

## RESEARCH ARTICLE

# Measurement of Eye-Gaze in Chimpanzees (*Pan troglodytes*)

EMILY J. BETHELL<sup>1,2\*</sup>, SARAH-JANE VICK<sup>1,3</sup>, AND KIM A. BARD<sup>1</sup>

<sup>1</sup>Department of Psychology, University of Portsmouth, Hampshire, UK

<sup>2</sup>Centre for Research in Evolutionary Anthropology, Roehampton University, London, UK

<sup>3</sup>Department of Psychology, University of Stirling, Stirling, Scotland, UK

Gaze cues are used as an index of social cognition in primates, yet the sensitivity to different forms of gaze, and consequently the cues required to test gaze-following abilities remain understudied. Whereas the eye is attributed special signal value in humans, the camouflaged ocular morphology of non-human primates has led to the consensus that head orientation may be a more salient cue. This study presents the first documentation of the surface eye movements of the chimpanzee, *Pan troglodytes*, in order to determine the behavioral forms of eye-gaze and their saliency as signals, document their functional variation, and address the signal value of the eyes distinct from head orientation. Movements of the eye were identified as Scan (continuous movement), Glance (a single movement <1 sec), or Fixate (no movement). Scans, glances, and fixations were reliably detected by humans during live observation and from video (Cohen's kappa over 0.70) and, therefore, are likely also to be detected by conspecifics. Eye-gaze comprised a nonunitary measure of visual attention, reflecting the attentional task demands of different activities. Specifically, chimpanzees spent significantly more time scanning while feeding and resting, than grooming,  $F(2,28) = 10.23$ ,  $P < 0.001$ , and spent significantly more time fixating while grooming, than feeding or resting,  $F(2,28) = 7.52$ ,  $P < 0.01$ . Further, eye-gaze was often incongruent with head movement, varying significantly with the form of eye-gaze: incongruence was found during 12–21% of fixations, during 42–49% of scans, and during 70–100% of glances,  $F(2,16) = 30.17$ ,  $P < 0.001$ . These findings provide the basis for discrimination of the adaptive significance of gaze-processing abilities with emphasis on sensitivity to eye-gaze distinct from head orientation. If we are to continue exploring gaze-processing abilities in primates, then we need greater consideration of the precise nature of the signals themselves. Here we present evidence for special consideration of the

Contract grant sponsor: Research Committee, Department of Psychology, University of Portsmouth, Portsmouth, UK.

\*Correspondence to: Emily J. Bethell, Centre for Research in Evolutionary Anthropology, School of Human and Life Sciences, Whiteland's College, Roehampton University, Roehampton, London, SW15 4JD UK. E-mail: E.Bethell@Roehampton.ac.uk

Received 5 April 2006; revised 29 June 2006; revision accepted 13 July 2006

DOI 10.1002/ajp.20376

Published online 10 January 2007 in Wiley InterScience (www.interscience.wiley.com).

**Key words:** visual attention; social cognition; eye movements; apes

## INTRODUCTION

The analysis of eye-gaze as a behavioral correlate of visual attention has typically been limited to studies of humans, *Homo sapiens* [e.g., Argyle & Cook, 1976]. This bias is due, in part, to the argument that there has been an increase in the signal value of human eyes compared to those of other primate species (Kobayashi & Kohshima [2001], but see Kaplan & Rogers [2002]) and interest in arguably *Homo*-specific sociocognitive capacities associated with the processing of eye-gaze, such as mental state attribution [Baron-Cohen, 1994].

Despite the wide use of gaze cues as an index of social cognition in the non-human primates (from here, “primate”), there is no consensus in the literature about the forms of gaze primates are sensitive to and hence the gaze cues required to test sociocognitive abilities. The camouflaged ocular morphology of primates has led to the suggestion that primate eyes hold low signal value to conspecifics [Kobayashi & Kohshima, 2001]. Others have suggested that among primate species that adopt a quadrupedal stance, head and body orientation may provide enough information with regard to direction of attention since “orientation of the body, head and eye gaze are in congruent directions for the majority of the time” [Emery, 2000; p 583]. Even recent studies of primate sociocognitive functioning, in line with those of humans, which directly address gaze-processing abilities (such as gaze-following and corresponding gaze-specific neuroanatomical features, see Emery [2000] for review) use pictorial [Fagot & Deruelle, 2002; Lorincz et al., 1999] or human [e.g., Vick & Anderson, 2003] gaze cues. While others have used video recordings of conspecifics to test gaze-following abilities, it is not clear whether the signals of attention are “eye-gaze” specifically or more general indicators of attention direction (“gaze”), such as head movement and orientation [e.g., Emery et al., 1997]. Recent studies have measured eye movements in response to conspecific cues and identified sensitivity to eye-gaze in rhesus monkeys [Deaner et al., 2005; Deaner & Platt, 2003; Lorincz et al., 1999]. However, the cues presented are single gaze shifts and do not reflect the transient nature of gaze as an information source within conspecific interactions.

The degree to which conspecific eye-gaze provides a salient behavioral cue to chimpanzees under naturalistic conditions therefore is unclear. We suggest that if this is to be remedied, and if previous experimental studies are to be placed within the ethological setting, we must address the signal dimensions of naturally occurring primate eye-gaze behaviors with direct reference to their functional context. Only once we have established the true nature of the signal itself can we begin to investigate the ability of the receiver to perceive it [Guildford & Dawkins, 1991]. This work presents the first consideration of the signal dimensions of the chimpanzee eye, exploring how these vary between and within individuals, and examining the extent to which the eyes provide information over that which can be gained from looking at the head alone.

The aims of this article are three-fold. It is our initial aim to determine whether chimpanzee eye movements hold potential signal value to onlookers by testing whether surface movements of the chimpanzee eye (indexing shifts in the most likely direction of visual attention) occur above the perceptual threshold for human observers (study 1). We suggest that if movements of the chimpanzee eye

are detectable to humans then they will also be detectable to conspecifics. This first aim is met through the application of an eye-gaze ethogram (EGE) during live observation and during observation from video. The value of the signal is assessed through analysis of the reliability with which two human observers record eye-gaze patterns according to predefined temporal and spatial parameters set out in the EGE. Comparison of live observations against microanalysis of video footage allows us to establish the validity of observations of shifts in eye-gaze during real-time recording. This study has practical implications for observational studies of gaze, and the efficacy of recording eye-gaze over head orientation during live observation of primates.

Our second aim is to explore the functional variation in chimpanzee eye-gaze patterns. We suggest that eye-gaze is not a unitary measure of visual attention but is employed flexibly and adaptively according to the attentional task demands of different activities. In the first instance we predict the frequency with which each eye-gaze pattern is employed will vary as a function of the attentional demands of feeding and grooming tasks. Specifically, we predict eye movements (categorized as scans and glances) occur more often during feeding times than during grooming episodes, due to foraging demands (identification, localization, and selection of food items) and the need to monitor conspecifics under increased levels of intragroup competition (e.g., Hare et al. [2001]; see also Deaner et al. [2005] for adaptive valuation of social information). Lack of eye movement (fixation) is predicted to occur more during grooming episodes, when focal animals would be expected to concentrate visual attention toward the spatially localized grooming task, and when levels of intragroup competition, and corresponding social monitoring, are generally low.

The third aim of this article is to address the extent to which the eyes provide information beyond that which can be obtained from the head alone (study 2). This will allow us to consider the adaptive value of sensitivity to the eyes (“eye-gaze”) over an ability to infer likely direction of visual attention based on head orientation (a component of “gaze”) in the chimpanzee. It has been suggested that humans and chimpanzees show a higher degree of eye movement independent of head movement compared with all other primates that have been tested [Kobayashi & Kohshima, 2001]. Therefore, eye orientation and head orientation cannot always be congruent measures of direction of visual attention in these two species. It should be noted, however, that we lack substantive data on the relative contributions of the head and eyes to the gaze “signal” in other primate species. We should therefore be circumspect in attributing increased signal value to human eye-gaze over that of other species (see Kaplan & Rogers [2002] for consideration of eye-gaze patterns in orangutans, *Pongo pygmaeus*, and Freedman & Sparks [1997] for rhesus macaques, *Macaca mulatta*). We test the relative signal value of the head with regard to how the eyes are moving in the chimpanzee through an analysis of the extent to which head movement is congruent with eye movement. The special signal value of the eyes is determined from the frequency with which shifts in eye-gaze would remain undetectable from sensitivity to head movement alone. This study will allow us to quantify the informational value of the eyes and “eye-gaze” as a signal over head movement and “gaze” more generally.

## STUDY 1: THE SIGNAL DIMENSIONS OF EYE-GAZE

The general aim of the first study was to determine the efficacy of coding eye-gaze in the chimpanzee. In the first instance we tested the reliability with which

chimpanzee eye-gaze could be measured using two different observational methods: live observation and coding from video. A secondary aim was to investigate the extent to which visual attention, as indexed by the EGE, is influenced by the task-specific attentional demands inherent in different activities. Variable eye movements were considered here to reflect different behavioral forms of visual attention since the duration of fixation on a target and eye movements between targets varied. As target of attention was not of interest in this study, the spatial parameter reflects only movement of the eye in space.

## Materials and Methods

### *Observers and Study Subjects*

Two coders, who trained for 8 hr in the application of the EGE (described below), collected data during live observation of 22 captive chimpanzees. Subjects comprised adult and subadult chimpanzees (*Pan troglodytes*: 17 females, mean age  $\pm$  standard deviation [SD] =  $19.18 \pm 9.67$  years; and five males, mean age  $\pm$  SD =  $29.80 \pm 8.58$  years), housed at the indoor enclosure at Chester Zoo, UK. All observations were conducted between March and May 2003. The  $\alpha$ - and  $\beta$ -males were categorized as high-ranking, and the remaining three males were categorized as low ranking. The dominant four adult females were categorized as high ranking and the remaining females were combined into one class of low rank (C. Caws, personal communication).

### *Observation Criteria*

Data were collected using focal-animal sampling [Altmann, 1974]. Each subject was selected for observation from a pseudorandomized predetermined list according to whether, at the start of the observation, that individual was 1) present in the indoor enclosure, 2) engaged in one of the three specified activities for study (feeding, grooming, and resting), and 3) had at least one eye visible to both observers. Activities were defined in general terms: "Feeding" was defined as any instance in which the animal had food in the mouth, held food in the hand, or was gathering food from the enclosure floor. Feeding times varied between days and consisted of scatter feeds of primate pellets, fruit and vegetables, and, on occasion, insects. Feeding always occurred in the presence of other group members and under a degree of competition for resources. "Grooming" was defined as all instances in which the focal animal groomed either another individual or parts of their own body. In addition, animals were observed while resting. This represents a heterogeneous category with no single dominant task feature, but which allows us to document background levels of eye movement in individuals not engaged in feeding or grooming activities. "Resting" was defined as all instances where an animal was primarily stationary in one area of the enclosure, sitting or lying down, and not engaged in feeding, grooming, or any other overtly physical task.

When a subject did not meet the above criteria, the observation session was postponed, the next name on the list selected, and the evaluation process repeated. Observation sessions that were temporarily postponed were reevaluated following the completion of the next observation session. This process was repeated such that morning and afternoon observations were obtained for each focal animal per day.

### *Recording Procedure*

All observations were made from the indoor public viewing area, which consisted of a two-way soundproof glass wall that spanned approximately two-fifths of the circumference of the circular enclosure. The size of the enclosure necessitated observation of animals at a distance of 2–10 m hence all information was collected using the naked eye. All data were collected independently, with no conferring, between 0900 and 1700 hr on each day.

For live observations a digital counter, set to sound at 1-sec intervals and kept at low volume, was used to keep time during observation sessions. The two observers remained within 1 m of each other during all observation sessions to enhance audibility of the counter and minimize deviations in the angle of observation.

For collection of video footage, one observer videotaped the eye region of the focal subject using a handheld Sony DCR-TRV16E digital camera, while one observer simultaneously coded eye movements live. Verbal signifiers of the beginning and end of each observation bout were spoken into the digital video camera, and the digital counter was audible on all tapes. Reliability between live observation and observations conducted from digital video were assessed more than 5 weeks after conducting the live observations. Digital material was coded through repeated playback using Adobe Premier Pro 1.5 software on a digital editing suite at Portsmouth University.

Three mutually exclusive and exhaustive categories [Bakeman & Gottman, 1997] of eye movement were defined. “Fixation” was defined as an instance where the eyes did not move (as if fixated on a target) for at least 1 sec. Any movement of the eyes signified the end of the fixation. “Glance” was defined as a horizontal or vertical shift of the eyes to break a fixation for less than 1 sec, returning to the same or a new position to fixate again. Glances were, by definition, always embedded within two fixation periods. “Scan” comprised all vertical or horizontal movements of the eyes that occurred sequentially and continuously where the eyes did not fixate on a target for more than 1 sec. A scanning bout ended when the eyes fixated for at least 1 sec. “Out of view” was included to account for all instances when neither eye was visible to the observer (when the head was turned away, obscured by an obstruction or shadow, or when the eyes were closed).

Each focal observation session lasted for 120 sec. The session was divided into six observation bouts of 10 sec each, separated by 10-sec inter-bout intervals (as pilot data collection revealed these were the optimal sampling intervals). The beginning and end of each observation bout was signified using verbal cues. The observers recorded continuous eye movement data from the focal animal on a second-by-second basis for each 10-sec observation bout during the 120-sec session.

### *Statistical Analyses*

Reliability between observers was assessed using Cohen’s Kappa,  $k$ , in which the observed agreement between two observers applying a series of mutually exclusive and exhaustive codes is adjusted by removing the agreement by chance alone [Bakeman & Gottman, 1997]. This gives a more accurate indicator of reliability between two coders than would percentage agreement. A  $k$  value of 1 indicates 100% agreement. A sliding scale of reliability was adopted whereby  $k \geq 0.75$  represents excellent agreement,  $0.6 \leq k < 0.75$  signifies good agreement, and  $0.4 \leq k < 0.60$  represents fair agreement [Bakeman & Gottman, 1997; Fleiss, 1981]. The margin of error was set within 2-sec.

To investigate main effects of activity on eye-gaze one-factor within-subjects factorial Analyses of Variance were conducted using SPSS 12.0.1. for Windows. Data were first considered for heterogeneity of variance using the Mauchly sphericity test. Where the assumption of sphericity was violated, a Greenhouse-Geisser adjustment to the degrees of freedom was applied.

## Results and Discussion

A total of 63 observation sessions (58 complete and five incomplete sessions) were conducted by two observers coding eye-gaze during live observation of 18 of the 22 subjects (four females were not observed due to high levels of absence from the indoor enclosure), producing a total of 3,510 sec of data. Reliability on the complete coding scheme was attained between the two observers with 82% observed agreement, and Cohen's  $k = 0.70$ . Because we were concerned with the reliability of detecting eye-gaze patterns, per se, we performed a second calculation checking reliability on the three eye-gaze patterns (i.e., removing of the out-of-view category, for which disagreement could simply reflect differences in visual perspectives between coders). In this more conservative estimate, reliability was attained at 88% observed agreement, with Cohen's  $k = 0.78$ , demonstrating that the eye-gaze categories can be coded by two independent observers during live observations with "good" to "very good" levels of agreement [Bakeman & Gottman, 1997]. We therefore conclude that movements of the chimpanzee eye can be categorized into mutually exclusive and exhaustive categories according to temporal and spatial parameters that are perceptible to humans during live observation.

A smaller sample, selected for good visibility at the start of the session, was used to assess reliability between live coding and observation from videotape (a total of 1,080 sec from 20 sessions for nine adult females). Reliability of the coding scheme was attained between live observation and coding from video footage with 80% observed agreement, and Cohen's  $k = 0.71$ . A more conservative estimate of agreement on eye movements (728 sec with the out of view category omitted) resulted in increased reliability estimates of 85% agreement, and Cohen's  $k = 0.73$ . The EGE coding scheme applied during live observation is reliable with that gained through observation from video. This validates the use of the EGE during live observation, when compared with second-by-second micro-analysis of video.

Once reliability between observers, and between live and videotaped observations, was established, data were compiled for consideration of the effects of task-specific attentional demands on eye-gaze. A total of 11,280 sec of data were collected during 218 observation sessions. Females were observed for a total of 8,220 sec (137 observation sessions; mean observation time  $\pm$  SE =  $525 \pm 41.95$  sec) and males were observed for a total of 3,060 sec (51 observation sessions; mean observation time  $\pm$  SE =  $612 \pm 74.46$  sec). Subjects' eyes were in view for 68% of the observation time (7,631 of the 11,280 sec) and there was no significant difference in the proportion of time for which males' (64%) and females' (69%) eyes were in view ( $t_{20} = 0.838$ ,  $P = 0.412$ , NS).

In order to examine variation in the frequency with which scans, glances and fixations were employed, adjusted time was used (i.e., including only those observation sessions for which the eyes were in view at least 50% of the time). This resulted in 7,920 sec of data (132 observation sessions). Females were observed for 5,880 sec (mean  $\pm$  SE =  $345.88 \pm 39.36$  sec) during 98 observation sessions and males were observed for 2,040 sec (mean  $\pm$  SE =  $408 \pm 89.80$  sec) over 34 observation sessions.

Data were collapsed for sex and rank respectively, as no main effects of either sex or rank on the frequency of different forms of eye-gaze were found. An ANOVA was conducted to examine variation in eye-gaze with activity. Our first prediction that scanning and glancing occur more often during feeding times than when grooming due to attentional task demands was partially supported. Scans occurred significantly more often during feeding than during grooming episodes ( $F_{2,28} = 10.258$ ,  $P < 0.001$ ,  $\text{Eta} = 0.423$ ,  $\text{Power} = 0.977$ ; Fig. 1a). Post hoc contrasts revealed time spent scanning during feeding bouts (mean  $\pm$  SE =  $25.28 \pm 1.94$  sec) differed from scan time during grooming (mean  $\pm$  SE =  $13.95 \pm 2.07$  sec), but did not differ from scan time during resting episodes (mean  $\pm$  SE =  $25.63 \pm 1.60$  sec). Frequency of glances did not vary significantly between activities (Greenhouse-Geisser adjusted:  $F_{1,18} = 3.426$ ,  $P = 0.072$  NS,  $\text{Eta}^2 = 0.197$ ,  $\text{Power} = 0.468$ ; groom:  $2.29 \pm 0.45$  sec; feed:  $1.86 \pm 0.32$  sec; rest:  $1.04 \pm 0.16$  sec; Fig. 1b). In support of our second prediction, fixations occurred most often during grooming episodes (mean  $\pm$  SE =  $35.33 \pm 2.71$  sec; Fig. 1c) compared with feeding (mean  $\pm$  SE =  $22.67 \pm 1.90$  sec) or resting (mean  $\pm$  SE =  $20.01 \pm 2.51$  sec) bouts ( $F_{2,28} = 7.520$ ,  $P = 0.002$ ;  $\text{Eta}^2 = 0.349$ ,  $\text{Power} = 0.918$ ), reflecting the localized attentional demands of the grooming task.

These results indicate that eye-gaze is employed adaptively and flexibly according to attentional task demands during feeding and grooming episodes. We suggest increased scan time during feeding reflects the need to search for scattered food items and monitor conspecifics in competition for this resource. Low levels of scanning and heightened levels of fixations during grooming episodes reflect the focused nature of the grooming task and the fact that grooming occurs when the group is restful and competition between individuals for resources is generally reduced.

In summary, two observers were able to reliably identify surface movements of the chimpanzee eye during live observation. We can conclude from these results that shifts in chimpanzee eye-gaze provide a detectable signal to human observers and are likely to also provide a detectable signal of visual attention among *P. troglodytes*. Further, the frequency with which different forms of eye-gaze are used varies as a function of the activity an individual is engaged in, but is not affected by sex or dominance rank. Variability in the frequency with which different forms of eye-gaze are deployed according to activity status indicates variability in the way this species attends to the external environment.

## STUDY 2: THE SIGNAL VALUE OF “EYE-GAZE” OVER “GAZE”

The aim of the second study was to determine how much information is provided by movement of the eyes that cannot be gained by looking at movement of the head alone. Determining the informational value of eye movement and head movement will enable us to calculate how often movements of the head inform us about shifts in the direction of eye-gaze. This will allow us to directly address conflicting reports of the utility of looking at the eyes as an information source over and above head orientation [cf., Emery, 2000; Kaplan & Rogers, 2002].

### Methods

#### *Observers and Study Subjects*

Two observers coded a sample of the video footage used in study 1 of five male and five female adult chimpanzees. Thirty video clips (one clip for each of the 10 subjects while engaged in feeding, resting and grooming activities) were selected

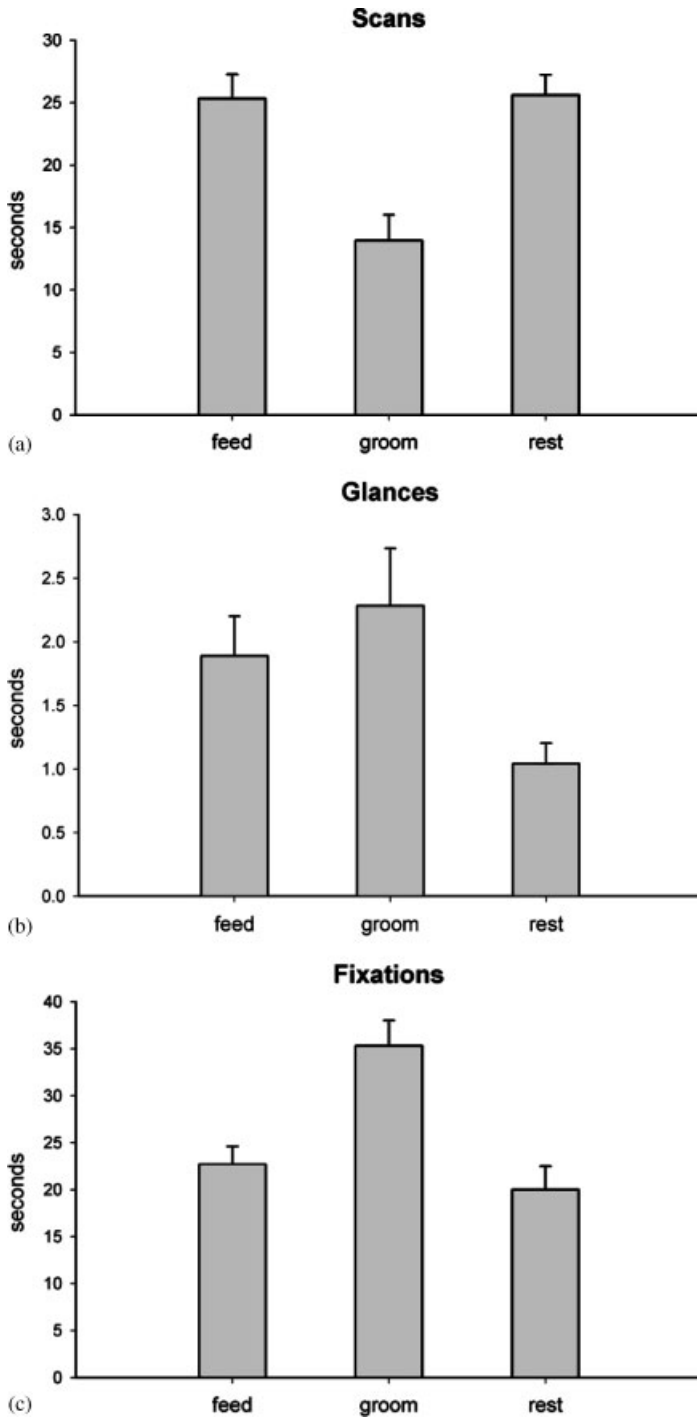


Fig. 1. Mean number of seconds per minute that adult male and female chimpanzees scanned (a), glanced (b), and fixated (c) while feeding, grooming, and resting.

using Premier software on a digital video-editing suite. Criteria for selection of video clips were good visibility of the subject and that at least one of the subject's eyes were visible to the observers at the start of the sequence.

### *Recording Procedure*

Video clips were coded using time sampling with the fOCUS II video coding software tool (an Open University resource: <http://observationskills.open.ac.uk/>) at 1-sec intervals. Three mutually exclusive and exhaustive codes (congruent, incongruent and out of view) were used to record whether head movement was indicative of eye movement. "Congruent" was coded whenever head movement reflected eye movement, namely when the eyes were seen to move (a "scan" or "glance") within the 1-sec interval and the head was also seen to move in the same direction. Similarly, congruent was coded when the eyes remained still ("fixate") and the head also remained still. "Incongruent" was coded whenever the eyes were seen to move (a "scan" or "glance"), but the head did not move. Similarly, incongruent was coded when there was head movement, but no perceivable eye movement ("fixate"). Incongruence was also recorded when the direction of the movement differed markedly between head and eyes (for example, where the head moved upwards while the eyes oriented downwards). "Out of view" was recorded when either the eyes or head were obscured from view.

### *Statistical Analyses*

Data were analyzed following the same procedure as study 1. For calculation of Cohen's  $k$  the margin of error was reduced to 1 sec.

## **Results and Discussion**

A total of 2,240 sec of footage were coded (males:  $n = 1,044$  sec, mean  $\pm$  SE =  $208.80 \pm 19.69$  sec; females:  $n = 1,196$  sec, mean  $\pm$  SE =  $239.20 \pm 11.4$  sec), of which a total of 1,569 sec were coded as in view and 671 sec coded as out of view (Table I). There was no difference between males and females in the proportion of time the eyes were in view ( $t_8 = 1.218$ ,  $P = 0.258$ , NS). Overall, males and females spent 42.96% of the time scanning, 1.69% glancing, and 26.56% fixating. The eyes were out of view for 28.79% of the time.

Interobserver agreement for the three codes "congruent", "incongruent" and "out of view" was reached at  $k = 0.62$ . This represents "good" reliability [Fleiss, 1981] between the two observers in coding (in)congruence of head and eye movement from video.

There was a significant effect of look type on incongruence of head and eye movement ( $F_{2,16} = 30.167$ ;  $P < 0.001$ ; Table II). Glances were highly incongruent with head movement; incongruence was found between 70–100% of the time. Fixations and scans occurred independently of head movement 12–21% and 42–49% of the time respectively. No significant effect of activity state on incongruence of eye movement with head movement was found for all three forms of eye-gaze (Scans:  $F_{2,18} = 1.411$ ,  $P = 0.270$ , NS,  $\text{Eta}^2 = 0.136$ , Power = 0.263; Glances:  $F_{2,18} = 0.753$ ,  $P = 0.485$ , NS,  $\text{Eta}^2 = 0.077$ , Power = 0.158; Fixations:  $F_{2,18} = 0.949$ ,  $P = 0.406$ , NS,  $\text{Eta}^2 = 0.095$ , Power = 0.189; Fig 2).

These results demonstrate that head movement is often not a reliable indicator of eye movement, especially in the case of glances and, to a lesser extent, scans. It is therefore necessary to record eye-gaze over and above head orientation to gain an accurate measure of how an individual's eyes are moving. Further, some forms of eye-gaze are more likely to be incongruent with head movement

**TABLE I. Observation Times (Sec) for Coding Congruency of Eye and Head Movement in Five Males and Five Female Chimpanzees Across the Three Activity States**

	Feed (sec)		Rest (sec)		Groom (sec)		Total observation time (sec)	
	In view	Total	In view	Total	In view	Total	In view	Total
<b>Males</b>								
Boris	29	63	48	65	60	83	137	211
Dillon	126	176	25	32	51	72	202	280
Nikki	13	17	92	117	59	74	164	208
Friday	37	54	36	68	35	55	108	177
Wilson	26	63	21	24	44	81	91	168
<b>Females</b>								
Sarah	29	63	74	86	57	59	160	208
Heidi	60	66	108	113	76	82	244	261
Rosie	72	115	53	85	33	55	158	255
Layla	46	63	65	92	58	60	169	215
Chrissie	35	76	71	149	30	32	136	257
Group total							1569	2240
Group mean							156.90	224.00
Group $\pm$ SE							13.90	11.86

**TABLE II. Mean Number of Seconds Per Minute That Scans, Glances, and Fixations Were Incongruent/Congruent With Head Movement**

	Scan (sec)		Glance (sec)		Fixate (sec)		Out of view (sec)
	Congruent	Incongruent	Congruent	Incongruent	Congruent	Incongruent	
<b>Males</b>							
Boris	13.06	9.89	0.31	0.72	13.12	1.34	21.57
Dillon	10.65	10.41	0.00	0.73	20.69	1.63	15.89
Nikki	16.68	11.64	0.27	0.54	12.51	5.33	13.03
Friday	14.20	12.35	0.36	0.66	8.71	0.73	22.98
Wilson	21.43	2.82	1.23	0.56	7.69	2.88	23.38
<b>Females</b>							
Sarah	22.35	8.11	0.00	1.57	8.30	5.42	14.26
Heidi	10.59	23.54	0.00	1.13	19.54	1.03	4.17
Rosie	15.63	12.56	0.00	0.00	7.35	1.45	23.01
Layla	11.70	8.78	0.00	1.65	23.90	2.04	11.93
Chrissie	10.48	10.94	0.00	0.40	15.40	0.27	22.51
Group mean	14.68	11.10	0.22	0.80	13.72	2.21	17.27
Group $\pm$ SE	1.38	1.65	0.12	0.16	1.89	0.57	2.05

than others. Glances, for example, are highly incongruent with head movement, and remain so regardless of activity state. In contrast, fixations are rarely accompanied by head movement. During scans the eyes provide information that head movement does not in approximately half of all cases. We therefore conclude that the eyes provide a detectable and potentially valuable signal with regards to shifts in direction of visual attention that has value over and above information

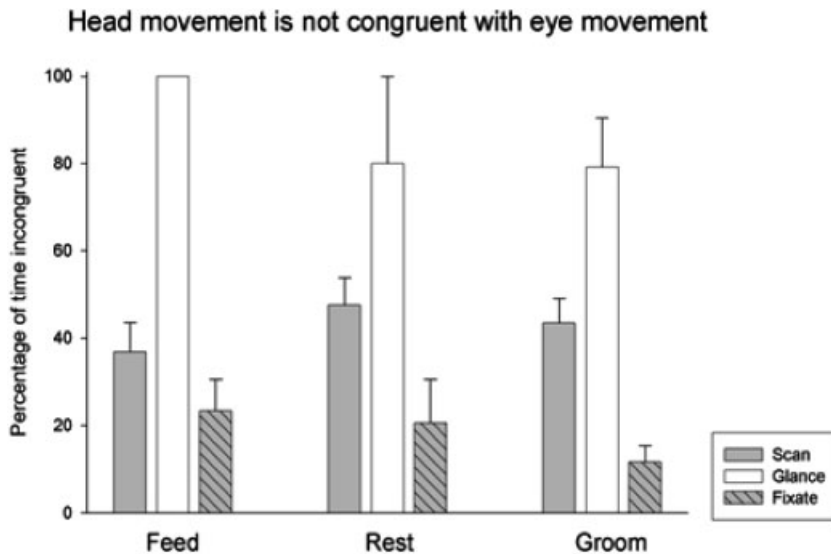


Fig. 2. Incongruence of head and eye movement for 10 adult chimpanzees (males:  $n = 5$ , females:  $n = 5$ ). Glances are highly incongruent with head movement and would go undetected if an observer was sensitive only to movement of the head. Fixations are highly congruent with head movement, and therefore sensitivity to the eyes would confer no advantage over sensitivity to head orientation in detecting these. Scans are 42–49% incongruent with head movement and would therefore go undetected, if an observer was sensitive only to movement of the head, in just under half of all cases.

that can be gained from sensitivity to head movement alone. Given the importance of sensitivity to eye-gaze for the development of sociocognitive skills in humans, the ability to access and use this social signal would confer a selective advantage on chimpanzees that possessed comparable sociocognitive abilities.

## GENERAL DISCUSSION

Our results demonstrate that 1) chimpanzee eye movements hold potential signal value to onlookers, they can be categorized into three quantifiable, mutually exclusive, and exhaustive categories (scans, glances and fixations) and be reliably observed during real-time observation; 2) eye-gaze patterns demonstrate functional variation according to the attentional task demands of feeding and grooming activities and resting behavior and 3) the eyes provide information about shifts in the direction of vision that cannot be gained from sensitivity to head movement alone.

From these results we conclude that chimpanzee surface eye movements provide a detectable signal to the human eye during live observation and, as such, may also provide a detectable signal to conspecific observers. This signal may provide information about underlying factors such as attentional stance and arousal which vary with activity status. Further, eye-gaze provides additional information over gaze, per se. These findings provide the basis for discrimination of the adaptive significance of gaze-processing abilities with particular emphasis on sensitivity to eye-gaze distinct from head orientation in the chimpanzee.

Our finding that variation in eye-gaze patterns reflects functional responses to the differential attentional task demands of grooming and feeding supports our argument that eye-gaze is not a unitary measure of visual attention but a flexible behavior that may be employed adaptively. Scans, glances and fixations differ

temporally and spatially reflecting functional differences in the way visual information is collected. Scans cover a larger range of visual targets than fixations by definition, while fixations are highly localized with respect to direction of vision. Heightened levels of scanning during feeding episodes were predicted to reflect visual search for scattered food and heightened social monitoring during foraging competition [e.g., Deaner et al., 2005; Hare et al., 2001]. Scanning occurred at a significantly higher rate during feeding than during grooming, and at a similarly high rate to feeding during resting episodes for all individuals regardless of sex or rank. Likewise, animals spent significantly more time fixating during grooming than when feeding or resting, reflecting the localized attentional demands of the grooming task. While we did not systematically record target of vision it was noted that fixations were almost exclusively directed towards the animal being groomed. We need further studies that are sensitive to target of visual attention in order to tease apart task-oriented- and socially-directed attention.

Our results demonstrate that sensitivity to shifts in eye-gaze would provide extra information about shifts in the direction of visual attention that could not be gained from sensitivity to head movement alone. The ability to detect shifts in eye-gaze, in addition to sensitivity to head orientation, would confer a selective advantage on chimpanzees exhibiting this cognitive ability [e.g., Langton et al., 2000; Perrett & Emery, 1994]. In particular it would provide individuals with an extended repertoire of behavioral indices on which to base assessment of others' knowledge states [e.g., Hare et al., 2001] and corresponding motivational and emotional states (eye-gaze has been shown to reflect likely motivational and emotional stance in the orangutan, *P. pygmaeus* [Kaplan & Rogers, 2002]; red-capped mangabey, *Cercocebus torquatus torquatus* [Blois-Heulin, 1999]; gray cheeked mangabey, *C. albigena albigena*: [Blois-Heulin & Girona, 1999]).

Additionally, these results have practical implications for researchers of vigilance behaviors in primates. Studies of primate gaze behaviors have applied a range of observational techniques for data collection, ranging from ad lib [e.g., Idani, 1995] to continuous focals [e.g., Caine & Marra, 1988] and scan sampling [e.g., Baldellou & Henzi, 1992]. Researchers have further tended to rely on head orientation as a less reliable, but more easily observed, behavioral indicator of likely direction of visual attention [e.g., Bethell, 2003; Tomasello et al., 1998]. However, as this study shows, eye-gaze may be observed reliably and accurately under captive conditions. With a sensitive coding scheme, such as the EGE, surface eye movements may be reliably observed in primate species such as *P. troglodytes*, using continuous sampling of pre-described behaviors within short time intervals (e.g., 10 sec). This level of analysis is important to capture the behavioral flexibility of eye-gaze reported here.

In conclusion, chimpanzee eye-gaze provides a salient behavioral measure to human observers and further studies are required to establish the signal value of the chimpanzee eye both as a measure of attention among conspecifics, and as an indicator of sociocognitive processes. If chimpanzees are sensitive to changes in the direction of the eyes, as humans are, then we must consider the implications of such a finding for future studies of social cognition. However, it is important to note that even the ability to perceive and respond to changes in eye-gaze need not reflect an epistemic understanding of "seeing" or "attention"; it may simply indicate sensitivity to the behavior of looking and its correlation with subsequent actions [e.g., Vick & Anderson, 2003]. Likewise, there may be nothing special about sensitivity to the eyes over head orientation for determining another's likely attentional stance, if both act as behavioral signals that inform the same

sociocognitive processes. It may simply be the case that under certain conditions (such as close proximity) eye-gaze provides a more reliable signal.

In either case experimental stimuli faithful to both the morphological characteristics and movement dimensions of the chimpanzee eye are required to test hypotheses concerning gaze-processing. Moreover, better understanding of the ethology of gaze can inform scientists in the use of gaze as a dependent variable; for example, frequency of looks and look duration may give divergent results [e.g., Emery et al., 1997], and serve as the basis for selecting appropriate measures of important processes, such as interest [Emery, 2000]. Reliable and precise methods to analyze eye-gaze are a requirement for investigating eye-gaze as an index of socio-cognitive abilities in the non-human primates. We hope this paper provides a substantive base for the identification of such stimuli and methods.

## ACKNOWLEDGMENTS

We are grateful to Chester Zoo for granting us permission to collect the data presented in this study, and to the Zoo staff for their assistance. Special thanks go to Clare Caws for information on dominance ranks, Bridget Waller for use of video material, and Paul Waby and Hester Duffy for technical support. We also thank two anonymous reviewers for helpful comments on the manuscript. E.B. was financially supported by a grant from the Research Committee, Department of Psychology, University of Portsmouth, Portsmouth, UK.

## REFERENCES

- Altmann J. 1974. Observational study of behavior: sampling methods. *Behavior* 49: 227–267.
- Argyle M, Cook M. 1976. *Gaze and mutual gaze*. 1st ed. Cambridge: Cambridge University Press. 221p.
- Bakeman R, Gottman JM. 1997. *Observing interaction: an introduction to sequential analysis*. 2nd ed. Cambridge: Cambridge University Press. 224p.
- Baldellou M, Henzi SP. 1992. Vigilance, predator detection and the presence of supernumerary males in vervet monkey troops. *Anim Behav* 43:451–461.
- Baron-Cohen S. 1994. The mindreading system: new directions for research. *Curr Psychol Cogn* 13:724–750.
- Bethell EJ. 2003. Rank effects on chimpanzee social monitoring. *Primate Eye* 80:4.
- Blois-Heulin C. 1999. Variability in social visual attention in the red-capped mangabey (*Cercocebus torquatus torquatus*) and the grey-cheeked mangabey (*Cercocebus albigena albigena*). *Folia Primatol* 70: 264–268. [Italian]
- Blois-Heulin C, Girona B. 1999. Patterns of social visual attention in the red-capped mangabey (*Cercocebus torquatus torquatus*) in the context of food competition. *Folia Primatol* 70:180–184. [Italian]
- Caine NG, Marra SL. 1988. Vigilance and social-organization in two species of primates. *Anim Behav* 36:897–904.
- Deaner RO, Khera AV, Platt ML. 2005. Monkeys pay per view: adaptive valuation of social images by rhesus macaques. *Curr Biol* 15:543–548.
- Deaner RO, Platt ML. 2003. Reflexive social attention in monkeys and humans. *Curr Biol* 13:1609–1613.
- Emery NJ, Lorincz EN, Perrett DI, Oram MW, Baker CI. 1997. Gaze following and joint attention in rhesus monkeys (*Macaca mulatta*). *J Comp Psychol* 111:286–293.
- Emery NJ. 2000. The eyes have it: the neuroethology, function and evolution of social gaze. *Neurosci Biobehav Rev* 24: 581–604.
- Fagot J, Deruelle C. 2002. Perception of pictorial gaze by baboons (*Papio papio*). *J Exp Psychol* 28:298–308.
- Fleiss JL. 1981. *Statistical methods for rates and proportions*. New York: Wiley. 352p.
- Freedman EG, Sparks DL. 1997. Eye-head coordination during head-unrestrained gaze shifts in rhesus monkeys. *J Neurophysiol* 77: 2328–2348.
- Guildford T, Dawkins MS. 1991. Receiver psychology and the evolution of animal signals. *Anim Behav* 42:1–14.

- Hare B, Call J, Tomasello M. 2001. Do chimpanzees know what conspecifics know? *Anim Behav* 61:139–151.
- Idani G. 1995. Function of peering behavior among bonobos (*Pan paniscus*) at Wamba, Zaire. *Primates* 36:377–383.
- Kaplan G, Rogers LJ. 2002. Patterns of gazing in orangutans. *Int J Primatol* 23:501–526.
- Kobayashi H, Kohshima S. 2001. Unique morphology of the human eye and its adaptive meaning: comparative studies on external morphology of the primate eye. *J Hum Evol* 40:419–435.
- Langton SRH, Watt RJ, Bruce V. 2000. Do the eyes have it? Cues to the direction of social attention. *Trends Cogn Sci* 4:50–59.
- Lorincz EN, Baker CI, Perrett DI. 1999. Visual cues for attention following in rhesus monkeys. *Curr Psychol Cogn* 18: 973–1003.
- Perrett DI, Emery NJ. 1994. Understanding the intentions of others from visual signals: neurophysiological evidence. *Curr Psychol Cogn* 13:683–694.
- Tomasello M, Call J, Hare B. 1998. Five primate species follow the visual gaze of conspecifics. *Anim Behav* 55: 1063–1069.
- Vick S-J, Anderson JR. 2003. Use of human visual attention by olive baboons (*Papio anubis*) in a competitive task. *J Comp Psychol* 117:209–216.