Physiology & Behavior 105 (2012) 489–492

Contents lists available at SciVerse ScienceDirect

Physiology & Behavior

journal homepage: www.elsevier.com/locate/phb

'Winner effect' without winning: Unresolved social conflicts increase the probability of winning a subsequent contest in a cichlid fish

Peter D. Dijkstra [a,b,*], Sara M. Schaafsma [a], Hans A. Hofmann [b,c], Ton G.G. Groothuis [a]

[a] Behavioural Biology Research Group, Institute for Behaviour and Neuroscience, University of Groningen, The Netherlands
[b] The University of Texas at Austin, Section of Integrative Biology, Austin, TX, USA
[c] The University of Texas at Austin, Institute for Neuroscience and Institute for Cellular and Molecular Biology, Austin, TX, USA

ARTICLE INFO

Article history:
Received 15 July 2011
Received in revised form 12 August 2011
Accepted 24 August 2011

Keywords:
Winner effect
Aggression
Androgens
Challenge hypothesis
Cichlid

ABSTRACT

Previous winning experience increases the probability of winning a subsequent contest. However, it is not clear whether winning probability is affected only by the outcome of the contest (winning or losing) or whether fighting experience itself is also sufficient to induce this effect. We investigated this question in the East African cichlid fish *Pundamilia* spec. To create an unresolved conflict we allowed males to fight their own mirror image prior to a real fight against a size-matched non-mirror-stimulated control male. When males fight their own mirror image, the image's response corresponds to the action of the focal animal, creating symmetrical fighting conditions without the experience of losing or winning. We found that mirror-stimulated males were more likely to win an ensuing contest than control males. Interestingly, in this species mirror stimulation also induced an increase in circulating androgens, which is consistent with the hypothesis that stimulation of these sex steroids during aggressive encounters may prepare the animal for subsequent encounters. Our results suggest that fighting experience alone coupled with an androgen response, increases the likelihood of winning, even in the absence of a winning experience.

© 2011 Elsevier Inc. All rights reserved.

1. Introduction

Almost all animal species respond to social challenges, such as territorial intrusion [1]. It has long been known that experiencing aggressive encounters affects the chances of winning future contests, independent of intrinsic fighting ability: winning a fight increases the probability of winning a subsequent contest (winner effect), whereas the experience of defeat has the opposite effect [2,3; reviewed in 4,5]. The winner effect can help to shape emerging social structures and the establishment of dominance hierarchies [2,3]. Despite the ubiquity of the winner effect, little is known about the physiological and cognitive processes that govern its formation [6,7]. Research indicates that the perception of victory is necessary to increase success in a later encounter [8], but it is also possible that fighting experience alone even in the absence of winning is sufficient.

The neuroendocrine system responds to social challenges and thus is well suited to mediate the winner effect [e.g. 1,7,8]. In males of a wide range of vertebrates, aggressive behavior is accompanied by a (transient) increase in androgens [9]. This correlation between androgens and the social environment is generally thought to modulate subsequent agonistic and reproductive motivation, in that it prepares the animal for future competitive situations ('Challenge Hypothesis', [9]; for recent reviews see [10–13]). Winners often exhibit elevated post-encounter testosterone levels, and several studies indeed suggest that in winners testosterone acts as a reinforcer of aggressive behavior in subsequent encounters, enhancing the chances of future victories [14,15]. However, most research suggests that the perception of winning itself, rather than fighting behavior alone, is instrumental in short-term increases in androgens and driving the winner effect [2,5,8,9]. It is unclear, however, whether the perception of victory is necessary to increase androgen levels and success in a later encounter or whether fighting experience alone even in the absence of winning is sufficient.

To examine this question, we allowed males of the Lake Victoria cichlid fish *Pundamilia* to fight their own mirror image or a non reflecting similar object before fighting a real fight. In mirror-elicited fights the focal male is given fighting experience without experiencing victory or defeat, i.e., the contest remains unresolved, because the mirror image's response is perfectly symmetric to the actions of the focal animal [16]. This paradigm allowed us to test the hypothesis that the experience of an unresolved (mirror-stimulated) fight increases the probability of winning a future encounter with a real opponent (Experiment I). In order to investigate whether success in later encounters after mirror fighting is mediated by androgens, we investigated in Experiment II whether escalated fighting during a mirror-stimulated fight is sufficient to induce an increase in circulating androgens. Previous research on this second question yielded contradictory results. Oliveira et al. [16] and Hirschenhauser et al. [17] failed to detect an androgen response

* Corresponding author at: The University of Texas at Austin, Section of Integrative Biology, 1 University Station-C0930, Austin, TX 78712, USA. Tel.: +1 512 475 7318.
E-mail address: pddijkstra@gmail.com (P.D. Dijkstra).

0031-9384/$ – see front matter © 2011 Elsevier Inc. All rights reserved.
doi:10.1016/j.physbeh.2011.08.029

during a mirror fight in the nile tilapia *Oreochromis mossambicus* and the Japanese quail (*Coturnix japonica*), respectively. However, these authors measured androgens in urine and feces, respectively, which are often assumed to correspond well with circulating levels [18–20]. However, several factors can affect the interpretation of such measures, such as the unclear temporal relationship between acute androgen responses in the circulation and their subsequent release into the environment via the digestive or excretory systems; the frequency of urination and defecation, which can depend on social cues; the metabolized nature of the hormones released this way; and possible cross-reactivity to metabolites from other steroid hormones [20–22]. It is therefore interesting to note that males of the cichlid fish *Astatotiapia burtoni* exhibited increased levels of circulating androgens during a mirror fight [23; see also 24]. This later result is consistent with our prediction that during a mirror fight hormones should increase in anticipation of further escalation of the fight against an equally strong opponent, likely increasing winning probability in later encounters.

2. Methods

2.1. Animals

We used 105 lab-bred, 18–24 months old adult males belonging to the haplochromine cichlid fish *Pundamilia* spec. from Lake Victoria. Haplochromine cichlids are polygynous, female mouth brooders without a pairbond and with strong male territoriality [25]. All aquaria contained a gravel substrate and were connected to a central biological filter system with continuously circulating water which was maintained at a temperature of 25 ± 2 °C. A natural tropical light: dark cycle of 12:12 h was maintained. The fish were fed flake food six times per week and a mixture of ground shrimps and peas twice per week. All experiments were carried out under animal experiment licenses (DEC 3137 and DEC 4335A) granted by the University of Groningen and in compliance with current laws in The Netherlands.

2.2. Experiment I

2.2.1. Procedure

Males were individually housed in separate compartments with visual but no physical access to other males at least 1 week prior to the experiments. At least 3 days before each test we placed pairs of size-matched males with no history of prior interactions in 100 liter test aquaria, which were subdivided by an opaque partition into two compartments, each of which contained a PVC tube as shelter. Thus, each male had no visual access to other males. Prior to combat, one randomly chosen male in each pair ($n = 40$) was presented with a mirror at one end of the compartment for 15 min; the corresponding control male was exposed to a sheet of black non-reflective glass instead to control for the presence of a novel object in the aquarium. The fighting behavior of the fish was recorded for 15 min using a focal continuous recording method. All aggressive displays (gill or frontal display and lateral display) and attacks (individual butts and bites at the mirror) were scored. We then removed the mirror/glass, and immediately lifted the opaque partition between the two experimental fish and the ensuing fight was observed from behind a blind. We identified winner and loser, defined as the winner chasing the loser at least three consecutive times [26]. We then immediately separated the fish. If there was no resolution within 30 min (fight duration, mean ± SE = 792 ± 88 s, $n = 40$), we separated the fish and called it a tie.

2.3. Experiment II

2.3.1. Procedure

For 7 days prior to the experiment, each male ($n = 25$) was housed in isolation in a 50 l aquarium with a PVC tube as a shelter. On Day 7, the fish were randomly divided into two groups; the first (experimental group, $n = 13$) was presented with a mirror at one end of the aquarium for 20 min; the second (control group $n = 12$) was exposed to a sheet of black non-reflective glass instead to control for the presence of a novel object in the aquarium.

We recorded the fighting behavior of the fish for 20 min using a focal continuous recording method. At the end of the 20-min test, we removed either the mirror or the sheet of black non-reflective glass. We then collected blood from the caudal vein using a 1 ml syringe and 0.5×16 mm needles. From approximately half of the fish in each group blood was collected within <5 min after the end of the test. Blood collection from the remaining animals occurred 30 min after the end of the test. We chose for these two time points to determine the temporal dynamics of the androgen surge after a mirror fight. Each sample was centrifuged at 12,000 rpm for 10 min to isolate the plasma portion of the blood, which was then stored at −80 °C until assayed for hormones.

We measured circulating levels of two androgens, T and 11-KT, in blood plasma using enzyme immunoassays (T: Assay Design, Ann Arbor, MI; 11-KT: Cayman Chemical Ann Arbor, MI) following protocols established by and exactly as described in Kidd et al. [27]. We used 7.2 and 3.6 μl blood plasma per sample to assay T and 11-KT, respectively. The intra-assay coefficient of variation (CV) was 1.58% and 2.57% for the T and 11-KT, respectively. The inter-assay CV was 6.56% and 4.46% for T and 11-KT, respectively. Cross-reactivity for these kits and sensitivities are shown in Kidd et al. [27].

2.4. Analysis

Hormone, aggression and fight duration data were log transformed ($\ln x + 1$) prior to analyses to meet assumptions of parametric testing. In Experiment I, we tested which males (mirror stimulated or control) had higher probabilities of winning using a binomial test. Hormone levels were compared between fish from the experimental and the control group, using ANOVA with time of sampling (0 or 30 min) and treatment as explanatory factors. We report means ± standard error. All quoted probabilities are for two-tailed tests of significance.

3. Results

3.1. Experiment I

Seven of 40 mirror-stimulated males did not show any response (neither agonistically nor submissively) toward their own mirror image. Of those seven individuals, three won and four lost the subsequent encounter. Eight of the 40 dyadic contests ended in a tie (i.e., remained unresolved after 30 min, without a clear winner). In the remaining 25 fights, 18 mirror-stimulated males defeated the control male in the subsequent fight; this winning success rate (72%) was significantly higher than expected by chance (binomial test, $p = 0.042$, $n = 25$). Neither the duration of the fight (Wald = 0.20, $df = 1$, $p = 0.65$), nor the rate of aggression against the mirror image (logistic regression: attack rate: Wald = 0.31, $df = 1$, $p = 0.58$; display rate: Wald = 0.65, $df = 1$, $p = 0.42$) significantly affected the probability of winning the ensuing fight.

3.2. Experiment II

All males exposed to a mirror reacted very aggressively to their own image, whereas males exposed to a non-reflective surface did not show any aggressive behavior at all (Fig. 1). Over the course of the testing period, the attack rate, but not the display rate of males in the mirror-stimulated group showed a non-significant upward trend over time (RM-ANOVA with the sum of attacks per five minute interval as repeat, attack: $F(1,12) = 4.095$, $p = 0.07$; display: $F(1,12) =$

Download English Version:

https://daneshyari.com/en/article/5925580

Download Persian Version:

https://daneshyari.com/article/5925580

Daneshyari.com