



Do mirrors reflect reality in agonistic encounters? A test of mutual cooperation in displays



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Animals frequently engage in mutual displays that may allow or at least help decisions about the outcome of agonistic encounters with mutual benefit to the opponents. In fish these often involve lateral displays, with previous studies finding evidence of population-level lateralization with a marked preference for showing the right side and using the right eye. Because both opponents tend to show this preference a head to tail configuration is formed and is used extensively during the display phase. Here we tested the significance of these lateral displays by comparing displays to a mirror with those to a real opponent behind a transparent barrier. The frequency of displays was lower to a mirror but the individual displays were of greater duration indicating a slower pace of the interaction with a mirror. This suggests that fish respond to initiatives of real opponents but as mirror images do not initiate moves the focal fish only moves when it is ready to change position. However, lateralization was still found with mirrors, indicating that the right-side bias is a feature of the individual and not of the interaction between opponents. We discuss implications for ideas about the evolution of mutual cooperation and information exchange in contests, as well as the utility of the use of mirrors in the study of aggression in fish.

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The outcomes of animal contests ensure the unequal distribution of vital resources (Arnott & Elwood, 2008) and thus drive evolution (Elwood & Arnott, 2012). The manner by which the outcome is determined is the subject of much debate, particularly concerning the degree to which animals gather information about the opponent (Arnott & Elwood, 2009a; Elwood & Arnott, 2012, 2013; Fawcett & Mowles, 2013; Mesterton-Gibbons & Heap, 2014). Some game theory models stress the importance of the contestant only monitoring its own state, termed self-assessment (Arnott & Elwood, 2009a; Taylor & Elwood, 2003), e.g. the energetic war of attrition (Payne & Pagel, 1996, 1997) and the cumulative assessment models (Payne, 1998). Others, such as the sequential assessment model (SAM; Enquist & Leimar, 1983), are said to involve mutual assessment, and stress the importance of gathering information about the opponent (Enquist & Leimar, 1983). With SAM there has been a presumption that the information about an opponent is compared with information about

oneself (Elwood & Arnott, 2013; Fawcett & Mowles, 2013). However, it has been noted that simple systems might exist that do not require the cognitive ability of comparison of two values (Elwood & Arnott, 2012). Irrespective of the cognitive process, this apparent ability to compare one's own ability with that estimated for the opponent has a distinct advantage over self-assessment models because it should enable an animal to quit a contest as soon as it perceives that it is likely to lose. Because this might occur at an early display stage, before the contest has escalated, the animal could avoid the cost of a fight it would inevitably lose (Arnott & Elwood, 2009a). The winner would also gain because it could get the resource more quickly and without paying the cost of escalation (see Mesterton-Gibbons & Heap, 2014 for relative costs of mutual and self-assessment for individuals of different strengths).

This leads to the idea that animals might cooperate in order to exchange information (Arnott, Ashton, & Elwood, 2011; Earley, 2010), enabling the contest to be resolved with minimum cost to both contestants (Arnott & Elwood, 2009a). This mutual benefit (West, Griffin, & Gardner, 2007) has been suggested as an important factor in the evolution of cooperative ritualized aggressive displays (Arnott et al., 2011). Such displays typically precede escalated physical contact; examples include the mutual vocal displays

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occurring between male red deer, *Cervus elaphus* (Clutton-Brock & Albon, 1979) and fallow deer, *Dama dama* (Jennings, Elwood, Carlin, Hayden, & Gammell, 2012). These ungulates also engage in a conspicuous lateral visual display during contests, termed the parallel walk, whereby the deer walk in the same direction a short distance apart, often adopting a stiff-legged gait (Jennings & Gammell, 2013). This lateral display has been interpreted as providing a means for males to assess the competitive ability of opponents (e.g. Clutton-Brock, Albon, Gibson, & Guinness, 1979; Jennings & Gammell, 2013), and contests may be settled during these early display stages (Jennings, 2012).

Fish also commonly show their flanks in early stages of a contest, engaging in so-called lateral displays, again typically interpreted as a means of allowing each contestant to observe the physical attributes of its opponent (Arnott & Elwood, 2009b, 2009c; Enquist, Leimar, Ljungberg, Mallner, & Segerdahl, 1990; Hurd, 1997). Fish, however, can align in two ways during lateral displays, with their heads either facing in the same direction (head to head) or in opposite directions (head to tail). Fish might also preferentially show one side to their opponent (Bisazza & de Santi, 2003; Reddon & Balshine, 2010). For example, competing convict cichlids, *Amatitlania nigrofasciata*, more commonly show their right than their left flank which results in the head to tail configuration being far more common than the head to head configuration (Arnott et al., 2011). It has been speculated that population-level lateralization of displays enables coordination of these agonistic interactions (Ghirlanda, Frasnelli, & Vallortigara, 2009). One way to test whether the head to tail posture is important in the coordination of displays is to prevent key features of the mutual display by the use of mirror images.

Mirrors are frequently used as a substitute for live opponents in studies on aggression in a range of species (e.g. crayfish, *Procambarus clarkii*, May & Mercier, 2007; Japanese quail, *Coturnix japonica*, Hirschenhauser, Wittek, Johnston, & Mostl, 2008), and this approach is particularly popular with fish aggression studies (e.g. Balzarini, Taborsky, Wanner, Koch, & Frommen, 2014; Earley, Hsu, & Wolf, 2000; Tinbergen, 1951; Verbeek, Iwamoto, & Murakami, 2007; Wilson, de Boer, Arnott, & Grimmer, 2011). They are popular because each fish used is a focal fish so fewer animals might be required and pseudoreplication is avoided, and because mirrors provoke strong aggressive responses. Further, the use of mirrors avoids welfare problems that arise from two animals being placed together when one may harm the other (Elwood, 1991). However, the suitability of mirror-elicited behaviour as a means of predicting contest performance or provoking the same behavioural and physiological responses as real contests is beginning to be questioned. Mirror images fail to elicit the same brain gene expression (Desjardins & Fernald, 2010) and the same hormonal responses (Oliveira, Carneiro, & Carneiro, 2005; but see Dijkstra, Schaafsma, Hofmann, & Groothuis, 2012) as live opponents. Balzarini et al. (2014) compared the displays of three cichlid fish species to a mirror and to a real opponent behind a clear barrier. Only one species showed positive correlations between the two situations for a number of different aspects of displays, which again casts doubt on the validity of using mirrors to elicit responses that would be informative for predicting behaviour against live opponents.

A key problem with using a mirror is that the reflection will not allow a head to tail posture and this might account for differences between displays to real opponents and mirror images (Arnott et al., 2011). A fish might turn to assume the head to tail posture but the reflection will turn simultaneously and the head to head alignment will persist. Thus, only the head to head posture is attained with a mirror and the common head to tail posture will be missing. This key element of mutual display, which appears to be

mediated by population-level lateralization, will be disrupted because the reflection fails to cooperate in the display (Arnott et al., 2011). Thus if fish repeatedly attempt to attain the head to tail posture we predict that with a mirror their responses will speed up resulting in more individual displays but with a shorter duration of each lateral display.

Alternatively, a mirror might not elicit the same response as a real opponent because real opponents initiate moves that elicit responses from the focal fish (e.g. Van Dyk & Evans, 2008). Mirror images, of course, do not initiate moves and thus a fish displaying to a reflection will only generate its own moves rather than responding to new moves of the opponent. We might envisage situations in which a focal fish waits for the real opponent to make a move that it will then counter. This leads to an alternative prediction that, with a mirror, the focal fish will not change position so frequently leading to fewer but longer individual displays to a mirror.

In this study we used convict cichlids to examine left lateral displays, right lateral displays and frontal displays of focal fish to mirrors and real opponents. In this species both sexes show territorial defence and lateralization of lateral displays with a preference for the right side (Arnott et al., 2011). We recorded the number of each display, the total duration of displays and the median duration of the displays in the two situations. This will reveal whether the fish faced with a mirror image speed up behavioural changes in an attempt to achieve a head to tail posture or slow down behavioural changes because the mirror does not initiate moves and therefore no counter displays are required. Further, if the mirror image fails to cooperate then the laterality noted with a real opponent might break down. Thus we also compared the laterality of displays to real opponents and mirror images.

METHODS

Twenty-six female, size-matched convict cichlids were obtained from a local supplier (Grosvenor Tropicals, Belfast, U.K.) in batches of six or seven and kept in individual glass tanks measuring 30 × 20 cm and 20 cm high with approximately 2 cm depth of gravel. A controlled artificial 12:12 h light:dark cycle was in place, the water aerated and kept to a depth of 15 cm and the temperature maintained at approximately 27 °C. Tanks were aligned end to end (Fig. 1) with opaque partitions visually isolating the fish outside of test sessions. Fish were fed every other day with flake food and on the experimentation day they were fed after observations had taken place. The fish were maintained isolated in their tanks for 1–2 weeks before experimentation, thus ameliorating any

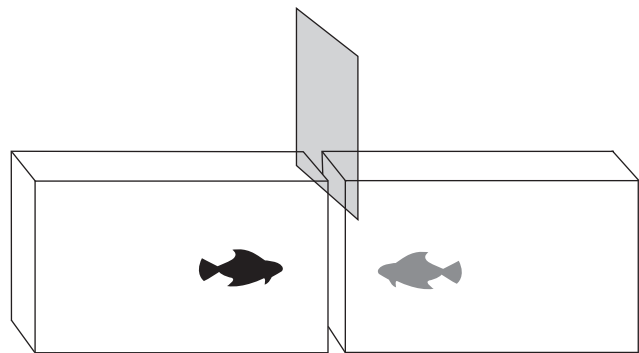


Figure 1. Experimental set-up. The two holding tanks were identical in condition and content and the grey opaque partition situated between the tanks was removable either to expose the focal fish to a real opponent or to allow insertion of a mirror. The fish coloured black is the focal fish in the procedure.

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