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Øverli, Øyvind; Korzan, Wayne J.; Larson, Earl T.; Winberg, Svante; Lepage, Olivier; Pottinger, Tom G.; Renner, Kenneth J.; Summers, Cliff H.. 2004
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Behavioral and neuroendocrine correlates of displaced aggression in trout

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Key words: Aggression, cortisol, displacement behavior, serotonin, stress, telencephalon

Abstract

In humans and other primates, violent actions performed by victims of aggression are often directed toward an individual or object that is not the original source of provocation. This psychological phenomenon is often referred to as displaced aggression. We demonstrate that displaced aggression is either rooted in evolutionarily conserved behavioral and neuroendocrine mechanisms, or represent a convergent pattern that has arisen independently in fish and mammals. Rainbow trout that briefly encountered large, aggressive fish reacted with increased aggression towards smaller individuals. There was a strong negative correlation between received aggression and behavioral change: Individuals subjected to intense aggression were subdued, while moderate assaults induced strong agitation. Patterns of forebrain serotonin turnover and plasma cortisol suggest that the presence of socially subordinate fish had an inhibitory effect on neuroendocrine stress responses. Thus, subordinate individuals may serve as stress reducing means of aggressive outlet, and displaced aggression towards such individuals appears to be a behavioral stress coping strategy in fishes.

Introduction

Aggressive actions in humans are often directed toward an individual or object that is not the original source of provocation, a psychological phenomenon referred to as displaced aggression (Marcus-Newhall et al., 2000). In the following, we review literature and report data which demonstrate that displaced aggression is either rooted in behavioral and neuroendocrine mechanisms of early evolutionary origin, or represent convergent patterns that have occurred independently in fish and mammals.

In primates, individuals that lose fights frequently attack a subordinate bystander that was not involved in the original conflict (Sapolsky and Virgin, 1997). This displaced, or re-directed, aggression in former victims of aggression is thought to represent either a stress-reducing behavioral outlet (Sapolsky and Virgin, 1997), or a signal of post-conflict state, i.e. continued motivation and ability to perform aggressive behavior and defend oneself (Kazem and Aureli, in press).

The hypothesis that aggression toward others functions as a stress-reducing behavioral coping strategy is frequently cited, but has rarely been tested. In rats, biting another individual has been reported to work as an effective outlet after stress (Levine et al., 1989). Other displacement behaviors such as wheel running or frequent self-induced feeding and drinking are also known to decrease plasma glucocorticoid concentrations (Dantzer, 1993). Circumstantial evidence indicates that similar mechanisms are operating in non-mammalian vertebrates (Knapp and Moore, 1995; Winberg et al., 1996).

As in mammals, social defeat has been shown to induce behavioral changes, chronically elevated plasma glucocorticoid levels, and altered brain neurochemistry in poikilothermic animals (Winberg and Nilsson, 1993; Øverli et al., 1998, 1999; Winberg

and Lepage, 1998; Höglund et al., 2001; Summers, 2002; Summers et al., 2003). Among the most characteristic effects of social stress is a widespread and sustained elevation in metabolism and release of the monoamine neurotransmitter serotonin (5-Hydroxytryptamine, 5-HT). Stress induced alterations in 5-HT activity is thought to be involved in the control of a range of behavioral and physiological stress responses, such as appetite inhibition, aggression, and glucocorticoid and peptide hormone release (Winberg and Nilsson, 1993; Winberg et al., 1997; Øverli et al., 1998, 1999; De Pedro et al., 1998; Larson and Summers, 2001; Höglund et al., 2002). During continued interaction in a stable hierarchy, winners of fights for social dominance show a rapid down-regulation of the 5-HT and glucocorticoid response to fighting (Øverli et al., 1999; Summers et al., 2003). In lizards (Knapp and Moore, 1995) and fish (Winberg et al., 1996) this reversal is absent or considerably delayed if all subordinate individuals are removed from the habitat of the dominant animal. Thus, it can be hypothesized that the prolonged presence of a subordinate has an inhibitory effect on the stress response in dominant animals.

The rainbow trout is a teleost species that forms strong dominance hierarchies when reared in small groups in the laboratory (Winberg and Lepage, 1998; Øverli et al., 1999). In the current study, juvenile rainbow trout were used to test the hypothesis that individuals of intermediate rank react to short-term social stress by increasing their aggression against smaller, subordinate fish. Furthermore, the ability to project aggression on other individuals was manipulated to determine if this behavior facilitated down-regulation of the physiological stress response in the aggressor. Along with

behavioral observations, forebrain and hypothalamic 5-HT activity and plasma cortisol was analyzed in an attempt to elucidate the underlying neuroendocrine mechanisms.

Material and methods

Prior to the experiment, juvenile rainbow trout (size range 70-200g) from a commercial fish farm had been kept indoors in holding tanks as described elsewhere (Øverli et al., 2002). Experiments took place in glass aquaria (100 x 50 x 50 cm), which were divided into four 50 l compartments by removable opaque PVC walls. Test fish weighed between 70-100 g at the time of the experiment, this size range was selected so that the size of the test fish was close to the mean of the population in the holding tank. Furthermore, a corresponding number of smaller (weight range 35-50 g) and bigger (weight range 140-200 g) individuals were distributed in the compartments next to the test fish so that one neighboring compartment contained a fish approximately half the size of the test fish, while a twice as large conspecific resided on the other side. The maximum allowed deviation from the 1-2-4 size ratio was 5%. The fourth compartment in each aquarium was either empty or contained a control fish weighing 70-100 g, which was held in isolation and left undisturbed throughout the experiment.

Fish were hand fed daily after transfer to rearing in isolation, and if one fish in a group of four failed to regain feed intake (eating at least 1% body weight/day) within one week in the observation aquaria, all fish in that group were discarded. In groups of fish that acclimated successfully (90% of all set-ups), the test fish was paired with its smaller neighbor by removing the PVC wall separating their individual territories. Previous experiments have shown this holding regime highly effective in inducing territoriality

and motivation to express aggressive behavior in rainbow trout (Winberg and Lepage, 1998; Øverli et al., 1999; Pottinger and Carrick, 2001). Although fish in individual compartments in this test system are only visually isolated, and may exchange pheromonal cues, the intensity of conflicts observed during encounters suggest that actual aggressive interaction is essential for hierarchy formation in salmonids. Sex differences have also been shown not to determine the outcome of fights for social dominance in reproductively immature rainbow trout (Øverli et al., 2004).

In all cases, the test fish won fights for social dominance with their smaller opponent. From the moment a fight winner was identified and the smaller fish stopped retaliating on aggressive acts performed by the test fish, we recorded the frequency of aggressive acts performed by the test fish in the established dominant-subordinate relationship. After 10 min of interaction in dominance-subordinate relationships, test fish were randomly assigned to one of three different treatments: **1) Defeat + re-establishment:** Test fish were paired with larger neighbors, while the smaller fish were isolated. Fights for social dominance were now always lost by the test fish, and the number of aggressive acts received by the test fish was recorded for 10 min. Test fish were then paired with their smaller partners again, and aggressive behavior was observed as above. **2) Defeat + isolation:** Interactions with small and large fish were carried out as above, but test fish were left in isolation for 16 min at the end of the experiment, corresponding to the mean duration of the final interaction with smaller, subordinate fish experienced by the defeat + re-establishment group. **3) No-defeat:** Test fish were allowed to establish social dominance repeatedly, but left in isolation instead of being defeated by a larger individual between encounters with subordinate fish. The isolation period lasted

13 min, corresponding to the mean duration of the encounters with larger fish experienced by other groups.

Immediately after the last observation/isolation period, test fish and corresponding controls were removed and anaesthetized in 0.5 g/ml Tricaine Methanesulfonate (MS 222). Blood samples were obtained and fish were decapitated and brains were removed and frozen at -80°C within 2 minutes of capture. These procedures adhered to the National Institutes of Health Guide for the Care and Use of Laboratory Animals and were approved by the Uppsala Animal Research Ethical Committee. Plasma cortisol was analyzed as described elsewhere (Øverli et al., 1999). Brain-punch microdissection on 300 µm sections were performed as described by Korzan et al. (2000), followed by analysis of brain serotonergic activity by detection of 5-HIAA and 5-HT in punched tissue samples by high-pressure liquid chromatography with electrochemical detection (Summers et al., 1997; Korzan et al., 2000). The hypothalamic preoptic area (POA), dorsal and lateral parts of the lateral zone of the dorsal area of the telencephalon (Dld-Dlv), and commissural and supracommissural nuclei of the ventral area of the telencephalon (Vc-Vs), putative homologues of the mammalian hippocampus and amygdala, respectively (Northcutt and Davis, 1983; Butler and Hodos, 1996), were identified for punching following Carruth et al. (2000).

The change in aggression (%) between repeated encounters with the same subordinate individual was calculated for the no-defeat and the defeat + re-establishment groups. These data were analyzed by t-test for single comparisons. Physiological data from all experimental groups including controls were analyzed by ANOVA followed by the least significant difference test for post-hoc comparisons, with an α -level of $p < 0.05$ as

criterion for statistical significance. Homogeneity of variance was checked by the Levene's test (Statistica for Windows software package, StatSoft Inc, Tulsa, OK).

Results

On average, test fish subjected to short-term defeat exhibit a 77% increase in aggression toward subordinate individuals (Fig. 1A). Fish that were left in isolation between encounters with a subordinate individual, in contrast, showed decreased aggression when re-introduced to the subordinate partner. This effect of experimental regime was highly significant ($t_{(14)}=3.45$, $p=0.004$). Moreover, change in aggression was negatively correlated to the number of aggressive acts launched against each test fish during the intervening period of social subordination (Fig. 1B).

Plasma cortisol and forebrain 5-HT neurochemistry in experimental groups and isolated, undisturbed controls is shown in Fig. 2. Elevated tissue concentrations of the 5-HT metabolite 5-hydroxyindoleacetic acid (5-HIAA) are considered indicative of increased release and turnover of the neurotransmitter (Fillenz, 1993). Most frequently, the concentration of 5-HIAA relative to that of 5-HT (5-HIAA/5-HT ratio) is used as a measure of neural activity. In both Vc-Vs ($F_{(3,24)}=9.16$, $p<0.001$) and Dld-Dlv ($F_{(3,26)}=7.05$, $p=0.001$) the ANOVA indicated that 5-HIAA/5-HT varied between experimental groups. Post-hoc tests revealed that this ratio was significantly elevated as compared to controls in fish that had been exposed to social subordination, but not in the no-defeat group. This elevation was evident in both brain parts, regardless of whether fish were held in isolation or allowed to interact with the original subordinate partner after defeat. Furthermore, according to post-hoc comparisons, presence or absence of a

subordinate individual in the original territory of the test fish after defeat had a significant effect on serotonergic activity in the Dld-Dlv: Defeated test fish allowed to interact with a subordinate displayed significantly higher 5-HIAA/5-HT ratios in this brain part than test fish left in isolation. A non-significant trend (post hoc $p=0.09$) towards the opposite pattern was seen in the Vc-Vs. Serotonergic activity in the POA was unaffected by social interaction in this experiment (data not shown). This slightly unexpected observation may be due to the relatively short time-course of behavioral interaction utilized in this experimental set-up. Previous experiments have shown that the telencephalon is the region in the brain that first shows measurable changes 5-HT metabolism following social stress in fish (Øverli et al, 1999).

Plasma cortisol was also significantly affected by social interactions ($F_{(3,27)}=4.59$, $p=0.01$). Similar to brain 5-HT activity, post-hoc comparisons indicated that cortisol was elevated in the defeat+isolation and defeat+re-establishment groups as compared to isolated controls. This elevation was not significant in fish that only interacted with a socially subordinate partner. The effect of the presence or absence of a subordinate on plasma cortisol did, however, not reach statistical significance (post hoc $p=0.08$).

Discussion

A striking observation in the current study is that fish subjected to short-term social stress reacted by increasing their aggression towards smaller individuals. This is the opposite of what happens when salmonid fish are subjected to longer periods of social stress (Höglund *et al.*, 2001). There was also a strong negative correlation between the amount of aggression an individual was subjected to, and the magnitude of the change in

behavior: Larger increases in aggression were seen in individuals that received fewer aggressive acts. Thus, it appears that individuals of intermediate social rank increase their aggression towards subordinates when subjected to moderate and short-term defeat. Increased intensity of received aggression, on the other hand, abolishes this response.

Social defeat led to increased 5-HT activity in both the Vc-Vs and the Dld-Dlv telencephalon areas, while 5-HT systems appeared unaffected by social interaction in fish paired repeatedly with a subordinate individual. Thus, as opposed to the inhibitory effect of 5-HT during long term social stress (Winberg and Nilsson, 1993; Höglund *et al.*, 2001) elevated forebrain 5-HT activity was associated with increased aggression in animals subjected to short-term defeat. This observation suggests that the relationship between 5-HT and aggressive behavior is time-, region-, and context- dependent, and the effect of 5-HT on aggression may be more complex than the purely inhibitory role that is usually ascribed to this neurotransmitter.

Interestingly, Dld-Dlv 5-HIAA/5-HT ratios were also higher in fish that were re-introduced to their original subordinate partner after being defeated (**defeat + re-establishment** group) than in fish that were left in isolation after interaction with dominant individual (**defeat + isolation** group). This indicates that release of 5-HT in this brain area was dependent on the presence or absence of a subordinate conspecific in the period directly following social defeat. Homologies between distinct pallial areas of teleosts and other vertebrates are debated (Butler, 2000; Saidel *et al.*, 2001; Portavella *et al.*, 2002; Rodríguez *et al.*, 2002; Holmes and Northcutt, 2003). Provided, however, that the Dld-Dlv in part corresponds to the mammalian hippocampus (Northcutt and Davis, 1983; Butler and Hodos, 1996), our data raise an interesting possibility: Projecting

aggression on another individual after a defeat may alter hippocampal modulation of the physiological stress response.

In mammals, the amygdala and hippocampus are thought to be important for control of the stress response in opposing ways: The amygdala is generally assumed to mediate excitatory effects on hypothalamus-pituitary-adrenal (HPA) function, while hippocampal stimulation inhibits most aspects of HPA activity, including circadian cycles and responses to stress (Jacobson and Sapolsky, 1991; Herman and Cullinan, 1997; López *et al.*, 1999). The presence or absence of a subordinate individual after stress led to largely opposite patterns of 5-HT activation in these two brain regions (*c.f.* figure 2). This observation supports the idea that displaced aggression towards subordinate individuals serve as a behavioral stress coping strategy that may modulate the physiological stress response (Sapolsky and Virgin, 1997).

It is currently not known whether 5-HT modulation stimulates or reduces hippocampal inhibition of glucocorticoid release. In mammals, serotonergic activity has been demonstrated to limit hippocampal output via 5-HT_{1A} receptors on pyramidal neurons; while 5-HT₄ receptor stimulation and 5-HT induced inhibition of GABAergic interneurons enhances hippocampal output (Andrade and Nicoll, 1987; Andrade and Chaput, 1991; Gulyás *et al.*, 1999; Kasamo *et al.*, 2001; Chapin *et al.*, 2002). In our data, there was a trend towards higher plasma cortisol concentrations in fish that were not re-introduced to their subordinate partners after social defeat (*c.f.* figure 2). Considering that this group simultaneously displayed decreased Dld-Dlv 5-HT turnover, these data do not support a stimulatory effect of hippocampal 5-HT on glucocorticoid release. It should be

kept in mind that temporal dynamics of the stress response may both influence and be influenced by social interactions (Summers, 2002; Summers *et al.*, 2003).

In conclusion, it appears that displaced aggression, a well known psychological phenomenon in humans, has counterparts in behavioral and neuroendocrine mechanisms that may have arisen at an early stage in vertebrate evolution. These observations support the view that studies in animals and humans must converge in order to increase our understanding of the biological mechanisms behind violent aggressive behavior. It would be of especially high interest to investigate whether it also holds true in humans that a moderate amount of received aggression induces a strong behavioral reaction, while no provocation as well as intense social subordination is associated with less violent behavior.

Acknowledgements

We thank Mrs. Patricia Crotwell; Dr. Michael Watt, and Dr. Gina Forster for valuable comments on this manuscript. This work was financially supported by NIH (grant no P20 RR15567 and 1 F31 MH64983-01) and the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS). Experiments were approved by the Uppsala Ethical Animal Research Committee. Special thanks to professor Bengt Meyersson and the FACIAS foundation for supporting and encouraging this experiment.

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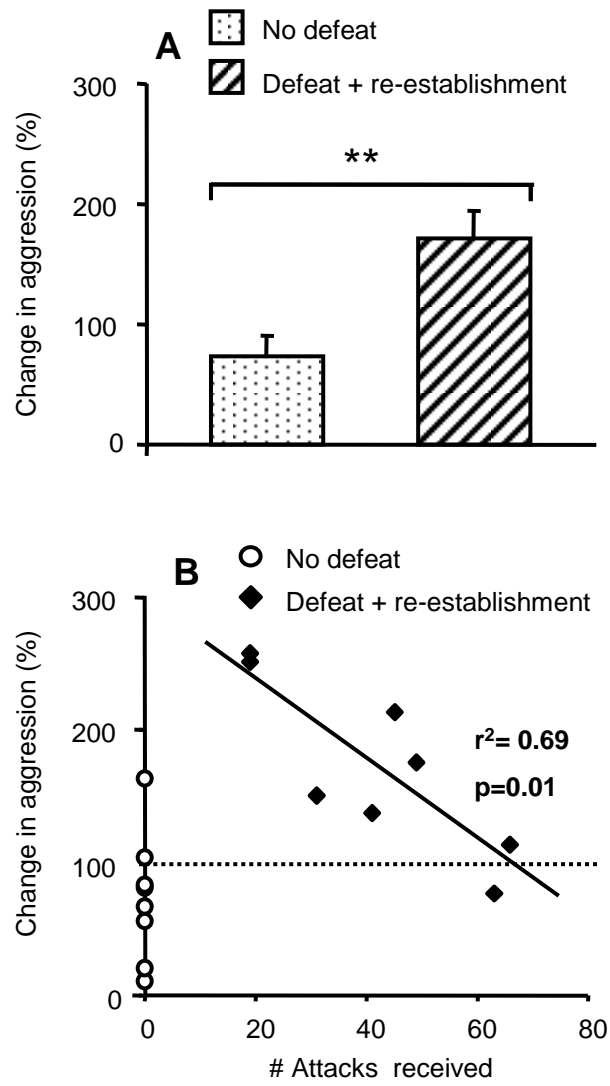
Figure legends

Fig.1. A. Change in aggressive behavior in rainbow trout of intermediate social rank subjected to repeated interaction with a subordinate individual, with or without intervening defeat by a dominant individual (average + S.E., ** = $p < 0.01$, two-tailed t-test). **No defeat** means fish held with subordinate partner, then in isolation, and finally with subordinate partner. **Defeat + re-establishment** means fish held with subordinate partner, then with dominant partner, and finally with subordinate partner.

B. Relationship between change in aggressive behavior and number of aggressive acts received during the intervening period of exposure to dominant fish (Pearsson r^2 and p values). The solid line is the linear model, least squares fitted trendline. The dotted line indicates the 100% level, equaling no change in aggression. Change in aggression for the **no defeat** group, i.e. fish receiving 0 aggressive acts, is shown on the y-axis (individual data points).

Fig. 2. Forebrain serotonergic activity (A: Vc-Vs, B: Dld-Dlv) and plasma cortisol (C) in rainbow trout of intermediate social rank exposed to different regimes of interaction in pairs. **No defeat** means fish held with subordinate partner, then in isolation, and finally with subordinate partner. **Defeat + re-establishment** means fish held with subordinate partner, then with dominant partner, and finally with subordinate partner. **Defeat + isolation** means fish held with subordinate partner, then with dominant partner, and finally in isolation. Different letters indicate a significant difference ($p < 0.05$) between experimental groups (ANOVA followed by least significant difference post hoc test).

Overli_fig 1



Overli_fig 2.

