experimental versus control conditions, suggesting that if animals were searching, they were looking specifically at the hidden location. In addition, it is inconsistent with the searching by Sq (Table 1), who moved to the viewing area and showed focussed looks, but whose demonstrator did not show facial expression indicating a conspecific. If this possibility is true, subjects, thus, had a representation of the hidden location as previously unseen, again requiring a representation of space, but not the capacity to follow gaze geometrically to a point outside the field of vision.

Arousal- or attention-based mechanisms may provide alternative explanations for the behaviour of the gaze following animals. Gaze followers may become more aroused by the changes in demonstrator behaviour during the experimental condition, and for that reason relocate and direct their attention towards the demonstrator, or simply look around more in general. We assumed that the more aroused an animal is, the more vigilant it will be, resulting in frequent changes of looking direction. However, overall, changes of looking direction were not significantly larger in the experimental compared to the control condition. In addition, relocations to the designated ‘viewing location’ did not differ significantly between the experimental and control condition. Moreover, prior to testing we had given the subjects experience with the different visual perspectives in the test-enclosure, which means that the animals had experienced that they could not see the demonstrator from the location from which they attempted to look around the barrier. We, therefore, conclude that it is unlikely that the gaze followers directed focussed looks from the viewing location because of the salience of the cue, because of elevated arousal or in an attempt to observe the demonstrator.

4.2. Experimental design

We considered focussed looks from a predefined position as the critical behaviour indicating gaze following, and not all movements towards this location by the subjects. Animals relocated on several other trials as well. Relocation to the viewing location, from which the subject could see the target location without focussed looking, may have been a result of the relatively lengthy trial duration (5 min) and the restrictions of the test-enclosure design, which meant that animals could only move in one direction if they moved at all. Therefore, relocation alone would have been an insufficient and uninformative cue of gaze following in this experimental set-up. A superior test-enclosure design would allow subject movement in two directions, but logistical constraints precluded this design. It is unlikely that the presented findings could be the result of order effects, since control trials that preceded and followed the experimental trial did not differ from one another in the various measures. Moreover, it is unlikely that the subject reacted differently to control and experimental condition due to the pulling of the panels itself, since any cues from pulling them up and their view from the viewing location was similar.

The use of a conspecific, in contrast to a human experimenter, may have made this task more salient to the animals. Many primate and non-primate species readily respond to human cues in basic gaze following tasks (Miklosi et al., 1998; Tomasello et al., 2001; Scheumann & Call, 2004; Kaminski et al., 2005), but advanced use of gaze cues seems more difficult to demonstrate with human experimenters (e.g., Anderson et al., 1996), although positive results have been obtained with hand-raised (ravens: Schloegl et al., 2007; wolves: Range & Virányi, 2011) and domesticated subjects (dogs, *Canis familiaris*: Bräuer et al., 2004). Conspecific individuals have been successful demonstrators and competitors in other paradigms testing gaze following capacities in animals (Tomasello et al., 1998; Itakura et al., 1999; Hare et al., 2001), indicating that a conspecific's gaze may be more salient than that of a human (Itakura et al., 1999). In addition, earlier studies showed that an affiliative signal increased gaze following responses in a simple gaze following task (Goossens et al., 2008; Teufel et al., 2010), the social responses of some demonstrators towards the mirror may be facilitating in a more complex situation like the barrier test. This is investigated by examining the behaviour of demonstrators and subjects in relation to the response of the subject.

4.3. Interactions with demonstrator behaviour

Only 5 of the 13 animals tested responded to the demonstrators by relocation with focussed looks around the barrier in the experimental condition. Thus, the magnitude of the observed gaze-following effect is weak. During all conditions the strength of the subject's gaze following was stronger when it looked more often at the demonstrator, supporting the suggestion that high general attention to the demonstrator may be a prerequisite for gaze following (Itakura, 1996). In addition, inter-individual differences in the cognitive capacity, motivation, or the propensity to perform this task may provide the additional explanations for the between-individual variation observed. Future studies should address these differences. We note that the difference between the experimental and control cues utilised in this study were likely weaker than comparable studies, where the control cue involved a demonstrator looking in a different direction and, thus, potentially drawing attention away from the barrier (e.g., Tomasello et al., 1999; Amici et al., 2009).

4.4. Conclusions

So far, great apes, some species of New World monkeys, wolves and ravens, but not bald ibises (Loretto et al., 2010), have been shown to follow another's gaze geometrically to a location hidden behind a barrier. They do this repeatedly, with different kind of barriers and irrespective of the presence of food at the location the experimenter's gaze is directed at (Povinelli & Eddy, 1996; Tomasello et al., 1999; Bugnyar et al., 2004; Bräuer et al., 2005; Amici et al., 2009). This ability requires geometric gaze following in combination with a representation of the hidden location. Geometric gaze following, without the barrier component, has been demonstrated in other species. For example, bee-eaters (*Merops orientalis*) differentiate between a predator looking at them or at their nest, indicating that they are able to exactly identify the target of another's gaze (Watve et al., 2002). Common marmosets (*Callithrix jacchus*) are able to follow gaze past distracting objects to an exact location within their visual field (Burkart & Heschl, 2006). With this study we provide suggestive evidence that the ability to follow gaze to hidden locations may also be present in a species of Old World monkeys, the long-tailed macaque.

Researchers agree that neither the geometrical nor the representational mechanisms of gaze following require a mentalistic understanding of the other's visual behaviour (Butterworth & Jarrett, 1991; Tomasello et al., 1999; Bugnyar et al., 2004), as it is not necessary to take the demonstrator's perspective to master the task we describe here. Yet in human infants this skill, exceeding simple co-orientation, has been proposed to signify progress in cognitive development (Butterworth & Jarrett, 1991). Recent work has begun to uncover a variety of visual behaviours in monkeys. Long-tailed macaques and Diana monkeys (*Cercopithecus diana*) have been shown to check-look (Scerif et al., 2004; Goossens et al., 2008), i.e., looking back and forth between the model and the looking direction when seeing nothing to be looked at in the direction of the other's gaze. This behaviour has been proposed to indicate the understanding that the other is looking at something specific (Scaife & Bruner, 1975; but see e.g., Corkum & Moore, 1995 for alternative explanations). Moreover, macaques follow gaze longer when the gaze is accompanied by a social facial expression, suggesting that gaze following is a flexibly employed response (Goossens et al., 2008; Teufel et al., 2010). Rhesus macaques (*Macaca mulatta*) respond to what a human competitor can and cannot see (Flombaum & Santos, 2005), which corresponds to behaviour described so far only in chimpanzees (*Pan troglodytes*) (Hare et al., 2000). Taken together with these other results, our findings that indicate a long-tailed macaque capacity to follow gaze geometrically to a point outside their field of vision, suggest that advanced gaze following capacities are present in monkeys and that the use of a conspecific demonstrator may be a valuable tool to reveal these capacities. In the wider perspective of cognitive evolution, we propose that apparently sophisticated cognitive capacities relating to interpreting the visual behaviour of others are widespread among non-human primates. This raises the possibility that these visual capacities may be a conserved primate feature. However, whether these capacities are limited to some taxa, among them primates, carnivores and corvids, or are widespread among vertebrates needs to be investigated by further comparative research.

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References

Amici, F., Aureli, F., Visalberghi, E. & Call, J. (2009). Spider monkeys (*Ateles geoffroyi*) and capuchin monkeys (*Cebus apella*) follow gaze around barriers: evidence for perspective taking? — J. Comp. Psychol. 123: 368-374.

Anderson, J.R., 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.

Anderson, J.R. & Roeder, J.J. (1989). Responses of capuchin monkeys (*Cebus apella*) to different conditions of mirror-image stimulation. — Primates 30: 581-587.

Angst, W. (1974). Das Ausdrucksverhalten des Javaneraffen *Macaca fasciculari*s Raffles 1821. — Forts. Verhaltensforsch. 15: 5-31.

Baldwin, D.A. & Moses, L.J. (1994). Early understanding of referential intent and attentional focus: evidence from language and emotion. — In: Children's early understanding of mind (Lewis, C. & Mitchell, P., eds). Erlbaum, Hillsdale, NJ, p. 133-156.

Baron-Cohen, S. (1995). Mindblindness: an essay on autism and theory of mind. — MIT Press, Cambridge, MA.

Bräuer, J., Call, J. & Tomasello, M. (2004). Visual perspective taking in dogs (*Canis familiaris*) in the presence of barriers. — Appl. Anim. Behav. Sci. 88: 299-317.

Bräuer, J., Call, J. & Tomasello, M. (2005). All great ape species follow gaze to distant locations and around barriers. — J. Comp. Psychol. 119: 145-154.

Bugnyar, T., Stöwe, M. & Heinrich, B. (2004). Ravens, *Corvus corax*, follow gaze direction of humans around obstacles. — Proc. Roy. Soc. Lond. B: Biol. 271: 1331-1336.

Burkart, J. & Heschl, A. (2006). Geometrical gaze following in common marmosets (*Callithrix jacchus*). — J. Comp. Psychol. 120: 120-130.

Butterworth, G. & Jarrett, N. (1991). What minds have in common is space: spatial mechanisms serving joint visual attention in infancy. — Br. J. Dev. Psychol. 9: 55-72.

Corkum, V. & Moore, C. (1995). Development of joint visual attention in infants. — In: Joint attention: its origins and role in development (Moore, C. & Dunham, P.J., eds). Erlbaum, Hillsdale, NJ, p. 61-83.

Deaner, R.O. & Platt, M.L. (2003). Reflexive social attention in monkeys and humans. — Curr. Biol. 13: 1609-1613.

D'Entremont, B., Yazbeck, A., Morgan, A. & MacAulay, S. (2007). Early gaze-following and the understanding of others. — In: Gaze-following: its development and significance (Flom, R., Lee, K. & Muir, D., eds). Lawrence Erlbaum Associates, Mahwah, NJ, p. 217-242.

Emery, N.J. (2000). The eyes have it: the neuroethology, function and evolution of social gaze. — Neurosci. Biobehav. Rev. 24: 581-604.

Flombaum, J.I. & Santos, L.R. (2005). Rhesus monkeys attribute perceptions to others. — Curr. Biol. 15: 447-452.

Gallup, G.G. (1970). Chimpanzees: self-recognition. — Science 167: 86-87.

Gallup, G.G. (1977). Absence of self-recognition in a monkey (*Macaca fascicularis*) following prolonged exposure to a mirror. — Dev. Psychol. 10: 281-284.

Gomez, J.C. (2005). Species comparative studies and cognitive development. — Trends Cogn. Sci. 9: 118-125.

Goossens, B.M.A., Dekleva, M., Reader, S.M., Sterck, E.H.M. & Bolhuis, J.J. (2008). Gaze following in monkeys is modulated by observed facial expressions. — Anim. Behav. 75: 1673-1681.

Hare, B., Call, J., Agnetta, B. & Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. — Anim. Behav. 59: 771-785.

Hare, B., Call, J. & Tomasello, M. (2001). Do chimpanzees know what conspecifics know? — Anim. Behav. 61: 139-151.

Itakura, S. (1996). An exploratory study of gaze-monitoring in nonhuman primates. — Jap. Psychol. Res. 38: 174-180.

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.

Kaminski, J., Riedel, J., Call, J. & Tomasello, M. (2005). Domestic goats, *Capra hircus*, follow gaze direction and use social cues in an object choice task. — Anim. Behav. 69: 11-18.

Loretto, M.-C., Schloegl, C. & Bugnyar, T. (2010). Northern bald ibises follow others' gaze into distant space but not behind barriers. — Biol. Lett. 6: 14-17.

Miklosi, A., Polgardi, R., Topal, J. & Csanyi, V. (1998). Use of experimenter given cues by dogs. — Anim. Cogn. 1: 113-121.

Moll, H. & Tomasello, M. (2004). 12-and 18-month-old infants follow gaze to spaces behind barriers. — Dev. Sci. 7: F1-F9.

Pack, A.A. & Herman, L.M. (2007). The dolphin's (*Tursiops truncatus*) understanding of human gazing and pointing: knowing what and where. — J. Comp. Psychol. 121: 34-45.

Povinelli, D.J. & Eddy, T.J. (1996). Chimpanzees: joint visual attention. — Psychol. Sci. 7: 129-135.

Povinelli, D.J., Parks, K.A. & Novak, M.A. (1992). Role reversal by rhesus-monkeys, but no evidence of empathy. — Anim. Behav. 44: 269-281.

Range, F. & Viranyi, Z. (2011). Development of gaze following abilities in wolves (*Canis lupus*). — PLoS ONE 6: e16888, DOI:10.1371/journal.pone.0016888.

Scaife, M. & Bruner, J.S. (1975). The capacity for joint visual attention in the infant. — Nature 253: 265-266.

Scerif, G., Gomez, J.C. & Byrne, R.W. (2004). What do Diana monkeys know about the focus of attention of a conspecific? — Anim. Behav. 68: 1239-1247.

Scheumann, M. & Call, J. (2004). The use of experimenter-given cues by South African fur seals (*Arctocephalus pusillus*). — Anim. Cogn. 7: 224-230.

Schloegl, C., Kotrschal, K. & Bugnyar, T. (2007). Gaze following in common ravens, *Corvus corax*: ontogeny and habituation. — Anim. Behav. 74: 769-778.

Shepherd, S.V., Deaner, R.O. & Platt, M.L. (2006). Social status gates social attention in monkeys. — Curr. Biol. 16: R119-R120.

Teufel, C., Gutmann, A., Pirow, R. & Fischer, J. (2010). Facial expressions modulate the ontogenetic trajectory of gaze-following among monkeys. — Dev. Sci. 13: 913-922.

Tomasello, M., Call, J. & Hare, B. (1998). Five primate species follow the visual gaze of conspecifics. — Anim. Behav. 55: 1063-1069.

Tomasello, M., Carpenter, M., Call, J., Behne, T. & Moll, H. (2005). Understanding and sharing intentions: the origins of cultural cognition. — Behav. Brain Sci. 28: 675-735.

Tomasello, M., Hare, B. & Agnetta, B. (1999). Chimpanzees, *Pan troglodytes*, follow gaze direction geometrically. — Anim. Behav. 58: 769-777.

Tomasello, M., Hare, B. & Fogleman, T. (2001). The ontogeny of gaze following in chimpanzees, *Pan troglodytes*, and rhesus macaques, *Macaca mulatta*. — Anim. Behav. 61: 335-343.

Watts, D.P. (1998). A preliminary study of selective visual attention in female mountain gorillas (*Gorilla gorilla beringei*). — Primates 39: 71-78.

Watve, M., Thakar, J., Kale, A., Puntambekar, S., Shaikh, I., Vaze, K., Jog, M. & Paranjape, S. (2002). Bee-eaters (*Merops orientalis*) respond to what a predator can see. — Anim. Cogn. 5: 253-259.