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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