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Research report

Laterality strength is linked to stress reactivity in Port Jackson sharks (*Heterodontus portusjacksoni*)

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HIGHLIGHTS

- Lateralization in *Heterodontus portusjacksoni* appeared to be highly individualized.
- Stronger lateralized individuals were more reactive to stress.
- Laterality did not correlate with boldness in *H. portusjacksoni*.
- Female *H. portusjacksoni* were more lateralized than males.

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ABSTRACT

Cerebral lateralization is an evolutionarily deep-rooted trait, ubiquitous among the vertebrates and present even in some invertebrates. Despite the advantages of cerebral lateralization in enhancing cognition and facilitating greater social cohesion, large within population laterality variation exists in many animal species. It is proposed that this variation is maintained due links with inter-individual personality trait differences. Here we explored for lateralization in Port Jackson sharks (*Heterodontus portusjacksoni*) using T-maze turn and rotational swimming tasks. Additionally, we explored for a link between personality traits, boldness and stress reactivity, and cerebral lateralization. Sharks demonstrated large individual and sex biased laterality variation, with females demonstrating greater lateralization than males overall. Stress reactivity, but not boldness, was found to significantly correlate with lateralization strength. Stronger lateralized individuals were more reactive to stress. Demonstrating laterality in elasmobranchs for the first time indicates ancient evolutionary roots of vertebrate lateralization approximately 240 million years old. Greater lateralization in female elasmobranchs may be related enhancing females' ability to process multiple stimuli during mating, which could increase survivability and facilitate insemination. Despite contrasting evidence in teleost fishes, the results of this study suggest that stress reactivity, and other personality traits, may be linked to variation in lateralization.

1. Introduction

Over the past three decades the demonstration of lateralization amongst all vertebrate groups and some invertebrates suggests that it is an evolutionarily deep-rooted trait and may even predate its evolution in vertebrates [1–3]. Much of recent evolutionary research has focused on the advantages and disadvantages of lateralization to understand the selective mechanisms for the evolution of cerebral lateralization, such as the enhancement of cognitive functions. For example, more strongly lateralized individuals are quicker to learn tasks and can process greater cognitive loading [4,5]. Additionally, lateralization enhances cohesive behaviours, such as shoaling and group foraging [6]. In visually complex habitats, such as coral reefs, the enhanced ability to process multiple stimuli and cooperate has been shown to enhance survivorship when predator abundance is high [7,8].

Despite these apparent fitness advantages of cerebral lateralization, substantial individual variation in both direction and strength of lateralization exists in many species [9–12]. The underlying mechanisms maintaining this individual variation are still poorly understood, but a recent hypothesis proposes that variation in lateralization is maintained through a link with consistent inter-individual personality and behavioural differences [13]. Aggression, for example, appears to be a highly lateralized trait among vertebrates and invertebrates [1,14,15]. During antagonistic responses, animals direct aggressive displays to conspecifics on

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the left side more than on the right side. This asymmetry has been recorded in toads [16], lizards [17], domestic chicks [18], gelada baboons [19], horses [20], and fruit flies [21]. On the other hand, other personality traits reveal confounding relationships that vary by sex and/or species [22]. Irving and Brown [23] found little evidence that laterality relates to boldness, sociability, or activity in *Poecilia reticulata*, and populations of the poeciliid *Brachyraphis episcopi* vary in strength of lateralization [9,24], as well as boldness [25], aggression [26], exploration, and activity [27].

The bulk of research that has examined the personality/lateralization relationship has focused on aggression and boldness; however, there is a paucity of research that has focused on stress reactivity (aka coping style or emotional reactivity). The few existing studies indicated that stress reactivity correlates with aggression, and suggested the existence of a relationship between stress reactivity and laterality [28]. Additionally, researchers commonly take advantage of the fact that laterality biases tend to be more pronounced in stressful situations, such as presence of predators or potential competitors. For example, when Bisazza & Vallortigara [29] placed male mosquitofish (*Gambusia holbrooki*) placed in a circular tank, laterality biases were only apparent when a predator was present in the middle of the tank; not during spontaneous swimming or when a female was used as a stimulus.

Measurement of physiological parameters have demonstrated that the right cerebral hemisphere is associated with expression of intense, often negative, emotions and controls hormonal states that accompany these states [30,31]. Therefore, it is expected that more strongly right lateralized individuals would exhibit stronger emotional and stress responses. Recent evidence that right lateralized marmosets were more pessimistic and avoided potentially stressful stimuli more than left lateralized conspecifics corroborate this prediction [32]. However, studies in dogs and domesticated chicks have shown that nonlateralized individuals to be more reactive, potentially as a result of the negative relationship between the development of lateralization and corticosterone levels during embryonic development [33,34]. While the relationship remains equivocal at best, it is apparent that studying the relationship between stress reactivity and laterality may provide valuable insight into the maintenance of individual variation in lateralization.

Studying lateralization in fishes has presented an especially interesting system for examining the evolution of vertebrate lateralization [15]. Fishes occur in a wide range of habitats that provides an opportunity to comparatively study the ecological conditions under which lateralization likely first evolved [1,35]. Additionally, in many fishes, optic fields do not overlap and primary visual projections ascend to neural structures on the contralateral hemisphere of the brain. Hence, observation of asymmetries is made particularly simple by examining which eye individuals use to observe particular cues or scenes [10,29]. Lateralized behaviours in fishes include inspection of conspecifics and predators [10,24], initiation of aggressive interactions [36], shoaling tendencies [6], predatory approaches [37], exploration [9,38], spatial abilities [5,39], and communication [40]. While teleost fishes have received a bulk of attention from research examining the evolutionary origins of lateralization in vertebrates, no study has yet examined laterality in elasmobranchs – one of the oldest vertebrate lineages, appearing some 450 million years ago.

Here we examined behavioural lateralization in Port Jackson sharks (*Heterodontus portusjacksoni*), a species thought to originate approximately 240 million years ago [41], using two different lateralization tests. We employed turn preferences in a T-maze and directional preferences for rotational swimming, two tests that have been successfully used to determine laterality in teleost fishes. Given the relationship between laterality and social interactions in teleost fishes and the social aggregating behaviours of Port Jackson sharks [42,43], we hypothesized that Port Jackson sharks will demonstrate a highly lateralized population bias, but we cannot predict the direction of laterality. We then examined for consistency of lateralization between turn and rotational preference. Lastly, sharks' boldness and stress reactivity were scored in a previous experiment [44], and relationships between these traits and laterality were examined. Based on teleost fish studies, we predicted that boldness would correlate with laterality, such that shyer individuals would be more strongly lateralized. Moreover, based on physiological evidence, we expected that right lateralized individuals (left eye use preference) would demonstrate higher stress reactivity than left lateralized individuals

2. Materials and methods

2.1. Subjects

Port Jackson sharks (*Heterodontus portusjacksoni*) were selected as study subjects due to their abundance in New South Wales coastal waters, as well as their small size and renowned hardiness, making them suitable for captive studies [43,45]. A total of 17 juvenile *H. portusjacksoni* were opportunistically collected from three sites in New South Wales, Australia: 1) Middle Head, Mosman, NSW (33°49′26.903″S 151°15′50.404″E); 2) Murray's Sandline, Jervis Bay, NSW (35°4′23.015″S 150°27′28.188″E); 3) Broken Bay, NSW (33°34′14.100″S 151°17′15.200″E). Sharks from Middle Head and Murray's Sandline were captured by hand, on snorkel, and sharks from Broken Bay were captured as by-catch on a commercial squid trawler. Sharks were housed at Sydney Institute of Marine Science (SIMS; Mosman, New South Wales) in four 1000-l housing tanks (1.25 m diameter × 0.90 m depth). Sharks were separated into housing tanks according to total length; tanks 1 and 2 contained sharks ≤30 cm and tanks 3 and 4 contained sharks >30 cm. Tanks were supplied with fresh seawater from Chowder Bay, Mosman, NSW at ambient temperature, aerated, and furnished with approximately 5 cm of sandy substrate (taken from Chowder Bay) and PVC structures to provide shelter. The sharks were exposed to a natural light cycle.

For individual identification, sharks were tagged subcutaneously with an inert polymer elastomer (North-West Marine Technology Inc., Shaw Island, WA, USA) for and total length was measured. After 24 h in captivity, sharks were fed to satiation with defrosted squid (*Loligo opalescens*). During non-experimentation periods, they were fed ~5% body weight five days per week on a mixed diet of squid (*L. opalescens* and *Nototodarus sloanii*) and shrimp (*Litopenaeus vannamei*). Post experimentation, subjects were released at their original site of capture. Research was conducted under a scientific marine research ethics permit (ARA 2014/003) obtained from Macquarie University. All sharks were collected under NSW Department of Primary Industries permit P080010-4.2 and Australian Government permit AU-COM2014-259.

2.2. Behavioural trait differences

Sharks used in this study had individual differences in boldness and stress reactivity predetermined in a previous experiment [44]. Personality trials were conducted over a 17-day period, from April 23 to May 9, 2015. To prevent temporal autocorrelation, trials were separated by at least three days. Boldness trials were conducted for each shark once on days one, four, seven, and 14, and stress reactivity trials were conducted on days 10 and 17 of the testing period.