



## Monoamines and decision making during contests in the hermit crab *Pagurus bernhardus*

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During fights animals are expected to make a series of strategic decisions that involve interactions between information about the contest and the individual's nervous system that produce a change in behaviour. Biogenic monoamines such as serotonin ('5-HT') and dopamine are thought to prime decision-making centres for appropriate responses during aggressive interactions in crustaceans, and circulating levels vary both between individuals and during agonistic encounters. Aminergic systems operate in diverse animal taxa and in this study we assayed circulating levels of 5-HT and dopamine following shell fights in the common European hermit crab, *Pagurus bernhardus*. The two roles in these fights, attacker and defender, perform different activities but, in both, 5-HT increased and dopamine declined in response to engaging in a fight. In defenders but not attackers, giving up was correlated with low 5-HT and dopamine. In attackers, motivation to initiate a fight was positively correlated with dopamine levels. Circulating monoamines are therefore involved in decision making during these aggressive encounters.

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Game-theoretical models of fighting behaviour explain the adaptive significance of fight activities such as the use of signals (Maynard Smith & Parker 1976) and their repeated performances (Payne & Pagel 1997) and may be tested by analysis of fight outcomes (e.g. Thornhill 1984), activities used during the encounter (e.g. Briffa et al. 1998) or relative or absolute sizes of the opponents (Taylor & Elwood 2003). Key assumptions are that fighting should be costly and that fighting animals gather information and make a series of decisions. Numerous studies have shown that fighting animals make decisions and recent work has focused on how such decisions are related to changes in energetic status that occur during contests (Smith & Taylor 1993; Thorpe et al. 1995; Neat et al. 1998; Sneddon et al. 1999; Briffa & Elwood 2001a, 2002, 2004, 2005; DeCarvalho et al. 2004). Less is known, however, about the functional role of other factors known to

be associated with decision making. Biogenic monoamines, for instance, 'alter the activity of specific neural decision-making centres' (Huber 2005, page 232) and are an important component in the link between information gathering and decision making. Most studies on the role of monoamines in crustacean aggressive behaviour (e.g. Huber et al. 1997a; Yeh et al. 1997; Doernberg et al. 2001) focus on the role of serotonin (5-hydroxytryptamine creatinine sulphate complex) or '5-HT'. 5-HT may act on several neural circuits, and experiments on crayfish, *Procambarus clarkii* (Yeh et al. 1996, 1997), for example, have shown that high levels of 5-HT in the lateral giant neuron trigger a rapid 'abdominal-flipping', forward-swimming escape response, an effect that may also be induced by artificially elevating circulating 5-HT levels. Thus, neuronal and perhaps circulating levels of 5-HT appear to modulate the decision to withdraw in subordinate individuals.

5-HT influences behavioural decisions in a wide range of taxa and this is thought to reflect an early evolutionary appearance of such 'aminergic' systems (Huber 2005). However, there appear to be key differences between taxa in 5-HT function. In vertebrates, elevated levels of 5-HT are associated with reduced aggression (e.g. Nelson

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& Chiavegatto 2001; Summers 2001; Winberg et al. 2001; Hoglund et al. 2005) but studies on crustaceans, involving 5-HT infusion, show the opposite effect. In the crayfish *Astacus astacus*, for example, subordinate individuals that have been subjected to 5-HT infusion are less likely to withdraw from contests (Huber et al. 1997b). Both experimental elevation and depletion of 5-HT in lobsters, *Homarus americanus*, result in increased aggression (Doernberg et al. 2001). Despite these differences between taxa, in the cases of both vertebrates (e.g. Matter et al. 1998; Emerson et al. 2000) and invertebrates (e.g. Sneddon et al. 2000) rapid changes in circulating 5-HT levels in response to aggressive encounters and other types of stressful situation suggest that monoamines are involved in short-term priming of the nervous system for appropriate responses to specific situations. Although these monoamines may exert their effects at the neuronal level, it is clear from these examples that circulating levels vary during behavioural encounters and elevated circulating levels influence behaviour.

An alternative approach to altering monoamine levels artificially is to assay for naturally circulating levels and relate these to fight outcomes and performance. Sneddon et al. (2000) found that 5-HT levels are elevated after fights over food in the shore crab *Carcinus maenas* and that eventual winners had higher levels before fighting than did eventual losers. The circulating levels of these compounds thus vary between individuals at rest and are dynamic within the timescale of agonistic interactions (approximately 0.25 h in the case of the shore crab study). Another monoamine, dopamine, also influences aggressive behaviour. It appears to be particularly important in decisions about the level of escalation (Sneddon et al. 2000), but it has yet to be examined with respect to variation in contest vigour.

Hermit crabs readily engage in agonistic interactions called 'shell fights'. They are initiated by the larger of the two opponents, the 'attacker' against a 'defender', in an attempt to gain a better-quality shell (one more suitable in size or of a preferred species). The attacker initiates a fight by first touching the defender's shell with its chelipeds and then grasping it with its walking legs; the defender then withdraws tightly into its shell. The attacker manipulates the defender's shell, gathering information about the quality of this resource (Dowds & Elwood 1983). At this point in the contest it is possible to determine the attacker's motivation for fighting by applying a novel stimulus that causes a startle response in the attacker (withdraw into shell), the duration of which is inversely proportional to the attacker's motivation (Elwood et al. 1998; Briffa & Elwood 2001b).

After this initial phase of the fight, the attacker may perform the key agonistic activity of 'shell rapping', where, using the abdominal muscles and walking legs, it vigorously swings the two shells together in a series of bouts separated by pauses. The defender remains tightly withdrawn into its shell until the encounter is resolved. After several bouts of rapping, the fight ends either by the defender giving up, in which case it allows the attacker to evict it from its shell, or by the attacker giving up without first evicting the defender. The key determinant of the

ability of attackers to effect an eviction is the 'vigour' with which they perform shell rapping. Successful attackers rap many times in each bout, leave short pauses between bouts (Briffa et al. 1998; Briffa & Elwood 2000a) and rap with a high power of impact (Briffa & Elwood 2000b, 2002; Briffa et al. 2003). The pattern of escalation is also important and, at the end of fights, successful attackers rap with increasing vigour from bout to bout whereas the vigour declines in attackers that give up (Briffa et al. 1998).

The fights therefore provide two outcomes, which clearly indicate that a giving-up decision has been made by either the defender or the attacker. It is also possible to quantify the prefight motivation and the subsequent vigour of fighting by attackers. Because of the nature of these fights, the role of defender is less amenable to behavioural analysis; nevertheless, we can observe their 'giving-up' decision. Our aims in this study were to investigate the relations between circulating levels of two key monoamines, 5-HT and dopamine, and the decisions to initiate fights in attackers and to terminate fights in attackers and defenders, and to determine whether monoamine levels are related to the vigour of the attacker's initial motivation and subsequent performance.

## METHODS

### Shell Preferences and Staging Fights

Crabs were collected from intertidal rock pools at Hannaford Point, Cornwall, U.K. They were transported back to the laboratory at Plymouth where they were maintained in 20-litre plastic containers, in batches of 150–200, in aerated sea water at 15°C and were fed ad libitum on catfish pellets.

To determine the preferred shell weight of a crab of a given size, we carried out a shell selection experiment as follows. We removed crabs from their shells, by cracking the shell in a bench vice and carefully removing the shell fragments without causing any injury to the crab. Naked crabs were then weighed, sexed by examination of the pleopods and males only (0.31–1.42 g,  $N = 100$ ) were isolated in separate crystallizing dishes 20 cm in diameter containing aerated sea water as above. Ten weighed *Littorina littorea* shells of varying weights were added to each crystallizing dish so that each crab had a free choice of shells to occupy. The crabs were left for 1 h and monitored at 30-min intervals until a crab had occupied the same shell for 2 h at which point it was deemed to have made a permanent choice of which shell to occupy. When the crab chose the smallest or largest shell available, we added a choice of smaller or larger shells to the dish and recorded any change in permanent choice as above. There was a significant positive relation between crab weight and preferred shell weight (regression:  $F_{1,99} = 95.2$ ,  $P < 0.0001$ ). All crabs that were used in the shell selection experiment were returned to the sea unharmed.

To stage fights, we first removed crabs from their shells and sexed them. Male crabs only, free of missing

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