Social status gates social attention in monkeys

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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.

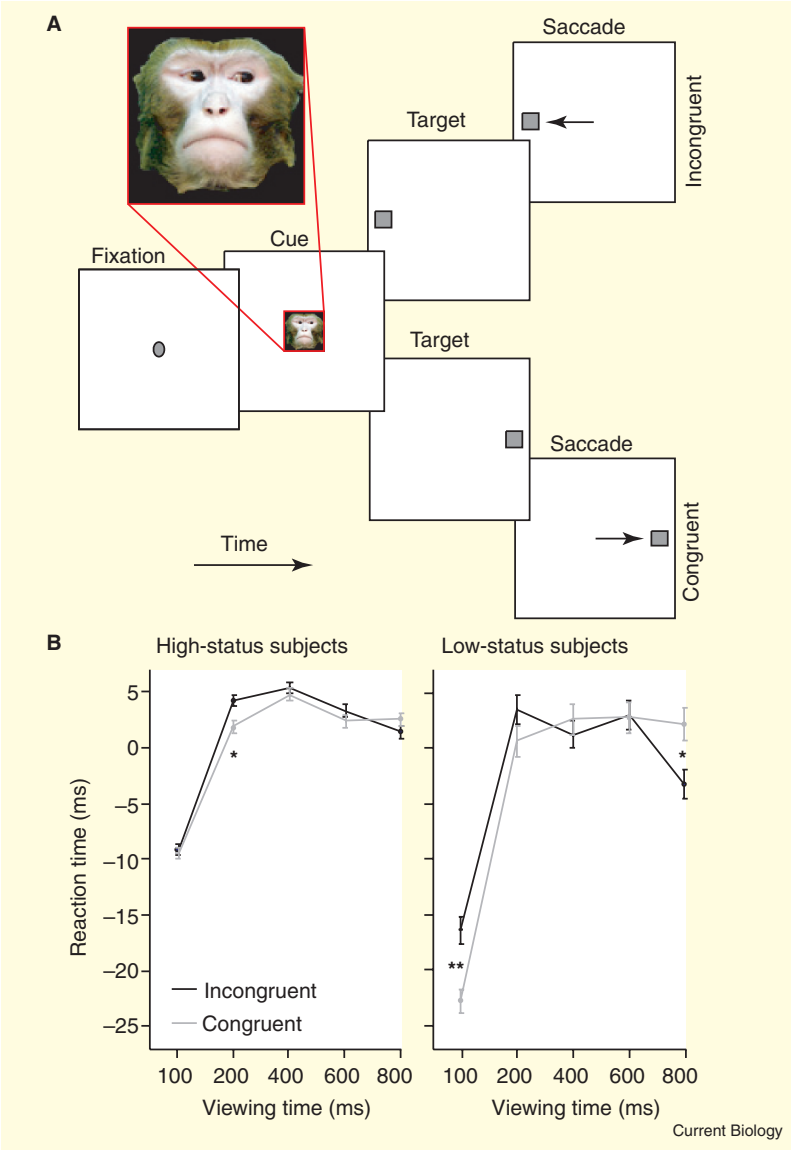

Figure 1. Observed gaze and social status influence saccade reaction times.

(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 (±3°) 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 10–15° 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 (±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.

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Supplemental data

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

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