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SHORT COMMUNICATION

Do facial gestures, visibility or speed of movement influence gaze following responses in pigtail macaques?

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Abstract This study investigated whether a human model's facial gestures, speed of head turn and visibility of face influenced gaze-following responses (GFR) in pigtail macaques. A human provided gaze cues by turning her head 90° in one of four directions. Head turns were immediately followed by a facial movement (pucker, eyebrow raise, tongue protrusion, neutral), or were executed swiftly (< 0.5 s), slowly (3 s) or whilst facing away from the monkeys. All monkeys reliably followed the gaze in all conditions with no differences between conditions. A greater frequency of GFR was found in females compared to males, and two hypotheses for this finding are discussed.

Keywords Gaze-following · Social cognition · Joint attention · Visual co-orientation · Pigtail macaque · Facial expression

Introduction

Several monkey species reliably follow the gaze of humans (e.g., Anderson and Mitchell 1999; Ferrari et al. 2000) as well as conspecifics (e.g., Tomasello et al. 1998; see also Itakura 2004). It is often claimed that following the gaze of others confers survival advantages such as being able to quickly and efficiently learn about food, predators and conspecifics in the immediate environment. However, monkeys who detect food, predators or conspecifics often do not restrict their behaviour to mere looking. Monkeys frequently react with facial gestures towards objects or events, e.g., fear grimaces towards potential threats or affiliative gestures towards friendly conspecifics. Critically, these facial gestures are directed at the external event, not the onlooking monkey, and they follow a gaze shift instead of preceding it.

In the present study we investigated what effects facial gestures may have on pigtail macaques' (*Macaca nemestrina*) gaze-following responses (GFRs). As in most other simian species, pigtail macaques' social relationships are regulated by facial expressions, e.g., pucker responses and eyebrow raises (Caldecott 1986; Maestripieri 1996). Given their signal function for potentially important events, we hypothesized that GFRs might increase when a model displays such social facial gestures (pucker, eyebrow raise) following a gaze shift compared to neutral and non-meaningful facial gestures (baseline, tongue protrusion; see Table 1). Furthermore, we hypothesized that a rapid change in gaze direction (indicating that something of interest was detected) may be more salient than a slow, gradual gaze shift (which may indicate nonspecific scanning of the environment). The final variable we manipulated was the visibility of the model's face. Monkeys do not always see other individuals face-on, but often detect only partial cues to others' gaze orientation, perhaps even with the eyes not being visible.

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Table 1 Description of all stimulus conditions

Condition	Description
Baseline	The experimenter's head was turned within 1 s, and the facial expression during the fixation remained neutral
Pucker	On completion of the experimenter's head turn, a pucker expression was displayed. A pucker consists of compressed and protruded lips, a raised forehead and eyebrows and is ascribed as an affiliative summoning function in pigtail macaques (Maestripieri 1996)
Eyebrow raise	On completion of the experimenter's head turn, an eyebrow raise expression was displayed. The experimenter's mouth was wide open, and the forehead and eyebrows were retracted. This facial gesture has been interpreted as a greeting display predominantly between adult males, with additional dominance overtones (Maestripieri 1996)
Tongue protrusion	The experimenter's head turn was followed by a protrusion of the tongue. This expression is not used by pigtail macaques as a facial gesture, and served as a control condition
Fast	The experimenter's head turn was executed fast (< 0.5 s), followed by a neutral facial expression
Slow	The experimenter's head turn was executed slowly (3 s), followed by a neutral facial expression
Back	The experimenter sat so that she faced away from the monkeys, and turned her head 45° whilst maintaining a neutral expression. This angle did not allow the monkeys to see the experimenter's eyes or face

We therefore investigated the sensitivity of pigtail macaques' GFRs to a model that faced away from the monkey and offered no eye cues.

Methods

Subjects and housing

The subjects were 10 pigtail macaques (*Macaca nemestrina*), five males (four adult, one sub-adult) and five females (all adult), all captive-born, mother-reared and aged 4—18 years. All monkeys were singly housed (cage measures: 100 × 160 × 100 cm), but had visual and physical contact with monkeys in adjacent cages. They were not food-deprived, and received their normal diet of fresh fruit, vegetables and monkey pellets several hours before the start of the experiment. Water was available ad libitum.

Procedure

In each test session, a female experimenter sat in front of the home cage, looking at the monkey with a neutral facial expression. Once the monkey was oriented towards her, the experimenter turned her head and eyes 90° in one of four directions (up, down, left, right). For trials involving a facial gesture, the gesture was displayed immediately following completion of the head turn. Gaze was held for 3 s before returning to the initial starting position with a neutral facial expression. The next trial started when the monkey reoriented towards the experimenter (resulting in approximately two trials per minute). A video camera positioned behind the experimenter recorded all sessions with both experimenter and monkey in view.

There were seven different conditions: baseline, pucker, eyebrow raise, tongue protrusion, fast, slow and back (described in Table 1). Twelve trials were run for each condition. The order of trials was randomized with two restrictions: gaze cue direction and type of trial could be identical for no more than two consecutive trials. To counter habituation, the monkeys were only tested once a day on up to 10 trials (total number of trials per monkey 84). GFRs were coded from the videotapes, starting when the experimenter initiated the head turn and ending when the experimenter returned to the starting position. The direction of the monkey's first gaze response after visual contact with the experimenter was coded. If the monkey did not look at the experimenter during the trial as determined from the video footage, the trial was re-run at a later session. Twenty percent of sessions were coded a second time to assess intra-observer reliability; codings were identical for 87% of trials, yielding Cohen's kappa of 0.83 ($P < 0.001$).

Results

Following Ferrari et al. (2000), we compared the monkeys' GFR against chance performance (chance = 25% correspondence with experimenter's gaze cues) using binomial tests. The monkeys followed the experimenter's gaze significantly above chance levels in all seven conditions (all $P < 0.001$). Furthermore, there was no correlation between trial position and GFRs, suggesting that the monkeys did not habituate to the gaze cues (rank biserial correlation $r_{pb} = 0.06$, $P > 0.05$). As we could make specific predictions about which conditions were expected to yield increased GFRs, we used paired-sample *t*-tests for the following comparisons: pucker versus baseline, pucker versus tongue, eyebrow versus baseline, eyebrow versus tongue, fast versus baseline, fast versus slow, and back versus baseline. No comparison reached statistical significance using a Bonferroni correction (all $P > 0.05$). To investigate potential sex differences, a repeated measure analysis of variance (ANOVA) with sex as a between-subject factor was run. This analysis revealed that females were more likely than males to follow the experimenter's gaze (on 53.58 versus 44.05% of trials, $F(1, 8) = 5.57, P = 0.046$; see Fig. 1). Nonetheless, when testing males and females separately against chance performance (25% GFR), both sexes scored significantly above chance levels in all conditions (all $P < 0.05$).

In order to determine a potential cause for the lack of effect of the model conditions, we counted the number of trials on which GFR occurred prior to the presentation of a facial gesture. The monkeys saw the facial gesture in only 55.8% of trials for the pucker condition and 63.3% of trials for the eyebrow condition. The percentage of GFRs in these trials was 46.7% for pucker and 35.5% for eyebrow. Comparing the percentage of GFRs when the monkeys saw the facial gesture with the percentage of GFRs when they did not, we failed to find any significant differences (Wilcoxon tests $z = -0.237$ for pucker and $z = -1.486$ for eyebrow, all $P > 0.1$).

Discussion

Pigtail macaques followed the gaze of a human significantly above chance across a range of head and eye movement conditions. Manipulations that we hypothesized might increase GFR (pucker and eyebrow gestures, fast movement) failed to do so when compared to control conditions (baseline, tongue protrusion, slow movement). Potential explanations for this negative result may be that GFRs occurred prior to the facial gesture, or a failure to interpret the facial gestures as

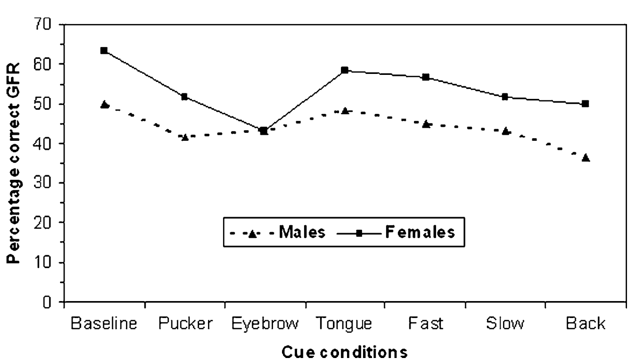

Fig. 1 Distribution of correct GFR across conditions

meaningful. However, the percentage of GFRs did not differ between trials in which the facial gesture was or was not detected. Furthermore, if we displayed facial gestures while directly looking at the monkeys, they often responded with facial expressions, suggesting that these facial movements carry meaning for them (see Ferrari et al. 2003). Neither hypothesis explains the non-impact on GFRs for trials that varied the speed of the gaze cue. It could be argued that failure to provide an external stimulus in the line of the model's gaze might have reduced the probability of GFRs, but as monkeys did not show any change in responsiveness across trials, habituation appears an unlikely cause. Possibly, a conspecific rather than a human may provide a more compelling model, and might yield different results.

The manipulations in the present study were chosen for their ecological validity: a model acts as if she sees something interesting currently out of sight of the subject, and reacts to it. Such events must be common in social situations, and GFRs in response to changes in facial expressions by conspecifics could be advantageous. Facial expressions might theoretically enhance GFRs by either being understood mentalistically (involving an attribution of mental states to the model), or through increased salience without mentalistic implications (see Emery 2000, for a review). Given the importance of eye and face cues for a mentalistic understanding, the results of the back condition, revealing high levels of GFRs despite the absence of face or eye cues, as well as the failure to find any effect of facial expressions and other social variables on GFRs suggests that macaques are extremely sensitive to gaze cues, but also that macaques' GFRs may be based on a non-mentalistic orienting response.

An unexpected result was that female macaques were more likely to follow gaze than males. In human adults, females show more interference from incongruent gaze cues than males, a finding that has been interpreted in terms of heightened automatic processing of social cues in females (Bayliss et al. 2005). One potential explanation for the observed sex difference in pigtail macaques relates to their social organization. Female pigtail macaques form the stable core of a group where they are the main caretakers of their infants; males are more peripheral and, although they may tolerate infants, they rarely interact with them (Caldecott 1986; Whitten 1987). It is the females who protect infants from potential dangers, including other group members. This role might have predisposed females to become more sensitive to gaze cues. Alternatively, factors related to the model might have had a significant impact on GFRs. Monkeys look more at dominant than at subordinate individuals (Chance 1967; McNelis and Boatright-Horowitz 1998), and they might also be more responsive to gaze cues of dominant individuals (Shepherd et al. 2006). Data from monkey-inhabited tourist sites suggest that adult macaques differentiate gender in humans by directing more aggression (bites) towards women rather than men (Fuentes and Gamerl 2005; Fa 1992). These observations are in line with the view that men, but not women, may be perceived as dominant by macaques. We used only one adult female human as a model, and she may have been perceived as dominant by female but not by male monkeys; the latter followed her gaze significantly less. This hypothesis might also explain why we found relatively low GFR scores (48.8% across conditions), compared to a study that used adult male humans as models (65—86% in Ferrari et al. 2000). Future studies might test both these hypotheses directly and detail the effects of dominance status and sex of the model on GFRs in macaques.

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