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Gaze following in monkeys is modulated by observed facial expressions

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Gaze following and the ability to understand that another individual sees something different from oneself are widely considered important components of animal social cognition. Recent studies suggest that gaze following is taxonomically widespread, yet for many species there is no evidence that gaze following is employed in a flexible manner and is more than a simple so-called 'orienting reflex'. Here, we measured the effect of social facial expressions, mimicking responses to social events, on gaze following in longtailed macaques, *Macaca fascicularis*, using a human demonstrator. Gaze-shifts accompanied by a socially meaningful facial expression (the Bare Teeth display) elicited stronger gaze-following responses than neutral gaze-shifts. Subjects also 'check-looked', that is, looked back and forth between the experimenter's face and their gaze direction, which has been proposed to indicate that a subject understands that another individual is looking at a specific stimulus. Monkeys' gaze following is thus modulated by the facial emotional expressions of the demonstrator, providing evidence that their gaze following is more flexible than was previously thought. This modulation may be due to a specific arousal- or attention-based mechanism or may be based on the subject understanding that the demonstrator is attending to something the subject cannot see.

Keywords: check-look; facial expressions; gaze following; longtailed macaques; *Macaca fascicularis*; social cognition

Gaze following, the ability to track the gaze direction of other individuals, has been proposed to be an important component of animal social cognition because it may be based on an individual's understanding that the perceptions of others can differ from its own. In human infants this understanding has been proposed to be a precursor to Theory of Mind (Baron-Cohen 1995), the capacity to understand another individual as a different mental agent with its own intentions, emotions and goals (Premack & Woodruff 1978). In addition, the observation and interpretation of another's gaze may play a key role in the development of a Theory of Mind in the life of an infant (Baron-Cohen 1995). However, for nonhuman primates the 'cognitive' interpretation of gaze following has been challenged (Povinelli & Eddy 1996a, b). Animals from various taxa (chimpanzees, *Pan troglodytes*; rhesus macaques, *Macaca mulatta*; ravens, *Corvus corax*; goats, *Capra hircus*; dogs, *Canis familiaris*; and seals, *Arctocephalus pusillus*; Miklosi et al. 1998; Tomasello et al. 2001; Bugnyar et al. 2004; Scheumann & Call 2004; Kaminski et al. 2005) attend to the gazing direction of others, but for many species it remains unclear whether gaze following is flexibly employed rather than a fixed response to another individual's sudden change of visual orientation (Emery 2000). It is also not known to what extent the social context in which an individual shifts gaze influences gaze following. We investigated whether gaze following in longtailed macaques, *Macaca fascicularis*, is flexibly employed by displaying facial expressions with social and emotional meanings during gaze-shifts. In this way, we could analyse whether subjects would take a mimicked social event into account as indicated by a change in their gaze-following response, potentially shedding light on their level of gaze interpretation.

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Among primates, there is substantial evidence for gaze following (or visual co-orientation) of both conspecifics and heterospecifics (Tomasello et al. 1998; Anderson & Mitchell 1999; Lorincz et al. 1999; Emery 2000; Bräuer et al. 2005). Chimpanzees and rhesus macaques can follow human gaze from an early age (Tomasello et al. 2001), even solely eye direction, irrespective of head and body posture (Ferrari et al. 2000). However, without extensive training, chimpanzees, rhesus macaques and capuchin monkeys, *Cebus apella*, do not appear to use human gaze as a cue to locate hidden food (Anderson et al. 1995, 1996; Call et al. 1998; but see Burkart & Heschl 2006 for evidence in common marmosets, *Callithrix jacchus*). This limited extent of gaze interpretation may indicate what has been termed an 'orienting reflex' or 'low-level' understanding (Povinelli & Eddy 1996a). A co-orienting response to an individual's gaze-shift may be conditioned by means of conspicuous objects or events in the line of sight that can act as reinforcers. The individual learns to attend and respond to the visual cue of another's gaze-shift. In this interpretation, the gaze-following individual does not necessarily know exactly where the other individual is looking nor does it have an expectation of what the other is seeing. Instead, it simply looks in the direction another looks, as a result of a reflex or conditioned response. This response may, however, be influenced by the context in which the other individual shifts its gaze. Such context-specific responses may also be learned, but would none the less indicate a more flexible interpretation of gaze following than the low-level explanation currently allows.

A cognitively more demanding interpretation of gaze following is that the gaze following individual understands that the other's attention is directed at something, for instance a conspecific. This explanation suggests that the gaze follower has the knowledge that the other individual is seeing something different from itself, which in turn is a prerequisite to understand that the other has different knowledge (Tomasello et al. 1999). The gaze-following individual matches another's looking direction, expecting to see the target the first individual is observing, possibly with an expectation about the nature of the target.

Recent evidence indicates that some animals may have some understanding of another's visual perception while or after following gaze. Chimpanzees, rhesus macaques, and orang-utans, *Pongo pygmaeus*, can judge whether another individual at a different location can see a food item they see (Hare et al. 2000; Flombaum & Santos 2005; Shillito et al. 2005), which indicates an appreciation of the other's visual perspective. Great apes, like humans, look back and forth between the experimenter's face and the experimenter's gaze direction (Scaife & Bruner 1975; Call et al. 1998; Bräuer et al. 2005; see also Scerif et al. 2004). This check-looking behaviour has been proposed to indicate an individual's understanding that another is looking at something (Scaife & Bruner 1975; but see Corkum & Moore 1995). In addition, chimpanzees and ravens follow the gaze of a human experimenter around physical barriers (Tomasello et al. 1999; Bugnyar et al. 2004), even when temporarily distracted by a conspicuous object in the line of sight (Tomasello et al. 1999). Thus, instead of merely turning their head in the correct direction, the animals relocate themselves to a position from where they can see what the other is seeing (Tomasello et al. 2005). These results suggest that chimpanzees and ravens can determine the location of the target to which another individual is attending and that their gaze following is more than a mere co-orienting reflex (Tomasello et al. 1999; Bugnyar et al. 2004). Although these results shed light on individuals' knowledge of the location of the targets others are looking at, it remains unclear whether and how the animals' gaze following is also influenced by the knowledge, intentions or emotions of another.

Primates are experts in recognizing facial expressions (Nahm et al. 1997; Gauthier & Logothetis 2000; Parr et al. 2000; Gothard et al. 2004) and in determining the direction another individual is looking (Keating & Keating 1982; Perrett & Mistlin 1991). Social interactions are a prominent part of primate life (Tomasello & Call 1997). The social context in which an individual shifts its gaze may therefore provide a naturalistic way to study gaze following and the flexibility with which this behaviour may be employed. In the present study, a human experimenter displayed social facial expressions during gaze-shifts, thereby mimicking a response to a social event. We assumed that animals would perceive facial expressions displayed by a human experimenter similarly to conspecific facial expressions (Paukner et al. 2007). We compared responses to gaze-shifts with a social expression to gaze-shifts with a neutral facial expression. By employing meaningful social expressions we took advantage of their important role in social interactions (Cheney & Seyfarth 1990) and consequent likely salience for the subjects. We also investigated the response to a novel facial expression not displayed in macaques to control for the possibility that social expressions were more salient than a neutral facial signal because they involved more muscular activity, rather than because they mimicked a species-specific signal. We predicted that longtailed macaques, like other primates, would follow the gaze of an experimenter. Furthermore, we predicted that gaze-shifts accompanied by a socially meaningful facial expression would elicit a stronger gaze-following response than a neutral gaze-shift or a meaningless face if the animals took into account the transmitted information of the facial expression.

METHODS

Subjects

Subjects were 13 captive adult longtailed macaques housed at the Ethology Station of Utrecht University. All subjects belonged to the same stable social group of 19 animals living in an 18-m^3 inside enclosure with access to a 160-m^3 outside compound. They were fed commercially available monkey chow daily and received additional fruits and vegetables weekly. Water was available ad libitum throughout. One animal (Pu) died of natural causes before starting experiment 3. The dominance hierarchy was established before experiments began using ad libitum observations of a unidirectional submissive behaviour (i.e. the silent Bare Teeth display). Subsequently the linearity-index h' was calculated using the program MatMan 1.1 (Noldus

Technology; de Vries 1998). This resulted in a linear hierarchy ($h' = 0.59$, directional consistency index = 0.92, $P < 0.001$). Since hierarchies in this species generally remain stable throughout prolonged periods (Veenema et al. 1997), we assumed that the ranks we assigned beforehand did not change during the course of the three experiments. We divided the group into low-, mid- and high-ranking individuals (Table 1). Subjects had participated in earlier studies on mate choice (Nikitopoulos et al. 2005) and neophobia (unpublished data) but had no experience with tasks similar to ours. Experiments were approved by the Ethical Committee of Utrecht University (DEC 04/197).

Test Procedure

Testing took place in a cage (1.00 × 0.90 × 1.00 m, height × width × depth) connected to the animals' inside home enclosure by a tunnel. Sliding doors were used to separate the subjects from the group. The test cage was elevated 1.80 m above the ground. Between the top of the cage and the ceiling there was a space of 1.40 m. During testing the experimenter was on eye level with the subject. Animals were trained to voluntarily separate from the group and enter the test cage. In the test cage the animals had no visual access to the social group, but limited auditory contact was possible. Two subjects (Ro, Ic) had infants, which they took with them into the test cage in most of the test sessions. The infants did not appear to affect the subjects' performance.

Experiment 1: Gaze Following with Neutral Facial Expression

Thirteen subjects were tested individually for their ability to follow the gaze of a human experimenter with a neutral facial expression using a design similar to that employed with apes (Call et al. 1998; Bräuer et al. 2005). We compared reactions in two different conditions. In the gaze-shift condition the experimenter suddenly shifted her gaze to a predefined location on the ceiling. In the look-straight condition she kept on looking at the subject's chest. The look was directed at the chest since longtailed macaques can perceive direct eye contact as a threat. Each subject received six trials, each lasting 10 s in both conditions, spread out over two sessions in a 3-week period. The order of conditions was pseudo-randomized with the restriction that one condition (either gaze-shift or look-straight) could be administered only twice in succession. One-half of the subjects received the gaze-shift condition as first trial, the other individuals the look-straight condition.

After separation from the group the experimenter captured the attention of the animal by feeding small treats (fruit or bread) and talking quietly to the animal. A trial would start only after the animal was attending to the experimenter. In the gaze-shift condition, the experimenter began a trial by shifting her gaze to a predefined location on the ceiling outside the cage while still offering a treat out of reach of the animal. In the look-straight condition, the experimenter announced the start of a trial to give a clear onset ('Start'). Since the experimenter was talking to the subject continuously between trials, we do not expect the acoustic signal ('Start'), uttered in the same soft tone of voice, to have influenced the subject's behaviour. A second experimenter videotaped the behaviour of the subject with a Sony Hi8 Handycam CCD-TR825E and timed the trials. After 10 s, the completion of the trial was indicated by the same experimenter ('Stop'). In both conditions the subjects received the food item that the first experimenter had offered during the trial. After reestablishment of the subject's attention the next trial started.

Table 1. Subjects of this study

Subject	Sex	Age (years)	Rank/category
Cl	M	9	1/high
Er	F	18	2/high
Vi	M	6	3/high
Li	F	7	4/high
Co	F	9	5/mid
Ic	F	10	6/mid
Su	F	10	7/mid
Ro	F	22	8/mid
Se	F	11	9/low
Ni	F	7	10/low
Lo	F	8	11/low
Me	F	7	13/low
Pu	F	10	14/low

The study group, excluding infants. M: male; F: female. Me and Ic stopped entering the test cage after completing the first experiment. Pu died from natural causes before the start of experiment 3. Ch (rank 12) did not participate in the experiments because she became highly stressed during pilot separations.

Experiment 2: Gaze Following with Social Facial Expression

We tested 11 animals in the experiment involving social facial expressions. Two animals that had participated in the previous experiment did not complete all sessions of this experiment because they were unwilling to enter the test cage. They were excluded from the analysis. There were three experimental conditions and one control condition. In all conditions the experimenter shifted her gaze to the same predefined location on the ceiling as in experiment 1. During experimental trials the experimenter displayed one of three facial expressions while looking up (Fig. 1), whereas the control condition was a gaze-shift at the ceiling with a neutral facial expression. The distinct experimental conditions consisted of three 'meaningful' faces, that is, part of the longtailed macaques' facial repertoire (Fig. 1). The expressions we used cover several domains of social life in macaques, namely aggression (Open Mouth), submission (Bare Teeth) and affiliation (Lip Smack) (Angst 1974). Two of these facial expressions are important for the establishment and maintenance of the dominance hierarchy (Open Mouth and Bare Teeth).

Figure 1. Emotional facial expressions. (Left to right) Bare Teeth, the signal for fear and submission, is shown from subordinate to dominant animals in both provoked and unprovoked situations. The Lip Smack shows affiliation between interaction partners. In contrast, the Open Mouth is used mostly in aggressive encounters to intimidate the opponent. Pilot experiments revealed that the animals would respond in a comparable way to the facial expressions when displayed by a human experimenter as they would to a conspecific.

The general procedure was the same as that in experiment 1 except for the intertrial intervals of at least 30 s in which the subject could eat the reward. Each subject was tested individually in six sessions spread out over a 7-month period. The sequence of the three meaningful facial expressions as well as the order of conditions was pseudo-randomized and counterbalanced across the animals. During a single session only one of the three facial expressions was tested in two experimental and two neutral-face control trials. This design was chosen to prevent confusion of the subjects due to the experimenter directing facial expressions with different social meanings to the ceiling within one single session.

Experiment 3: Gaze Following with Meaningless Facial Expression

To control for the possible effect of any extraordinary human face involving random contractions of the facial muscles we subsequently tested the animals' reaction to a fourth facial expression. We used a facial expression that was not part of the monkeys' or the human facial repertoire and thus most likely did not convey any meaning. Ten subjects received a total of four control and four experimental trials in a pseudo-randomized order spread out over two sessions. The procedure was otherwise the same as that for experiment 2.

Facial Expressions

Four facial expressions were displayed by the experimenter during the gaze-shift in experimental trials. The first three facial expressions are part of the animals' behavioural repertoire (Angst 1974) whereas the fourth was artificial and created by us for the purpose of this study. Facial expressions in longtailed macaques are very characteristic and stereotyped (Angst 1974; Fig. 1). We assumed that animals would perceive facial expressions displayed by a human experimenter similarly to those displayed by conspecifics. It has been shown that monkeys look at human and conspecific faces in a similar way when a facial expression is displayed (Nahm et al. 1997). In addition, during pilot experiments we had observed that the animals would respond appropriately to species-specific facial expressions when performed by a human experimenter. In general, animals responded to human lip smacking with affiliative behaviour (lip smacking or lifting of the eyebrows), whereas human Open Mouth threats resulted in escape and gaze avoidance or return of the threat, depending on the individual. Baring teeth to a threatening individual would often result in ceasing of the threat.

(1) Bare Teeth: Eyebrows are lifted and lips are pulled up, so that teeth and gums are visible. The Bare Teeth display is a submissive and fearful behaviour exclusively shown by a subordinate to a dominant animal, even when not provoked.

(2) Lip Smack: The mouth is opened fast and repeatedly while looking at the interaction partner with raised eyebrows. The signal is mostly used in a friendly, affiliative context.

(3) Open Mouth: Eyes are wide open, sometimes with lifted eyebrows, and fixed at interaction partner. The mouth is open with lips covering the teeth. This display is used in aggressive encounters to threaten the interaction partner.

(4) Meaningless Face: Cheeks are blown up in an extreme way. The mouth is closed. To our knowledge, this expression is meaningless to macaques and humans. This facial expression was matched with the other facial expressions in the degree and area of facial movement involved, since it involves movement of the mouth that also affects the area around the eyes.

Data Analysis

Two observers, blind to the experimental conditions, recorded the total number of looks up and down per trial. If a subject ceased its earlier gaze up, returned to the face of the experimenter and gazed up again immediately, we defined this as a check-look. All occurrences within every trial were scored. Because longtailed macaques, like various other primates, can monitor their surroundings by inconspicuous glancing (Emery 2000), we also included subtle looks or eye-only looks. Therefore, to record the looks in a systematic way, we defined a look up as a deviation of head and/or eyes with an angle of at least 45° above an estimated horizontal line between the eyes of the experimenter and the subject. The minimum duration of a look was set at 20 ms. In few trials, some of the subjects climbed up to the cage ceiling (perhaps to get a better view of the experimenter's face). While climbing, they mostly looked up straight in the direction of climbing. In those cases it was difficult to distinguish whether the gaze was due to the direction of movement or to the cue provided by the experimenter. We therefore defined a relevant look as a deviation of head and/or eyes towards the spot the experimenter was focusing compared to the direction the individual was climbing. As a measure of general gazing activity the number of looks down was recorded. We scored a look down as any deviation downwards from (1) the estimated horizontal line between the experimenter's and the subject's eyes or (2) the estimated line between the subject's eye and the food the experimenter was presenting, whichever was lowest. In addition, the scratching rate, defined as the number of quick repeated movements of hand and/or foot through the fur per trial, was scored because it indicates current levels of stress and anxiety (Schino et al. 1988; Pavani et al. 1991; Maestripieri et al. 1992). Interobserver reliability was high with 83% agreement on the number of looks per trial and a Cohen's kappa of 0.75 ($P < 0.001$).

Data were analysed with SPSS 12.1. Where data met the requirements of parametric tests paired *t* tests and repeated-measures ANOVA were applied; otherwise exact Wilcoxon signed-ranks test and exact Friedman's ANOVA were used (Mundry & Fischer 1998). In experiment 2 Bonferroni corrections were applied to the pairwise comparisons of the number of looks, and thus *P* values below 0.017 should be considered statistically significant. In the same experiment, one-tailed tests were used for the pairwise comparison of the different facial expressions with the respective controls and with the average control because we had a clear prior prediction, whereas all other tests were two tailed.

RESULTS

Experiment 1: Monkeys Follow the Gaze of a Human Experimenter

Subjects directed significantly more looks up during the gaze-shift condition than during the look-straight condition (Fig. 2a; paired *t* test: $t_{12} = 8.78$, $P < 0.001$). The

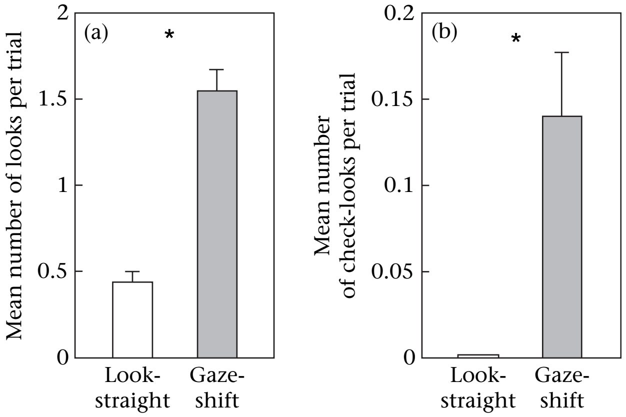

Figure 2. (a) Mean ± SE number of looks up per trial in the look-straight and the gaze-shift conditions. Subjects followed gaze significantly more often when the experimenter shifted her gaze to the ceiling than when she looked straight ahead (*$P < 0.001$). (b) Mean ± SE number of check-looks per trial in the look-straight and the gaze-shift conditions. Subjects performed significantly more check-looks in the gaze-shift than in the look-straight condition: they directed significantly more looks back at the experimenter and up again after having followed her gaze and subsequently looked up again (*$P < 0.01$).

animals followed the experimenter's gaze direction (i.e. looked up) in 90% of the gaze-shift trials, compared to 40% of the control trials. The response to gaze-shifts did not differ significantly between the two sessions (paired t test: $t_{12} = 1.83$, $P > 0.2$), providing no evidence that animals habituated to the experimental procedure. In addition, there were more check-looks (for definition see Methods) in the gaze-shift condition than in the look-straight condition (Fig. 2b; exact Wilcoxon signed-ranks test: $T = 0$, $N = 13$, $P < 0.01$). Eight of 13 individuals engaged in check-looking during at least one gaze-shift trial.

Experiment 2: Gaze Following Is Modulated by Facial Expression

Subjects looked up significantly more often when the experimenter displayed a facial expression than when she looked up with a neutral face (repeated-measures ANOVA: $F_{1,10} = 6.80$, $P < 0.03$). Gaze following was significantly more frequent in response to a signal of fear/submission (Bare Teeth; Fig. 3; paired t test: $t_{10} = 2.54$, $P = 0.014$, one tailed), while gaze-shifts with two other facial expressions did not have a significant effect (Fig. 1, Open Mouth and Lip Smacking). The response to Bare Teeth was also significantly greater than the average response during the combined controls (paired t test: $t_{10} = 2.57$, $P = 0.014$, one tailed; average control: $\overline{X} \pm \mathrm{SE} = 1.09 \pm 0.13$; Bare Teeth: $\overline{X} \pm \mathrm{SE} = 1.38 \pm 0.16$), suggesting that the effect was not due to an especially low response in the Bare Teeth control trials. Subjects had a tendency to check-look more often during gaze-shifts accompanied by a social facial expression than when the experimenter looked up with a neutral face (exact Wilcoxon signed-ranks test: $T = 0$, $N = 11$, $P = 0.12$). There was no decrease in response to the neutral facial expression between the sessions (repeated-measures ANOVA: $F_{5,50} = 0.841$, $P > 0.5$). The number of looks down, recorded as a measure of general gazing activity, did not differ significantly between a gaze-shift accompanied by a facial expression and a neutral face (repeated-measures ANOVA: $F_{1,10} = 0.03$, $P > 0.8$) nor did it significantly differ between the three different facial expressions (repeated-measures ANOVA: $F_{2,20} = 0.48$, $P > 0.6$). We did not find significant differences in scratching rate between any of the social versus neutral faces (exact Friedman's ANOVA: $\chi^2_5 = 3.81$, $P > 0.7$).

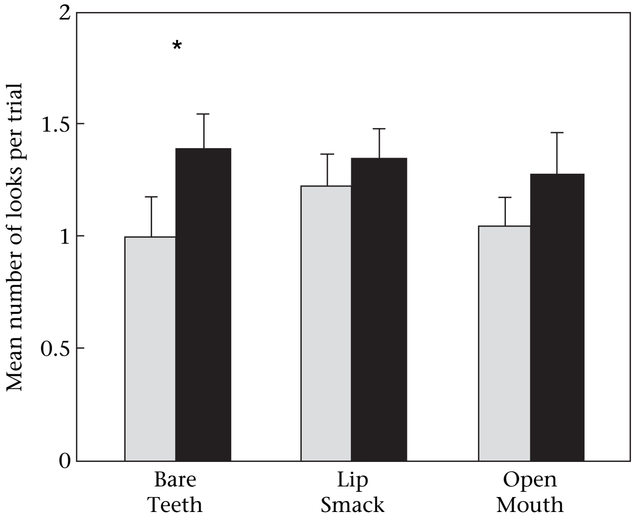

Figure 3. Mean ± SE number of looks up per trial when the experimenter shifted her gaze with a meaningful or a neutral facial expression. Black bars illustrate the response to a gaze-shift accompanied with one of the facial expressions; white bars indicate the levels of response to the neutral face. The subjects directed significantly more looks up when the experimenter's gaze-shift was accompanied by a social facial expression. Post hoc analysis revealed that the gaze-following response to one of the expressions was significantly different from its respective control, namely the Bare Teeth display, which communicates fear and submission of the signaller (*$P < 0.02$).

Experiment 3: There Is No Differential Responsiveness to Neutral and Meaningless Facial Expressions

There was no significant difference between the number of looks up in response to the gaze-shift accompanied by a meaningless or a neutral facial expression (Fig. 4; $t_9 = 1.00$, $P > 0.3$). In addition, there was no difference in response to the neutral facial expression in the two sessions (paired t test: $t_9 = 0.017$, $P > 0.8$).

Change in Responsiveness between Experiments

Over the course of the experiments there was a change in response towards the neutral gaze-shift (repeated-measures ANOVA: $F_{2,18} = 22.40$, $P < 0.001$). Pairwise comparisons revealed that this was due to a decrease in response to the neutral gaze-shift between experiments 1 and 2 ($P < 0.01$).

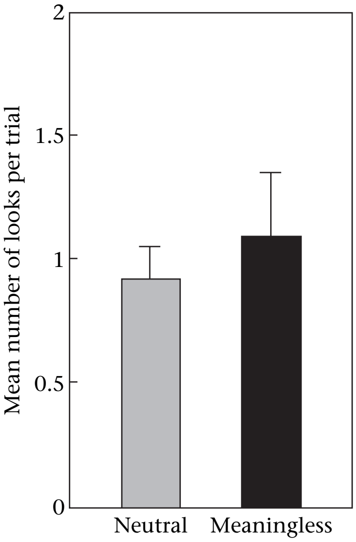

Figure 4. Mean ± SE number of looks per trial when the experimenter displayed a neutral versus a meaningless facial expression. No significant difference between these conditions was found.

However, and of particular relevance to the interpretation of the results, there was no decrease in the number of looks up between experiments 2 and 3 ($P > 0.5$).

DISCUSSION

The monkeys in this study followed the gaze of a human experimenter with frequent check-looks, compared to a control condition in which there was no gaze-shift. In addition, the animals showed stronger gaze-following responses when the human's gaze-shift was accompanied by a social facial expression. Gaze following was significantly more frequent in response to a signal of fear and submission than to a neutral facial expression, whereas gaze-shifts accompanied by two other social expressions or a meaningless facial expression did not have this effect. Thus, gaze following in monkeys was modulated by the outward expression of the emotional state of the signalling individual. Our findings suggest that gaze following is flexibly employed according to the facial expression that is observed.

Additionally, we found that the monkeys frequently looked back at the signalling individual and looked up again (check-looks) during experimenter's gaze-shifts, thereby confirming earlier results on the presence of check-looking in human infants and some nonhuman primate species (Scaife & Bruner 1975; Call et al. 1998; Scerif et al. 2004; Bräuer et al. 2005). Moreover, check-looking responses seemed to be stronger during gaze-shifts accompanied with facial expressions. Check-looking has been proposed to indicate that the gaze-following individual understands that the signaller is seeing something different from itself (Scaife & Bruner 1975; Butterworth & Cochran 1980). Although there are alternative explanations for this behaviour (for instance, a repeatedly triggered gaze-following response) (e.g. Corkum & Moore 1995), it suggests that the gaze-following individual checks back on the demonstrator because it fails to see what the other is seeing (Scaife & Bruner 1975; Butterworth & Cochran 1980).

The effect of a social facial expression on gaze following indicates that the animals may have responded based on the understanding that the experimenter was reacting to something socially relevant and meaningful that the subjects could not see themselves. However, the greater responsiveness to the experimenter's gaze-shift when accompanied by a facial expression (displayed by a human) could also be explained by an elevated general level of attention or arousal. That is, the level of attention or arousal caused by the movement involved in displaying Bare Teeth or the emotional content of this facial expression might have been greater than that for the other facial expressions. However, there are several arguments against this interpretation. First, although pilot studies revealed that monkeys respond appropriately to a human displaying species-specific facial expressions it remains possible that the animals are not able to read the meaning of the facial expression and respond only to the facial movement involved. In that case, Lip Smacking may be expected to elicit the strongest response since it involves repeated lip movements and sounds. We found no indication that this was the case. Second, assuming that the animals recognize the meaning of the facial expression, the highest level of emotional arousal would be expected in response to the aggressive signal (Open Mouth display), which often precedes a physical attack. Although the signal is not directed at the subject, it still indicates a physical conflict in which the subject may become involved. Contrary to this expectation, the gaze-following response to the Open Mouth display was the lowest of all three social expressions. Third, an elevated emotional arousal may result in increased scanning behaviour. As a measure of general gazing and scanning activity we counted the looks down during experimental and control conditions. The number of looks down did not differ significantly between conditions. Moreover, emotional arousal will likely result in elevated anxiety, which can be measured by scratching rates (Pavani et al. 1991; Maestripieri et al. 1992). We found no evidence for differences in anxiety between conditions because scratching rates did not differ between conditions or facial expressions. Fourth, the animals did not respond more strongly to the meaningless facial expression than to the neutral face. Although conclusions drawn from this comparison should be treated with caution because of the low statistical power, the result suggests that the animals do not respond to a face with a random muscular contraction as strongly as they do to a face that mimics a facial expression with which they are familiar and which in this case signals fear and submission of the sender. Together, these arguments suggest that elevated general arousal is unlikely to cause the modulating effect of the Bare Teeth display on gaze-following responses.

Our results conflict with findings in human infants (Flom & Pick 2005). Seven-month-old infants followed gaze less when a facial expression conveying a certain emotion (such as happy or sad) was displayed: infants seemed to pay more attention to the facial expression than to the gazing direction, which the authors interpreted as the infants' inability to understand the referential nature of the mothers' signal (Flom & Pick 2005). Studies on human adults are consistent with our results because adults' responses to averted gazes are stronger with accompanying fearful or angry faces than neutral faces (Holmes et al. 2006; Putman et al. 2006). Yet the response of the macaques in our study contrasts with other findings in macaques that did not show stronger gaze-following responses to displays of affiliation and greeting than to a neutral facial expression (Paukner et al. 2007). This difference may be due to the wider range of emotional facial expressions we employed in this study, including expressions that communicate fear and threat. Our results may suggest that the macaques were responding to the significance of a social event that the experimenter was signalling, in particular during the Bare Teeth display. In interactions with conspecifics, only fearful and threatening events or dominant individuals evoke this display. It seems plausible that the Bare Teeth signal, which indicates a potentially threatening stimulus, elicits stronger responses than affiliative signals, which do not indicate a potential threat (Parr & Hopkins 2000).

Surprising, however, was the finding that the Open Mouth display did not elicit an increase in the gaze-following response because this signal can also indicate a social event that may affect the subject. Signals communicating fear may be more important to an individual than aggressive displays since fear clearly and unmistakably communicates a threat (e.g. the presence of a dominant conspecific) in close proximity. Accordingly, fear in others is a highly salient stimulus facilitating acquisition of knowledge about fearful objects (Olsson & Phelps 2007). A threatening display on the other hand may not directly concern the gaze-following individual itself because it is obviously meant for someone else, most likely a subordinate individual. Therefore the message of this signal may be more ambiguous. Alternatively, individuals of different ranks might be affected differently by facial expressions of aggression and submission, which are used in the establishment and maintenance of the dominance hierarchy. To address this we conducted an exploratory analysis by examining the effect of social dominance rank (categories: high – mid – low; Table 1) on gaze following. Although the small number of subjects limited the possibilities for statistical analysis, we did note apparent differences in responsiveness to gaze-shift with expression according to subject's social rank, particularly in the Open Mouth condition, where high-ranking animals were least responsive and mid-ranking animals most responsive. For high-ranking individuals it may not be relevant whether and to whom subordinate individuals (or individuals outside the hierarchy such as a human) direct an aggressive display. It may, however, be of more interest to mid- or low-ranking individuals because for instance the approach of a threatening animal could have severe consequences for them. The differential response to an agonistic facial expression other than the Bare Teeth display is in line with the recent finding that gaze following is dependent on the social rank of the gazing individual (Shepherd et al. 2006) and moreover strengthens the interpretation that gaze following is flexible and is more than a simple reflex. Further research on social facial expressions, the identity of the signaller and its relationships to the observing individual is required to better understand the influence of rank on the response to a gaze-shift accompanied by facial expressions.

Our findings suggest that longtailed macaques exhibit gaze following in a flexible way. Two possible explanations may account for this: (1) the behaviour may be based on a specific arousal- or attention-based mechanism that enhances gaze-following responses only during the most salient facial expressions (one of which may be Bare Teeth) but does not affect our measures of general visual scanning or anxiety or (2) the behaviour may be based on a voluntary response. The second explanation implies that the monkeys took into account the social event indicated by the experimenter's facial expressions and that gaze-following responses were guided by the knowledge that the other individual was attending to a feared stimulus. Evidence is emerging that monkeys know more about the perceptions of others than previously thought, such as the significance of the eyes in the process of seeing (Perrett & Mistlin 1991; Ferrari et al. 2000) or whether another individual can see or hear them (Flombaum & Santos 2005; Santos et al. 2006). Adding social facial expressions to the study of gaze following may shed light on how animals respond to gazes that convey a meaning, that is, that indicate social events, highly relevant in animal groups with complex relationships. The question of whether gaze following in monkeys is based on a mentalistic understanding of the observing animal about the other's visual target still remains open. None the less, we show that gaze following can be adjusted to the social context in which the gaze-shift takes place. This suggests that gaze following in monkeys is flexibly employed, which, combined with other recent findings, indicates that monkeys' abilities regarding social cognition have been underestimated.

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