RESEARCH ARTICLE

Male Long-Tailed Macaques (*Macaca fascicularis*) Understand the Target of Facial Threat

ANNE M. OVERDUIN-DE VRIES[1,2], FREDERIQUE A.A. BAKKER[3], BERRY M. SPRUIJT[2], AND ELISABETH H.M. STERCK[1,2]*
[1]*Animal Science Department, Biomedical Primate Research Center, Rijswijk, The Netherlands*
[2]*Animal Ecology, Utrecht University, The Netherlands*
[3]*Behavioral Biology, Leiden University, The Netherlands*

The cognitive demands of group living have resulted in the development of social competences in a wide range of animal species. Primates are well aware of the complex social structure within their group and infer information about social status by observing interactions of others. A capacity used to infer this information, Visual Perspective Taking (VPT), is present in apes and in monkeys. However, it is unclear whether monkeys really understand that another individual is looking at a specific target. We investigated whether monkeys understand the target of attention of conspecifics using a new paradigm, based on expectancy violation. Subjects were exposed to pictures of scenes involving group members. These pictures either represented congruent (agonistic signals consistent with the dominance hierarchy) or incongruent (signals contradict the dominance hierarchy) social situations. The only difference between scenes concerned the looking direction, that is, the target of attention, and facial expression of the central monkey in the picture. Female subjects did not differ in their looking times to incongruent and congruent scenes, but results may be confounded by their longer looking times at scenes involving kin than non-kin. Male subjects looked significantly longer at incongruent than congruent scenes, suggesting that they understand the target of attention of other individuals. Alternative explanations involving simpler cognitive capacities were excluded. This implies that monkey species share social cognitive capacities underlying VPT with apes and humans. Am. J. Primatol. 78:720–730, 2016.   © 2016 Wiley Periodicals, Inc.

Key words: visual perspective taking; gaze following; social cognition; primate; attention

INTRODUCTION

Many animal species live in large social groups [Alcock, 1993] that provide individual benefits such as allocare [eusocial insects, fish, birds, and mammals: Riedman, 1982; birds: Koenig and Dickinson, 2004], protection against predators [Edmunds, 1974], and collecting resources unavailable to non-social individuals, for example, by cooperative hunting [review: Packer and Rutan, 1988; humans: Alvard, 2003; spiders: Avilés, 1997; Buskirk, 1981; chimpanzees, *Pan troglodytes*: Boesch and Boesch, 1989; African wild dogs, *Lycaon pictus*: Creel and Creel, 1995; spotted hyenas, *Crocuta crocuta*: Mac Donald, 1983; and lions, *Panthera leo*: Scheel and Packer, 1991]. However, living in large groups increases intraspecific foraging competition, and limits access to resources per individual [Altmann, 1974; Caro, 1989; Leighton and Leighton, 1982; Sterck et al., 1997]. In order to maximize the benefits and minimize the costs of group living, animals have developed social strategies that help them to cooperatively achieve common goals [Dugatkin, 2002] or to outcompete their group members [Isbell, 1991].

A common feature minimizing the costs of group living is the establishment of a dominance hierarchy [Hand, 1986; Isbell, 1991], which limits the amount and severity of aggression in the group. Adequate responses to group members prevent injury. Therefore, it is important for a social animal to know its own and its group members' position in

the dominance hierarchy. Indeed, there are indications that animals from a wide range of taxa are well aware of their dominance rank and of the rank of group members. For example, they notice rank reversals in playback experiments [hamadryas baboons, *Papio hamadryas*: Bergman et al., 2003; vervet monkeys, *Chlorocebus aethiops*: Borgeaud et al., 2015; chacma baboons, *P. cynocephalus*: Cheney et al., 1995; ravens, *Corvus corax*: Massen et al., 2014]. Animals learn the dominance hierarchy within their group not only from their own interactions, but also from observing conflicts of (unknown) conspecifics [*Astatotolapia burtuni*: Grosenick et al., 2007; pinyon jays, *Gymnorhinus cyanocephalus*: Paz-y-Mino et al., 2004]. Most of these studies are based on experimentally arranged conflicts between two individuals that are unknown to each other, observed by a third bystander individual [Grosenick et al., 2007; Paz-y-Mino et al., 2004]. However, in real societies, conflicts occur in the presence of other individuals and, in established groups, often involve subtle threat behaviors rather than serious conflicts [Dunbar, 1988; Roseth et al., 2007].

Social strategies such as the establishment of a dominance hierarchy may have selected for specific social cognitive capacities such as Visual Perspective Taking (VPT; understanding what others can see). In order to procure valuable information from subtle threat or submissive behaviors in the social dynamics of animal groups, an observing individual requires the cognitive skill to understand that another individual looks at a specific target. Specific social cognitive capacities, such as Visual Perspective Taking or its constituting parts, may be employed. Understanding the target of attention of others is part of the cognitive capacity VPT. VPT has been tested with several paradigms: for example, gaze following; and a competitive food task with conspecific or human competitors.

Within the gaze following paradigm, individuals co-orient with the gaze direction of others. Gaze following is a widespread naturally occurring behavior [Emery, 2000]. It can result from one of two mechanisms [Brauer et al., 2005]: first, reflexive co-orienting comprising instinctive following of another individual's gaze. Note that no understanding of the target of attention is required. Second it can result from VPT, where individuals voluntarily follow others' gaze, because they know they may see something. Hence, for VPT-based gaze following, individuals have to understand that the gazer has a specific target of attention.

Great apes show VPT [Okamoto-Barth et al., 2007; Shillito et al., 2005] and follow another's gaze past distractors and around barriers [Brauer et al., 2005; Tomasello et al., 1999] implying that they understand the target of attention of conspecifics. They succeed in these tasks, even if they have to move in the opposite direction in comparison with the gaze direction of the demonstrator [Tomasello et al., 1999, wall condition]. Thus, great apes do not simply orient to the location others are oriented to, but actively search for the object that got the attention of the other.

In contrast with earlier studies [Burkart and Heschl, 2006; Cheney and Seyfarth, 1990a; Hare et al., 2003; Kummer et al., 1996; Povinelli et al., 1991 but see Flombaum and Santos, 2005], recent studies on gaze following in monkeys support the VPT model. Monkeys show higher gaze following responses to human demonstrators [Goossens et al., 2008] or conspecifics [Teufel et al., 2010] with facial expressions than with neutral faces. This voluntary co-orienting implies an understanding that demonstrators with facial expressions may see something relevant. Moreover, gaze following depends on the quality of the relationship between a gazing monkey and the gaze follower [Micheletta and Waller, 2012] and on both individuals' dominance rank [Shepherd et al., 2006], confirming flexibility of gaze following. Additionally, monkeys were able to follow a human [Amici et al., 2009] or conspecific's [Goossens et al., 2012] gaze around a barrier and relocate to a position where they could look behind the barrier. This may indicate that the gaze follower understands that the other individual is seeing something that was not visible for the individual itself. However, it is unknown whether they simply move in the direction of gaze of the demonstrator [Amici et al., 2009; Burkart and Heschl, 2006], or whether the movement was caused by limited alternative directions to move in [Goossens et al., 2012]. Moreover, some results [Goossens et al., 2008, 2012; Teufel et al., 2010] may be explained by higher arousal levels in subjects due to the facial expressions of the demonstrators. Although measurements of anxiety and general visual scanning did not reveal any difference between different conditions [Goossens et al., 2008, 2012], this does not exclude that some sort of arousal may have caused a higher level of gaze following [Goossens et al., 2008; Teufel et al., 2010] or a higher chance of passing the barrier [Amici et al., 2009; Goossens et al., 2012]. Additionally, although long-tailed macaques (*Macaca fascicularis*) showed check-looking behavior [Goossens, 2008], repeated looking in the direction of the demonstrator's gaze that is considered an indicator of VPT [Brauer et al., 2005; Call et al., 1998; Scaife and Bruner, 1975; Scerif et al., 2004], this behavior was absent in brown capuchin monkeys (*Cebus apella*) and spider monkeys (*Ateles geoffroyi*) [Amici et al., 2009].

A paradigm that has successfully shown VPT in apes [chimpanzees: Hare et al., 2000], is a setting where a subordinate individual can choose between one food item visible or one invisible for a dominant competitor. Common marmosets (*Callithrix jacchus*)

assigned food as belonging to their opponent when the opponent had gazed at the food, and thus showed no VPT [Burkart and Heschl, 2007]. Similarly, results with brown capuchin monkeys were most consistent with behavior reading [Hare et al., 2003]. This behavior reading is a simpler mechanism than VPT, since this requires the perception of an opponent's gaze cue and an operant conditioned rule. Recently, the paradigm has been successful with long-tailed macaques [Overduin-de Vries et al., 2014]. Subordinate subjects were able to choose the food item invisible for their dominant competitor, despite a one-way mirror that prevented the dominant opponent from giving gaze cues.

Overall, these studies outline that monkeys understand that opaque objects within the line of sight of an opponent give them the opportunity to grab a contested item [Overduin-de Vries et al., 2014] and that a conspecific's gaze may help them find interesting objects [Amici et al., 2009; Goossens et al., 2008, 2012; Teufel et al., 2010]. Nonetheless, a central question remains whether they actually understand that another individual looks at a specific target.

Some evidence that monkeys understand how conspecifics direct their gaze at specific targets comes from a study with Diana monkeys (Cercopithecus diana). Diana monkeys were shown photographed conspecifics with a shifted gaze while a picture of a toy, representing the target of attention, appeared next to the pictured conspecific at a location either compatible or incompatible with the gaze. Subjects re-inspected the picture more often if the target appeared at a location incompatible with the gaze cue [Scerif et al., 2004]. However, an alternative explanation for this result is that in the incompatible situation monkeys experience more difficulty finding the target [cf. Deaner and Platt, 2003] and therefore look more often at other locations, including the conspecific. Therefore, it remains unclear whether monkeys understand the target of attention of others.

We employed a new paradigm to investigate whether macaques understand the target of attention, using the well assessed facts that monkeys know the dominance hierarchy in their social group [long-tailed macaques: Cheney and Seyfarth, 1990b], that they can recognize group members from pictures [rhesus macaques, *Macaca mulatta*: Parr et al., 2000; Silwa et al., 2011; Barbary macaques, *Macaca sylvanus*: Schell et al., 2011; grey-cheeked mangabeys, *Lophocebus albigena*: Bovet and Deputte, 2009; brown capuchin monkeys: Pokorny and De Waal, 2009], that they recognize facial expressions from pictures [crested macaques, *Macaca nigra:* Micheletta et al., 2015] and that agonistic facial expressions in long-tailed macaques are typically unidirectional [van Hooff, 1962], providing information about the target of attention. In this new paradigm, monkeys were shown pictures of social scenes involving three of their group members that were either congruent or incongruent concerning their group's dominance hierarchy. The pictures consisted of three monkeys in a row; the central monkey had a dominance rank in between those of the two flanking monkeys. The facial expression and gaze direction of the central monkey varied. For example, the central monkey looking aggressively at the higher-ranking monkey, representing an incongruent situation, while the central monkey looking aggressively at the lower-ranking monkey is a congruent situation. Since in general unexpected situations increase attention, following expectancy violation [Lewis and Goldberg, 1969], monkeys are expected to look longer at these incongruent than at congruent scenes. The only differences between the pictures are the facial expression and gaze direction, and with that the target of attention of the central monkey. The experiments make use of the expectancy violation paradigm, which predicts that individuals look longer at unexpected (incongruent) than at expected (congruent) situations [Cheney et al., 1995; Kim and Spelke, 1992]. Therefore, we assume that if monkeys look longer at incongruent scenes, they understand the target of attention of the central monkey.

METHODS

Subjects

Long-tailed macaque subjects with ages ranging from 2 to 20 years lived in three different groups: (A) a mixed sex group of 22 individuals; (B) a group of four males; and (C) a mixed sex group of six individuals (Table I), housed at the Biomedical Primate Research Center in The Netherlands. Since subjects participated on a voluntary basis, we tested respectively 15, four and five individuals. The three groups were formed from one social group for management reasons. From June 30, 2009 group B was split off from group A; on May 10, 2010, one individual was removed from group A; and from October 08, 2010 group C was split off from group A. Some individuals in group A and C were tested both before and after the group splitting. After the split, 21 subjects received pictures of current group members, while three individuals did not return in a social group, and received pictures of former group members. The groups consisted of five matrilines, we considered animals that are descendants up to the fourth generation (great grand children) of the one founding female to form one matriline.

This research was approved by the Animal Ethical Committee of the Biomedical Primate Research Center (DEC#628) and complies with the Dutch legal requirements. The research adhered to the American Society of Primatologists principles for the ethical treatment of primates.

TABLE I. Test Subjects, Their Dominance Rank, Sex, and Age at the Start of the First Experiment

Group/monkey	Rank	Sex	Age (years)	Bared-teeth experiment (N sets)	Open-mouth experiment (N sets)
Group A					
Regilio	1 (1)	M	15, 2	3	2
Annika	3 (5)	F	5, 4	3	2
Kraa	4 (2)	F	19, 5	3	2
Salsaa	6 (12)	F	11, 4	1	2
Caya	8 (13)	F	12, 9	1	0
Cordoba	9 (15)	F	5, 8	4	3
Alfaa	- (3)	F	23, 1	2	–
Rastafa	- (8)	F	15, 4	3	–
Santiago	- (21)	M	6, 3	3	–
Plopsa	?	F	2, 6	2	3
Metallica	?	F	1, 7	2	2
Nirgendwo	?	M	2, 6	2	2
Bonobo	- (?)	M	6, 4	3	3
Inlimbo	- (?)	M	8, 1	3	3
Rijstevla	?	F	2, 5	1	2
Group B					
Just-so	1	M	6, 8	1	1
Tabasco	2	M	6, 7	1	1
Tonko	3	M	8, 6	1	1
Burkina-faso	4	M	5, 8	1	1
Group C					
Ontarijo	1 (7)	M	7, 5	2	–
Tres-bella	2 (10)	F	10, 2	4	1
Latifa	3 (11)	F	15, 1	2	1
Mega	4 (19)	F	9, 1	2	1
Risotto	?	M	2, 3	3	3

The dominance rank ranged from 1 (the most dominant individual) to 11 (group A) or 4 (group B and C). For individuals from group A and C their rank before the group split is given in brackets. The rank of juveniles was unknown, since their hierarchical position in the group was not stable. The ranks of bonobo and inlimbo were unknown since they left the group before the dominance hierarchy was determined.

Hierarchy

Prior to testing, the dominance hierarchy of each group was established by calculating Landau's modified h [de Vries, 1998; Schmid and de Vries, 2013] on the basis of a matrix of submissive signals [Overduin-de Vries et al., 2012]. Because of the high number of inconsistencies for juveniles, their dominance ranks were unreliable and we excluded pictures of juveniles (<3 years) from the stimuli. In group A, the adults' dominance hierarchy was significantly linear ($h' = 0.95$, $P < 0.0001$). The dominance hierarchy of group B and C was linear, but this was not significant due to the small group size (group B: $h' = 1$, $P = 0.38$; group C: $h' = 1$, $P = 0.39$). However, since at least seven interactions per dyad were observed with no inconsistencies, we assume linearity.

Experiments

Two experiments were run: "the Bared-teeth experiment" and "the Open-mouth experiment." They had the same procedure, but differed in the stimuli used. The Bared-teeth experiment tested whether monkeys recognize the incongruity of a dominant individual giving a submissive (bared-teeth) display towards a subordinate individual. The Open-mouth experiment tested whether monkeys recognize the incongruity of a subordinate individual giving a threatening (open-mouth) display towards a dominant individual.

Testing Procedures

The test room ($10 \, \text{m}^2$) was part of their home cage with a sawdust bedding and wire mesh partition, which could be closed off from the rest of the cage. After a subject entered the test room on a voluntary basis, it was encouraged to sit in front of the screen (HP Compaq, 19 inches) with a reward. Subsequently, a trial commenced by simultaneously playing a trivial sound, to attract the attention of the monkey to the screen, and showing a picture on the screen. The picture remained visible for 1 min. The subject's responses were recorded with two video cameras (Sony, DCR-SR72): one handheld camera following the subject, the other mounted on a tripod continuously focusing on the area in front of the television.

On a test day, the subject monkey was shown only one picture. If the subject failed to look at the screen during picture exposure, it was cued back in front of the television and the same picture was shown again. If a monkey did not look at the picture after three trials, it received the same picture the next day. Once the subject had looked at a picture, that picture was never shown to that subject again.

Test Stimuli

The pictures were constructed using Photoshop (version CS2) and displayed three monkeys in a row, which were (former) group members of the subject monkey. Each of the pictured monkeys measured approximately 5.5×3 inches on the screen. The central monkey had a dominance rank in between those of the flanking monkeys. All pictures had their outdoor cage as a background, suggesting that the three individuals were together in the same environment. By varying the facial expression and looking direction of the central monkey, a four-picture-set was created (Fig. 1). In each experiment, subjects received one to three different four-picture-sets (Table I) (each subject saw in each experiment 4, 8, or 12 different pictures). The order of picture exposure within a four-picture set was randomized, but different four-picture sets were not mixed. Within each four-picture-set, the appearance of the flanking monkeys and the body of the central monkey were identical. The central monkey's head with a neutral or agonistic facial expression originated from a different photograph than its body. The central monkey directed its gaze either to the right or to the left, by randomly using mirrored images, balancing the proportion of mirrored images between conditions. The identity of the central monkey always differed between four-picture sets shown to one subject, and the flanking monkeys were changed as much as possible (i.e., in both the Bared-teeth and Open-mouth experiment, only two subjects saw scenes containing one of the flanking monkeys that they had seen in another configuration). Stimuli monkeys were both male and female monkeys. We had 38 unique four-picture sets (Bared-teeth experiment: $N = 23$, Open-mouth experiment: $N = 15$), which could share one or two of the monkeys in the picture, but at least one of the monkeys was different.

The Bared-teeth experiment was conducted between March 4, 2010 and May 25, 2010 and between February 8, 2011, and April 26, 2011. The Open-mouth experiment was conducted between February 16, 2011 and May 6, 2011. Subjects first completed the Bared-teeth experiment before starting with the Open-mouth experiment. The facial expression of the central monkey in the Bared-teeth experiment was either a neutral face or submissive bared-teeth display. Stimuli in the Open-mouth experiment were similar to those used in the Bared-teeth experiment, but showed a neutral face and a threatening open-mouth display (Fig. 1).

Data Analyzes

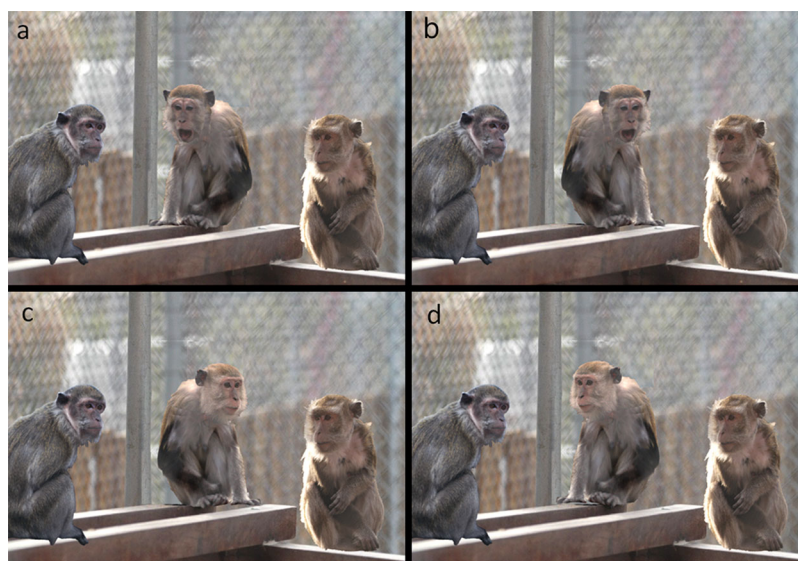The video recordings conveyed 25 frames per second. Looking times were measured by counting

Fig. 1. One example of a four-picture set used in the Open-mouth experiment: (**a**) open-mouth display towards dominant; (**b**) open-mouth display towards subordinate; (**c**) neutral face directed towards subordinate; and (**d**) neutral face directed towards dominant. Original stimuli were randomly mirrored.

the number of frames a monkey was looking at the screen during the total 60 sec that the stimulus was presented. The scoring observer was blind to the stimuli presented to the subject.

The response of each individual was calculated by subtracting the mean looking time for congruent scenes from the mean looking time at incongruent scenes.

The main test of this study was whether the subject's expectancy was violated when confronted with incongruent scenes. We used R [R-Core-Team, 2014] and lme4 [Bates et al., 2012] to perform a linear mixed effects analysis (using the lmer function) of the relation between the incongruence of a picture (i.e., experimental condition) and the time monkeys spent looking at it (lookingtime). As dependent variable we entered the time a subject spent looking at the picture. Fixed and random effects were added to the model based on their assumed contribution to variance in the data. Fixed effects were the experimental condition (congruent versus incongruent pictures), sex of the subject (male or female), and kinship (whether the central

pictured individual was from the same matriline as the subject yes or no). Random effects included random intercepts for subjects ($N = 24$), gaze accuracy (how well the central individual on the picture gazed at one of the flanking monkeys, $N = 7$ degrees of accuracy), and rank difference (the mean difference in dominance rank between the central individual on the picture and both flanking monkeys, $N = 9$ degrees of rank difference), as well as by-subject random slopes for the effect of condition on looking time. We allowed random slopes, because we expect individuals to react differently to the experimental conditions. This resulted in the following model: lookingtime $\sim$ experimental condition + sex + kinship + (1 + condition + sex|subject) + (1|gaze accuracy) + (1|rank difference). Visual inspection of residual plots revealed that for the Bared teeth experiment these deviated from normality and homoscedasticity. Therefore, we log transformed the lookingtimes. Inspection of the residuals from this same model with LOG (lookingtime) as dependent variable revealed that now the residuals hardly deviated from normality

TABLE II. Impact of Experimental Condition on Looking Time

Bared-teeth experiment, males and females

Fixed effects	$\beta \pm SE$	X2	df	P
Condition	0.07 ± 0.15	0.21	1	0.644
Kinship	0.21 ± 0.22	0.83	1	0.363
Sex	-0.01 ± 0.22	0.00	1	0.952
Random effects	Variance $\pm SE$			
Subject (random intercepts)	0.10 ± 0.31	0.91	2	0.633
Subject (random slopes for condition)	0.00 ± 0.04	0.04	2	0.980
Gaze accuracy (random intercepts)	0.00 ± 0.00	0.00	1	1
Rank difference (random intercepts)	0.02 ± 0.14	0.10	1	0.753

Open-mouth experiment, males

Fixed effects	$\beta \pm SE$	X2	df	P
Condition	-70 ± 27	5.17	1	0.023
Kinship	3 ± 24	0.01	1	0.911
Random effects	Variance $\pm SE$			
Subject (random intercepts)	34243 ± 185	8.18	2	0.017
Subject (random slopes for condition)	4402 ± 66	1.79	2	0.413
Gaze accuracy (random intercepts)	1979 ± 44	2.82	1	0.093
Rank difference (random intercepts)	0 ± 0	0	1	1

Open-mouth experiment, females

Fixed effects	$\beta \pm SE$	X2	df	P
Condition	64 ± 34	0	1	1
Kinship	14 ± 35	0.15	1	0.697
Random effects	Variance $\pm SE$			
Subject (random intercepts)	6957 ± 83	2.01	2	0.366
Subject (random slopes for condition)	5211 ± 72	2.23	2	0.328
Gaze accuracy (random intercepts)	0 ± 0	0	1	1
Rank difference (random intercepts)	0 ± 0	0	1	1

Effect values for all random and fixed factors in the GLMM were obtained by means of a likelihood ratio test where we compared the full model with the model in which this effect was removed. The dependent variable for the bared-teeth experiment was looking time (in number of counted video frames) and for the open-mouth experiment log (looking time).

and homoscedasticity. For the Open mouth experiment visual inspection of residual plots did not reveal any obvious deviations from normality or homogeneity. For each of the effects we obtained its *P*-value by means of a likelihood ratio test, using the anova function, where we compared the full model with the model in which this effect was removed.

RESULTS

Bared-Teeth Experiment

In the Bared-teeth experiment, pictures were shown of congruent and incongruent submissive displays. There was no significant difference in looking time between congruent and incongruent pictures (GLMM: $X2 = 0.21$, df $= 1$, $P = 0.64$) (Table II) (Fig. 2). No effect of kinship, gaze accuracy, or rank was found (Table II). There was no significant difference in looking time between both control pictures (GLMM: $X2 = 0.77$, df $= 1$, $P = 0.38$).

Open-Mouth Experiment

In the Open-mouth experiment, pictures were shown of congruent and incongruent threat displays. There was a significant interaction effect between sex and the experimental condition (GLMM: $X2 = 7.71$, df $= 1$, $P = 0.005^{**}$). Therefore, both sexes were analyzed separately. Males significantly looked longer at incongruent pictures than at congruent pictures (GLMM: $X2 = 5.17$, df $= 1$, $P = 0.023^*$ (Table II) (Fig. 3)). Incongruency increased looking times by about 2.80 ± 1.10 seconds. No difference was found for females ($X2 = 0$, df $= 1$, $P = 1$) (Table II) (Fig. 3). No effect of kinship, gaze accuracy or rank

was found for either sex (Table II). There was no significant difference in looking time between both control pictures (GLMM: $X2 = 2.11$, df $= 1$, $P = 0.15$).

DISCUSSION

With a new expectancy violation paradigm we investigated whether long-tailed macaques can assess the target of attention of monkeys in pictured social scenes, a capacity underlying Visual Perspective Taking (VPT). Our results indicate that male monkeys look longer at pictured monkeys in incongruent threat scenes than those in congruent scenes. This shows that they understand the incongruity of the target of the facial threat and that they thus perceive the difference in looking direction, and may understand the target of attention of the central monkey. However, since results were not uniform, neither for the two tested facial expressions nor for the two sexes, they need further discussion.

In the Bared-teeth experiment subject monkeys did not discriminate between congruent and incongruent submissive interactions. This was not expected, because bared-teeth displays are highly unidirectional in this species [van Hooff, 1962]. In a similar long-tailed macaque group of our colony the bared-teeth display was observed within 195 dyads, and only in one of these dyads the display was exchanged in both directions [Preuschoft, 1995]. The absence of an effect in our Bared-teeth experiment cannot be explained by a general disinterest in submissive interactions, because bared-teeth displays increase gaze following behavior in this species, whereas open-mouth displays do not [Goossens et al., 2008]. An alternative explanation may be found in the consequences for the audience of
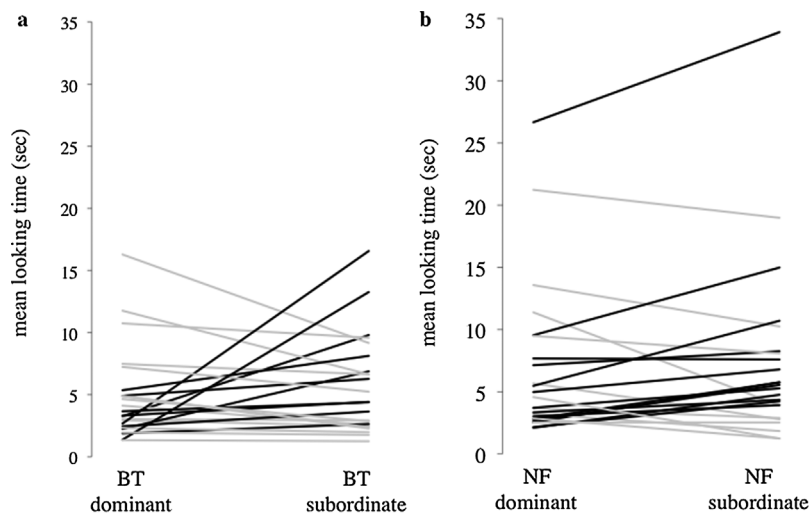

Fig. 2. Looking times in the Bared-teeth experiment: (**a**) the congruent, bared-teeth display toward dominant (BT dominant) and incongruent, bared-teeth display toward subordinate (BT subordinate) condition and (**b**) both control image conditions (Neutral face (NF) towards dominant or subordinate). Separate lines correspond to the responses of individual macaques. Black lines indicate macaques that responded in correspondence with expectancy violation, whereas grey lines indicate contradictive responses.
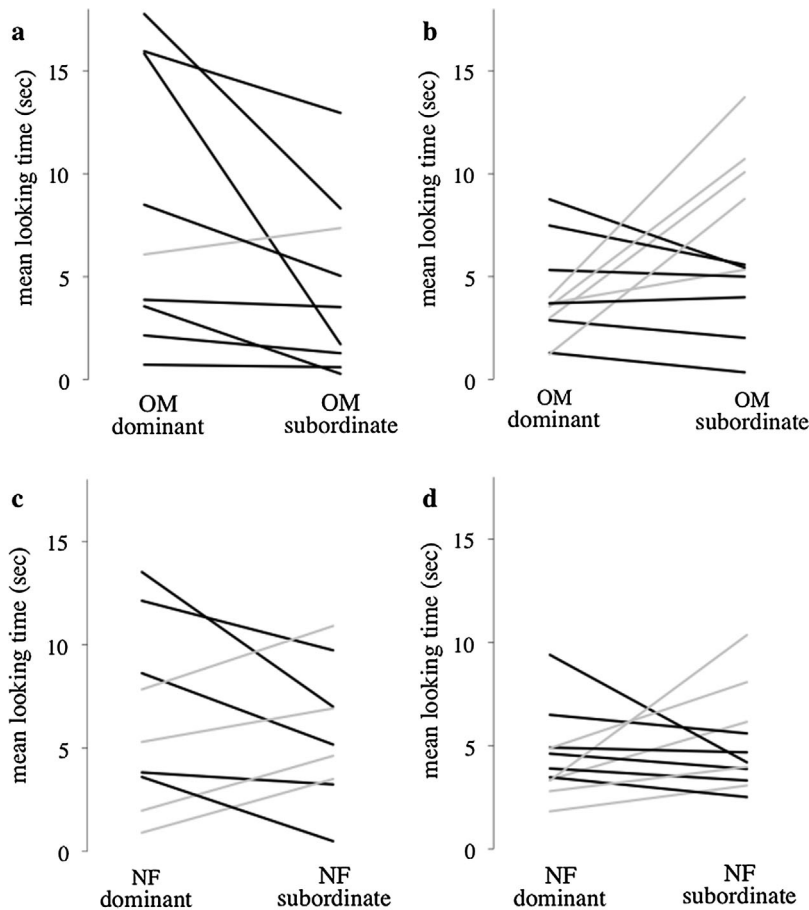
Fig. 3. Looking times in the Open-mouth experiment. The separate graphs represent male (**a**) and female (**b**) responses to the incongruent (OM dominant) and congruent (OM subordinate) scenes. Additionally, male (**c**) and female (**d**) responses to both control images, a neutral face (NF) towards dominant and subordinate, are given. See for explanation of lines the legend of Figure 2.

an incongruous behavior. Although rank-reversals are considered relevant [e.g., Bergman et al., 2003], third parties may be particularly interested when these are expressed in aggression, as exemplified by the open-mouth threat in our experiment or the vocally mimicked fights in hamadryas baboons [Bergman et al., 2003], since they may involuntary get involved. A submissive bared-teeth display directed at a subordinate, although indicating a rank reversal, is possibly not directly threatening. This suggests that not all signals used in a social interaction are equally important for third parties. To our knowledge, this is the first experiment using stimuli with rank reversed submissive signals in the absence of threat signals. Therefore, it would be interesting to further investigate how much animals pay attention to rank reversals expressed in submissive signals.

In the Open-mouth experiment, we found a significant difference in response between male and female subjects. Whereas males showed more interest in incongruent than congruent threat scenes, females did not. The absence of an effect in

females is against our expectations. First, females should be equally interested in agonistic scenes. In our test, no significant difference in the time spent looking at the picture was found between male and female subjects for the congruent Open-mouth stimuli (Wilcoxon rank sum test: $U = 66$, $N_1 = 9$, $N_2 = 11$, $P = 0.2299$). Therefore, females compared to males did not walk away or look away more often before assessing the pictured scene properly. This is consistent with the involvement of long-tailed macaque females in aggressive behavior [Sterck and Steenbeek, 1997] and the sex independent involvement in aggression by macaques [rhesus macaques: Reinhardt, 1987]. Second, females were not more distracted during picture exposure than males. We checked this by looking at the general noise value in the female data, which could have been increased by distraction of subjects. The absolute difference in looking time between the two control images for each individual, a measure of noise, did not differ significantly between males and females (Wilcoxon rank sum test: $W = 34.5$, $N = 9,11$, $P = 0.27$). Third, female monkeys should be able to

understand the incongruity of agonistic scenes. For example, baboon females have increased interest in playbacks of fight sequences involving incongruent than congruent call sequences [Bergman et al., 2003]. Moreover, in vervet monkeys, females are even more sensitive to rank reversals than males [Borgeaud et al., 2015]. Long tailed macaque females, like vervet females, are the philopatric sex [van Noordwijk and van Schaik, 1985] and are thus expected to have advanced developed skills for attaining social knowledge. Finally, variation in female responses may be due to the identity of the pictured animals. Although no significant effect of kinship was found in the GLMM, the central monkey was more often kin of female than of male subjects and this may have caused noise in the data. Additionally, the attention of macaque males, like that of human males, may not depend on the kinship of the gazer, while for human females it does [Deaner et al., 2007]. Therefore, future studies should take the relationship between the subject and the pictured monkeys into account.

In contrast with females, the results for males in the Open-mouth experiment may indicate an understanding of the target of attention in the pictured social scenes. Several alternative explanations involving cognitive capacities simpler than VPT for this result can be precluded, because of the configuration of our stimulus pictures and the controls. First, in natural aggressive interactions, dominant individuals are often in proximity of a subordinate, and thus it could be argued that associative learning took place. However, within our stimuli pictures, the proximity of a dominant or subordinate to a threatening monkey did not differ between picture conditions, and, therefore, could not be used by the subjects to discriminate between pictures. Second, the results cannot be explained by a higher interest of subjects in pictures where the central monkey is gazing at the dominant than where it is gazing at the subordinate, since subjects were not more interested in control pictures with neutral gazes at the dominant than at the subordinate. Third, since both congruent and incongruent scenes show an agonistic facial display, differences in arousal cannot be explained by the facial expression alone. Moreover, if arousal was higher due to the incongruity, this would actually show that they understand the target of attention. In conclusion, the most plausible explanation of our results is that male subjects may understand the target of attention of a pictured conspecific.

Understanding the target of attention of conspecifics is crucial for higher level visual perspective taking. Great apes show an understanding of the target of attention of conspecific when they follow another's gaze past distractors, not simply orienting to objects others are oriented to, but actively searching for the object that got the attention of the other [Tomasello et al., 1999, wall condition]. The current study suggests that understanding the target of attention of conspecifics is a conserved primate feature that great apes share with monkeys. Although additional research with other species is required to confirm this proposition, these results, in combination with the earlier studies on monkeys [Amici et al., 2009; Flombaum and Santos, 2005; Goossens et al., 2008, 2012; Overduin-de Vries et al., 2014; Scerif et al., 2004; Teufel et al., 2010], imply that monkey species share high-level cognitive capacities underlying VPT with apes and humans.

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