



Effects of isotocin on social responses in a cooperatively breeding fish

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Oxytocin and its nonmammalian homologues play an important role in modulating a diverse array of social behaviours. Recently, it has been suggested that one of the key functions of oxytocin is to direct attention towards socially relevant stimuli, increase social motivation and guide social decision making. Here, we test whether an exogenous increase in isotocin (the teleost homologue of oxytocin) increases the response to social information in a cooperative breeder, the highly social cichlid fish, *Neolamprologus pulcher*. In our first experiment (a simulated territorial contest), we found that *N. pulcher* injected with isotocin were more sensitive to the size of their opponent regardless of whether their opponent was a live rival or a mirror image. Isotocin-treated fish fought in accordance with the size of their opponent whereas control fish fought according to their intrinsic aggressive propensity. In our second experiment (a social group context), we found that isotocin-treated *N. pulcher* were more responsive to aggressive feedback and produced more submissive displays (an important social signal in this species). These experiments provide evidence that isotocin increases responsiveness to social information and further support the function of the oxytocin family of nonapeptides as a highly conserved regulator of social behaviour across vertebrates.

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The evolution of sociality represents one of the most enduring and important questions in behavioural biology (Székely et al. 2010). Why do some species show complex social behaviour, while other closely related species living in similar ecologies spend the majority of their lives in solitude? To answer this question, it is crucial that we develop an integrative perspective on social behaviour that includes a thorough understanding of the proximate mechanisms that generate social behaviour (Insel & Fernald 2004; Young 2009; Soares et al. 2010). The nonapeptide oxytocin (and its nonmammalian homologues; e.g. isotocin in teleost fish, mesotocin in birds and reptiles) represents a promising candidate system for the modulation of social behaviour (for recent reviews see: Donaldson & Young 2008; Goodson 2008; Lee et al. 2009; Ross & Young 2009; Goodson & Thompson 2010; Insel 2010).

Oxytocin acts both as a central neuromodulator and a peripheral hormone (Lee et al. 2009). In the periphery, oxytocin is involved in parturition and milk letdown (Lee et al. 2009). Centrally, oxytocin is essential for the regulation of behaviours related to reproduction, including pair bonding and parental care (Insel & Young 2001). A growing body of research has linked variation in oxytocin and its receptor to social behaviours outside of the realm of reproduction,

including affiliation, attachment, trust, generosity, the formation of social memories and the suppression of social anxiety (MacDonald & MacDonald 2010). Taken together, this research suggests that the oxytocin system may be a very general mechanism involved in the regulation of social behaviour (Ross & Young 2009; Goodson & Thompson 2010).

The oxytocin system is highly pleiotropic, affecting an impressive diversity of behaviours across functional contexts (e.g. parental care, cooperation, aggregation, anxiety and aggression). One possible explanation for this functional diversity is that oxytocin may be centrally involved in a higher-order regulatory system with downstream effects on a wide variety of social behaviours transcending functional context (Ross & Young 2009; O'Connell & Hofmann 2011). Recently, a unifying principle has been proposed for the function of oxytocin as a central modulator of attention to social stimuli (Ross & Young 2009). Individuals or species with greater expression of oxytocin (higher circulating levels and/or greater receptor density) may be more attentive to socially relevant stimuli and as a result may be more socially motivated. In support of this idea, it seems that the effects of oxytocin manipulations are specific to explicitly social contexts, while other functionally similar but nonsocial behaviours remain unaffected (Nelson & Panksepp 1996; Ferguson et al. 2000; MacDonald & MacDonald 2010). For example, Kosfeld et al. (2005) found that humans treated with exogenous oxytocin were more accepting of risk in a socially framed economic game (which the authors interpreted as

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increased trust) but not so in a mathematically identical, but nonsocial, version of the game. In animal models, oxytocin suppresses fear associated with social interactions and activates reward centres in the brain (Insel & Shapiro 1992; Insel & Young 2001). Oxytocin appears to be important in the evaluation of the salience and valence of social stimuli, and thus is emerging as a key element of the neural machinery for social decision making (O'Connell & Hofmann 2011). Previous work in nonmammalian vertebrates suggests that the social functions of oxytocin may be evolutionarily ancient (Goodson et al. 2009). Thompson & Walton (2004) found that treatment with exogenous isotocin increased sociability in goldfish, consistent with a role for isotocin in increasing social motivation and interest in social stimuli. Similarly, Braida et al. (2012) found that zebrafish showed greater social motivation after treatment with isotocin. The characterization of the central function of oxytocin as a highly conserved and general regulator of attention to social stimuli and hence social motivation is intuitively satisfying in that it unifies many diverse findings on the social functions of oxytocin into a single conceptual framework.

In the current paper we set out to explore the role of the teleost oxytocin homologue, isotocin (IT), in the social behaviour of the cooperatively breeding cichlid fish, *Neolamprologus pulcher* (also known as *Neolamprologus brichardi*; Duftner et al. 2007). *Neolamprologus pulcher* is a small freshwater fish endemic to Lake Tanganyika, Africa, that forms permanent social groups containing a single dominant breeding pair and several (1–20) adult subordinate helpers (Taborsky & Limberger 1981; Balshine-Earn et al. 1998; Balshine et al. 2001; Heg et al. 2005; Wong & Balshine 2011a). Individual *Neolamprologus pulcher* engage in a rich variety of social behaviours and frequently interact with other members of their own group and with individuals in nearby groups (Taborsky 1984, 1985; Wong & Balshine 2011a). In an experimental context, *N. pulcher* are highly motivated to interact with conspecifics (Jordan et al. 2010; Reddon et al. 2011a). The social complexity of group life observed in *N. pulcher* is highly unusual amongst the fishes and presents an excellent opportunity to test the hypothesis that IT plays a general role in modulating responses to social information.

Here, we report the results of two experiments designed to investigate the role of IT as a regulator of social information use in *N. pulcher*. First, we explored the effects of an experimental increase in IT on behaviour in staged aggressive contests against both mirror images and live rivals. We investigated the general effect of IT on aggression and the effect of IT on opponent assessment (especially, how perceived opponent body size regulates aggression under IT administration compared to control). Opponent body size is an important determinant of contest dynamics in animals (Arnott & Elwood 2009), including *N. pulcher* (Mitchell et al. 2009; Reddon et al. 2011b), and is a vital component of mutual assessment models of contest behaviour, where the relative asymmetry of the contestants is the strongest predictor of fight dynamics and outcome (Parker 1974; Enquist & Leimar 1983; Arnott & Elwood 2009). We predicted that increasing IT would increase sensitivity to social information, and as a result, increase the importance of opponent assessment, thereby strengthening the correlation between opponent fighting ability and focal behaviour. Specifically, we expected that IT-treated fish would be less aggressive against more formidable opponents. In our second experiment, we explored the effects of an experimental increase in IT on social behaviour within a fish's normal social group. In particular, we were interested in the effects of IT on the regulation of aggressive, affiliative and submissive behaviours in permanent social groups where responses to social feedback from other group members are an important part of an individual's daily life. We predicted that experimentally increasing IT would increase responsiveness to social feedback from other group members, resulting in more

dramatic responses to pro- and antisocial acts received from group members. Together, these two experiments increase our understanding of the role of IT as a regulator of social information use in a highly social, nonmammalian vertebrate.

GENERAL METHODS

Subjects and Housing

We used 55 adult *N. pulcher* (27 males and 28 females) in these experiments. Experimental fish were all laboratory-reared descendants of wild-caught fish. Each fish was used only once. The fish used in experiment 1 were housed in one of two 527-litre, mixed-sex communal aquaria (183 × 48 × 60 cm) prior to the experiment. These fish had been randomly assigned to these communal tanks as juveniles after being hatched within the social groups maintained in the laboratory. The fish used in experiment 2 were adult subordinate helpers from long-term social groups maintained in our laboratory. Each social group is housed in a 189-litre (92 × 41 × 50 cm) aquarium and consists of a single dominant breeding pair and several (mean: 10; range 7–15) subordinate adult helpers. Water temperature was maintained at 26 ± 2 °C. All fish were fed six times per week on commercially prepared cichlid flakes.

Dosage and Injections

Fish received intraperitoneal injections of isotocin (IT, 1 µg/g of body mass) dissolved in 0.9% saline and/or a 0.9% saline control. Injection volume was tailored to the mass of the fish (25 µl/g). The IT dose was based on previous nonapeptide research in other species (Propper & Dixon 1997; Semsar et al. 2001; Lema & Nevitt 2004; Santangelo & Bass 2006; Mennigen et al. 2008; Filby et al. 2010) and pilot testing in *N. pulcher* in our laboratory. Experiment 1 was a between-subjects design and each fish received only one of the two treatments (IT or saline control). Experiment 2 was a within-subjects design and each fish received both treatments separated by 7 days.

Ethical Note

The fish showed no adverse effects from the injections and resumed normal behaviour within a minute or two. No fish suffered any detectable injury or mortality as a result of the injections or behavioural testing. Focal fish were marked in experiment 2 with a dorsal fin clip to allow for visual identification. Fish recovered immediately from this procedure and showed no adverse effects from the marking. The methods for animal housing, handling and experimental protocols were assessed and approved by the Animal Research Ethics Board of McMaster University (Animal Utilization Protocol number 10-11-71) and adhere to the guidelines of the Canadian Council for Animal Care and ASAB/ABS Guidelines.

EXPERIMENT 1: TERRITORIAL AGGRESSION

Methods

Thirty-six *N. pulcher* (18 females, 18 males; mean standard length = 51.1 mm, range 39.4–62.8 mm) were used in this experiment. Fish were tested for aggressive tendencies in two contexts, first against their mirror image and then against a live same-sex rival across a transparent barrier. Fish were tested in a 38-litre aquarium divided into two compartments by a pair of barriers, one transparent and one opaque, running down the centre (Fig. 1). The far ends of the aquarium were covered with a mirror hidden from

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