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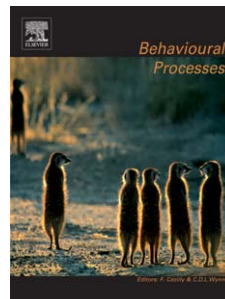
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1 **Pictorial gaze cues do not enhance long tailed macaques' performance on a computerised**
2 **object-location task**

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11 **Abstract**

12 The perception of pictorial gaze cues was examined in long-tailed macaques (Macaca
13 fascicularis). A computerised object location task was used to explore whether the monkeys
14 would show faster response time to locate a target when its appearance was preceded with
15 congruent as opposed to incongruent gaze cues. Despite existing evidence that macaques
16 preferentially attend to the eyes in facial images and also visually orient with depicted gaze
17 cues, the monkeys did not show faster response times on congruent trials either in response to
18 schematic or photographic stimuli. These findings coincide with those reported for baboons
19 testing with a similar paradigm in which gaze cues preceded a target identification task (Fagot
20 and Deruelle 2002). When tested with either pictorial stimuli or interactants, non human
21 primates readily follow gaze but do not seem to use this mechanism to identify a target object;
22 there seems to be some mismatch in performance between attentional changes and manual
23 responses to gaze cues on ostensibly similar tasks.

24 **Keywords:** nonhuman primate, gaze following, object-choice task, cueing.

1 **Introduction**

2 The study of gaze understanding in nonhuman primates has been assessed using two basic
3 methodologies: a gaze following paradigm, in which the respondent visually co-oriens with a
4 model's gaze (Itakura, 1996), and various object-choice tasks which require the animal to select
5 an object on the basis of gaze cues (Anderson et al. 1995). These two approaches have revealed
6 what has been described as a 'functional dissociation' (Gomez 2005); primates readily gaze
7 follow of both humans and conspecifics (Tomasello et al, 1998) but successful performance on
8 object-choice tasks is less consistent and may require learning over a number of sessions (e.g.
9 Vick and Anderson 2000)¹. There is apparently some divergence between knowledge and
10 action as measured by the dependent variables of visual attention and manual responses,
11 respectively.

12 Several species of nonhuman primates have been shown to change their visual
13 orientation to track a human interactant's head and eye direction or eye gaze alone (Ferrari et
14 al. 2000; Okamoto et al. 2002; Tomasello et al, 1999). Similar studies which have used live
15 conspecific models are largely unable to control which cues are present or attended to so that it
16 is unclear which factors (such as bodily orientation and head direction) influence responses
17 (Tomasello et al. 1998). As conspecific cues are difficult to vary systematically, studies have
18 also used photographic images rather than interactants and have reported clear evidence for
19 visual co-orientation (Deaner and Platt 2003; Emery et al. 1997; Lorincz et al. 1999; Scerif et
20 al. 2004; Shepherd, Deaner and Platt, 2006). In addition, presenting video or photographic
21 stimuli may allow more control over timing and cues, while removing any social constraints
22 upon interactions with either humans or conspecifics (Fagot and Deruelle 2002). Although
23 there is still debate regarding the understanding of pictorial representations in nonhumans
24 (Bovet and Vauclair 2000; Martin-Malivel and Fagot 2001; Pascalis et al. 1999), it is clear that

1 both video and static images are valuable in the study of social cognition in monkeys
2 (Capitanio 2002; Dasser 1987; Kyes et al. 1992).

3 There are consistent patterns in terms of how monkeys look at images of faces;
4 macaques reliably allocate most attention to the eyes, even when images were inverted or
5 scrambled (Guo et al. 2003). Moreover, this same basic pattern is found, in terms of viewing
6 time, number of fixations, and other temporal and spatial characteristics, whether the facial
7 stimuli presented is conspecific, chimpanzee, human or even simple schematic images (Keating
8 and Keating 1982; Gothard et al. 2004; Guo et al. 2003; Sato & Nakamura, 2001). Human
9 facial images have sometimes been used in gaze studies as cues may be more readily controlled
10 (Fagot and Deruelle 2002; Vick et al 2001). To date, very few studies using conspecific stimuli
11 have manipulated both head and eye direction; using scanning patterns as a measure, rhesus
12 macaques have been shown to respond to both head and eye direction alone by shifting
13 attention to a congruent quadrant of space (Lorincz et al 1999). Deaner and Platt (2003) also
14 found that non-predictive head and eye-gaze cues enhanced gaze shifts to detect peripheral
15 targets by rhesus monkeys (and humans tested within the same paradigm).

16 While monkeys readily co-orient and visually inspect cued locations, the attention to the
17 target object itself appears ambiguous at best. Emery et al (1997) demonstrated that objects
18 which appeared in a location congruent with depicted visual attention were inspected more than
19 identical distractors. However, most attention was directed at central monkey image prior to
20 object appearance and there was no significant difference between target and distractor when
21 only these remained on screen. Similar results with Diana monkeys also show coorientation to
22 a spatial location congruent with the gaze direction of a photographed conspecific, in terms of
23 significantly more first looks, and more frequent and longer visual inspections. However,
24 attention to target and anti-target locations *following* the appearance of the object itself was not

¹ While success is more readily found with competitive paradigms that require non-attended items to be selected (Flombaum and Santos, 2005; Hare et al, 2000; 2001; Vick and Anderson, 2003), the nature of the relationship

1 reported; thus, it impossible to ascertain the relationship between gaze following and
2 subsequent levels of interest in the target rather than just the cued location (Scerif et al. 2004).

3 Measurement of eye movement and other forms of visual co-orientation can certainly
4 inform about nonhuman primates' responses to gaze as a social signal, but the absence of any
5 subsequent response to targets means that it is difficult to assess how attention shifts are
6 translated into action. Moreover, the timing of both independent and dependent variables differ
7 in gaze following and object choice approaches. Object choice studies typically involve
8 presenting a cue for a few seconds to ensure that the subject has time to attend, but even
9 relatively brief delays between cue and response is detrimental to chimpanzee performance
10 (Barth et al. 2004). In comparison, studies using visual fixations as a dependent measure have
11 shown effects within a few seconds and even at first fixation (e.g. Deaner and Platt 2003; Scerif
12 et al. 2004). It may be that temporal contiguity of target and cue is crucial as attention shifts
13 occur rapidly and then quickly dissipate.

14 One way to examine whether manual responses or timing are detrimental to object-
15 choice performance is to modify procedures in order to make the gaze following and object
16 response tasks more comparable. Only one study to date has combined pictorial gaze stimuli
17 with a manual response, rather than measuring visual scan patterns alone. The impact of
18 schematic and photographic (human) gaze cues upon accuracy and response times was
19 examined in baboons using a joystick to respond on a go no-go target identification task (Fagot
20 and Deruelle, 2002). This approach resembles the object choice task in terms of gaze cues
21 preceding a manual response, but also allows more subtle differential effects of cue type on
22 reaction times (RTs) to be measured. Moreover, the presentation of gaze cues was much briefer
23 than in traditional manual response tasks with the delay between the appearance of cue and

between competitive tasks and a tendency to co-orient with others is less clear.

1 target, or stimulus onset asynchrony (SOA), being 300ms.² However, Fagot and Deruelle
2 (2002) found that targets were not detected more accurately or more rapidly when preceded
3 with congruent as opposed to incongruent gaze cues.

4 The current study aims to further explore this type of cueing paradigm by examining the
5 relationship between gaze cues and manual responses in long-tailed macaques. Firstly, the only
6 cue presented by Fagot and Deruelle was eye gaze, but a fuller exploration considering a
7 variety of attention cues and their interactions is warranted (Langton 2000; Lorincz et al. 1999;
8 Perrett and Emery 1994). The present study therefore presents a variety of head and eye
9 direction cues to examine the relative influence of these information sources. Schematic faces
10 and matched scrambled control images were also presented to examine the basic features that
11 might affect responses, such as face-like configuration and overall perceptual asymmetry of
12 stimuli (Quadflieg, Mason & Macrae 2004). Secondly, the current study uses a wider range of
13 SOAs to explore more systematically the issue of timing of cues and responses (drawing upon
14 human literature on reflexive gaze following, see also Deaner and Platt 2003). Thirdly, whereas
15 the baboons were tested within a pre-learned go-no go joystick task which required object
16 discrimination (Fagot and Deruelle 2002); we used a less cognitively demanding and more
17 strictly spatially based task requiring a response directly to the target location using a touch-
18 screen. If target location is facilitated by co-orientation we should see faster reaction times to
19 congruent than incongruent targets, and this pattern may vary systematically with differing cue-
20 target timings (Deaner and Platt 2003).

21 **Materials and Methods**

22 **Subjects**

²SOA later modified to 800ms, the cue-target distance was also reduced and the baboons were trained to attend to the central area of the monitor but these changes had no impact on the results obtained.

1 The monkeys tested were 9 long-tailed macaques (Macaca fascicularis: 8 females and 1 male,
2 age range 9-26 years, mean age 14.6 years) housed in a large social group (46 individuals) at
3 the Ethology Station, University of Utrecht, The Netherlands. The group had access to a large
4 indoor/outdoor enclosure (80m²) but could be isolated in a smaller indoor experimental area
5 (0.5m x 1.2m) for testing, while maintaining auditory and limited visual contact with their
6 group. The monkeys were fed twice daily with commercial monkey pellets and twice a week
7 this was supplemented with fruit or vegetables and grain. Treats such as nuts, raisins and cereal
8 were used as reinforcers during testing.

9

10 **Apparatus**

11 A 14-inch (640 x 480 pixels) Apple Macintosh monitor was secured in front of an opening in
12 the mesh of the test area. The monitor was fitted with a Micro-Touch touch-screen and was
13 connected to an Apple Macintosh computer which controlled presentation of trials and recorded
14 responses using Authorware Professional software. Correct responses were rewarded with food
15 items (grain and raisins) delivered by a Universal Feeder (G5912 Gebrands Corporation) that
16 was connected to the computer. A video camera was secured above the test area so that the
17 experimenter could monitor the monkeys' general behaviours as they performed the task.

18

19 **Procedure**

20 **Training**

21 The monkeys had previously been trained and tested on delayed non match to sample tasks
22 using the touch-screen (Veenema, 1998). The monkeys were re-familiarised firstly to the
23 experimental area and subsequently to the apparatus. Once the monkeys reliably responded to
24 the touch-screen and could be readily separated from the group for at least 10 minutes, testing
25 commenced.

1 **Testing**

2 Once a monkey had entered the test area, they were separated from the rest of the group using a
3 sliding partition. The computer program was then initiated and the experimenter observed the
4 session from an adjacent room via the video link. The monkey remained in the test area until a
5 maximum of 50 trials had been presented or 25 minutes had elapsed. If the monkey ceased
6 responding for over 3 minutes or was became distressed (for example, when group fights broke
7 out in the adjacent enclosure), the session was terminated and the monkey was released back
8 into the group. As entry into the testing area was voluntary, not all animals were tested on all
9 days (data from additional subjects completing only a few sessions each were excluded from
10 analysis). Subjects were tested with a schematic stimulus set for 5 weeks and with photographic
11 images for the following 4 weeks; order of presentation was not counterbalanced due to the
12 group testing situation.

13

14 **Stimuli**

15 Schematic faces: these were line drawings (150 x 150 pixels) of faces and scrambled faces.
16 Pupils appeared positioned in one of five locations: up, down, left, right or central (a neutral
17 condition which offered no directional cue towards peripheral locations) relative to the centre
18 point of the face (depicted by the nose). Photographs: these were colour images (150 x 150
19 pixels) of a human female with variations in head and eye direction. In this set, the face cued
20 only along the horizontal axis, e.g. head and/or eyes to the right/left. Any asymmetry in the
21 photographs was accommodated by using reversed right images to create left images (see
22 Scerif et al 2004). There were three variations of cue available: congruent head and eye cue
23 with the head turned in full profile to left or right, eyes only directed to either the left or right or
24 displaying direct gaze, and half-profile images in which the head was turned 30 degrees from
25 centre with eyes either congruent with head turn or fixated centrally (direct gaze).

1

2 **The task**

3 Following a 30-second delay during which the monitor was uniformly black, a
4 schematic face or control (scrambled face) stimulus appeared; the monkey touching this central
5 stimulus initiated the trial. After a 500msec delay, pupils appeared in the face or control image.
6 Following another delay of 100ms, 300ms or 1000ms (stimulus onset asynchrony: SOA) the
7 central image was removed and a target square (100 x 100 pixels) appeared in one of the four
8 locations (up, down, left, right). Figure 1 shows an example of a presentation sequence. For the
9 photograph stimulus set the pre-trial stimulus was modified; a white square that appeared in the
10 centre of the screen was used. The square disappeared when touched and the trial commenced
11 with the stimulus photograph appearing in the centre of the screen after a 500ms delay (see
12 Figure 2).

13 Each cue type for both stimulus sets was presented as congruent and incongruent (i.e.
14 cues were non-predictive) with the subsequent target at each of the three SOAs. For the
15 schematic images, the trials varied according to four factors: Stimulus type (Face and Control),
16 timing of SOA (100ms, 300ms and 1000ms), and Cue condition (Congruent, Incongruent and
17 Neutral); the four target locations (up, down, left, right) were used to ensure that cues were
18 non-predictive and were not considered in the subsequent analyses. For the photographic
19 stimuli, the trials varied in terms of face type (profile, half profile, frontal), timing of SOA
20 (100ms, 300ms and 1000ms), and Cue condition (Congruent, Incongruent and Neutral). The
21 monkey responded by touching the target, which then disappeared, and a reward was then
22 delivered by the automatic feeder. The next trial commenced after a 30-second inter-trial
23 interval. If the monkey failed to touch the initial image within 30 seconds, it re-appeared after a
24 10-second time-out. If the monkey initiated a trial but subsequently failed to touch the target
25 within 30 seconds a new trial was presented without any reward being delivered. Trials were

1 pseudo-randomly presented with no more than three consecutive trials with the same stimulus
2 type, SOA, target location or congruence value. Responses on each trial were recorded in terms
3 of latency and the co-ordinates of each touch to the screen; response time (RT) was measured
4 in ms and timed from the target onset.

5 -----
6 **Fig. 1 and Fig 2. about here**
7 -----

10 **Data Analysis**

11 Target location response times of less than 100msec (anticipations) or greater than 3000msec
12 (time outs) were excluded from the analysis; only rapid responses which were likely to be
13 related to gaze cues were considered, with a 3 second interval comparable to the duration used
14 in scan measurement studies. The percentage of trials eliminated by this procedure was 11.6%
15 (347/3003) and 7% (226/3226) for schematic and photographic stimuli, respectively. Incorrect
16 responses (first touches to areas of the screen other than to the target area) were also excluded
17 from analysis, removing a further 9.4% (281) trials and 11.4% (368) trials (with only 16 and 14
18 trials being touches to locations cued by incongruent gaze cues) for schematic and
19 photographic conditions, respectively.

20 Mean RTs were calculated for each individual in each condition; means were used
21 instead of medians as trial numbers were unequal (Miller, 1998). Repeated measures analyses
22 of variance were conducted on the mean RT data. Repeated measure Anovas were also
23 conducted on error rates (Friesen and Kingstone, 1998) for schematic (all $p > 0.1$) and
24 photographic images (all $p > 0.05$) and revealed no systematic variation in error rates. The data
25 was also analysed for each individual monkey; there were a small number of significant

1 interactions but no response patterns indicative of reflexive gaze and individual performances
2 are therefore not reported further here.

3

4 **Results**

5 **1. Schematic images**

6 A repeated measures anova conducted on mean RTs (See Table 1) revealed no significant main
7 effects, that is, response times did not differ according to whether or not a face or control image
8 was presented ($F_{1,8} = 0.01$, $p = 0.98$), SOA ($F_{2,16} = 0.77$, $p = 0.48$) or as a function of the cue's
9 predictive value ($F_{2,16} = 2.77$, $p = 0.09$). There were no significant interactions (Face x SOA,
10 $F_{2,16} = 1.52$, $p = 0.25$, Face x Cue, $F_{2,16} = 1.83$, $p = 0.19$, Cue x SOA, $F_{4,32} = 0.88$, $p = 0.48$,
11 Face x Cue x SOA, $F_{4,32} = 1.12$, $p = 0.37$). There was no evidence that responses differed to
12 schematic and scrambled images. Further, there is no evidence to suggest that congruence
13 between cue and target in terms of either direction or timing had any impact upon response
14 times in this target location task.

15

16

17

Table 1

18 **2. Photographic images**

19 Each face type was examined separately in order to allow all cue combinations to be
20 thoroughly analysed.

21 **Head direction:** As head direction was either congruent or incongruent with the target
22 location, a 3 (SOA) x 2 (Cue) repeated measures Anova was conducted on group data (see
23 Table 2 for mean RTs). There were no significant main effects; RTs did not differ according to
24 SOA ($F_{2,16} = 3.12$, $p = 0.086$) or whether the target was congruent or incongruent ($F_{1,8} = 0.32$, p
25 $= 0.59$). There was also no significant interaction between SOA and Cue condition ($F_{2,16} =$

1 2.37, $p = 0.13$). These results suggest that depicted head direction did not impact upon
2 response times, in terms of either spatial or temporal cue-stimulus contiguity in the target
3 location task presented.

4

5 **Eye direction:** As eye direction could either be congruent, incongruent or neutral regarding the
6 target location, a 3 (SOA) x 3 (Cue) repeated measures Anova was conducted on group data
7 (see Table 2 for mean RTs). Exploration of the SOA main effect showed that 100ms SOA trials
8 were responded to faster than longer SOAs (mean 100ms = 938ms, 300ms = 1011ms and
9 1000ms = 1008) but this effect did not reach significance ($F_{2,16} = 3.40$, $p = 0.059$). There was a
10 main effect of Cue condition, with neutral stimuli receiving the fastest responses (Neutral =
11 946ms, Congruent = 999ms and Incongruent = 1012ms: $F_{2,16} = 3.86$, $p = 0.043$). Fisher's tests
12 revealed that responses were faster to neutral compared with incongruent targets ($t_1 = 4.16$, $p =$
13 0.03), while responses to congruent targets were not significantly different from either. Overall,
14 the data from the eye-direction conditions fail to demonstrate that congruent cueing of the
15 target led to faster response times, although it does seem that neutral images (direct gaze) may
16 have speeded responses.

17

18 **Half-profile:** As head and eye direction could be either congruent or incongruent with one
19 another, the data were analysed on the basis of head orientation alone (i.e. ignoring eye
20 direction), and also taking account of whether or not eye gaze was compatible with head
21 direction. When the data were analysed on the basis of head direction alone in a 3 (SOA) x 2
22 (cue condition) repeated measures Anova, there were no significant effects or interactions
23 (SOA $F_{2,16} = 1.54$, $p = 0.24$; Cue $F_{1,8} = 0.73$, $p = 0.42$; SOA x Cue $F_{2,16} = 2.13$, $p = 0.15$; see
24 Table 2 for mean RTs). To examine whether head and eye direction interacted, a 3 (SOA) x 4
25 (Cue condition: head and eye directions) repeated measures Anova was also conducted; there

1 were no significant main effects or interactions RTs did not differ according to SOA or Cue
2 (SOA $F_{2,16} = 1.203$, $p = 0.33$; Cue $F_{3,24} = 0.84$, $p = 0.49$; SOA x Cue $F_{6,48} = 1.02$, $p = 0.42$).
3 Unlike direct gaze within a frontal face, direct gaze as depicted within a half-turned face did
4 not influence RTs, even when data were analysed simply on the basis of whether the eyes were
5 engaging in direct gaze or were averted ($F_{1,8} = 1.51$, $p = 0.254$). These results suggest that half-
6 profile cues do not facilitate faster responses, and further, that systematically varying the eye
7 direction with the half-profile face does not influence response patterns in this target location
8 task.

9 -----
10 Table 2
11 -----
12

13 Discussion

14 The current study aimed to tap into spontaneous gaze following responses and examine how
15 these are translated into subsequent actions on attended objects. The results with both
16 schematic and photographic stimuli fail to demonstrate any advantage of congruent gaze cues
17 upon the macaques' subsequent response times to locate a target. Responses were slightly faster
18 overall for photographic rather than schematic images, however due to possible order effects it
19 is difficult to conclude whether this is a meaningful difference in terms of face processing.
20 These negative findings are in line with previous research using a target identification task in
21 baboons (Fagot and Deruelle 2002), suggesting that our spatially based target location task did
22 not differ substantially from their identification task. In addition, the macaques were no more
23 likely to respond to the more salient cue of profile views than eye gaze alone, and there was no
24 systematic influence of temporal contiguity of cue and target. That is, these modifications did
25 not impact upon response times following congruent and incongruent cues.

1
2 A potential problem with the current study is that the current task did not require the central
3 gaze stimuli to be actively processed (due to brief SOA), as responses were only needed to start
4 a trial and to locate the target. Firstly, this seems unlikely as the monkeys were monitored via a
5 video link throughout the session; they were highly motivated to perform the task and, while
6 eye direction was not measured directly, the monkeys were reliably oriented towards the screen
7 for the vast majority of a session. It could also be argued that a gaze following response could
8 lead the monkeys to look beyond the computer screen rather than to the target object per se.
9 While eye measurement studies can control for this by training subjects to only foveate within
10 defined boundaries (Gothard et al 2004), the current study was dependent upon natural gaze
11 shifts. In any case, it is likely that gaze following should still lead to differential response times
12 in detecting cued and uncued targets; orienting in the wrong direction would slow detection
13 more than orienting in the same general direction as the target. Secondly, in humans reflexive
14 gaze is robust even when participants are specifically asked to ignore the central image. As
15 identified in the introduction, primates have an innate interest in viewing social stimuli such as
16 faces, with the eyes consistently of greatest interest (e.g. Gothard et al. 2004). The finding that
17 direct gaze photographs did shorten response times further suggests that the monkeys were
18 processing the central stimuli on some level; direct gaze is considered a distinct percept which
19 captures attention (Baron-Cohen 1994; von Grunau & Anston, 1995).

20 Together, these studies with baboons and macaques seem to conflict with growing
21 evidence that monkeys visually co-orient in response to pictorial stimuli. Although Fagot and
22 Deruelle (2002) suggested that co-orientation in other studies may reflect learning, this seems
23 unlikely as co-orientation responses are not subject to differential reinforcement (Emery et al.
24 1997; Lorincz et al. 1999; Scerif et al. 2004). Both the current study and Fagot and Deruelle's
25 (2002) also avoided differential reinforcement by using non-predictive cues and rewarding both

1 cued and uncued target location and identification, respectively. However, the baboons were
2 subsequently shown to learn to use these same gaze cues when these were repeatedly presented
3 contingently with the target (Fagot and Deruelle 2002), suggesting that they can learn to use
4 gaze in a problem solving situation (Vick & Anderson, 2000).

5 Two factors which have received attention in the gaze following literature appear
6 particularly relevant for our findings: whether the problem is presented in a competitive or
7 cooperative context and whether the model is human or conspecific. In relation to recent
8 research using more competitive paradigms, and reporting better performance when responses
9 are made to an unattended object (e.g. Hare, Call and Tomasello 2000; Flobaum and Santos
10 2005; Vick and Anderson 2003), it could be argued that in fact slower responses should be
11 expected to cued objects. If there is some inhibition of responses to attended objects, avoiding
12 the direction of another's gaze could potentially lead to faster detection of the target on
13 incongruent trials. However, this is an unlikely explanation for the absence of cueing benefits
14 due to the robust nature of the visual co-orienting response in primates, and the absence of any
15 systematic variation in favour of uncued targets either.

16 Perhaps the inter-specific stimuli deserves further attention; the visible morphology of
17 the human eye is distinct from those of other primates, notably in the amount of visible white
18 sclera (Kobayashi and Koshima 2001; Perrett and Mistlin 1990), and this may mean that the
19 psychophysics of gaze detection will similarly differ (e.g. see Ricciardelli et al. 2000 for human
20 gaze perception). Nonetheless, there is evidence that macaques scan human and monkey faces
21 in a comparable manner (Guo et al. 2003) and moreover respond to a wide range of gaze stimuli
22 with visual co-orientation (Lorincz et al. in press). While the social context of gaze in certainly
23 due further study (e.g. Shepherd, Deaner & Platt, 2006), we suggest instead that the
24 considerable variations in performance across methodologies are likely to result from the
25 different response demands of visual co-orientation studies and object based paradigms. While

1 it is difficult to understand how space-based responses would not improve target detection
2 within that space, this dichotomy has even been shown within the same subjects (Povinelli et
3 al. 1999, see also Call et al. 1998). Moreover, both the current study and Fagot and Deruelle's
4 (2002) indicate that even when object response tasks have a temporal framework which is
5 comparable to that of eye movement studies, this central difference remains.

6 An alternative approach to examining gaze following and subsequent actions is to ask
7 whether nonhuman primates are able to recognise the relationship between gaze and targets in
8 other individuals. For example, using an expectancy violation paradigm in which an individual
9 is shown attending to one of two objects before manipulating either the attended or ignored
10 object. During familiarisation trials, only attended objects are acted upon so that the viewer's
11 visual interest diminishes; understanding the relationship between attention and action should
12 lead to increased interest (measured in looking patterns) when incongruent gaze-action trials
13 occur in which the previously ignored object is manipulated. However, findings using this
14 paradigm are inconsistent; cotton-top tamarins have shown differential responses (Santos and
15 Hauser 1999); but capuchins and squirrel monkeys do not (Anderson et al. 2004). As with other
16 co-orientation responses, it is not clear whether it is unusual changes in orientation within trials
17 that are unexpected rather than an understanding between gaze and object of attention per se.
18 Interestingly, Scerif et al. (2004) also report something akin to expectancy violation in Diana
19 monkeys with the monkeys checking back (see also Call et al. 1998) to the stimulus monkey
20 photograph when a target appeared at a incongruent location. This indicates that the
21 relationship between attention and target is processed in some manner, but further study is
22 needed to ascertain precisely what this might mean in terms of cognitive processing. Thus,
23 research focusing upon the recognition rather than production of the gaze-action relationship
24 has also failed to reveal a clear pattern. Nonhuman primates are clearly sensitive to others'
25 direction of gaze but the underlying mechanisms remain unclear. In order to better understand

1 the functional dissociation between perception and action in response to gaze information,
2 future research should attempt to measure these responses in parallel.

3

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9

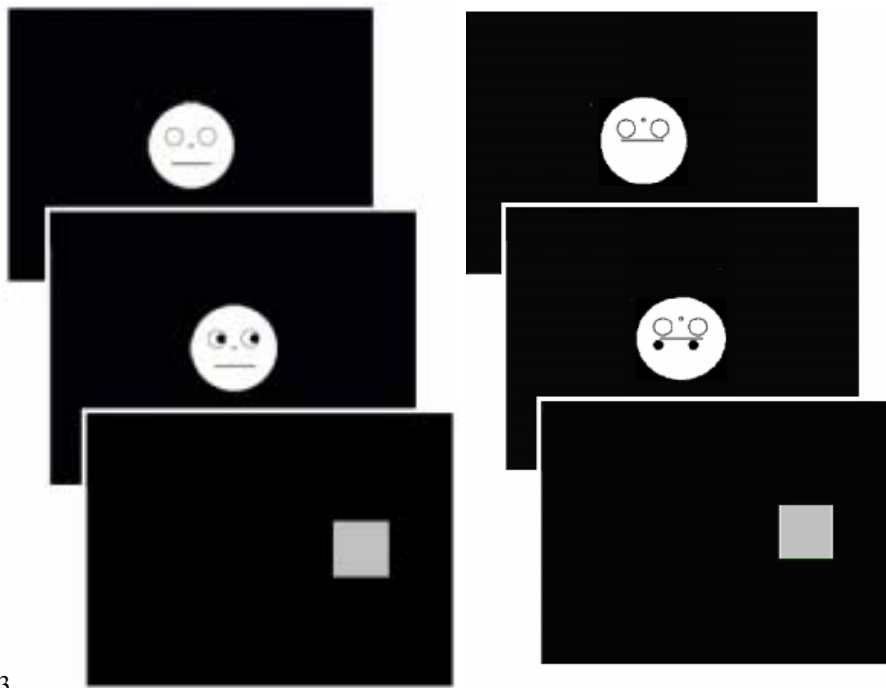
1 **References**

- 2 Anderson JR, Mitchell RW (1999). Macaques but not lemurs co-orient visually with humans.
3 *Folia Primat.* 70: 17-22.
4
- 5 Anderson JR, Sallaberry P, Barbier H (1995) Use of experimenter-given cues during object-
6 choice tasks by capuchin monkeys. *Anim Behav* 49:201-8
- 7 Anderson JR, Kuroshima H, Kuwahata H, & Fujita K (2004). Do squirrel monkeys (*Saimiri*
8 *sciureus*) and capuchin monkeys (*Cebus apella*) predict that looking leads to touching? *Anim*
9 *Cogn*, 7, 185 – 192.
- 10 Baron-Cohen S (1994). How to build a baby that can read minds: cognitive mechanisms in
11 mindreading. *Curr Psych of Cogn* 13: 513-552.
- 12 Barth J, Reaux JE, Povinelli DJ (2004) Chimpanzees' (*Pan troglodytes*) use of gaze cues in
13 object-choice tasks: different methods yield different results. *Anim Cogn* 8: 84-92
- 14 Bovet D, Vauclair J (2000). Picture recognition in animals and humans. *Behav Brain Res* 109:
15 143-165.
- 16 Call J, Hare BA, Tomasello M (1998) Chimpanzee gaze following in an object-choice task.
17 *Anim Cog* 1: 89-99.
- 18 Capitanio JP (2002). Sociability and responses to video playbacks in adult male rhesus
19 monkeys (*Macaca mulatta*). *Primates* 43: 169-177.
- 20 Dasser V (1987). Slides of group members as representations of the real animals (*Macaca*
21 *fascicularis*). *Ethol* 76: 65-73.
- 22 Deaner RO, Platt, ML (2003) Reflexive social attention in monkeys and humans. *Curr Biol* 13:
23 1609-1613.
- 24 Emery N (2000). The eyes have it: the neuroethology, function and evolution of social gaze.
25 *Neurosci and Behav Rev* 24: 581-604.
- 26 Emery NJ, Lorincz EN, Perret DI, Oram MW, Baker CI (1997). Gaze following and joint
27 attention in rhesus monkeys (*Macaca mulatta*). *J of Comp Psych* 111: 286-293.
- 28 Fagot J., Deruelle C. (2002). Perception of pictorial gaze by baboons (*Papio papio*). *J of Exp*
29 *Psych* 28: 298-308.
- 30 Fagot J, Martin-Malivel J, Dépy D (1999). What is the evidence for an equivalence between
31 objects and pictures in birds and nonhuman primates? *Curr Psych of Cogn* 18: 923-949.
- 32 Flombaum JI, Santos LR (2005) Rhesus Monkeys Attribute Perceptions to Others. *Curr Biol*
33 15: 447-452.
- 34 Friesen CK, Kingstone A (1998). The eyes have it! Reflexive orienting is triggered by
35 nonpredictive gaze. *Psychonom Bull and Rev* 5: 490-495.

- 1 Gómez J-C (2005) Species comparative studies and cognitive development. *Trends in Cogn.*
2 *Sci* 9:118-125.
- 3 Gothard KM, Erickson CA, Amaral DG (2004) How do rhesus monkeys (*Macaca mulatto*)
4 scan faces in a visual paired comparison task? *Anim Cogn* 7: 25-23
- 5 von Grunau M, Anston C (1995). The detection of gaze direction: A stare in the crowd effect.
6 *Perception*, 24, 1297-1313.
- 7 Guo K, Robertson RG, Mahmoodi S, Tadmor Y, Young MP (2003). How do monkeys view
8 faces? A study of eye movements. *Exp Brain Res* 150: 363-374.
- 9 Hare B, Call J, Agnetta B, Tomasello M (2000). Chimpanzees know what conspecifics do and
10 do not see. *Anim Beh*, 59, 771-785.
- 11 Hare B, Call J, Tomasello M (2001). Do chimpanzees know what conspecifics know? *Anim*
12 *Beh* 61: 139-151.
- 13 Kobayashi H, Kohshima S (2001). Unique morphology of the human eye and its adaptive
14 meaning: comparative studies of external morphology of the primate eye. *J Human Evol*, 40,
15 419-435.
- 16 Kyes RC, Mayer EK, Bunnell BN (1992). Perception of stimuli presented as photographic
17 slides in cynomolgus macaques (*Macaca fascicularis*). *Primates* 33: 407-412.
- 18 Langton SRH (2000). The mutual influence of gaze and head orientation in the analysis of
19 social attention direction. *Quart. J Exp. Psych.* 53A: 825-845.
- 20 Langton SRH, Bruce V (1999). Reflexive visual orienting in response to the social attention of
21 others. *Visual Cogn.* 6: 541-567.
- 22 Lorincz EN, Baker CI, Perret DI (1999). Visual cues for attention following in rhesus monkeys.
23 *Curr Psych of Cogn* 18: 973-1003.
- 24 Lorincz EN, Jellema T, Gomez J-C, Barraclough N, Xiao D, Perret, DI (in press) Do monkeys
25 understand actions and minds of others? Studies of single cells and eye movements. In *From*
26 *Monkey Brain to Human Brain* (Dehaene S, ed.), Oxford University Press.
- 27 Martin-Malivel J, Fagot J (2001) Perception of pictorial human faces by baboons: Effects of
28 stimulus orientation on discrimination performance. *Anim Learn Behav* 29: 10-20
- 29 Miller JO (1988). A warning about median reaction time. *J Exp. Psych: Human Perception and*
30 *Performance*, 14, 777-778.
- 31 Okamoto S, Tomonaga M, Ishii K, Kawai N, Tanaka M, Matsuzawa T (2002). An infant
32 chimpanzee (*Pan troglodytes*) follows human gaze. *Anim. Cogn.* 5: 107-114.
- 33 Pascalis O, Petit O, Kim J, Campbell R (1999). Picture perception in primates: the case of face
34 perception. *Cahiers de Psychologie Cognitive* 18, 889-922
- 35 Perrett DI, Emery NJ (1994). Understanding the intentions of others from visual signals:
36 Neurophysiological evidence. *Curr Psych Cogn*, 683-694.

- 1 Perrett DI, Mistlin, AJ (1990). Perception of facial characteristics by monkeys. In WC Stebbins
2 and MA Berkley (Eds.) *Comparative Perception - Volume II: Complex Signals* . (pp. 187-213).
3 New York: John Wiley and Sons.
- 4 Povinelli DJ, Eddy TJ (1996). *What Young Chimpanzees Know about Seeing*. Chicago:
5 University of Chicago Press.
- 6 Povinelli DJ, Bierschwale DT, Cech CG (1999) Comprehension of seeing as a referential act in
7 young children, but not juvenile chimpanzees. *British J Dev Psych*. 17: 37-60.
- 8 Quadflieg S, Mason MF, Macrae CN (2004) The owl and the pussycat: Gaze cues and
9 visuospatial orienting. *Psych Bull & Rev*, 11, 826-831
- 10 Ricciardelli P, Baylis G, Driver J (2000). The positive and negative of human expertise in
11 gaze perception. *Cogn*. 77: B1-14.
- 12 Santos LR, Hauser MD (1999) How monkeys see the eyes: Cotton-top tamarins' reaction to
13 changes in visual attention and action. *Anim Cogn*, 2, 131 - 139.
- 14 Scerif G, Gomez J-C, Byrne RW (2004). What do Diana monkeys know about the focus of
15 attention of a conspecific? *Anim Behav* 68: 1239-1247
- 16 Shepherd SV, Deaner RO and Platt ML (2006) Social status gates social attention in monkeys.
17 *Curr Biol* 21, 19-20.
- 18 Tomasello M, Call J, Hare B (1998). Five primate species follow the visual gaze of
19 conspecifics. *Anim Beh* 55: 1063-1069.
- 20 Veenema H (1998). *Social influences of aging in group-living long-tailed macaques*. Doctoral
21 thesis, Universiteit Utrecht.
- 22 Vick S-J, Anderson JR (2000). Learning and limitations of eye gaze an an experimenter-given
23 cue in an object choice task by capuchin monkeys (*Cebus apella*). *J Comp Psych* 114: 200-
24 207.
- 25 Vick S-J, Bovee D, Anderson JR (2001). Discrimination of gaze cues by olive baboons (*Papio*
26 *anubis*). *Anim Cogn* 4: 1-10.
- 27 Vick, S-J, Anderson JR (2003). The use of visual orientation cues in a competitive task by olive
28 baboons (*Papio anubis*). *J Comp Psych* 117: 209–216.

- 1 Figure 1: An example of a i) congruent schematic face trial and ii) an incongruent scrambled
- 2 face trial.



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1 Figure 2: An example of an incongruent head trial

2



1 **Table 1: Mean (+ S.E.) RTs (in ms) according to stimulus type, SOA and cue type.**
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 3

Stimulus	SOA	Congruent	Incongruent	Neutral
Face	100ms	1169 (101)	1182 (57)	1206 (75)
	300ms	1329 (70)	1142 (99)	1180 (86)
	1000ms	1326 (61)	1159 (81)	1360 (84)
Control	100ms	1329 (66)	1312 (57)	1201 (62)
	300ms	1126 (62)	1214 (83)	1222 (100)
	1000ms	1239 (66)	1173 (72)	1240 (84)

4
 5
 6 **Table 2: Mean (+S.E) RTs (in ms) for detecting targets cued by congruent and**
 7 **incongruent and neutral cues at 100ms, 300ms and 1000ms SOAs.**
 8

Stimulus	SOA	Congruent	Incongruent	Neutral
Head	100ms	959 (42)	928 (53)	--
	300ms	988 (44)	1099 (48)	--
	1000ms	1049 (67)	1028 (62)	--
Half profile	100ms	991 (61)	1041 (48)	--
	300ms	1012 (34)	880 (26)	--
	1000ms	1021 (34)	997 (65)	--
Eyes	100ms	954 (41)	916 (44)	944 (36)
	300ms	1033 (39)	1078 (32)	923 (34)
	1000ms	1010 (60)	1043 (53)	971 (43)

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