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

Douglas P. Chivers [a, *], Mark I. McCormick [b], Donald T. Warren [b], Bridie J. M. Allan [b],
Ryan A. Ramasamy [b], Brittany K. Arvizu [b], Matthew Glue [b], Maud C. O. Ferrari [c]

[a] Department of Biology, University of Saskatchewan, Saskatoon, SK, Canada
[b] ARC Centre of Excellence for Coral Reef Studies, and College of Marine & Environmental Sciences, James Cook University, Townsville, QLD, Australia
[c] Department of Biomedical Sciences, WCVM, University of Saskatchewan, Saskatoon, SK, Canada

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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

* Correspondence: D. P. Chivers, Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, SK S7N 5E2, Canada.
E-mail address: doug.chivers@usask.ca (D. P. Chivers).

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 nonlateralized 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.
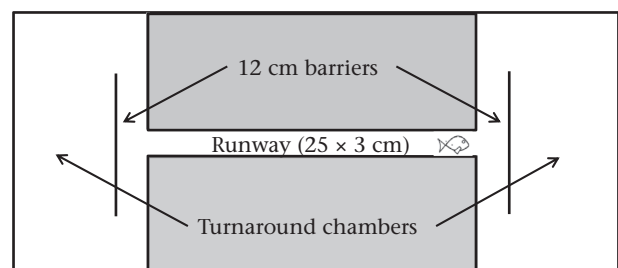
METHODS

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.

Experiment 1: Predator Learning

A total of 198 fish were screened for their lateralization tendencies using a standard detour test (see below). Thirty three fish scored 80% or more right turns and were defined as right-biased, 30 fish scored 80% or more left turns and were defined as left-biased. Forty-five fish scored equally right and left were defined as not biased ('nonbiased'). The remaining 90 fish were not included in the experiment.

Right-biased, left-biased and nonbiased fish were then trained to recognize a novel predator using a well-established one-time conditioning protocol, involving the simultaneous pairing of the predator odour with cues from injured conspecifics (Ferrari, Wisenden, & Chivers, 2010). Many prey species innately respond to cues from injured conspecifics with an overt antipredator response, and these cues facilitate the association between fear and the previously unknown stimulus (Ferrari, 2010). The following day, fish were tested for their response to the predator odour alone and their antipredator response was recorded.

Training protocol

Left-biased, right-biased or nonbiased fish were placed, individually, in 3-litre tanks containing a sand substrate, an airstone and a 15 cm branching coral object serving as a shelter. Each fish was left to acclimate for 3 h. Each tank then received 5 ml of injured conspecific cues (alarm cues) paired with 5 ml of predator odour. Predator odours were obtained by soaking two dottybacks (*P. fuscus*, a common predator of settling juvenile fish; total length: 6.4 and 7.1 cm) in 3 litres of water for 1 h. Injured conspecific cues were prepared by sacrificing, via cold shock, two randomly selected donor fish from our stock tank. Using a scalpel, we made 10 superficial cuts on each side of the donors and rinsed them with 100 ml of water, which was enough cues to train 20 fish (5 ml per tank). Once injected in the 1-litre tanks, the final concentration was ~two cuts/litre. This concentration has previously been shown to elicit overt antipredator responses in this species (Chivers et al., 2014). The fish were left undisturbed for 1 h and were then transferred into 5-litre testing tanks, fed and left undisturbed overnight.

Testing assay

The following day, each fish was tested for its antipredator response to the odour of the predator or a water control, using a well-established methodology. We first injected 2 ml of food (*Artemia* nauplii solution containing ~100 individuals/ml) through an injection tube and waited for 3 min. We then injected another 2 ml of food and started the 3 min prestimulus observation. We recorded the number of feeding strikes, regardless of success of the fish, as a measure of foraging. We also recorded activity, counting the number of lines crossed by the fish during the observation period. A 4×4 cm grid was drawn on the side of the tank to facilitate measurement. At the end of the observation, we injected another 2 ml of food followed immediately by 5 ml of sea water or 5 ml of predator odour (prepared as previously described) and started the 3 min post-stimulus observation, recording the same variables as previously described. Food and chemical cues were always flushed into the tanks with 20 ml of tank water. The change in behaviour between the pre- and post-stimulus periods indicates the response of the fish to the cues. Typical antipredator responses include decreased foraging and activity (Chivers et al., 2014). The observer was blind with respect to the lateralization status of the test animals.
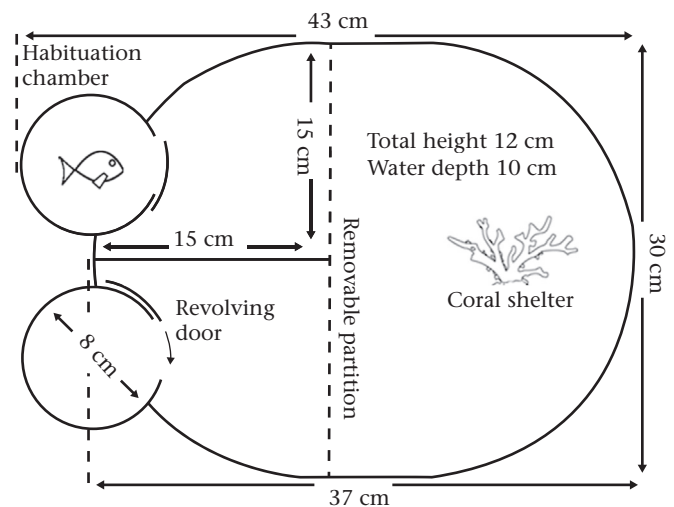
Experiment 2: Competition Experiment

As in experiment 1, fish were first screened for their lateralization tendencies using a standard detour test, to identify left-biased,

right-biased and nonbiased fish. Of the 147 fish screened, 22 were defined as left-biased, 9 were defined as right-biased, 29 were nonbiased and the remainder represented other groups. We then staged paired encounters between nonbiased fish and fish that were either right- or left-biased and quantified attacks, displays and competitor avoidance.

Testing assay

Size is known to influence the outcome of competitive interactions (McCormick, 2009). Consequently, fish were measured and pairs of biased and nonbiased fish were matched for standard length. The mean (± SE) percentage difference in size among biased and nonbiased fish was $3.5 \pm 0.5\%$. The fish pairs were tested the day following their measurement to decrease the effect of handling stress on the outcome. Fish were fasted for 12 h prior to competitive trials. Our competition trials followed those of Killen et al. (2014) using slightly modified experimental arenas. Our arena consisted of a rectangular tank with rounded corners, divided by a clear removable partition, with a fragment of live coral (~5 cm^3) in one half and two habituation chambers in the other (Fig. 2). Habituation chambers were separated by a solid fixed divider to prevent fish from seeing each other. At the start of the trial, fish were placed individually in the habituation chambers for 5 min. After the habituation period, revolving doors on both chambers were opened simultaneously, allowing fish to emerge independently and explore their portion of the arena. Emergence time was recorded for each fish. Once both fish exited their chambers, the clear partition was raised, exposing both fish to one another as well as the coral fragment. The coral provided shelter and served as a resource for competition. Competitive interactions were videorecorded for 5 min and later analysed in slow motion for three behaviours: (1) displays, defined as a lateral flare of its fin towards the opponent; (2) attacks, defined as a chase or biting of the opponent; and (3) avoidances, swimming away from an opposing attack or display. Using slow-motion video was crucial because individuals were sized-matched and the competitive interactions occur quickly for a human observer. The observer was blind with respect to the lateralization status of the test animals.

Figure 2. Diagram of competition arena used in experiment 2. Fish were placed into habituation chambers at the beginning of a trial for 5 min. Next, revolving doors were opened simultaneously, allowing fish to exit and explore their portion of the arena. Once both fish had emerged, a clear removable partition was lifted, exposing fish to the coral shelter and each other. A 5 min video recording was taken starting from the first interaction. Neither the fish nor the coral are drawn to scale.

Statistical Analysis

Experiment 1

Pre- and post-stimulus data were computed into a proportion change in behaviour ((post – pre)/pre), and the resulting variables were used in subsequent analyses.

We ran two-way ANOVAs testing the effect of lateralization bias (right-biased versus nonbiased versus left-biased) and test cue (water versus predator odour) on the pre-stimulus data first (to ensure no existing biases among treatment groups) and then on the behavioural change data for both response variables. One-way ANOVA followed by Tukey post hoc tests were then performed to clarify the nature of any interaction. There was a marked lack of homoscedasticity for the change in activity data, so we ranked the data prior to analysis and performed a nonparametric ANOVA (Scheirer–Ray–Hare extension of the Kruskal–Wallis test; Sokal & Rohlf, 2012).

Experiment 2

We first tested for size bias in the outcome of the interaction by running a chi-square test looking at the association between size (large or small) and outcome (winner or loser). We also compared the emergence time between biased and nonbiased fish using a two-way ANOVA, with lateralization as a fixed factor and pair as a random factor. The data were not normal, so the number of events were log transformed to normalize the data. We tested the effect of lateralization bias (biased versus nonbiased) and side of lateralization (the side of lateralization, left versus right, was determined for each pair based on the side bias of the lateralized fish) on the frequency of occurrence of each behaviour (attacks, displays and avoidance) using a two-way repeated measures design, where lateralization was our within-subject effect and side of lateralization was our between-subject effect. In this analysis, pair, not fish, was used as our unit of replication ($N = 29$).

The number of interactions among pairs ranged from 4 to 61, so we repeated the same analysis using proportion of attacks, displays and avoidance per fish (i.e. proportion of attack = number of attacks/sum (attack + displays + avoidance)) to remove the potential biasing effect of highly interactive pairs on the results. Proportion data were arcsine transformed to normalize the data.

All data met parametric assumptions. Analyses were performed with SPSS 23 (IBM, Armonk, NY, U.S.A.).

Ethical Note

Fish were collected in accordance with an Australian Marine Park Authority Permit (G12/35117.1) and Queensland Fisheries Permit (number 170251). Care was taken to reduce unnecessary stress to the fish during all stages of the experiment. Following capture, fish were maintained in flow-through containers supplied with fresh sea water. Shelter was provided to the fish and the fish were fed several times per day with live food. At the end of the experiments all fish were returned to the reef. All experimental methods were carried out in accordance with relevant guidelines and regulations; all protocols were approved by the James Cook University Animal Ethics Committee (Approval numbers: A2080 and A2005).

RESULTS

Experiment 1

Fish did not differ in their pre-stimulus behaviours, either for feeding (lateralization bias: $F_{2,84} = 0.3$, $P = 0.9$; cue: $F_{1,84} = 1.0$, $P = 0.7$; interaction: $F_{2,84} = 0.9$, $P = 0.4$) or for activity (lateralization bias: $F_{2,84} = 2.8$, $P = 0.1$; cue: $F_{1,84} = 2.1$, $P = 0.2$; interaction: $F_{2,84} = 0.3$, $P = 0.7$).
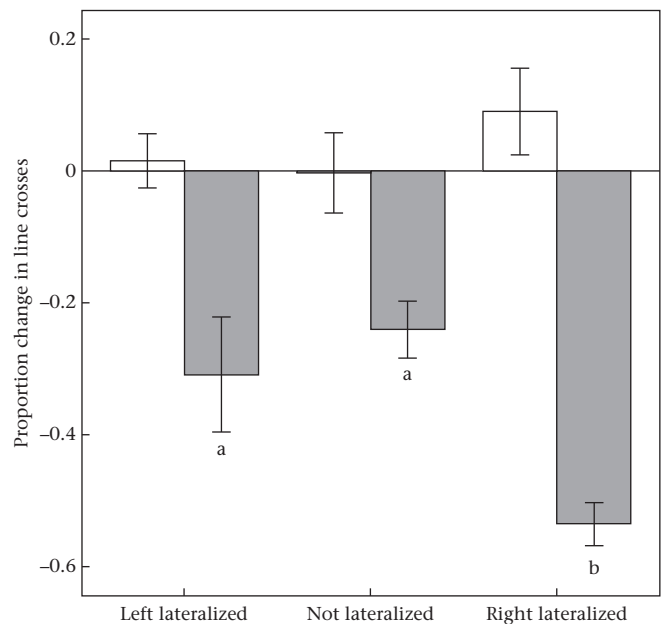
Change in feeding was affected by an interaction between lateralization bias and cue ($F_{2,84} = 10.2$, $P < 0.001$; Fig. 3). Splitting the analysis by cue revealed that fish from different lateralization groups did not differ in their response to water ($F_{2,27} = 0.5$, $P = 0.6$). However, they differed in their response to the predator ($F_{2,57} = 43.7$, $P < 0.001$), with both right- and left-biased fish displaying equally strong responses to the predator odour (post hoc Tukey test: $P = 0.3$), while nonbiased fish responded with a significantly weaker antipredator response (post hoc Tukey tests: both $P < 0.001$) to the same cue.

Change in activity was also affected by an interaction between lateralization bias and cue ($H_{2,84} = 5.7$, $P = 0.005$; Fig. 4). Once again, fish from different lateralization groups did not differ in their response to water ($H_{2,27} = 0.8$, $P = 0.5$). However, they differed in their response to the predator odour ($H_{2,57} = 8.6$, $P = 0.001$). The post hoc comparisons revealed that contrary to the feeding response, the activity response was similar between the left-biased and nonbiased fish ($P = 0.6$), which were both significantly weaker than the response displayed by the right-biased fish (both $P < 0.01$). Upon visual inspection of the data (see Fig. 5), however, we found that the heterogeneity in variance originated from a single group, the left-biased fish, which displayed very inconsistent responses to the predator odour compared to fish from the two other groups.
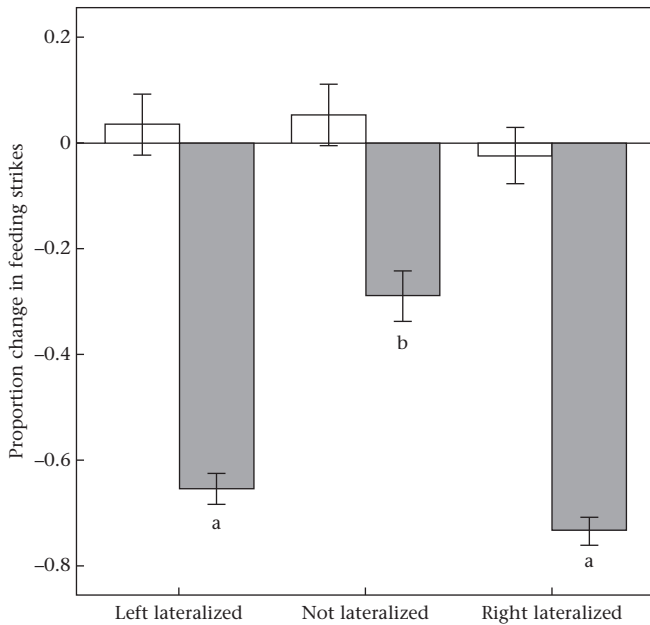
Experiment 2

There was no association between size and contest outcome ($\chi^2_c = 2.4$, $P = 0.14$). Winners consisted of 11 larger and 18 smaller individuals, ruling out size bias in the outcome of the interactions. Emergence time did not differ between fish with a lateralization bias and nonbiased fish ($F_{1,28} = 1.1$, $P = 0.31$).

Nonbiased fish displayed higher numbers of attacks ($F_{1,27} = 5.5$, $P = 0.027$), higher numbers of displays ($F_{1,27} = 11.2$, $P = 0.002$) and lower numbers of avoidance behaviour ($F_{1,27} = 5.7$, $P = 0.025$) than biased fish (Fig. 6). The side of lateralization bias did not have an

Figure 3. Mean (±SE) proportion change in feeding strikes for lateralized (left, right) and nonlateralized damselfish exposed to predator odour (grey bars) or control sea water (white bars) following conditioning. Letters indicate statistical differences at $\alpha = 0.05$.
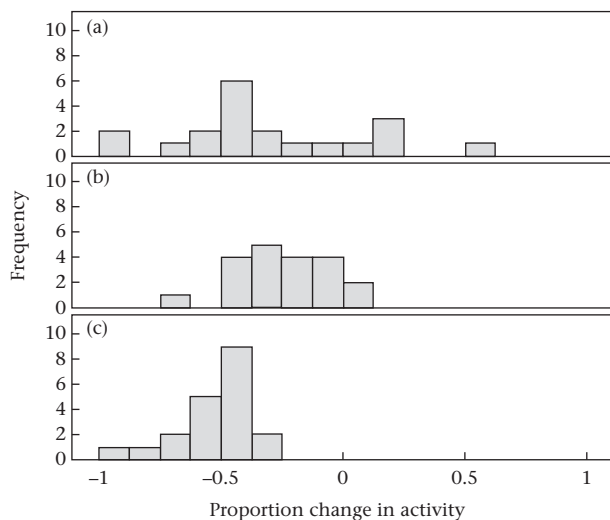
Figure 4. Mean (±SE) proportion change in line crosses for lateralized (left, right) and nonlateralized damselfish exposed to predator odour (grey bars) or control sea water (white bars) following conditioning. Letters indicate statistical differences at α = 0.05.
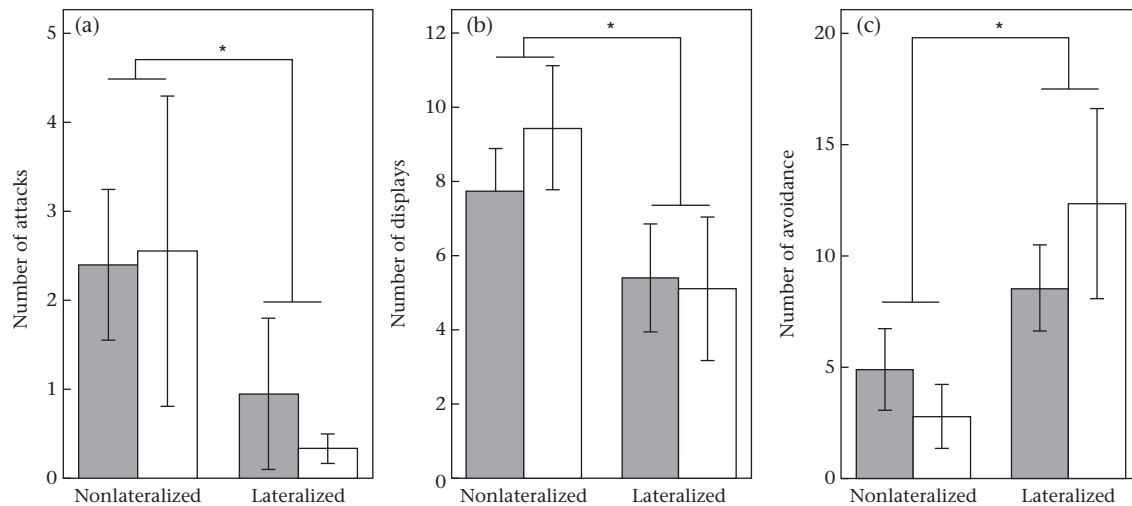
DISCUSSION

Despite any potential cognitive advantage of lateralization, researchers observe a large range of lateralization scores among wild animals (Bisazza, Cantalupo, Capocchiano, & Vallortigara, 2000; Chivers et al., 2016). This broad distribution of lateralization phenotypes suggests that there is some balancing of costs and benefits. Our experiment provides strong empirical support for this supposition. Our results demonstrate that juvenile coral reef fish with differing lateralization scores differ in the responses they display to learned predators and also how they interact during competitive interactions.

Experiment 1 provides strong evidence that fish from all groups (left-biased, right-biased and nonbiased) showed learning of the predator based on our well-established conditioning protocol. Lonnstedt et al. (2012) demonstrated that damselfish that learned predators through this mechanism have higher survival in the wild than naïve fish. In our experiment, we found that right-biased fish responded more strongly to the predator odour as a threat than fish in the nonbiased group. This was consistent across both behavioural measures. Right-biased fish reduced feeding and activity more than nonbiased fish. For left-biased fish, we observed very strong reductions in feeding upon detecting the predator odour, but the activity responses of left-biased fish were highly variable. Some individuals appeared to respond to the threat in the same way as the right-biased fish, while others seemed to maintain or even increase activity. This may indicate an alternate strategy whereby the individual may seek additional information about the nature of the threat. We interpret the stronger behavioural responses of biased fish to predator cues as evidence of altered cognition (Shettleworth, 2009), and as such, our results provide support for the hypothesis that there are benefits to lateralization that may counteract its costs. Our results are in accordance with other studies showing enhanced cognition of lateralized animals over nonlateralized animals (Bibost & Brown, 2014; Magat & Brown, 2009). Our study is the first to show this in a predator recognition context.

In experiment 2, we observed a strong effect of lateralization bias on competitive interactions. Nonlateralized damselfish showed much higher rates of attacks and more displays and were less likely to be attacked than were fish with a lateralization bias. The poor showing during competitive interactions by lateralized fish occurred regardless of whether the fish were left- or right-biased. Our results suggest that nonbiased animals may adapt their fighting strategy when they are interacting with individuals with a left-bias versus a right-bias. Future work should address whether this pattern holds for higher vertebrates where the outcome of competitive interactions may depend on greater cognitive ability.

Lateralization in fishes has recently been linked with sex and with personality traits such as boldness and activity (Dadda, Domenichini, Piffer, Argenton, & Bisazza, 2010; Irving & Brown, 2013; Reddon & Hurd, 2009). While we did not specifically consider these variables in our experiment, our results suggest that these behavioural traits may not be linked to lateralization. In experiment 1, we failed to find a pre-stimulus difference in activity and foraging tendencies between biased and nonbiased fish, and in experiment 2, emergence time did not differ between biased and nonbiased fish.

When damselfish recruit to the reef, they face two major selection pressures. First, predation pressure is immense with upwards of 50−60% predation-related mortality in the first 2 days after settlement (Almany & Webster, 2006). Fish need to immediately start cataloguing potential predators and nonpredators (Chivers et al., 2014; Mitchell, McCormick, Ferrari, & Chivers, 2011). This immense selection would suggest that fish should come to the

effect on the magnitude or direction of these results (attack: $F_{1,27} = 0.01$, $P = 0.9$; display: $F_{1,27} = 0.2$, $P = 0.6$; avoidance: $F_{1,27} = 0.6$, $P = 0.4$). Lateralization bias and side of lateralization did not interact (attack: $F_{1,27} = 0.04$, $P = 0.8$; display: $F_{1,27} = 0.6$, $P = 0.5$; avoidance: $F_{1,27} = 0.9$, $P = 0.3$).

When we looked at the proportion of events, we found similar results. Nonlateralized fish displayed proportionally more attacks ($F_{1,27} = 5.4$, $P = 0.028$), more displays ($F_{1,27} = 5.9$, $P = 0.022$), and less avoidance ($F_{1,27} = 8.2$, $P = 0.008$) than fish with a lateralization bias. Once again, the side of lateralization did not matter (attack: $F_{1,27} = 0.04$, $P = 0.9$; display: $F_{1,27} = 0.01$, $P = 0.9$; avoidance: $F_{1,27} = 0.1$, $P = 0.7$) and the lateralization bias did not interact with side of lateralization (attack: $F_{1,27} = 0.02$, $P = 0.9$; display: $F_{1,27} = 0.7$, $P = 0.4$; avoidance: $F_{1,27} = 0.4$, $P = 0.5$).

Figure 5. Frequency distribution of proportion change in activity for (a) left-lateralized, (b) nonlateralized and (c) right-lateralized damselfish exposed to predator odour following conditioning.

Figure 6. Mean ± SE (a) number of attacks, (b) aggressive displays and (c) avoidance behaviour displayed by nonlateralized and lateralized fish during a 5 min paired contest. ■: Contests between nonlateralized and left-lateralized fish; □: contests between nonlateralized and right-lateralized fish. Asterisks indicate statistical differences at α = 0.05.

reef highly lateralized and in tune to risk (Ferrari, McCormick, Allan, Choi, Ramasamy, Johansen, et al., 2015). However, free territories of high quality are of short supply on reefs. Given that fish are under immense selection to compete for territories (Holbrook & Schmitt, 2002; McCormick & Weaver, 2012), this would indicate that fish should come to the reef being nonlateralized and ready to compete the best they can. How do fish balance these two conflicting demands? Does the intensity of predation or the intensity of competition drive differences in lateralization? To gain an appreciation of the importance of this balance we need to be able to put these questions into the broader context of the pressures over the life period, from the end of the larval period, through settlement transition, to when the fish successfully joins the juvenile population. At each life stage the fish will interact with different animals within the different environmental contexts (McCormick & Makey, 1997). Currently the factors that promote or devalue lateralization are unknown for any life stage. Interestingly, several researchers recently showed that lateralization is highly flexible and that increases in predation pressure over days to weeks results in dramatic increases in lateralization (Broder & Angeloni, 2014; Chivers et al., 2016; Ferrari, McCormick, Allan, Choi, Ramasamy, & Chivers, 2015; Ferrari, McCormick, Meekan, et al., 2015). Whether changes in competition over the same time span can likewise change lateralization is not known, but coral reefs experience pulses of recruitment and hence a dynamic competition environment (Poulos & McCormick, 2014). It seems conceivable that at some times, or in some places on the reef, there is more competition for shelter while at other times or in other places, predation is more important. This spatiotemporal variation may lead to the maintenance of differences in lateralization. However, variation in lateralization may also stem from frequency-dependent selection whereby the fitness associated with different lateralization phenotypes changes based on the frequency of other phenotypes.

Our work points to the fact that we need a comprehensive assessment of costs and benefits of lateralization in different animals (Dadda, Zandonà, Agrillo, & Bisazza, 2009). In our study, we concentrated on studying two factors that have opposing effects on the benefits and costs of lateralization. We encourage additional work that can simultaneously address multiple ecological pressures. For example, future researchers should ask whether individuals that are highly lateralized have lower foraging efficiency because they are better at detecting resources on one side. Are individuals that are nonlateralized able to make enhanced sexual display because they

have different movement patterns? Understanding the cost and benefits of lateralization will require a comprehensive approach whereby the relative costs and benefits are compared across a range of ecological conditions and animal taxa.

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