Competitive superiority versus predation savvy: the two sides of behavioural lateralization

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Many animals respond differentially to stimuli on one side of their body compared to the other. This is a reflection of being lateralized, and is a feature common in vertebrates. Given that any particular stimulus that an animal encounters, be it food, a predator or a competitor, has an equal probability of coming from either side of the body, there may be negative selection for lateralization. However, the costs of lateralization may be offset if being lateralized confers a considerable advantage in other contexts, including cognition. Here, we showed that learned responses of juvenile ambon damselfish, *Pomacentrus amboinensis*, to a novel predator was strongly influenced by the degree of lateralization. While both lateralized and nonlateralized fish were able to learn the predator, lateralized fish showed much stronger responses to the learned predator than nonlateralized fish. When we paired lateralized and nonlateralized fish and allowed them to interact over a shelter resource, we observed that lateralized fish were poorer competitors. They attacked less often, showed fewer displays and exhibited greater avoidance of their competitor. For many gregarious species, the expression of lateralization likely reflects a fine balance of competing selection pressures. Our work highlights the need for integrative studies.

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It is common for a variety of vertebrates to show cerebral lateralization, whereby one hemisphere of the brain is specialized for a particular function, leaving the other hemisphere to perform other functions (Bisazza & Brown, 2011). Cerebral lateralization often results in behavioural asymmetry. For example many animals show more aggression towards conspecifics on one side of their body than the other or orient their body in a specific direction towards a rival (Deckel, 1995; Robins, Lippolis, Bisazza, Vallortigara, & Rogers, 1998; Rogers, 1991). Feeding responses likewise are often biased towards one side of the body (Mench & Andrew, 1986; Wilzeck & Kelly, 2013). If we consider that any particular stimulus, be it food, a competitor or a predator, has an equal probability of coming from either side, there could be negative selection for lateralization (Vallortigara & Rogers, 2005). It behooves animals to respond to predators coming from their right just as much as from their left. The argument is the same for acquiring resources or competing with conspecifics for mates or territories.

Cognition refers to mechanisms by which animals, acquire, process, store and act on information from the environment. These include perception, learning, memory and decision making (Shettleworth, 2009). Levy (1977) has argued that cognitive benefits of lateralization likely outweigh the obvious costs of lateralization, and indeed, there is some support for this notion. For example, highly lateralized fish perform better in spatial tasks (Sovrano, Dadda, & Bisazza, 2005) and have enhanced numerical skills over nonlateralized individuals (Dadda, Agrillo, Bisazza, & Brown, 2015). Highly lateralized parrots likewise have enhanced cognition (Magat & Brown, 2009). Given the unforgiving nature of predation, we should expect that this is one realm where we should observe very clear evidence of enhanced cognitive abilities. However, little work has considered the cognitive benefits that differently lateralized individuals might have with regards to predator exposures (Lucon-Xiccato, Chivers, Mitchell, & Ferrari, 2016).

In fishes, lateralization may be manifested as a turning bias, with some individuals showing a left bias, others a right bias and others no bias (Bisazza & Brown, 2011). Here, we screened juvenile ambon damselfish, *Pomacentrus amboinensis*, for their turning bias and then trained individuals to recognize a common reef predator, the dusky dottyback, *Pseudochromis fuscus*, using a well-established

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conditioning protocol. Our specific aim was two-fold: (1) to test whether individuals that were strongly lateralized, regardless of the direction of their turning bias, showed differential responses to the learned predator cues compared to nonlateralized individuals, and (2) to test whether individuals with a right-turning bias showed the same response intensity to the learned predator cues as those with a left-turning bias. There is evidence in larval woodfrogs (*Lythobates sylvaticus*) that individuals with a right-turning bias show strong predator learning while those with a left-turning bias do not (Lucon-Xiccato et al., 2016). In rainbowfish, individuals with a left lateralization bias, as measured by the eye preferentially used to view their mirror image, perform better in a food-conditioning task compared to those with a right bias (Bibost & Brown, 2014).

Despite any potential cognitive advantage of lateralization, researchers observe a large range of lateralization scores among wild animals, including many animals that show little evidence of lateralization (Bisazza & Brown, 2011; Chivers et al., 2016). This broad distribution of lateralization phenotypes suggests that there is some balancing of costs and benefits. Here, we considered whether individuals with no lateralization bias have advantages over biased individuals in other contexts, specifically competition. Individuals that exhibit a specific turning bias are likely to encounter individuals that lack that same bias, or have the opposite bias. Raymond, Pontier, Dufour, and Møller (1996) argued that left handedness in humans resulted from frequency-dependent selection whereby rare left-handed fighters have an advantage during fights with right-handed fighters. The strength of the advantage should increase when the frequency of left-handed individuals declines. Consistent with the left-hand fighting advantage, Raymond et al. (1996) reported a higher proportion of left-handed individuals in interactive sports, which reflects fighting ability, but not in noninteractive sports. These results suggest that individuals with the minority phenotype have an advantage over individuals with the majority phenotype, but they have equal performance when facing other rare phenotype individuals. Individuals with the majority phenotype should do equally well against others with the same phenotype but loose to individuals with the rare phenotype. Following from this supposition, we should consider whether individuals that are non-lateralized have an overall advantage over lateralized individuals if they can adapt their agonistic interactions to compete with either left- or right-biased individuals. This may be akin to the batting advantage of switch-hitting baseball players that alter their batting handedness based on the handedness of the pitcher (Goldstein & Young, 1996). Here, we screened juvenile damselfish for their turning bias and then paired individuals with a turning bias with those that lacked a turning bias, and allowed them to fight for a coral head. This allowed us to specifically test whether nonlateralized individuals are competitively superior (in terms of fighting ability) over lateralized individuals. Fighting ability would suggest that this is the case, however, fighting ability has a cognitive component, and hence more lateralized individuals may also have a fighting advantage over nonlateralized individuals. Indeed, Reddon and Hurd (2008) showed that highly lateralized cichlids were more likely to be aggressors.

METHODS

Test Species

The ambon damselfish, is a common planktivorous fish that lives in the shallow waters around the coral reefs of the Indo-Pacific. Fish settle to the reef after a pelagic larval phase of 15–23 days (Kerrigan, 1996), and juveniles prefer live coral over rubble habitat when given a choice (McCormick, Moore, & Munday, 2010). A combination of differential mortality associated with higher survival near territorial males (McCormick & Meekan, 2007) and

interspecific competition (McCormick & Weaver, 2012) results in juveniles being in highest abundance at the base of shallow reefs in a mixture of sand, rubble, and live and dead coral. Both intraspecific and interspecific competition, as well as an ability to quickly catalogue predators and nonpredators, is important in determining who survives during the first few weeks after settlement (Chivers, McCormick, Mitchell, Ramasamy, & Ferrari, 2014; Ferrari, McCormick, Allan, Choi, Ramasamy, & Chivers, 2015; Ferrari, McCormick, Meekan, & Chivers, 2015; Lonnstedt, McCormick, Meekan, Ferrari, & Chivers, 2012; McCormick, 2009).

Settlement-stage juvenile ambon damselfish were collected overnight using light traps moored in open water around Lizard Island (14′40°S, 145′28°E), in the northern Great Barrier Reef, Australia in November 2015. The juveniles were then placed in 20-litre flow-through holding tanks and fed three times a day with brine shrimp (*Artemia* nauplii). At the time of testing the fish ranged from 11.7 to 15.1 mm in total length. Fish were held in the laboratory for 1–3 weeks prior to testing.

Lateralization Assay

To assess the behavioural lateralization of the fish, we used a standard detour test pioneered by Bisazza, Facchin, Pignatti, and Vallortigara (1998). The chamber consisted of a runway (25 long × 3 wide × 12 high cm) at the end of which sat two opaque barriers (12 long × 12 high cm), 3 cm ahead of each end (Fig. 1). Curtains surrounding and above the tank were used to remove outside disturbance. At the start of each trial, a single fish was introduced into the middle of the runway and left to acclimate for 2 min. The fish was then gently manoeuvred towards the end of the runway using a plastic ruler. Upon reaching the end of the runway it had to make a decision to turn left or right around the barrier. After turning either direction, the fish found itself in a common turn-around chamber. When the fish subsequently exited the turnaround chamber it found itself in the runway moving towards the opposite end where it would make its second choice to turn left or right. This process continued until the fish had made 10 consecutive turning choices. There was no time between trials. To avoid fish taking a familiar route, the fish entered the runway from a different side from which they exited. In the event that the fish did not leave the turnaround chamber within 1 min, it was manoeuvred into the runway with the plastic ruler. Turning was scored by direct observation. We summed the number of times the fish turned left or right when exiting the runway. To avoid changes in water temperature and dissolved oxygen levels, both of which have been found to influence neural function (Domenici, Lefrancois, & Shingles, 2007), the tank water was changed every five trials. Water in the experimental tank was 6 cm deep and was maintained at 27–28 °C.
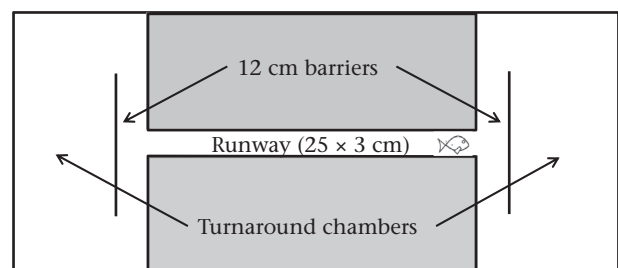
Figure 1. Diagram of the lateralization chamber. Fish started the trial in the centre of the runway. When they reached the barrier they had to make a decision to turn left or right. Upon doing so the fish found themselves in a common turnaround chamber. When the fish subsequently exited the turnaround chamber it found itself in the runway moving toward the opposite end of the chamber where it would make its next choice to turn left or right. Each fish made 10 choices in the chamber.