Watching fights raises fish hormone levels

Cichlid fish wrestling for dominance induce an androgen surge in male spectators.

Social interactions among the animals in a group affect their subsequent behaviour, manifesting as dominance hierarchies or territoriality, for example, and meaning that behaviour is adjusted to social context[1]. These interactions are thought to be modulated by androgens, allowing the agonistic motivation of individuals to adjust to changes in their social environment; androgen production is itself determined by sexual status and by social contacts among conspecifics[2]. Here we show that the adaptive value of socially modulated androgen levels in male cichlid fish can be extended to bystanders who watch but who do not participate in social confrontation.

The 'challenge hypothesis' proposes that an individual's androgen production responds to their social interactions with other group members[2]. We investigated whether this hypothesis can be extended to bystanders by monitoring the effect of watching fights between conspecifics on the androgen levels of adult male cichlid fish, *Oreochromis mossambicus*. Males of this species defend mating territories in leks during the breeding season.

Fish of comparable size and age and raised in similar conditions were placed in social isolation for 7 days (phase 1) to minimize the influence of previous social experience on androgen levels. Bystander males were allowed to watch two isolated conspecific male neighbours through a one-way mirror for a period of 3 days (phase 2). After this time, the opaque partition keeping the two neighbours apart was removed at 9 a.m. to allow a one-hour fight for dominance to take place. The fight was watched by the bystander through the one-way mirror (phase 3).

We collected urine at different stages from bystanders for radioimmunoassay to determine the concentrations of testosterone and 11-ketotestosterone, the principal fish androgens[3]. Samples were taken 2 hours before the start of phase 3 to act as a reference for androgen levels in the presence of two conspecific males; at 30 minutes after the end of the fight; at 2 hours after the end of the fight; and at 6 hours after the end of the fight. Urine from controls (who witnessed no fight because the opaque partition was kept in place, preventing interaction between the bystander's two neighbours) was also collected at the time points corresponding to these stages.

If androgens are produced in response to a social interaction among conspecifics, androgen concentrations in urine from bystander fish should rise in the experimental situation but not in the controls. We found that 30 min after witnessing fights among conspecifics, the amounts of both testosterone and 11-ketotestosterone were significantly raised in the urine of the bystander, with 11-ketotestosterone remaining above basal concentrations for a further 3 hours after the fight (Fig. 1a, b). By contrast, in the control situation there was a continuous decline in both steroids, which is largely explained by the normal daily variation in basal urinary androgen, being highest in the early morning, at the start of phase 3, and then decreasing during the day (Fig. 1c).

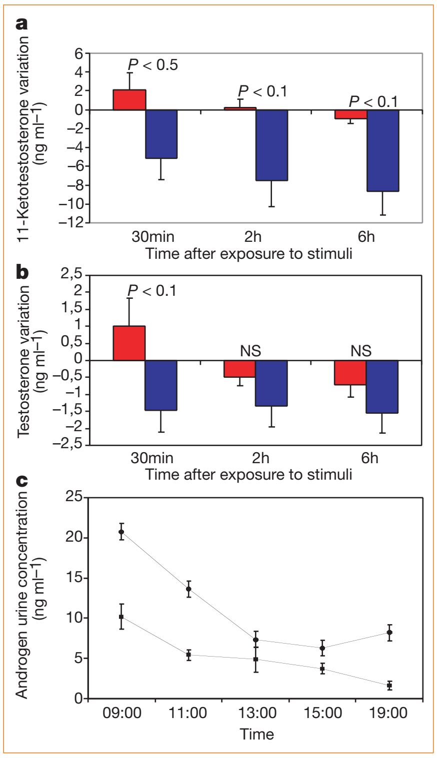

Figure 1 Social interactions modulate androgen levels of bystanders. **a, b,** Variation of bystander (red) total (free + sulphate + glucuronide) urinary levels of 11-ketotestosterone (**a**) and testosterone (**b**) after witnessing a conspecific fight relative to the pre-test reference values (concentration before watching the fight minus the concentration after watching the fight). Blue, controls. **c,** Daily variation in testosterone (bottom curve) and 11-ketotestosterone (top curve) in males after 7 days of social isolation. Sample size (n) was 18 fish, apart from the 11-h sample point, for which $n = 17$, and the 11-ketotestosterone 19-h sample point, for which $n = 13$. Urine was collected into 1.5-ml Eppendorf tubes by applying gentle pressure to the ventral area of the fish flanks. Sample processing radioimmunoassay characteristics have been described elsewhere[4,10,11]. P values refer to Mann–Whitney tests.

Our results indicate that the endocrine system of spectators responds to social interactions in which they do not themselves participate. Androgen levels pertaining in combatants 30 min after the start of a fight are a good predictor of the individual's position in the final hierarchy[4], so the presence of increased concentrations in spectators suggests that these hormones mediate changes required for sharpening awareness and readiness to challenge. The potential adaptive benefits of increasing androgen levels during social challenge include a positive effect on cognitive tasks, promoting an animal's success socially by enhancing social attention, learning and memory processes[5,6].

Animals use information from previous interactive experiences to adjust their behaviour in subsequent social situations (as evidenced by the winner–loser effect[7], eavesdropping[8] and audience effects[9], for example). Androgens are the likely mediators of these effects, acting by modulation of cognitive mechanisms underlying animal communication. We conclude that the 'challenge hypothesis' can be extended to bystander individuals. Androgens may eventually be viewed not only as sex steroids, but also as competition hormones that respond to the social environment and prepare the individual for competitive situations, rather as corticosteroids are considered as stress hormones in addition to their everyday function as metabolic regulators.

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