



Know thine enemy: fighting fish gather information from observing conspecific interactions

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Many of the signals that animals use to communicate transmit relatively large distances and therefore encompass several potential signallers and receivers. This observation challenges the common characterization of animal communication systems as consisting of one signaller and one receiver. Furthermore, it suggests that the evolution of communication behaviour must be considered as occurring in the context of communication networks rather than dyads. Although considerations of selection pressures acting upon signallers in the context of communication networks have rarely been expressed in such terms, it has been noted that many signals exchanged during aggressive interactions will transmit far further than required for information transfer between the individuals directly involved, suggesting that these signals have been designed to be received by other, more distant, individuals. Here we consider the potential for receivers in communication networks to gather information, one aspect of which has been termed eavesdropping. We show that male *Betta splendens* monitor aggressive interactions between neighbouring conspecifics and use the information on relative fighting ability in subsequent aggressive interactions with the males they have observed.

Keywords: visual signalling; agonistic interactions; *Betta splendens*; eavesdropping

1. INTRODUCTION

Communication is a ubiquitous behaviour underlying much of the social organization of animals, but most studies of the topic only consider dyads of one signaller and one receiver. Given that the average spacing between individuals is often small relative to the transmission distance of most signals, many signallers and receivers will be within the range of one another and form communication networks (Dabelsteen 1992; McGregor 1993; McGregor & Dabelsteen 1996). In territorial systems, communication networks are more apparent because the spacing between individuals is more regular and constant.

Considerations of selection pressures acting upon signallers in the context of communication networks have rarely been expressed in such terms, although they do exist. Good examples are the timing of signals in chorusing frogs and insects either to avoid or to promote signal overlap (Otte 1974; Ryan *et al.* 1981; Wells 1988; Greenfield *et al.* 1997). Similarly, it has been noted that many signals exchanged during aggressive interactions will transmit far further than required for information transfer between the individuals directly involved, suggesting that these signals have been designed to be received by other, more distant,

individuals (Zahavi 1979). The idea that such an audience can affect signalling behaviour has been demonstrated experimentally (Gyger *et al.* 1986; Karakashian *et al.* 1988; see Gyger (1990) for a review of alarm calling). One consequence of signalling in a communication network is that specialized behaviour or signals must be involved to direct a signal towards a particular receiver rather than to the network as a whole. The ability of squid to produce different visual displays on opposite sides of the body when flanked by different individuals (Moynihan & Rodaniche 1977) is an example of directing signals to a particular part of the network.

By contrast with signallers, the selection pressures on receivers in communication networks have been considered infrequently. One aspect that has been discussed in some detail is based on the observation that aggressive interactions between individuals of the same species contain information on relative aspects such as fighting ability, condition and motivation that could not be gained from the signals alone (McGregor & Dabelsteen 1996). The advantage to receivers in a communication network eavesdropping on such interactions are that the relative information can be gathered at no risk, at little cost, and before any interaction with the interacting individuals (McGregor 1993). This behaviour could be considered to be an aspect of receiver psychology (Guilford & Dawkins 1991, 1993) and there is some evidence that such behaviour occurs. In the red-capped cardinal (*Paroaria gularis*), Eason & Stamps (1993) demonstrated that individuals are more likely to detect sooner an intruder if it has just been evicted from a neighbour's territory than if it does not come from

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an adjacent territory. Eavesdropping in the territorial context may provide information not only on the presence of an intruder, but also on its competitive ability. Experimental data on red-winged blackbirds (*Agelaius phoeniceus*) indicates that territorial males may assess the competitive ability of neighbours by watching contests. Freeman (1987) presented mounts to territorial *A. phoeniceus* males and scored the aggressiveness with which the male attacked the mount, and then recorded the subsequent territorial intrusions suffered by the focal male. His data show that neighbours are more likely to intrude upon individuals that attacked the mount less vigorously. Such a mechanism was also proposed by Chase (1985) to explain the occurrence of transitive relationships in social dominance hierarchies. An experiment with nightingales (*Luscinia megarhynchos*) showed that subjects paid attention to a vocal interaction (stimulated by playback) between two conspecifics and responded differently according to which of the two conspecifics overlapped the other's song, a signal of readiness to escalate a dispute (Naguib & Todt 1997). The aim of the experiments reported in this paper was to investigate whether eavesdropping occurs in a visually signalling territorial fish.

The Siamese fighting fish (*Betta splendens*) is an anabantid from south-east Asia. Males defend territories in the water column near the surface, which are centred on a bubble nest built by the male (Forselius 1957). This species is very aggressive and has very stereotyped social displays, leading to its wide use in laboratory studies of signalling and aggressive interactions, and there is gambling on the outcome of staged fights in south-east Asia. The social displays of *B. splendens* have been described in detail by Simpson (1968) and include gill cover erection and fin spread. Fights are dangerous, often involve physical damage to the fish, and can result in the death of one of the opponents. Therefore, we would expect information on the fighting ability of potential opponents gathered before a fight to have high survival value.

We tested the hypothesis that male Siamese fighting fish pay particular attention to displays between other males and use information extracted from these interactions in subsequent contests with the males they have observed. In a first experiment, we tested if subjects watched displaying individuals more than non-displaying individuals. In a second experiment, we investigated whether they used the information gathered in such observations in subsequent aggressive interactions.

2. MATERIALS AND METHODS

Male Siamese fighting fish were obtained from a local supplier (Nottingham). Males ranged in size (standard length) from 3.2 cm to 5.0 cm (mean \pm s.d. = 4.18 ± 0.39 cm, $n = 47$). Fish were individually housed in tanks (20 cm \times 30 cm \times 35 cm) at 28 °C with a 12 h L:12 h D cycle. In the first experiment, a large tank (100 cm \times 30 cm \times 35 cm) was divided into three compartments separated by one-way mirrors. The subject was placed in the central compartment (60 cm \times 30 cm \times 35 cm), and two conspecifics separated by an opaque partition were placed in each end compartment (20 cm \times 30 cm \times 35 cm). The three major compartments of the tank were watertight; therefore, the subject could not have used chemical cues (e.g. Noakes 1982). Markings on the tank delimited the 5 cm of the central compartment closest

to each end compartment. All five fish were introduced to their respective compartments and allowed to acclimatize for 1 h. After 1 h, the opaque partitions that separated the central compartment from each end were removed and the opaque partition separating the two males in one end was replaced with a clear partition. These two males engaged in mutual agonistic displays across the clear partition. Differential lighting of the central compartment meant that the subject could see the four stimulus fish without itself being seen. We noted the time spent within 5 cm of each end, the time within 5 cm of each end spent facing the conspecifics, and the time spent displaying towards the conspecifics. Facing was defined as being orientated towards, and gazing at, the conspecifics. The measures were taken using a scan sampling procedure with a sampling period of 10 s.

3. RESULTS

Subjects spent significantly more time within 5 cm of each end and gazing at the two interacting males (% of time gazing (mean \pm s.e.): 5.2 ± 0.9 (non-interacting neighbours) versus 13.1 ± 3.4 (interacting neighbours); Wilcoxon matched-pairs test, $z = 2.56$, $n = 17$, $p = 0.01$). This difference cannot be explained by an end bias because (i) the end that held the interacting two males was randomized, and (ii) there was no significant difference in time spent at each end (% of time spent at each end (mean \pm s.e.): 30.8 ± 4.7 (non-interacting neighbours) versus 28.1 ± 4.6 (interacting neighbours); Wilcoxon matched-pairs test, $z = 0.57$, $n = 17$, $p = 0.57$). Similarly, subjects did not differ significantly in the amount of time spent displaying between the two ends (% of time displaying (mean \pm s.e.): 9.6 ± 3.0 (non-interacting neighbours) versus 7.3 ± 3.0 (interacting neighbours); Wilcoxon matched-pairs test, $z = 0.70$, $n = 17$, $p = 0.49$). Our interpretation of these data is that subjects pay more attention to interactions between neighbouring males, and therefore fulfil a prerequisite for eavesdropping.

To test if the subjects were using the information on relative fighting ability contained in the interactions they observed we conducted a second experiment (the experimental procedure for which is detailed in figure 1). In this experiment, subjects were allowed to observe interactions with a clear winner (W) and a clear loser (L). They were not allowed to see a simultaneous comparable interaction (winner = w, loser = l). If subjects have gathered information and use it in a subsequent interaction with one of the observed individuals, we would predict an initial difference in response towards the seen winner (W) when compared with the seen loser (L). However, we would predict no such difference towards the unseen winner (w) when compared with the unseen loser (l). Figure 2a shows that the two measures of initial response in the interaction differ as predicted. The subjects took significantly longer to approach and longer to display to seen winners (W) than to seen losers (L), but there was no such difference for unseen winners (w) and losers (l). In this experiment, latency could be taken as an indication of the subject's willingness to engage in a fight. Figure 2a shows that they are more willing to fight individuals that they have seen lose than to fight individuals they have seen win relative to their intermediate response to unseen individuals. We would not expect previously gathered information to influence measures of response over the entire interaction,

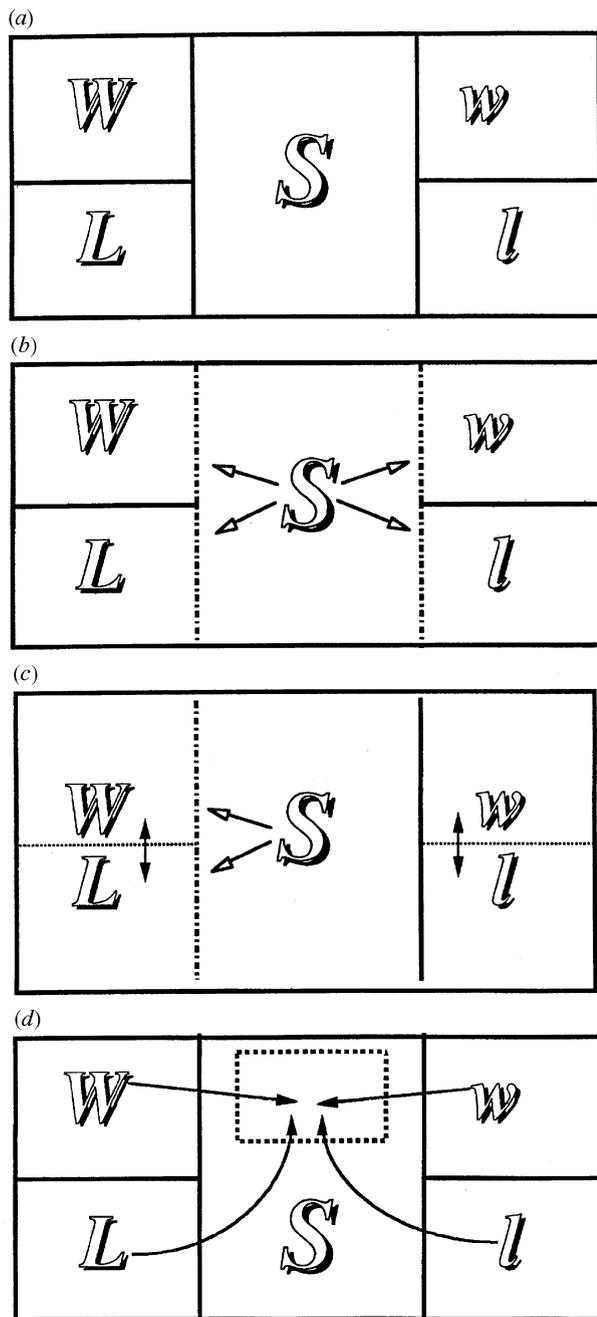


Figure 1. (Experiment 2) A tank (60 cm \times 30 cm \times 35 cm) was divided into three compartments of equal size separated by one-way mirrors, so that, as in the first experiment, the subject could see the four stimulus fish without itself being seen. The subject (S) was placed in the central compartment and two conspecific males were added to each lateral compartment, separated from each other by two partitions: one opaque and one clear Plexiglass. All five fish were introduced to their respective compartments and allowed to acclimatize for 20 min (a). (Stage 1) The opaque partitions between the central and the lateral compartments were removed, and the four conspecifics could be seen by the subject for 10 min to control for familiarization effects (b). (Stage 2) One of the opaque partitions was replaced between the central tank and one of the lateral compartments, while the opaque partitions inside the lateral compartments were removed, so that agonistic interactions started at the same time between the two pairs of conspecifics but only one interaction could be seen by the subject (c). These interactions lasted for 15 min. (Stage 3) All the opaque partitions were replaced resulting

because such measures are influenced by the dynamics of the interaction in progress. Moreover, as the subject always interacted with the stimulus fish (W, L, w and l) in its own tank, a prior residence effect would be expected (Bronstein 1985), and because all five fish were matched for size (Bronstein 1984), we would expect a standard level of response by the subject towards the intruders in overall measures. Display frequency and duration are such measures, and figure 2b shows no significant effect of whether opponents were seen/unseen or winner/loser. Although the subject took longer to respond to the seen winner (W), it tended to escalate to a higher level (measured by the proportion of subjects that attempted to bite the intruder: seen fights, $n=24$, $W=29.1\%$ versus $L=8.3\%$, two-tailed difference between the two proportions, $p=0.06$; unseen fights, $n=24$, $w=29.1\%$ versus $l=29.1\%$, two-tailed difference between the two proportions, $p=1.0$). These results are consistent with the subject having identified the intruder as a strong opponent.

4. DISCUSSION

Several alternative explanations for our results are excluded by various controls. Our experiment allowed us to control for winner/loser effects, which are known to be important in determining the outcome of successive fights (Jackson 1991; Chase *et al.* 1994). This effect would predict a difference in the subject's response towards both seen and unseen winners and losers (W versus L and w versus l). However, figure 2a shows that there is a significant difference only between seen winners and losers (W versus L). *A posteriori*, we were able to test whether winners and losers differed in features likely to elicit different responses from the subject, other than the outcome of the observed interaction. There were no significant differences in size, colour brightness or competitive ability of the winner (body size (standard length) differences between winners and losers: W versus L, $z=0.97$, $n=24$, $p=0.33$; w versus l, $z=1.53$, $n=24$, $p=0.13$; colour brightness (0 to 5 scale) differences between winners and losers: W versus L, $z=1.08$, $n=24$, $p=0.28$; w versus l, $z=0.141$, $n=24$, $p=0.89$; competitive ability (time spent displaying) differences between the winners of the seen and the unseen

Figure 1. (*continued*) in visual isolation of all five fish. We then introduced each of the four conspecifics one at a time into a clear box in the subject's compartment and recorded the interaction of the subject with the other fish for 10 min (d). As we were interested in the differences in response to winners and losers within the seen category and the same difference within the unseen category, the order of introduction was balanced within the seen categories (W introduced first as often as L was introduced first) and within the unseen categories (w introduced first as often as l was introduced first). The four conspecifics were classified as winner of a seen fight (W), loser of a seen fight (L), winner of an unseen fight (w) and loser of an unseen fight (l), according to the time spent displaying during the interaction, which showed a large and significant difference (seen fights (WL): Wilcoxon matched-pairs test, $z=4.14$, $n=24$, $p<0.0001$; unseen fights (wl): Wilcoxon matched-pairs test, $z=4.0$, $n=24$, $p<0.0001$). This criterion was used because Simpson (1968) showed that time spent displaying was a good predictor of outcome of fights.

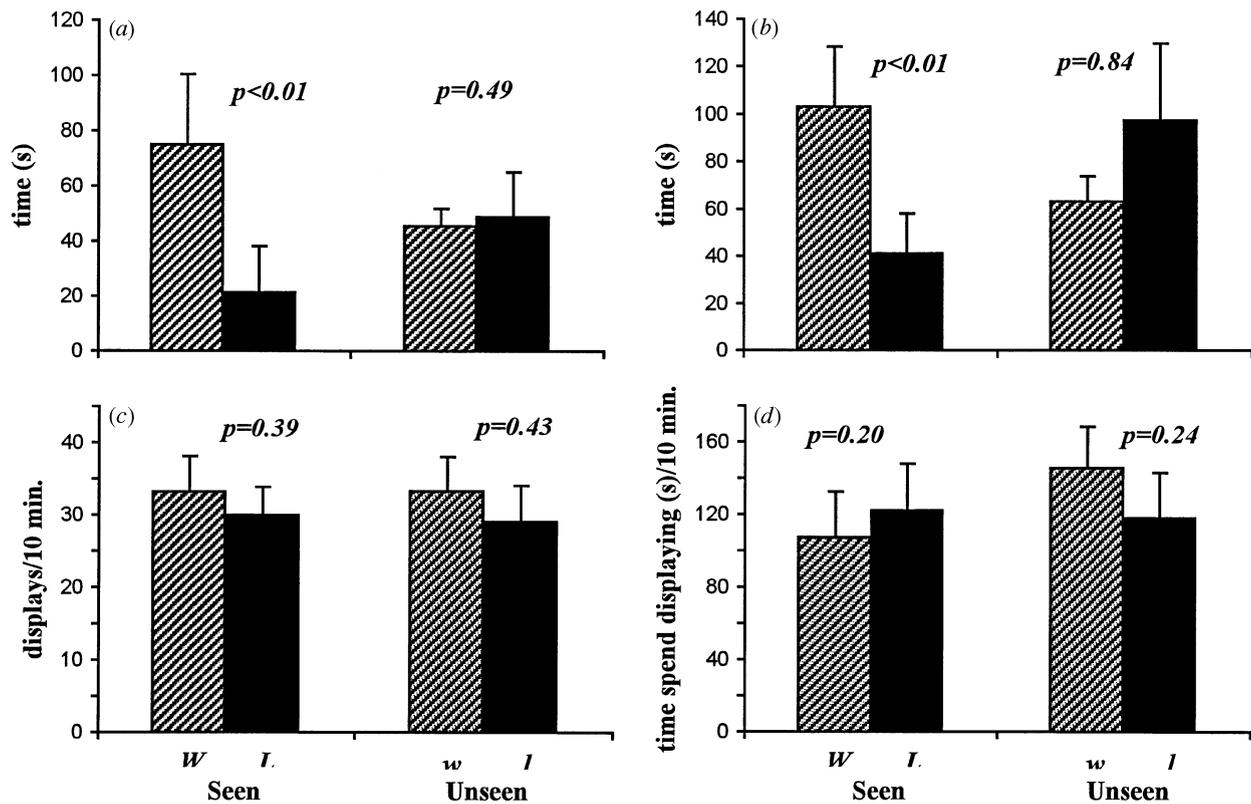


Figure 2. The mean responses (\pm s.e.) of 24 subjects to males introduced into the subject's compartment one by one. The introduced males had previously been seen winning (W) or losing (L) interactions, or had been unseen winners (w) or losers (l). (a, b) Initial responses: the latency of subjects to approach (a) and to display (b). (c, d) Responses over 10 min: the frequency (c) and duration (d) of fin-spreading and gill cover erection displays. p values refer to Wilcoxon matched-pairs tests.

fighters: W versus w, $z = 0.73$, $n = 24$, $p = 0.47$), nor were there any differences in intensity between the seen and unseen fights (intensity of the fight differences between seen and unseen contests (WL versus wl): time spent displaying, $z = 0.49$, $n = 24$, $p = 0.63$; number of agonistic acts, $z = 0.21$, $n = 24$, $p = 0.83$). Therefore, the most parsimonious explanation of our results is that male fighting fish can eavesdrop on interactions between other males.

In summary, these experiments support the idea that male *B. splendens* gather information on the fighting ability of potential opponents by eavesdropping on other male–male interactions. These results have wider implications for communication networks and cognitive abilities of receivers. Although the effect of an audience on the behaviour of signallers has been noted for some time (Gyger *et al.* 1986; Karakashian *et al.* 1988; Gyger 1990), there has been little consideration of the effect on, and opportunities for, signal receivers in a network context. This is particularly true of females as receivers (e.g. the role of eavesdropping in female assessment of extra-pair males is discussed by Otter *et al.* (1998)). Our study supports the claim that eavesdropping should be an important feature of receiver behaviour in a communication network (Dabelsteen 1992; McGregor 1993; McGregor & Dabelsteen 1996). Preliminary results from a study of a territorial song bird (McGregor *et al.* 1997) showed a similar initially cautious response to an apparently aggressive opponent, just as we found in the present study. This similarity emphasizes the role that eaves-

dropping could play in territorial systems in widely different vertebrate groups that use different communication modalities.

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