

Increased behavioural lateralization in parasitized coral reef fish

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Abstract Preferential use of one side of the body for cognitive or behavioural tasks (lateralization) is common in many animals, including humans. However, few studies have demonstrated whether lateralization is phenotypically plastic, and varies depending on the ecological context. We studied lateralization (measured as a turning preference) in the bridled monocle bream (*Scolopsis bilineatus*). This coral reef fish is commonly infected by a large, ectoparasitic isopod (*Anilocra nemipteri*) that attaches to the left or right side of its host's head. Fish that were parasitized showed no turning bias with respect to the side on which the parasite had attached. On average, however, parasitised fish were significantly more lateralized (i.e. had a strong side bias) than unparasitized fish. The extent of lateralization declined significantly when we experimentally removed the parasite. Our results indicate that lateralization can vary with the ecological context. One possible explanation is that lateralization shortens the response time until fish

flee after encountering a predator. A stronger side bias might be advantageous for parasitized individuals to overcome their recently documented lower maximum swimming speed.

Keywords Behavioural side bias · Cymothoid isopod parasite · Great Barrier Reef · Handedness · Laterality · Morphological asymmetry · *Scolopsis bilineatus*

Introduction

Behavioural lateralization, the preferential use of one side of the body, is commonly reported in many invertebrates and vertebrates, including humans (Rogers and Andrew 2002; Vallortigara and Rogers 2005; Schaafsma et al. 2009; Jozet-Alves et al. 2012). Recent research suggests that the strength of lateralization can be context dependent rather than fixed, as previously thought (Mandel et al. 2008). For instance, in humans, a strong hand preference when writing is not always apparent when performing other tasks, suggesting that handedness is a relatively plastic trait (Geuze et al. 2012). Such context-dependent or task-dependent changes in lateralization are, however, still poorly understood both in humans and non-humans.

Some of the strongest evidence for an adaptive role of behavioural lateralization comes from teleost fish. For example, lateralization has been shown to be advantageous in fish schooling (Bisazza and Dadda 2005), escape responses (Dadda et al. 2010), multitasking (Dadda and Bisazza 2006a, b) and spatial reorientation (Sovrano et al. 2005). The enhanced performance of lateralized individuals in such cases is generally attributed to the specialisation of certain cognitive or motor tasks by one hemisphere of the brain (Rogers and Andrew 2002). This potentially avoids the duplication of costly neural pathways, and allows for the simultaneous processing of information from different stimuli (Rogers and Andrew 2002; Rogers et al. 2004; Vallortigara and Rogers 2005). However,

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there are potential costs to favouring one side of the brain, since ecologically relevant stimuli generally occur equally often on both sides of the body (e.g. predator approach; Vallortigara and Rogers 2005; Dadda et al. 2009). The balance between such costs and benefits will determine how strongly each individual is lateralised. Frequency-dependent selection is then likely to determine the skew, or lack thereof, in the population distribution of lateralization (whether or not most individuals are biased towards the same side) (Hori 1993; Lee et al. 2012).

A few recent studies have shown that changes in abiotic (water pH) and biotic (presence of predator versus conspecifics) factors as well as changes in the environment (novel vs. familiar) can affect how strongly individuals are lateralized (Bisazza et al. 1997b; Brown et al. 2004; Reddon and Hurd 2009; Domenici et al. 2012), but there is still limited evidence that side biases vary in different ecological contexts (Brown et al. 2004).

On the Great Barrier Reef, the cymothoid isopod *Anilocra nemipteri* parasitizes the bridled monocle bream, *Scolopsis bilineatus* (Grutter 1994; Roche et al. 2013b), with up to 30 % of fish infected at some sites (Roche et al. 2013b). A single isopod typically attaches to a fixed location on one side of the host. Parasites can grow to almost one third of the fish's standard length (D.G. Roche, unpublished data) and reduce host growth and survivorship (Adlard and Lester 1994; Fogelman et al. 2009; Roche et al. 2013b). *A. nemipteri* does not exhibit any side bias in attachment preference on either the left or right side of the host's body (Roche et al. 2013b). These parasites impair the swimming ability of *S. bilineatus*, mostly by increasing drag at high speeds and decreasing the host's critical swimming speed (U_{crit}) (Binning et al. 2013). Parasite attachment on one side of the body results in morphological asymmetry (Takeuchi et al. 2010), which can create uneven drag and/or weight distribution across the fish's body (Östlund-Nilsson et al. 2005), potentially affecting the host's centre of mass and pivot point. This could influence the fish's turning behaviour, causing parasitized individuals to turn more frequently towards/away from the side of their parasite. Since cymothoids significantly reduce swimming performance (Binning et al. 2013), increased lateralization could be particularly advantageous for parasitized fish when escaping from predators as lateralization has been associated with earlier responses to threatening stimuli (Dadda et al. 2010).

We tested the context dependency of lateralization by comparing the turning preferences of naturally unparasitized and parasitized *S. bilineatus*. We then compared the extent of lateralization of fish before and after we experimentally removed their parasite. We hypothesised that parasitism would increase lateralization and predicted that: (1) experimentally removing parasites would reduce lateralization to

the level of uninfected fish; (2) the side bias of a parasitized fish would depend on the side to which the parasite had attached.

Material and methods

Parasitized (11.82 ± 2.50 cm; mean \pm s.d.) and unparasitized (14.75 ± 1.47 cm; mean \pm s.d.) *S. bilineatus* were collected using barrier nets from the lagoon at Lizard Island, Northern Great Barrier Reef, Australia ($14^\circ 40'S$; $145^\circ 28'E$), in March and April 2012 (Fig. 1). Fish were transported in buckets to the Lizard Island Research Station and held in flow through aquaria under a natural light and temperature regime. Fish were fed to satiation once a day with raw prawn and fasted for 24 h prior to the experiments. All animals were kept in aquaria for a minimum of 3 days before performing swim trials to ensure all fish were healthy.

We used a detour test to assess behavioural lateralization (Dadda et al. 2010; Domenici et al. 2012). A single fish was introduced into a T maze, consisting of a large opaque tank ($102 \times 51 \times 50$ cm, length \times width \times height) with a runway down the middle ($70 \times 15 \times 20$ cm, length \times width \times height; Fig. 2). The water height in the tank was kept at 13 cm and water temperature was maintained at 27 ± 1 °C via a flow-through system with enough flow to ensure adequate aeration, but not to create a current in the tank. To initiate a trial, a fish was placed at the starting end of the runway and maintained there with an acrylic divider for 3 min. The experimenter then lifted the divider from behind the tank and gently pushed the fish with a dip net to initiate movement (Dadda et al. 2010; Domenici et al. 2012). The fish would swim to the end of the runway and reach a barrier (25×20 cm, width \times height; Fig. 2), positioned perpendicular to the runway, forcing it to turn left or right. We ran ten consecutive trials per fish (3-min



Fig. 1 The parasitic cymothoid isopod *A. nemipteri* infecting the bridled monocle bream, *S. bilineatus* (photo D.G. Roche)

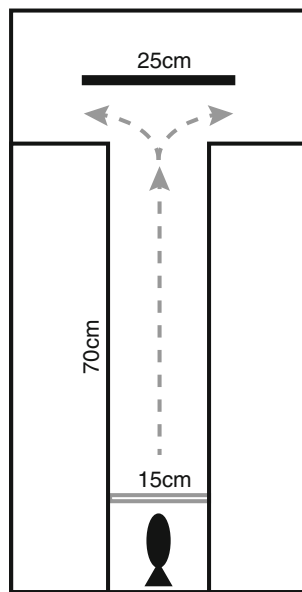


Fig. 2 Schematic representation of the T maze used for the detour test. During each trial, the holding barrier was raised, allowing the fish to swim down the runway. The fish faced a barrier at the end of the runway and would turn either left or right. The direction chosen by the fish was then recorded by the experimenter

rest between trials) and recorded the fish's turning direction. We then calculated a relative lateralization index (L_R) (Bisazza et al. 1997b; Domenici et al. 2012): $L_R = ((\text{Turn to the right} - \text{Turn to the left}) / (\text{Turn to the right} + \text{Turn to the left})) \times 100$. A score of -100 indicates an absolute preference for left turns and of 100 an absolute preference for right turns (Domenici et al. 2012). If an entire population is lateralized in the same direction, we expect an extreme high (close to 100) or extreme low (close to -100) population-level L_R score (Bisazza et al. 1998). A mean L_R close to zero indicates that a population (or sample of a population) is neither left nor right biased in its turning preference (Bisazza et al. 1998).

Even if a population as a whole is not left or right biased in its turning preference, it may still contain individuals that are themselves lateralized. In other words, individual fish may display distinct preferences for turning left or right irrespective of whether the population itself is lateralized. Therefore, we used the absolute lateralization index L_A ($L_A = |L_R|$) to calculate the strength of lateralization at the individual level, irrespective of the direction of lateralization. L_A ranges between 0 (individuals that turn left and right equally) and 100 (individuals that turn either left or right all the time) (Bisazza et al. 1998; Domenici et al. 2012).

Forty-one individuals were initially tested (25 unparasitized and 16 parasitized fish). We then removed parasites from the parasitized fish by holding the fish in a shallow water bath and gently unhooking the isopod with forceps (see Binning et al. 2013). We waited 24 h and retested the fish in the T maze.

We used goodness-of-fit G -tests to compare the proportion of left versus right turns per fish to the expected binomial distribution when $p=q=0.5$ for unparasitized, parasitized and parasite-removed fish. Lack of fit could be due to overdispersion (i.e. individuals have side-biases) even if $L_R \neq 0$ and/or a systematic side-bias at the population level (i.e. $p \neq 0.5$, equivalent to $L_R \neq 0$). We then ran a generalised linear model (GLM) with quasibinomial errors (given overdispersion; see "Results") to test for differences in the mean side-bias (i.e. L_R) between parasitized and unparasitized fish, and whether either mean differed from $p=0.5$ (i.e. $L_R=0$). Next, we calculated an absolute lateralization index L_A ($L_A = |L_R|$) for individuals in each of the three groups to evaluate the strength of lateralization of individuals, irrespective of the direction (Bisazza et al. 1997a; Domenici et al. 2012). We then compared L_A between unparasitized and parasitized fish using a Mann–Whitney U test. We also compared L_A between parasitized and parasite-removed fish with a Wilcoxon paired-sample test. Finally, we used a GLM with quasibinomial errors to test whether parasitized fish turned more often towards or away from the side to which their parasite was attached. Statistical analyses were conducted in R v2.15.0 (R Development Core Team 2010).

Results

The distribution of individuals' side biases (L_R) deviated from the null binomial distribution for unparasitized ($G=44.8$, $p<0.01$), parasitized ($G=88.7$, $p<0.001$) and parasite-removed fish ($G=56.6$, $p<0.001$) (Fig. 3). In all three groups, fish were significantly more lateralized than expected by chance; the observed deviations from a binomial distribution ($p=0.5$) were due to significant overdispersion ($\omega=5.8$) because individual fish tended to show side-biases. Fitting a GLM showed no significant difference in mean L_R between unparasitized and parasitized fish ($t=0.91$, $p=0.37$), and the estimated mean L_R did not differ significantly from zero ($t=0.70$, $p>0.45$). The mean L_R for all three groups was close to zero: unparasitized -10.4 ± 13.5 (mean \pm s.e.); parasitized 11.25 ± 21.7 ; and parasite-removed fish 16.3 ± 14.3 (Fig. 3). There was therefore no tendency for different fish to turn in the same direction (i.e. no population skew towards left or right turning fish). There was also no evidence that the turning bias of infected fish depended on which side their parasite was attached ($t=0.077$, $p=0.94$).

The absolute lateralization index L_A indicated individual-level side biases were significantly weaker for unparasitized than parasitized fish ($U=119.5$, $p=0.026$; Fig. 4). Intriguingly, L_A was also significantly smaller for parasite-removed fish compared to parasitized fish ($Z=2.58$, $p=0.01$; Fig. 4),

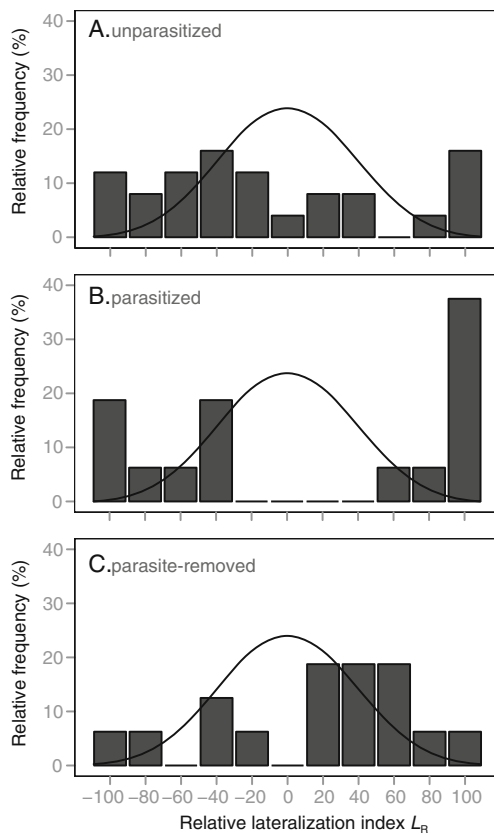


Fig. 3 The distributions of L_R in **a** unparasitized fish, **b** parasitized fish and **c** parasite-removed fish. The curve shows a binomial distribution with $p=q=0.5$. Positive values are right turns; negative values are left turns. Values of $|100|$ indicate fish that turned in the same direction (all left or all right) in all 10 trials

indicating that the additional lateralization induced by a parasite is readily reversed (i.e. within 24 h of parasite removal). We found no significant relationship between host size and L_A ($p=0.67$, $r^2=0.01$).

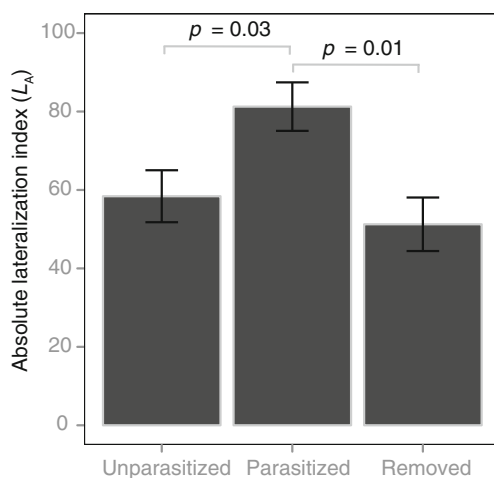


Fig. 4 L_A (mean \pm s.e.) for unparasitized, parasitized and parasite-removed fish. Significance levels are shown for pairwise contrasts (see text)

Discussion

Although there was no population level lateralization, individual bridled monocle bream tended to have a side-bias when turning at a barrier. The strength of this behavioural lateralization was associated with attachment of the ectoparasite *A. nemipteri*. Parasitized fish showed a significantly stronger side-bias than unparasitized fish, providing evidence that the strength of individual lateralization can vary with the ecological context.

A simple proximate explanation for these differences in lateralization could be that the asymmetric attachment of the parasite on one side of the fish creates a directional cue on the host's body (Takeuchi et al. 2010). When facing a barrier, some parasitized individuals might deal with the combination of having to turn and carrying a directional cue by consistently turning towards or away from the cue. Unparasitized fish that do not carry a directional cue, in contrast, would be less likely to show a strong turning bias when facing a barrier. Studies argue that directional bias in lateralization may lead to behavioural predictability in prey escape responses resulting in enhanced predator success (e.g. Reddon and Balshine 2010). This could explain why parasitized fish, although lateralized, did not show a consistent directional bias in lateralization towards or away from the parasite cue, which predators could learn to anticipate.

There are also adaptive explanations for the higher lateralization of parasitized fish. Notably, functional left–right cerebral asymmetries are important determinants of fish behaviour, particularly during predator–prey interactions (Dadda et al. 2010; Domenici et al. 2012). For example, behavioural lateralization helps avoid simultaneously initiating opposing directional responses when fleeing from a predator (Vallortigara and Rogers 2005). In a study of the surfperch *Cymatogaster aggregata*, Dadda et al. (2010) also found that lateralization likely increases escape success by lowering the response latency of fish to threatening stimuli. They attributed the increased reactivity of lateralized individuals to a lower sensory threshold required to activate the Mauthner cells (Dadda et al. 2010), a pair of giant reticulospinal neurons responsible for short (<50 ms) escape response latencies (Eaton et al. 2001).

Recently, Binning et al. (2013) showed that parasitized *S. bilineatus* suffer from decreased swimming performance in critical swimming speed (U_{crit}) trials due to increased drag. U_{crit} measurements provide rough estimates of maximum sustained (aerobic) swimming speed (Plaut 2001), but typically involve burst (anaerobic) swimming towards the end of the trial (Farrell 2007; Svendsen et al. 2010; Roche et al. 2013a). Prolonged and burst swimming are often used by fishes to escape from predators, particularly from ram feeders (as opposed to suction feeders) that chase their prey prior to capture. Faster responses owing to a stronger side

bias might confer a fitness advantage to parasitized individuals that are poorer swimmers. In addition, *A. nemipteri* attaches very close to the eye, which might decrease the host's visual range. Rapid responses triggered by other sensory stimuli (e.g. olfactory and mechano-acoustic stimuli; Domenici 2002; Stewart et al. 2013) might compensate for a reduced field of vision and otherwise elevated host vulnerability to predation.

Biologically relevant visual stimuli occur equally on both sides of the body, so strong lateralization is not always advantageous (Rogers and Andrew 2002; Vallortigara and Rogers 2005). The extent of lateralization probably represents a trade-off between faster decision making in lateralized individuals and the ability of non-lateralized fish to better process stimuli originating from all directions (Dadda et al. 2009; Reddon and Hurd 2009; Domenici et al. 2012). Reduced swimming performance presumably shifts the balance of this trade-off toward stronger lateralization and faster decision making in parasitized hosts that are potentially more vulnerable to predators. In contrast, the balance would shift away from strong lateralization and towards the ability to process stimuli on both sides of the body for unparasitized individuals with good swimming abilities. This trade-off could explain why *S. bilineatus* became more weakly lateralized once their parasite was removed. This change in lateralization strength unlikely resulted from testing fish twice since fish that were tested more than once in preliminary trials ($n=8$) displayed consistent lateralization indices.

Behavioural flexibility within different ecological contexts is often advantageous, especially for organisms living in complex habitats, such as coral reefs. For instance, coral reef fishes adjust their swimming behaviour (fin use) in response to varying hydrodynamic conditions, presumably to save energy (Heatwole and Fulton 2012). Similarly, parrotfishes vary their flight-initiation distance depending on the perceived risk of predation (Gotanda et al. 2009). It is therefore plausible that the changes in lateralization of *S. bilineatus* are adaptive in the context of predator–prey interactions. The observed plasticity in laterality is consistent with evidence that the preferential use of one eye is not necessarily fixed for individual fish (Brown et al. 2004). The rapid decrease in lateralization following parasite removal also supports recent findings that the negative physiological effects of *A. nemipteri* on *S. bilineatus* are reversed within 24 h post removal (Binning et al. 2013).

Predation is thought to play a key role in the evolution of lateralized behaviour. Previous studies have shown that lateralization varies between conspecific populations exposed to different predation pressures (Brown et al. 2004). Here, we show that parasitism might interact with the strong selection imposed by predators to favour phenotypic plasticity in behavioural lateralization. Further studies are needed that test

the extent to which greater lateralization improves the fitness of parasitized *S. bilineatus* when they encounter predators. More broadly, our results highlight the need to test for adaptive phenotypic plasticity in behavioural lateralization among other species.

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Ethical standards Research was conducted under the Australian National University animal ethics permit A2012/02 and the Great Barrier Reef Marine Parks Authority collection permit G12/34805.1. Animals were released at their site of capture at the end of the study and none were harmed as a result of the parasite removal.

Conflict of interest The authors declare that they have no conflict of interest.

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