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Serotonin-manipulated juvenile green sea turtles *Chelonia mydas* exhibit reduced fear-like behaviour

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ABSTRACT: Animals display fear-like behaviours before escaping from predators. This response triggers both behavioural and physiological changes in multiple body systems, allowing animals to escape danger and ensure survival. Fear-like behaviour is modulated by the serotonergic system in the brain of vertebrates, which shapes social behaviour and cooperative behaviours. Using fluoxetine (FLX), a common pharmaceutical that alters the levels of serotonin in the brain, we aimed to clarify whether the same is true in solitary animals like green turtles *Chelonia mydas*. Green turtles exhibit individual differences in their response to risk. If fear-related behaviours are regulated by the serotonin system in turtles, the fear-like responses of individuals injected with FLX could change. We therefore assessed the effect of FLX injection on the behavioural responses to a fear stimulus in 9 wild juvenile green turtles in an aquarium setting. We inserted a hand net as a stimulus into the aquarium (within a designated inspection zone) to elicit a fear-like behaviour and measured the time that turtles spent in this zone. All turtles exhibited fear-like behaviour and fled from the stimulus prior to any injection treatment. Turtles with control injection (no FLX) also fled and avoided the inspection zone with the fear stimulus. FLX injection appeared to reduce the turtles' fear of the stimulus: The total time turtles injected with FLX spent in the inspection zone was significantly longer than for turtles that received a control medium injection. Control turtles fled from the stimulus and were initially vigilant and avoided the area with the stimulus, but then moved throughout the aquarium, including the inspection zone. These data suggest that fear-like behaviour is modulated by the serotonin-mediated nerve system in juvenile green turtles.

KEY WORDS: Fear-like behaviour · Serotonin · Juvenile green sea turtle · Solitary animal

1. INTRODUCTION

Animals show fear-like behaviours to avoid or escape from predators. Avoiding predation is a preeminent selective force in nature because failing to do so immediately reduces the individual's future fitness (Werner & Peacor 2003). Fear response triggers both behavioural and physiological changes in multiple body systems to allow individuals to avoid danger (Cezario et al. 2008, Adolphs 2013). For example, sharks are predators of sea turtles, and antipredator responses in turtles have been shown to enable hiding, predator deterrence, flight and vigilance (Heithaus et al. 2008). The time an animal spends forag-

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ing can be affected by the presence of predators; thus, antipredator responses are essential fitness components that can influence an animal's survival (Heithaus et al. 2002, 2005, 2008, Higgins 2006). However, physiological changes in fear responses have not been studied in sea turtles.

Fear-like behaviours are known to be associated with the brain serotonin system in animals (Adolphs 2013, Beis et al. 2015). Serotonin (5-hydroxytryptamine, 5-HT) is a neurotransmitter released in the brains of several vertebrates in response to stress (Puglisi-Allegra & Andolina 2015). Serotonin participates in the modulation of stress and defensive behaviour in fish (Herculano & Maximino 2014, Winberg & Thörnqvist 2016, Soares et al. 2018) and has been implicated in vertebrate social behaviour (Insel & Winslow 1998, Soares et al. 2018) and cooperative behaviours (Paula et al. 2015). These findings indicate that serotonin may be involved in the mediation of cooperative and defensive behaviours in situations when animals are in fear. In fact, when the guppy treated with fluoxetine (FLX), a commonly prescribed antidepressant in the family of selective serotonin reuptake inhibitors that alters the levels of serotonin in the brain, was exposed to the stimulus of predator animation, it was found to spend more time near the predator image and freezing and less time avoiding the predator. This observation suggests the role of serotonin in cooperative behaviours (Pimentel et al. 2019).

Animals that form groups as a type of cooperative behaviour are able to detect predators sooner than solitary individuals in part due to the improved vigilance effect, so predators seem to be less successful when their prey is fully aware of their presence (Caro 2005). However, sea turtles are primarily solitary animals (Thomson et al. 2015), although some adult green turtles in the Florida Keys are found in groups (Bresette et al. 2010). Green turtles detect a danger signal, respond to danger and show vigilance without external help. In addition, turtles respond to a fear stimulus, including non-lethal factors such as humans (Griffin et al. 2017), hand nets (Kudo et al. 2021), shark decoys (Wang et al. 2010) and boats (Heithaus et al. 2002), with fear-like behaviours and flee from predators. In this situation, it is unclear whether fear-like behaviours in green turtles are similar to the serotonin-derived behaviours displayed by animals that form groups in cooperative behaviours.

The green sea turtle, *Chelonia mydas*, is under threat from human activities, of which fisheries bycatch has the greatest impact (Lewison et al. 2013). The conflict between conservation and human activity needs to be addressed. Much research, e.g. the development of turtle excluder devices, has already been conducted to solve this problem, and understanding how individual animals respond to disturbance, for example to determine what triggers an avoidance response in animals, will be useful for commercial fisheries (Higgins 2006, Wang et al. 2010, 2013, Bostwick et al. 2014). If we can understand what incites fear, we can incorporate some of these stimuli into fishing nets to reduce sea turtle by-catch.

After several years in the pelagic zone juvenile turtles return to coastal waters and occupy various habitats during their development until they reach sexual maturity (Musick & Limpus 1997). Green turtles in tropical and sub-tropical foraging areas establish narrow home ranges during foraging periods in Florida (Makowski et al. 2006), Hawaii (Brill et al. 1995), Mexico (Lamont et al. 2015) and Japan (Kameda et al. 2013). Wild green sea turtles suffer high mortality in their natural habitat for several reasons (e.g. fishing nets, boats, predators); thus, various circumstances can teach them fear (Ishihara et al. 2014). In a study of stimulus presentation experiments, green turtles from the coast of Japan exhibited fear-like responses to hand nets in an aquarium setting: turtles confronted with a net fled immediately and avoided the area with the net for longer than in a control setting (i.e. without a net) (Kudo et al. 2021). However, it is unclear whether these behaviours correspond to the serotonin-derived behaviours in social interaction.

Therefore, this study aimed to clarify whether fear-like behaviour is modulated by serotonin in juvenile green turtles. Green turtles, known to be solitary, exhibit individual differences in their responses to a fear stimulus. If fear-like behaviours are induced by the serotonin system in turtles, the fleeing responses of individuals whose serotonin levels in the brain have been increased by FLX, i.e. pharmaceuticals which affect the serotonergic systems, are likely to change.

2. MATERIALS AND METHODS

2.1. Study site and sea turtle collection

The present study was conducted from June to November 2019 on the Hazako coast (32° 56′ N, 132° 2′ E) in Oita Prefecture, Japan. Nine wild juvenile green turtles (*Chelonia mydas*) of standard carapace length, 353–425 mm and body mass of 7.3–11.0 kg were ob-

tained opportunistically from accidental catches in coastal set nets of commercial fisheries and marked with a plastic tag (obtained from the Oita environmental conservation forum) attached to the left rear limb after it had been pierced. The turtles were kept for 2–4 wk in a circular holding tank (diameter: 260 cm, height: 94 cm). Ambient seawater was continuously circulated in the aquarium, and water temperature was maintained at 21–25°C. The holding tank was illuminated by natural light at 80–120 lux. The turtles were provided with defrosted fish daily but did not feed initially after transfer to the holding tank. When they started to feed, they were considered acclimatised to the holding tank and ready for the experiments. At this point, each individual was fed 3–5 thawed silver-stripe round herring every morning.

2.2. Experimental setup and design

All tests were conducted in an experimental aquarium (300 × 200 × 100 cm; Fig. 1). A video camera (VCC-H 154 equipped with 540 HF 3.5 M - 2 lens, Digimo Innovations) was installed 230 cm above the water surface and the centre of the experimental aquarium to film turtle behaviour during the experiments. Images were recorded on a computer using the LRH 1540 v movie Image recording control system software. A black mesh covered the frame on which the camera was installed (see Fig. 1) to avoid direct sunlight as the reflection in sunlight would have made it impossible to see the image of the turtle. The inspection zone (200 × 100 cm) was designated as anywhere within 1 m of the wall on which the stimulus was presented (Fig. 1).

Trials were conducted over 4 d, with behavioural trials on Days 1 and 2 (Trials 1 and 2, respectively) and FLX trials on Days 3 and 4 (Trials 3 and 4, respectively; Fig. 2). All animal experimentation protocols were approved by the Institutional Animal Care and Use Committee of the University of Tokyo (permit no. P18-15). The study was carried out in accordance with the National Institutes of Health guide for the care and use of laboratory animals (NIH Publications No. 8023, revised 1978) and in compliance with the ARRIVE guidelines (https://arriveguidelines.org/arrive-guidelines).

2.2.1. Behavioural tests: Trials 1 and 2

We used a hand net as a fear stimulus to elicit a fear-like response based on the results of a previous experiment (Kudo et al. 2021). In the first behavioural trial, one turtle at a time was moved from the circular holding aquarium to the experimental aquarium and allowed 20 min to acclimatise to the experimental

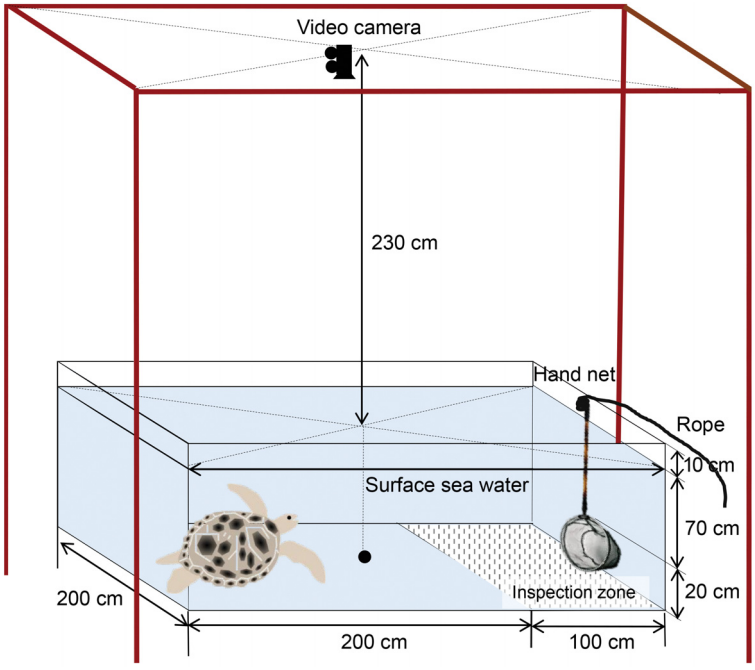

Fig. 1. Experimental setup for the behaviour test

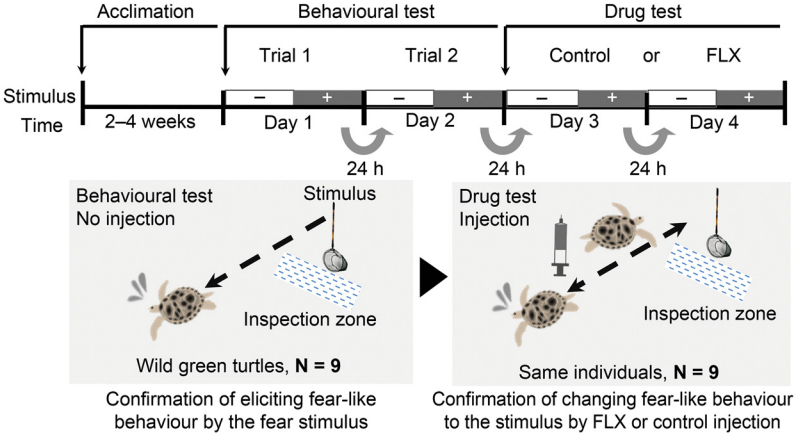

Fig. 2. Timeline of the behaviour and drug tests. FLX: fluoxetine

aquarium without stimulus. Then we threw a hand net tied to a rope into the centre of the experimental tank and pulled the rope towards the wall to place the hand net within the inspection zone. The stimulus was left in place while the turtle was filmed for 20 min before being returned to the holding tank. The same turtle was tested the next day using the same procedure. The order of the turtles being tested was decided haphazardly for Trial 1, and the same order was used the next day for Trial 2. The time each turtle spent in the inspection zone during each trial was measured based on the recording of the behavioural tests.

2.2.2. FLX tests: Trials 3 and 4

On Day 3, the day after the 2nd behavioural trial, the turtles were haphazardly assigned to either the control or the FLX treatment group and injected intraperitoneally with 0.5 ml per kilogram body weight (kg BW^{-1}) control medium (1% by vol of Tween® 80, 1% by weight of methylcellulose and H_2O; Inagaki et al. 2005) or control medium + FLX (Tokyo Chemical Industry; 20 mg FLX per ml control medium, equivalent to 10 mg FLX kg BW^{-1}), respectively. We chose this dose of FLX, because it was the lowest does that elicited a fear-like stimulus response in all 9 animals in preliminary tests (data not shown). In those tests, we started with injections of 60 mg kg BW^{-1} based on Deckel (1996). However, at this concentration, movements of treated turtles were getting sluggish, and they did not respond to the fear stimulus. Each turtle was moved to the experimental aquarium 15 min after injection and underwent the same procedure as during the behavioural trials. The FLX trial was repeated on Day 4, with each turtle being assigned to the other treatment group (i.e. control turtles received the FLX injection and vice versa).

2.3. Statistical analysis

All of the data met assumptions of normality and homogeneity of variances (Kolmogorov-Smirnov one-sample test, $p > 0.05$) and homogeneity of variances (Levene's test, $p > 0.05$). In order to confirm whether turtles would flee from the stimulus and consistently respond to the stimulus over time, we compared the total time turtles spent in the inspection zone between the 2 repeated behavioural trials for each individual using paired *t*-tests. Next, we used paired *t*-tests to compare the total time each turtle spent in the inspection zone during the 2 behavioural tests (Trials 1 and 2) in the 20 min before versus in the 20 min after the stimulus was added to the tank. The aim of this analysis was to validate the stimulus that was used in the behavioural tests (i.e. without injections). We also compared the time that turtles spent in the inspection zone between the control and FLX treatment groups using paired *t*-tests. All statistical analyses were performed using SPSS software v25.0 and a significance level of 0.05.

3. RESULTS

Generally, the total time turtles spent in the inspection zone was significantly shorter in both behavioural tests (Trials 1 and 2) when the hand net was present compared with when it was absent (paired *t*-test, Trial 1: $t_8 = -3.988$, $p < 0.05$, mean ± SD without stimulus : 207.3 ± 107.9 s, with stimulus: 53.2 ± 36.7 s; Trial 2: $t_8 = -3.603$, $p < 0.05$, without stimulus: 228.5 ± 112.9 s, with stimulus: 59.2 ± 50.2 s, n = 9 for both trials, Fig. 3). The hand net was therefore deemed a suitable stimulus for investigating fear-like behaviour in green sea turtles. Comparisons between Trial 1 and Trial 2 showed that test results for each individual were significantly correlated (Pearson's correlation: with stimulus, $r = 0.85$, $p < 0.01$, n = 9; without stimulus: $r = 0.87$, $p < 0.01$, n = 9), indicating that all individuals consistently showed fear-like behaviour.

In the presence of the hand net, the green turtles injected with FLX remained in the inspection zone for a significantly longer period than the turtles that received a control medium injection (paired *t*-test: $t_8 = -2.805$, $p < 0.05$, mean ± SD for the medium control 53.0 ± 45.0 s, and 96.2 ± 39.9 s for the FLX treatment, n = 9, Fig. 4).

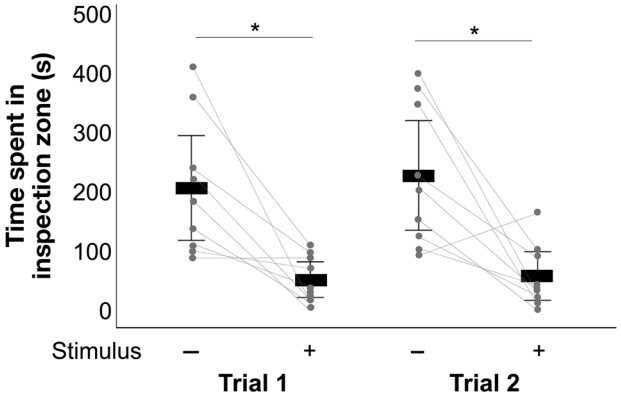

Fig. 3. Comparison of times spent in the inspection zone with (+) and without (–) each stimulus. Black bars: average value; error bars: 95% CIs; grey dots: measured values; grey lines connect the same individuals; *$p < 0.05$

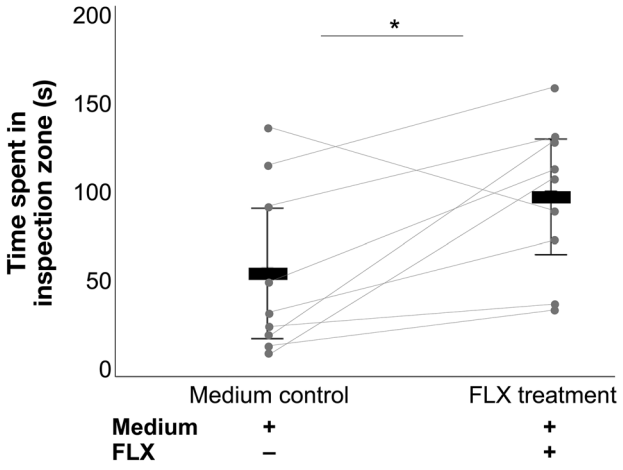

Fig. 4. Comparison of times spent in the inspection zone with stimulus control injection and fluoxetine (FLX) injection. Black bars: average value; error bars: 95% CIs; grey dots: measured values; grey lines connect the same individuals

4. DISCUSSION

In this study, juvenile green sea turtles fled from the fear stimulus, and the stimulus elicited turtle responses that indicated fear-like behaviour. The turtles injected with FLX remained in the inspection zone for a longer time than those injected with the control injection. This result indicates that the response of the turtles injected with control medium was changed by the FLX injection, causing them to be less fearful of the stimulus. These results suggest that regulation by the serotonin-mediated nervous system has effects on the response to a fear stimulus in juvenile green turtles.

Sea turtles are primarily solitary animals (Thomson et al. 2015); however, Bresette et al. (2010) reported that adult (>90 cm standard carapace length [SCL]) and large subadult green turtles (65–90 cm SCL) observed on their foraging ground were found in small groups of 4 or 5 individuals, while juvenile turtles (<65 cm SCL) were not seen grouping. Since the green turtles we examined had SCLs of 35.3–42.5 cm, they were juveniles and probably solitary.

In mammals, such as mice, FLX treatment increases the serotonin level in the amygdala (Marcinkiewcz et al. 2016). Regulation of the serotonin-mediated nervous system with serotonin and selective serotonin reuptake inhibitors suppresses fear-like behaviour (Salchner & Singewald 2002, Spennato et al. 2008, Ravinder et al. 2011, Burghardt et al. 2013, Deschaux et al. 2013). Fear-like behaviour is also related to the expression of genes associated with serotonin synthesis, regulation, uptake and degradation (Thörnqvist et al. 2015). Many previous clinical studies have demonstrated that FLX treatment reduces fear and anxiety in mice, rats and humans (Salchner & Singewald 2002, Spennato et al. 2008, Ravinder et al. 2011, Burghardt et al. 2013, Deschaux et al. 2013). Given that FLX treatment suppressed fear-like behaviour in juvenile green sea turtles in the present study, a similar phenomenon may occur in other solitary animals.

All turtles in the behavioural trials (i.e. without injection) consistently showed fear-like behaviour over time (Trial 1 vs. Trial 2) in our study. The turtles' response was changed by the FLX injection, causing the turtles to be less fearful of the stimulus (i.e. spending more time in the inspection zone, see Fig. 4). Similarly, manipulation of the serotonin-mediated system with FLX affected personality traits such as shyness and boldness in sticklebacks: shy sticklebacks under FLX treatment spent more time near the image of a predator (Abbey-Lee et al. 2019). In our study some of the turtles we considered to be shy (i.e. those which had spent less time in the inspection zone after the stimulus was added than other turtles in the control medium injection group) showed a trend towards greater boldness when treated with FLX (i.e. these turtles then spent more time in the inspection zone with the stimulus relative to turtles we considered bold based on their control treatment behaviour); however, this trend could not be analysed statistically due to the small sample size.

Fear-like behaviour is generally associated with the serotonin system coupled with experience and memories of fearful experiences in animals (Zanette et al. 2019). The fear caused by a predator in the past can have long-lasting effects which modify the animal's subsequent reactions to predators (Clinchy et al. 2011, 2013, Manzur et al. 2014, Zanette & Sih 2015, Zanette & Clinchy 2017, Crane et al. 2018). Predator-induced fear can even cause post-traumatic stress disorder-like changes in the brains and behaviours of wild animals (Zanette et al. 2019). There are many occasions on which wild green sea turtles along the Pacific coast from northeast to southwest Japan can experience fear on their natural foraging ground, because they are frequently captured in the coastal set nets of commercial fisheries (Ishihara et al. 2014, Narazaki et al. 2015). The density and methods of fisheries vary among locations in Japan, with turtle mortality rates of 0.6–40% as a result of bycatch in set nets (Ishihara et al. 2014, Narazaki et al. 2015). Thus, solitary sea turtles may respond to fear stimuli on the basis of past traumatic experiences, which could reflect the level of pressure from fish-

eries in their habitat. Fear-like behaviour is modulated by serotonin in green sea turtles. This indicates that green sea turtles, like mammals, show a negative emotional reaction as fear. Understanding what incites fear and triggers an avoidance response in green sea turtles can lead to the design and effective deployment of a fisheries tool to reduce sea turtle bycatch.

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