

Social status gates social attention in monkeys

Stephen V. Shepherd¹,
Robert O. Deaner¹ and
Michael L. Platt^{1,2,3}

Humans rapidly shift attention in the direction other individuals are looking, following gaze in a manner suggestive of an obligatory social reflex [1–4]. Monkeys' attention also follows gaze, and the similar magnitude and time-course of gaze-following in rhesus macaques and humans [5] is indicative of shared neural mechanisms. Here we show that low-status male rhesus macaques reflexively follow the gaze of all familiar rhesus macaques, but high-status macaques selectively follow the gaze only of other high-status monkeys. These results suggest that gaze-following in monkeys involves reflexive and voluntary components, and that the strength of these mechanisms varies according to social status.

We probed the impact of social status on gaze-following in rhesus macaques performing a simple visual orienting task [5] (Figure 1A). Each monkey (four high-status, three low-status) fixated a central target which was replaced by an image of a familiar monkey's face looking left or right. After 100, 200, 400, 600 or 800 ms, the face disappeared and a peripheral target appeared randomly to the left or right; monkeys then shifted gaze to the target to receive a juice reward. Crucially, the face's gaze direction did not predict the target location. We demonstrated previously that saccade reaction times for monkeys and humans are faster on those trials in which observed gaze is congruent with target location; reaction time savings thus served as our operational definition of gaze-following. We hypothesized that monkeys would generally follow gaze, but that the strength and timing of gaze-following would be modulated by social status.

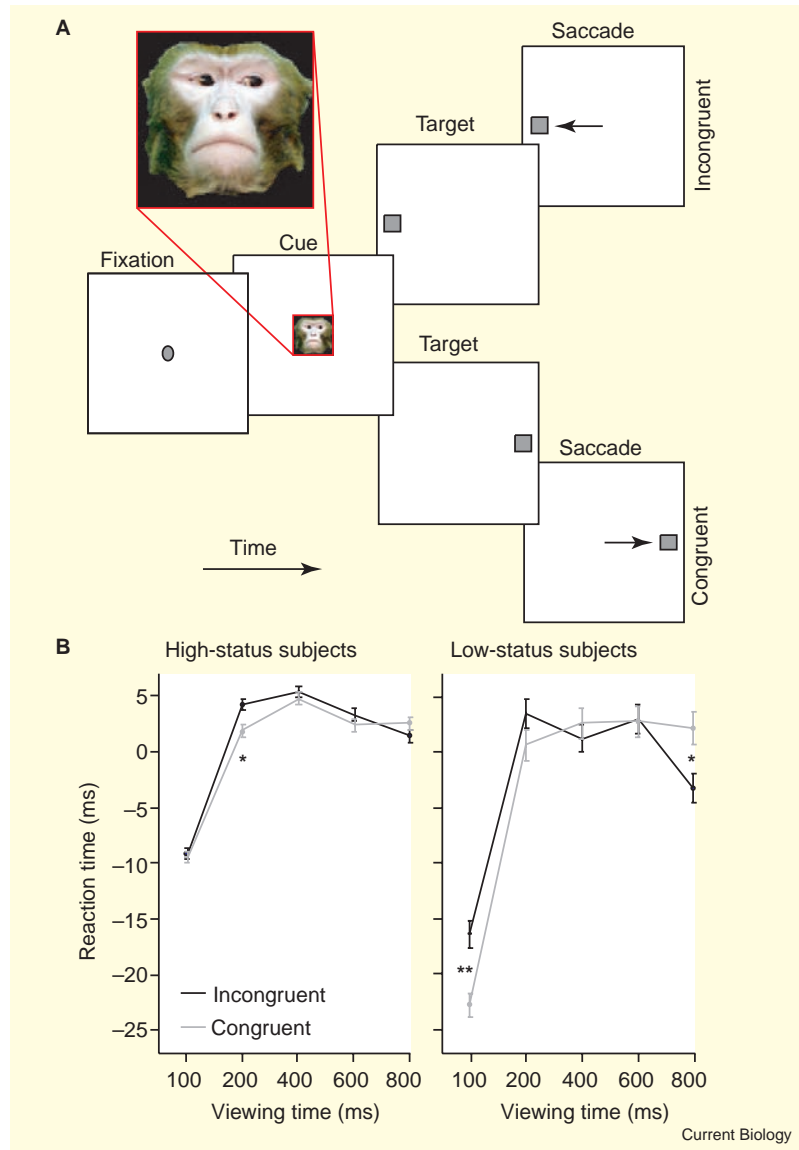


Figure 1. Observed gaze and social status influence saccade reaction times. (A) Visual orienting task. The impact of social status on gaze-following was examined by comparing reaction times for saccades made to a peripheral target after viewing an image of a familiar monkey looking left or right. Each monkey first fixated a central yellow square ($\pm 3^\circ$) for 200–500 ms. The yellow square was then extinguished and a monkey face, shown here in inset, was illuminated centrally for a variable duration. If the monkey maintained fixation, the face was extinguished and a peripheral yellow square simultaneously illuminated at one of two fixed positions located symmetrically $10\text{--}15^\circ$ to the left or right. Gaze shifts to the peripheral target within 350 ms were rewarded with a small squirt of juice. (B) Gaze-following dynamics vary with social status in male rhesus macaques. Average (\pm S.E.M.) saccade reaction times plotted as a function of face viewing duration on congruent and incongruent trials, for high-status (left) and low-status (right) subjects. For high-status monkeys, gaze cues evoked significant reaction time savings only at the 200 ms viewing duration. For low-status monkeys, both early reaction time savings and later inhibition of return (IOR) were observed. **post-hoc test $p < 0.00005$; *post-hoc test $p < 0.005$; all other contrasts $p > 0.05$.

Overall, monkeys followed gaze at 100 ms (LSD, $p < 0.005$) and 200 ms (LSD, $p < 0.005$) but showed inhibition of return (IOR) at 800 ms (LSD, $p < 0.01$). More importantly, social status significantly influenced

gaze-following (Figure 1B; ANOVA, $p < 0.005$). The three low-status monkeys showed initial gaze-following at 100 ms (LSD, $p < 0.00005$) followed by IOR at 800 ms (LSD, $p < 0.005$). Although reaction times differed significantly

amongst individuals (ANOVA, $p < 0.05$), every low-status monkey followed gaze at 100 ms (Mann-Whitney U $p < 0.05$) and tended to show IOR at 800 ms. The four high-status monkeys, by contrast, all showed gaze-following at 200 ms (ANOVA, $p < 0.05$; LSD, $p < 0.005$) with no IOR (800 ms, LSD, $p = 0.4$). To control for experience, we repeated the analyses using only the first 500 correct trials from each monkey, finding an identical pattern of results (ANOVA, $p < 0.005$). Rapid gaze-following and IOR in low-status monkeys implies reflexive attention, whereas delayed gaze-following and lack of IOR in high-status monkeys implies voluntary attention [6–8].

We next examined whether the social status of the cuing monkey influences gaze-following. Across all viewing durations, gaze-following by low-status monkeys was unaffected by cue status (ANOVA, $p = 0.6$); high-status monkeys, by contrast, only followed the gaze of other high-status monkeys (ANOVA, $p < 0.01$; low-status cues, LSD, $p = 0.7$; high-status cues, LSD, $p < 0.005$). This difference may arise from the distinct time course of gaze-following in each group: across all subjects, late (> 400 ms cue duration) gaze-following was stronger to high- than low-status monkeys (pooled subjects, ANOVA, $p < 0.005$; high-status only, ANOVA, $p < 0.01$; low-status only, ANOVA, $p < 0.05$).

This influence of cue social status complements reports [9–11] that nonhuman primates preferentially attend to high-status individuals, and suggests that preferential attention extends in the direction these animals look. The time course is consistent with the observation that neurons in macaque temporal cortex discriminate identity in a viewpoint-independent manner only after 150–400 ms [12,13].

Our results confirm prior reports that gaze-following in nonhuman primates, as in humans, is composed of reflexive and voluntary components [14,15], and shows that the strength of these mechanisms varies with social status. We speculate that

variation in reflexive and voluntary gaze-following among monkeys may share features with variation in social attention in humans. For example, the balance of reflexive and voluntary social attention may be set by neuromodulatory systems [16,17] associated with differences in personality or temperament [18,19]. Low social status may correlate with heightened arousal and scanning behavior [10,18,20] supporting fast, reflexive gaze-following; high social status may require selective monitoring of only other high-status monkeys [10,11]. Though macaque social status does not predict plasma cortisol levels (indexing anxiety), it does predict levels of testosterone [17]. All high-status males in our study had larger testes than all low-status males (Mann-Whitney U, $p < 0.05$), suggesting higher circulating testosterone levels [19]. Given the recent report that human males follow gaze less robustly than human females [21], these data suggest individual variation in androgen-linked masculinization may contribute to differences in the strength of reflexive and voluntary gaze-following in primates.

Acknowledgements

We thank Michael Bendiksbj by for additional data, Sheila Roberts for technical assistance, and Jeff Klein for comments. This work was supported by MH066259 (M.L.P.), the Cure Autism Now Foundation (M.L.P.), and a postdoctoral NRSA (R.O.D.). The authors declare no competing financial interests.

Supplemental data

Supplemental data including experimental procedures are available at <http://www.current-biology.com/cgi/content/full/16/4/R119/DC1/>

References

1. Friesen, C.K., and Kingstone, A. (1998). The eyes have it! Reflexive orienting is triggered by nonpredictive gaze. *Psychon. Bull. Rev.* 5, 490–495.
2. Langton, S.R.H., and Bruce, V. (1999). Reflexive visual orienting in response to the social attention of others. *Vis. Cogn.* 6, 541–567.
3. Driver, J., Davis, G., Kidd, P., Maxwell, E., Ricciardelli, P., and Baron-Cohen, S. (1999). Gaze perception triggers reflexive visuospatial orienting. *Vis. Cogn.* 6, 509–540.
4. Hietanen, J.K., and Leppanen, J.M. (2003). Does facial expression affect

attention orienting by gaze direction cues? *J. Exp. Psychol. Hum. Percept. Perform.* 29, 1228–1243.

5. Deaner, R.O., and Platt, M.L. (2003). Reflexive social attention in monkeys and humans. *Curr. Biol.* 13, 1609–1613.
6. Jonides, J. (1981). Voluntary versus automatic control over the mind's eye's movement. In *Attention and Performance*, Vol. IX, J. Long and A. Baddley, eds. (Erlbaum), pp. 187–203.
7. Posner, M.I., and Cohen, Y. (1984). Components of visual orienting. In *Attention and Performance*, Vol. X, H. Bouma and D. Bouwhuis, eds. (Erlbaum), pp. 531–556.
8. Klein, R.M. (2000). Inhibition of return. *Trends Cogn. Sci.* 4, 138–147.
9. Chance, M.R.A. (1967). Attention structure as the basis of primate rank orders. *Man* 2, 503–518.
10. Keever, E.B., Leonard, R.A., Scruton, D.M., and Young, S.K. (1978). Visual monitoring in social groups of Talapoin Monkeys. *Anim. Behav.* 26, 933–944.
11. Deaner, R.O., Khara, A.V., and Platt, M.L. (2005). Monkeys pay per view: adaptive valuation of social images by rhesus macaques. *Curr. Biol.* 15, 543–548.
12. Sugase, Y., Yamane, S., Ueno, S., and Kawano, K. (1999). Global and fine information coded by single neurons in the temporal visual cortex. *Nature* 400, 869–873.
13. Eifuku, S., De Souza, W.C., Tamura, R., Nishijo, H., and Ono, T. (2004). Neuronal correlates of face identification in the monkey anterior temporal cortical areas. *J. Neurophysiol.* 91, 358–371.
14. Tomasello, M., Hare, B., and Fogleman, T. (2001). The ontogeny of gaze following in chimpanzees, *Pan troglodytes*, and rhesus macaques, *Macaca mulatta*. *Anim. Behav.* 61, 335–343.
15. Friesen, C.K., Ristic, J., and Kingstone, A. (2004). Attentional effects of counterpredictive gaze and arrow cues. *J. Exp. Psychol. Hum. Percept. Perform.* 30, 319–329.
16. Amaral, D.G. (2002). The primate amygdala and the neurobiology of social behavior: implications for understanding social anxiety. *Biol. Psychiatry* 51, 11–17.
17. Sapolsky, R.M. (2004). Social status and health in humans and other animals. *Annu. Rev. Anthropol.* 33, 393–418.
18. Clarke, A.S., and Boinski, S. (1995). Temperament in nonhuman primates. *Am. J. Primatol.* 37, 103–125.
19. Bercovitch, F.B., and Ziegler, T.E. (2002). Current topics in primate socioendocrinology. *Annu. Rev. Anthropol.* 31, 45–67.
20. Caine, N.G., and Marra, S.L. (1988). Vigilance and social organization in two species of primates. *Anim. Behav.* 36, 897–904.
21. Bayliss, A.P., diPellegrino, G., and Tipper, S.P. (2005). Sex differences in eye gaze and symbolic cueing of attention. *Q. J. Exp. Psychol.* A 58, 631–650.

¹Department of Neurobiology,

²Department of Biological Anthropology and Anatomy, Duke University Medical Center, Durham, North Carolina 27710, USA. ³Center for Cognitive Neuroscienc, Duke University, Durham, North Carolina 27710, USA.

Supplemental Data: Social status gates social attention in monkeys

Stephen V. Shepherd, Robert O. Deaner, & Michael L. Platt

Supplemental Experimental Procedures

Seven pair-housed male rhesus macaques (*Macaca mulatta*) from our colony at the Duke University Medical Center Vivarium served as subjects; each was assessed as high-status or low-status relative to its cagemate based on unidirectional submissive displays[S1]. Moreover, pairwise status extended to all other members of the colony (i.e., all low-status monkeys averted gaze from all other high-status monkeys) during controlled confrontation tests[S1]. All animals were originally reared in naturalistic social groups; cage position and composition for the macaques in our colony remained unchanged for more than three years prior to the initiation of this study. All animal procedures were approved by the Duke University Medical Center Institutional Animal Care and Use Committee and were designed and conducted in compliance with the Public Health Service's Guide for the Care and Use of Animals.

Experiments were run on a Dell Precision 220 Pentium IV computer using custom software (ryklinsoftware.com). Monkeys viewed stimuli on a 24" Sony Trinitron monitor running at a resolution of 1024x768 and refresh rate of 60 Hz. Subjects were seated with their eyes 45 cm from the center of the monitor. Eye position was monitored using a magnetic search coil surgically implanted beneath the conjunctiva of one eye and sampled at 500 Hz[S2, S3] while head position was maintained with a surgically

implanted stainless steel prosthesis (Crist). All surgical procedures were performed aseptically, followed with appropriate analgesics and antibiotics, and in all other ways followed standard protocols described previously[S4].

Monkey faces displayed at fixation were drawn from 32 images of four familiar macaques (two high- and two low-status) looking either left or right. Each monkey and gaze direction was represented with two eye-averted and two head-and-eyes-averted images. Face images were standardized by cropping the head from the background, centering the midpoint of the eye region (eyes-only) or the centermost eye corner (head-and-eyes), and resizing to 115x115 pixels, approximately 5°. All stimuli were presented on a black background. All monkeys, both subjects and cues, were approximately 8 years old at the time they participated in this experiment.

We operationalized gaze-following as a decrease in reaction time for saccades toward targets at the location viewed by the cue image relative to saccades toward targets located opposite the direction of gaze in the cue image. All statistical tests consisted of ANOVA, with post-hoc tests between groups by Fisher's Least Significant Difference (LSD) or by Mann-Whitney U, as noted. Statistical tests were performed as follows: first we confirmed the presence of time-varying gaze-following across all our macaque subjects, controlling for variation in the number of trials successfully completed by each macaque whenever possible (ANOVA, normalized RT by congruence by cue duration with subject ID as variable of no interest). Significant differences between individuals were present and were found to vary significantly with social status (ANOVA, normalized RT by subject status by congruence by cue duration). Gaze-following dynamics of low- and high-status monkeys were probed

separately using ANOVA (normalized RT by congruence by cue duration with subject ID as variable of no interest).

We additionally examined the responses of low- and high-status subjects to cues from monkeys of differing social status. We first separately analyzed low- and high-status individuals pooled across cue viewing times (ANOVA, normalized RT by cue social status by congruence with subject ID as variable of no interest), and then examined the overall responses of pooled low- and high-status monkeys as a function of time (ANOVA, normalized RT by cue social status by cue duration with subject identity as a variable of no interest).

Finally, we examined the impact on gaze-following of low-level cue features, including luminance, contrast, head area, and saturation, using multiple regression and found no significant effects. Although we examined the distribution of eye positions during cue fixation, both from each monkey and relative to each specific cue image, we were unable to find any systematic differences relating to either social status or reaction time. However, we do not currently exclude the possibility that fixations toward the cuing monkey's eye region may correlate with subsequent gaze-following (e.g. [S5]): We note that for the images and fixation windows used in this experiment, successful task performance generally positioned at least part of the cuing monkey's eye-region within the subject's fovea.

Onset and offset of task-related saccades were defined using a velocity criterion (onset, $\geq 60^\circ/\text{s}$ for ≥ 8 samples; offset, $\leq 30^\circ/\text{s}$ for ≥ 3 samples). We gathered 1000-7000 successful trials from each macaque, excluding saccades initiated faster than 90 ms or

slower than 280 ms. The average number of successful trials collected in a single session was 754, with no session contributing more than or 35% the subject's total. "Incidental" successes, defined as successful trials that occurred despite a $\geq 50\%$ fail rate within ± 2.5 -minute time window, were excluded from analysis. To minimize the variance in reaction time due to transient spatial biases or changes in motivation, we normalized our data by subtracting the mean successful reaction time for each monkey and target direction across a 15-minute moving window within each dataset.

All monkeys had extensive experience with nonsocial visual orienting tasks. However, to investigate the effects of experience in this specific paradigm, we parameterised the training history at every data point by noting the log chronological order in which each data point was gathered from a given subject. Neither training history nor the local (± 2.5 -minute) success rate interacted with gaze-following or the temporal dynamics thereof as continuous predictors of normalized reaction time in a homogeneity-of-slopes general linear model (training history on congruence, $p=0.3$, training history on cue duration by congruence, $p=0.09$; local success rate on congruence, $p=0.3$, local success rate on cue duration by congruence, $p=0.4$). We found an identical pattern of subject status effects using only the first 500 correct trials from each monkey, confirming that training history was not responsible for the subject effects reported here.

Morphometric data was recorded in one day while monkeys were anaesthetized for a routine physical exam. To estimate circulating testosterone, we used callipers to measure the testicles of each subject across their longest axis: these measurements, cubed, estimate testicular volume and thus the rate of testosterone production[S6].

- S1. Deaner, R.O., Khera, A.V., and Platt, M.L. (2005). Monkeys pay per view: adaptive valuation of social images by rhesus macaques. *Curr Biol* 15, 543-548.
- S2. Fuchs, A.F., and Robinson, D.A. (1966). A method for measuring horizontal and vertical eye movement chronically in the monkey. *J Appl Physiol* 21, 1068-1070.
- S3. Judge, S.J., Richmond, B.J., and Chu, F.C. (1980). Implantation of magnetic search coils for measurement of eye position: an improved method. *Vision Res* 20, 535-538.
- S4. Deaner, R.O., and Platt, M.L. (2003). Reflexive social attention in monkeys and humans. *Curr Biol* 13, 1609-1613.
- S5. Dalton, K.M., Nacewicz, B.M., Johnstone, T., Schaefer, H.S., Gernsbacher, M.A., Goldsmith, H.H., Alexander, A.L., and Davidson, R.J. (2005). Gaze fixation and the neural circuitry of face processing in autism. *Nat Neurosci* 8, 519-526.
- S6. Bercovitch, F.B., and Ziegler, T.E. (2002). Current topics in primate socioendocrinology. *Annual Review of Anthropology* 31, 45-67.