

Elasmobranch cognitive ability: using electroreceptive foraging behaviour to demonstrate learning, habituation and memory in a benthic shark

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Abstract Top predators inhabiting a dynamic environment, such as coastal waters, should theoretically possess sufficient cognitive ability to allow successful foraging despite unpredictable sensory stimuli. The cognition-related hunting abilities of marine mammals have been widely demonstrated. Having been historically underestimated, teleost cognitive abilities have also now been significantly demonstrated. Conversely, the abilities of elasmobranchs have received little attention, despite many species possessing relatively large brains comparable to some mammals. The need to determine what, if any, cognitive ability these globally distributed, apex predators are endowed with has been highlighted recently by questions arising from environmental assessments, specifically whether they are able to learn to distinguish between anthropogenic electric fields and prey bioelectric fields. We therefore used electroreceptive foraging behaviour in a model species, *Scyliorhinus canicula* (small-spotted catshark), to determine cognitive ability by analysing whether elasmobranchs are able to learn to improve foraging efficiency and remember learned behavioural adaptations. Positive reinforcement, operant conditioning was used to study catshark foraging behaviour towards artificial, prey-type electric fields (Efields). Catsharks rewarded with food for responding to Efields throughout experimental weeks were compared with catsharks that were not rewarded for responding in order to assess behavioural adaptation via learning ability.

Experiments were repeated after a 3-week interval with previously rewarded catsharks this time receiving no reward and vice versa to assess memory ability. Positive reinforcement markedly and rapidly altered catshark foraging behaviour. Rewarded catsharks exhibited significantly more interest in the electrical stimulus than unrewarded catsharks. Furthermore, they improved their foraging efficiency over time by learning to locate and bite the electrodes to gain food more quickly. In contrast, unrewarded catsharks showed some habituation, whereby their responses to the electrodes abated and eventually entirely ceased, though they generally showed no changes in most foraging parameters. Behavioural adaptations were not retained after the interval suggesting learned behaviour was not memorised beyond the interval. Sequences of individual catshark search paths clearly illustrated learning and habituation behavioural adaptation. This study demonstrated learning and habituation occurring after few foraging events and a memory window of between 12 h and 3 weeks. These cognitive abilities are discussed in relation to diet, habitat, ecology and anthropogenic Efield sources.

Keywords *Scyliorhinus canicula* · Efield · Electroreception · Behavioural adaptation · Search path

Introduction

Cognitive ability is fundamental for optimising crucial animal behaviours such as locating and acquiring food and mates, navigating and avoiding predators. It is especially important for animals that inhabit complex, dynamic environments with unpredictable sensory stimuli. Recent research suggests that relative brain size in vertebrates is

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linked with the ability to adapt and persist in novel and changing environments (Reader and MacDonald 2003; Sol et al. 2008; Maklakov et al. 2011). Coastal environments are particularly changeable, both spatially and temporally, due to the convergence of dynamic marine, freshwater, terrestrial, atmospheric and, increasingly, anthropogenic factors. Organisms that inhabit such an environment should theoretically exhibit behavioural flexibility to enable them to function and survive by adapting to changing conditions and thereby maximise ecological fitness (Dill 1983). Learning and memory are crucial means with which to facilitate such adaptation.

The cognitive ability and adaptability of marine mammals when foraging is well supported (Schusterman and Kastak 2002) as evidenced by, for example, development of intentional stranding (Guinet and Bouvier 1995), herding (Similä and Ugarte 1993), vocal learning (Shapiro et al. 2004) and cooperation (Visser et al. 2008). The current, general consensus is that many teleosts (bony fish) also possess significantly more cognitive ability than previously believed (reviewed in Laland et al. 2003; Brown et al. 2006) with, for example, foraging adaptability demonstrated by learning in sticklebacks (Croy and Hughes 1991), salmon (Brown et al. 2003) and mosquito fish (Brown and Braithwaite 2005), and memory in trout (Bryan and Larkin 1972) and sticklebacks (Mackney and Hughes 1995).

Conversely, chondrichthyans (cartilaginous fish) have received relatively little attention with respect to cognitive ability. This is surprising given that certain elasmobranchs (sharks, skates and rays) possess brain to body mass ratios that overlap those of some mammals and birds (Demski and Northcutt 1996). Until very recently, the few examples of investigations into elasmobranch cognitive ability were relatively old and involved visual discrimination to gain food rewards (Clark 1959, 1961; Wright and Jackson 1964; Aronson et al. 1967; Graeber and Ebbesson 1972; Graeber et al. 1978). More recently, Schlüssel and Bleckmann (2005) demonstrated spatial memory of environment in juvenile freshwater stingrays, Kuba et al. (2010) demonstrated tool use in a similar species, Meyer et al. (2010) suggested tiger sharks may use cognitive maps to navigate between distant foraging areas, and Guttridge et al. (2012) demonstrated social learning in juvenile lemon sharks. Based on this limited evidence for cognitive ability in elasmobranchs, we hypothesised that when using their primary sensory mode, electroreception, the cognitive abilities of benthic elasmobranchs would be clearly demonstrable and behaviourally adaptive.

Electroreception is the last in a hierarchy of senses utilised by elasmobranchs whilst foraging (Kalmijn 1971); it aids precise location of prey and jaw orientation and has been demonstrated to override all other

senses over short distances (Kalmijn 1971; Heyer et al. 1981). It is particularly crucial for the foraging success of benthic species that forage for inconspicuous prey owing to burial, refuging or crypsis (see Tricas and Sisneros 2004 for review). As such, it can be considered fundamental for the feeding success and subsequent somatic and gonadal growth of these predators. Electroreception can also be utilised during the location of and communication with conspecifics, the detection of predators and possibly in aiding navigation (Tricas and Sisneros 2004). Flexibility in their responses to electric stimuli within their environment via learning and memory should provide tangible ecological benefits to the life processes of these predators. When considered in conjunction with the repeatability of the behaviour under laboratory conditions (Kalmijn 1971), the importance of electroreception makes it an ideal tool to attempt to measure behavioural adaptation. Furthermore, the need to assess the cognitive ability of elasmobranchs has been accentuated recently amid questions raised by environmental assessments in coastal waters worldwide. Given the burgeoning deployment of subsea electric cables (e.g. associated with offshore renewable energy and grid connection development), suggestions of electromagnetically ultra-sensitive elasmobranchs potentially being affected have arisen (Gill et al. 2005; Sutherland et al. 2008). The principal question relates to whether the elasmobranchs will be able to learn about electrical stimuli to enable them to distinguish between those that provide an energetic return (such as prey located via their bioelectric fields) and those that are anthropogenic in origin and that provide no food return (Kimber et al. 2011).

The objective of this study was therefore to investigate the ability of a model species of benthic elasmobranch, the small-spotted catshark (*Scyliorhinus canicula*), to learn to adapt its electroreceptive foraging behaviour towards profitable (in terms of food gain) and non-profitable (i.e. no food gain) electrical stimuli and remember learned adaptations. Such results would support the growing body of evidence that cognitive ability is beneficial in novel and changing environments among a variety of predators and provide useful information for environmental assessments.

In this context, laboratory studies were designed to study catshark behaviour using operant conditioning. Experiments investigated the foraging behaviour of catsharks rewarded with food for operant responses to an electrical stimulus. Contrasting treatment experiments were undertaken during which no food rewards were provided for responses to the electrical stimulus. Experiments were then repeated after an interval with previously rewarded catsharks receiving no food and vice versa to assess memory.

Methods

Animals and apparatus

Twenty-four size-matched (mean total length = 61.8 ± 4.8 cm standard deviation), mixed-sex small-spotted catsharks (*S. canicula*) were caught on a Marine Biological Association of the UK (MBA) research vessel off Plymouth, southwest England (station L4: 50°15'N, 4°13'W). They were randomly assigned to one of four groups (1–4) and tagged just below their dorsal fin with different coloured, individually numbered T-bar anchor tags (FLOY TAG Inc., Seattle, Washington, DC, USA) following licensed UK Home Office animal welfare regulations. Catsharks were maintained in 2,242 litre holding aquaria (1.83 m diameter × 0.43 m depth) supplied by a sea water flow and return system at the MBA in which they acclimatised for 3 weeks. Twice weekly, they were each fed a 20 g food ration equivalent to 3 % wet body mass per feed to standardise feeding motivation (Sims and Davies 1994). Food consisted of mixed squid (*Loligo forbesi*), whiting (*Merlangius merlangus*) and marine pellets with liposome spray (New Era Aquaculture Ltd., Thorne, UK).

Salt-bridge electrode circuits and apparatus were used to present catsharks with prey-type electric fields (sensu Kimber et al. 2009). A trap-door mechanism and hidden food compartment were attached to the underside of an opaque, raised and gently ramped electrode plate. The food compartment was positioned against the plate and sealed with silicone gel to prevent food scent seepage. A hydraulic system of BD Luer Lok syringes and Nalgene 380 PVC tubing allowed the food compartment to be opened and closed remotely, smoothly, quickly and silently by the observer. This permitted presentation of food rewards to catsharks in close proximity to the dipole, immediately after a response to an electric field, and with minimal disturbance.

Experimental procedure

Six 792 litre acrylic aquarium tanks supplied with filtered seawater were used as behavioural arenas (1.65 m L × 0.80 m W × 0.60 m D). The six catsharks from group 1 were transferred to randomly chosen arenas (one catshark per arena) and allowed to acclimatise for 60 h. Each catshark was then presented with an Efield produced by a 9 µA direct current twice per day for 5 days, a total of 10 experimental sessions, forming an experimental week. The Efield was chosen due to its similar strength to prey bioelectric fields and demonstrated elicitation of voluntary (operant) feeding responses in these benthic sharks (Kalmijn 1971, 1972). These feeding responses consist of rapidly turning towards and biting upon the electrodes

(often repeatedly) once the Efield is detected. Three randomly selected catsharks were positively reinforced by rewarding them with offer of approximately 1.3 g of food immediately after their first bite upon the electrodes in each experimental session. Catsharks not consuming all of their rewards were fed the remainder of their weekly 13 g ration after the experimental week was completed. This reduced feeding ration (approximately 2 % wet body mass per week: Sims and Davies 1994) ensured satiation was not reached and hunger and normal foraging behaviour persisted during the week. The other three catsharks acted as contrasting treatments, whereby they were not rewarded for biting the electrodes, but were instead fed a 13 g food ration after the experimental week was completed.

On completion of the experimental week, the group 1 catsharks were transferred back to the holding aquaria and replaced with the catsharks from group 2. After 60 h acclimatisation, group 2 then underwent a similar experimental week. This procedure was repeated for groups 3 and 4. Once group 4's first experimental week was complete, each group (1–4 in turn) then underwent a second experimental week, similar except that those catsharks that were previously rewarded were not rewarded and vice versa. There was therefore a 3-week interval between each group's two experimental weeks.

Prior to each particular experimental session, a salt-bridge apparatus was introduced into a randomly chosen arena, and at a randomly chosen end (to ensure catsharks were not simply learning to associate the food with a particular location), with the power switched off and water flow halted to allow the catsharks to settle down. After 20 min, the power was switched on and 20 ml of food scent (sieved squid and whiting added to water) was introduced into the arena approximately 7.5 cm from the dipole. Since one of the first hierarchical senses used during foraging by elasmobranchs is olfaction (Hodgson and Mathewson 1971), it is necessary to use a dose of scent to stimulate foraging behaviour and attract the catsharks towards the electrode plate (sensu Kalmijn 1971). Once in close proximity of the electrodes, electroreception is known to override all other senses. For the relatively small, benthic *S. canicula*, this predominantly occurs within approximately 5 cm to 10 cm (Dawson et al. 1980; Kimber et al. 2009) in comparison with up to 30 cm for larger, pelagic species (Kalmijn 1971; Heyer et al. 1981).

Sessions lasted for no more than 15 min and were recorded using overhead cameras. The following hierarchical response variables of each catshark were compiled by reviewing video footage: (a) the number of times the catsharks passed within 5-cm of the electrodes, (b) the latency of turns towards and bites upon the electrodes, (c) the frequency of turns towards and bites upon the electrodes, (d) after which bite (i.e. first, second, etc.) and

what latency a food reward was taken (note rewards were not always taken immediately), and finally, (e) the search paths the catsharks undertook from their starting position (when scent detected) to their first response at the electrode dipole. The latter were traced from video footage on a large monitor. These traces were then converted to JPEG files using an HP Designjet 815mfp scanner and subsequently converted to polyline shape files and geo-referenced to arena size using ArcGIS software. An index of the path directness to the dipole was then calculated by dividing search path lengths by the direct distance between starting position and the electrodes.

Upon completion of all experiments, tags were removed from catsharks and the attachment points treated. The catsharks were held in holding aquaria and after a short period of observation were certified for release to the sea off Plymouth (Fig. 1).

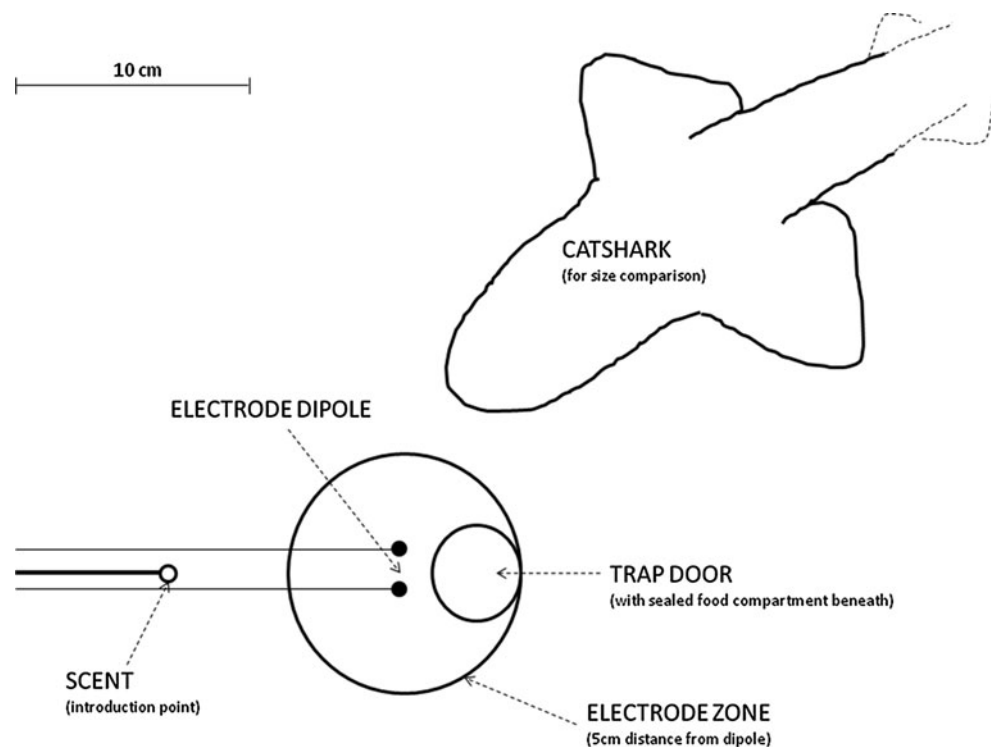
Data analysis

Statistica 8.0 and Genstat 10.0 software were used to run the statistical models that analysed differences in electro-receptive foraging behavioural parameters (a–e) between rewarded (R) and not rewarded (N) catsharks, between experimental weeks 1 and 2, and also changes in the parameters throughout experimental sessions (i.e. within experimental weeks). Depending upon the hypothesis being tested and data type (count, continuous or path directness index), either hierarchical generalised linear

mixed models (HGZLMM), hierarchical general linear models (HGLM) or general linear models (GLM) were used with relevant distributions (poisson, log link, identity or normal). Fixed effects were reward (yes or no) and experimental week (1 or 2) for tests between rewarded and unrewarded catsharks and between experimental weeks 1 and 2, and experimental session (1–10) or individual number for tests within experimental weeks. This ensured that each data point for each catshark was used only once during each analysis. If replication (non-independence) was not already accounted for within these models, the relevant random effects (individual number and/or session) or continuous predictors (session) were also used. These carefully formulated models robustly and powerfully dealt with the complex data to generate accurate descriptions of biologically relevant effects (*sensu* Nakagawa and Cuthill 2007).

Estimates of effects generated by modelling and presented here represent either relative differences between means (whereby rewarded catshark effects are compared to the zero reference, unrewarded catsharks between experimental weeks) or regression coefficients (within experimental weeks). The latter were back-transformed to the units of original measurement to enable fitted curve plots to be produced (raw data was omitted owing to the effects of individual catsharks being partially confounded with experimental session). For all model results reported, the distributions of residuals (using transformations as required) were close to Normal and therefore the models

Fig. 1 Plan view of the electrode plate experimental apparatus



were assumed to be satisfactory. Residual degrees of freedom ranged between approximately 215 and 460 unless otherwise stated.

Results

Learning and habituation

Averaged over all ten experimental sessions, rewarded catsharks passed within 5 cm of the electrodes significantly more than unrewarded catsharks (relative difference between means = 0.725, standard error (SE) = 0.141, $t = 5.15$, $P \ll 0.0001$). Throughout an experimental week, the high number of passes rewarded catsharks made before their first response to the electrodes significantly decreased (regression coefficient = -0.0678 , SE = 0.0148, $t = 4.59$; $P < 0.001$; Fig. 2). There was no change in the low number of passes unrewarded catsharks made before their first response to the electrodes (regression coefficient = -0.0001 , SE = 0.0328, $t = 0.00$; $P = 1.0$; Fig. 2).

Throughout an experimental week, the time latency of first response to the electrodes of rewarded catsharks significantly decreased (regression coefficient = -0.0677 , SE = 0.0274, $t = 2.47$, $P = 0.014$; Fig. 3). There was no change in the time latency of first response of unrewarded catsharks (regression coefficient = -0.0039 , SE = 0.0366, $t = 0.11$, $P = 0.91$; Fig. 3). Averaged over all ten experimental sessions, rewarded catsharks turned towards and bit the electrodes significantly more than unrewarded catsharks (relative different between means = 0.866 and 0.851, SE = 0.162 and 0.153, $t = 5.35$ and 5.57, respectively, both $P \ll 0.0001$). Throughout an experimental week, the higher number of turns and bites made by rewarded catsharks

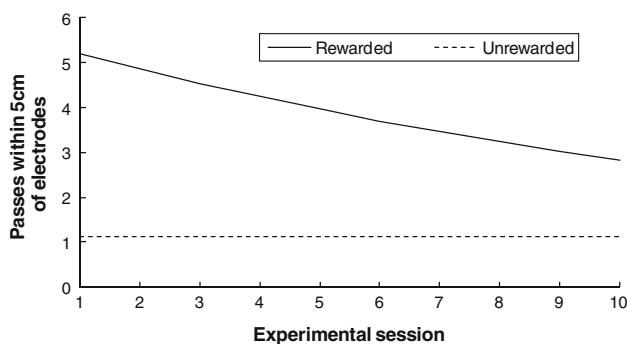


Fig. 2 Changes in the number of passes within 5 cm of electrodes throughout experimental week plotted by back-transforming estimates of effects to original units of measurement for fitted curve (Rewarded: constant = 1.72, regression coefficient = 0.068, error = 0.015; Unrewarded: constant = 0.12, regression coefficient = 0.0001, error = 0.033)

significantly decreased (regression coefficient = -0.0547 and -0.0940 , SE = 0.00816 and 0.0114, $t = 6.70$ and 8.27, respectively, both $P < 0.0001$; Fig. 4). So, too, did the lower number of turns and bites made by unrewarded catsharks, but more sharply (regression coefficient = -0.151 and -0.205 , SE = 0.0140 and 0.0206, $t = 10.77$ and 9.93, respectively, both $P < 0.0001$; Fig. 4), such that on average, they ceased to bite upon the electrodes altogether after approximately six or seven experimental sessions.

As the catsharks swam and searched for food rapidly, they did not always manage to take food rewards immediately after being offered them following their first bite upon the electrodes. If this was the case, however, they would almost invariably turn back swiftly (and repeatedly) to bite the electrodes again (rewarded catsharks responded to the electrodes greater than once in more than 97 % of treatments). The bite after which they took the food reward was therefore not necessarily the first. The bite number and time after which rewarded catsharks managed to attain the food reward throughout an experimental week decreased significantly (regression coefficient = -0.0716 and -0.0844 , SE = 0.0182 and 0.0294, $t = 3.94$ and 2.87, respectively, $P = 0.0001$ and 0.004, respectively; Fig. 5). The search paths undertaken by rewarded catsharks throughout an experimental week also significantly decreased (regression coefficient = 1.904, SE = 0.0288, SS = 5.91; $P < 0.019$; Figs. 6, 7). In contrast, on average, the paths undertaken by unrewarded catsharks did not change throughout an experimental week (regression coefficient = 1.61, SE = 0.0347, SS = 0.137; $P = 0.69$; Figs. 6, 7).

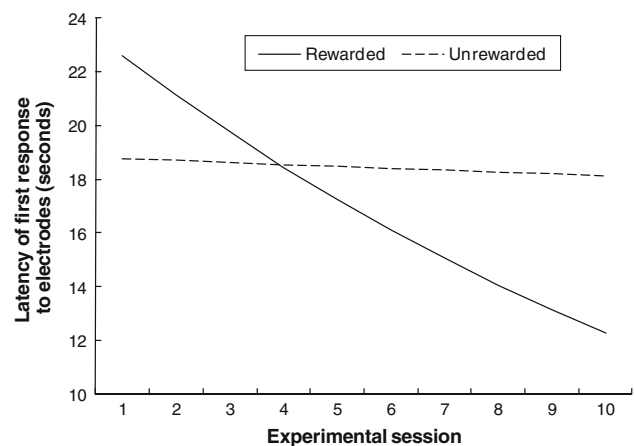


Fig. 3 Changes in the latency of first response to the electrodes throughout experimental week plotted by back-transforming estimates of effects to original units of measurement for fitted curve (Rewarded: constant = 8.18, regression coefficient = 0.068, error = 0.027; Unrewarded: constant = 8.43, regression coefficient = 0.004, error = 0.037)

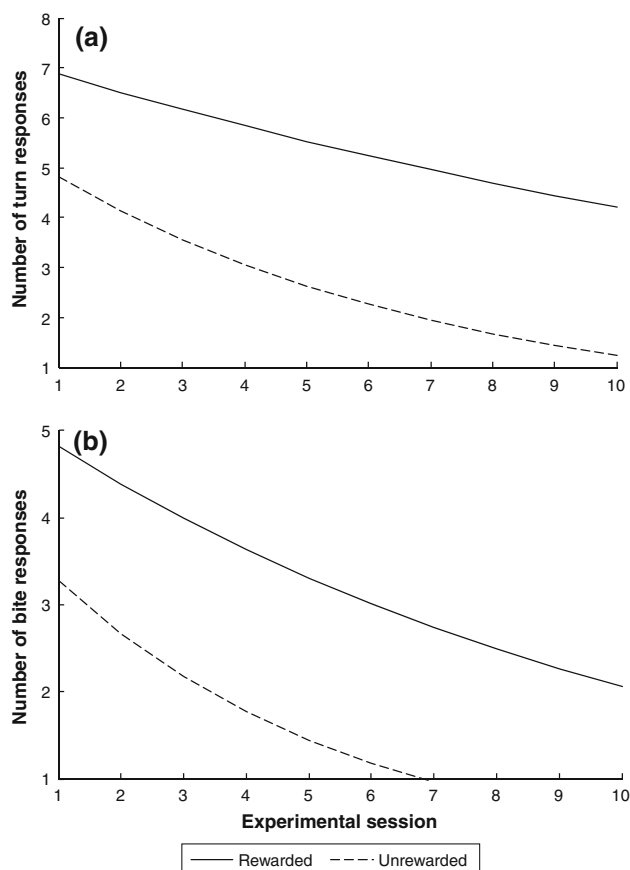


Fig. 4 a, b Changes in number of turn and bite responses to electrodes throughout experimental week plotted by back-transforming estimates of effects to original units of measurement for fitted curve (Turns—Rewarded: constant = 1.98, regression coefficient = 0.005, error = 0.008; Unrewarded: constant = 1.72, regression coefficient = 0.151, error = 0.014; Bites—Rewarded: constant = 1.67, regression coefficient = 0.094, error = 0.011; Unrewarded: constant = 1.39, regression coefficient = 0.205, error = 0.021)

Memory

Table 1 shows that when rewarded and unrewarded catshark data were grouped together and compared between experimental weeks before and after the 3-week interval, there were no significant differences in any behavioural parameters other than a slight difference in the latency of first response to the electrodes. Neither were any interactions observed between reward (yes/no) and week (1 and 2) for any of the parameters (Table 1). Therefore, on average, foraging behaviour was independent of whether a catshark was rewarded before the interval and unrewarded after the interval or vice versa. These results suggest that behavioural alterations were not retained beyond the interval.

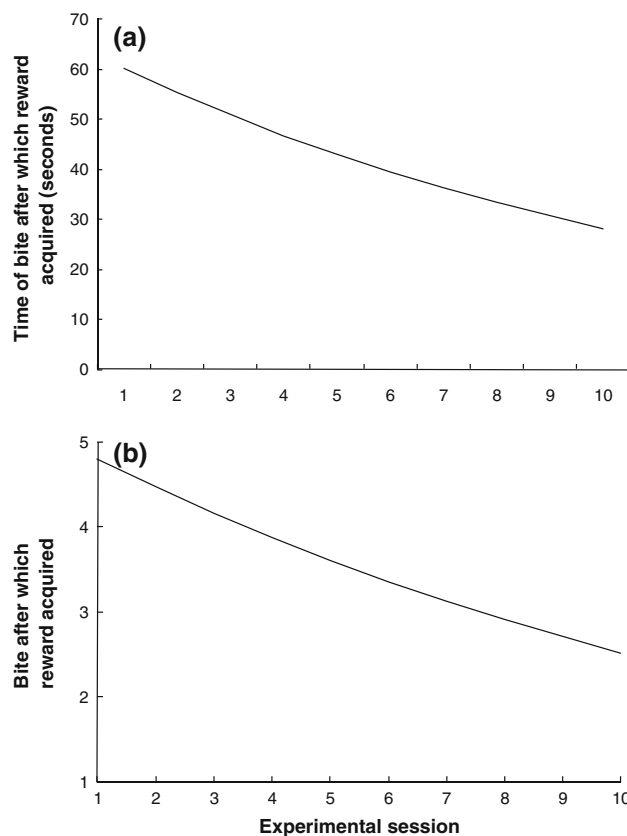


Fig. 5 a, b Changes in the time and bite number after which rewarded catsharks acquired food reward throughout experimental week plotted by back-transforming estimates of effects to original units of measurement for fitted curve (Time: constant = 7.18, regression coefficient = 0.084, error = 0.029; Bite: constant = 1.64, regression coefficient = 0.072, error = 0.018)

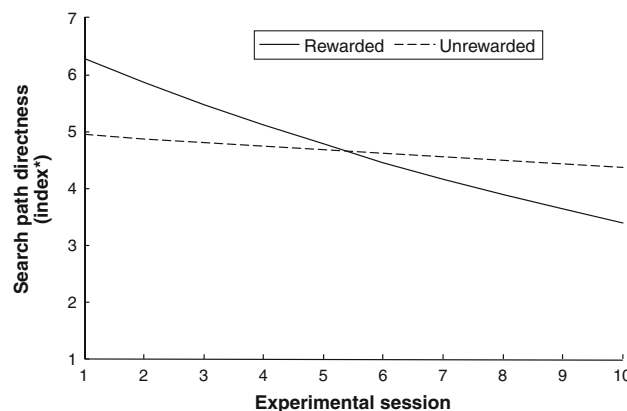
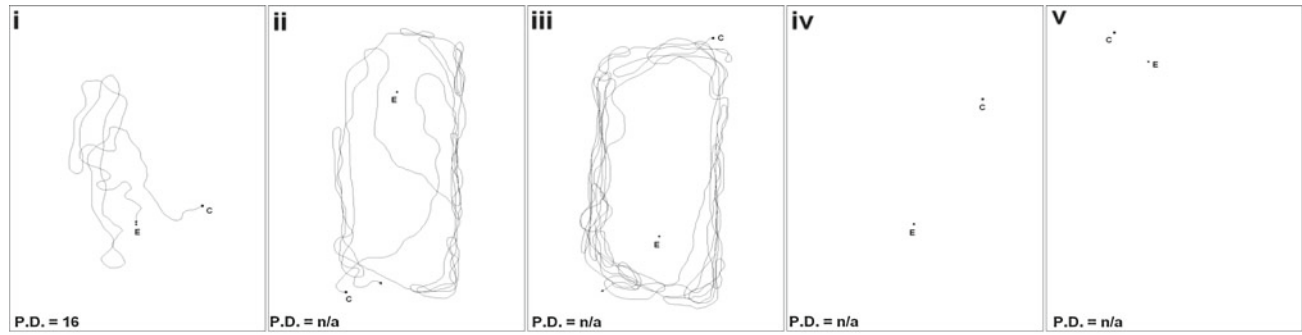
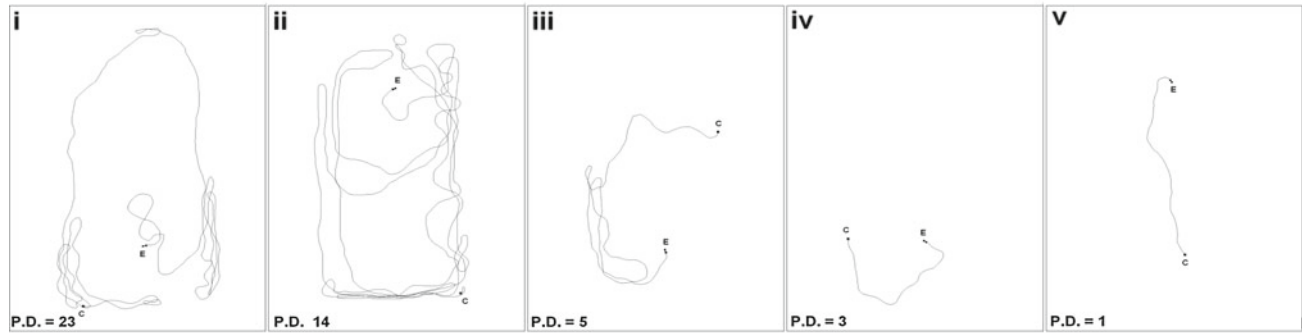


Fig. 6 Changes in path directness to electrodes throughout experimental weeks plotted by back-transforming estimates of effects to original units of measurement for fitted curve (Rewarded: constant = 1.90, regression coefficient = 0.068, error = 0.029; Unrewarded: constant = 1.61, regression coefficient = 0.014, error = 0.035), *index calculation provided in methods

Before interval: **UNREWARDED**

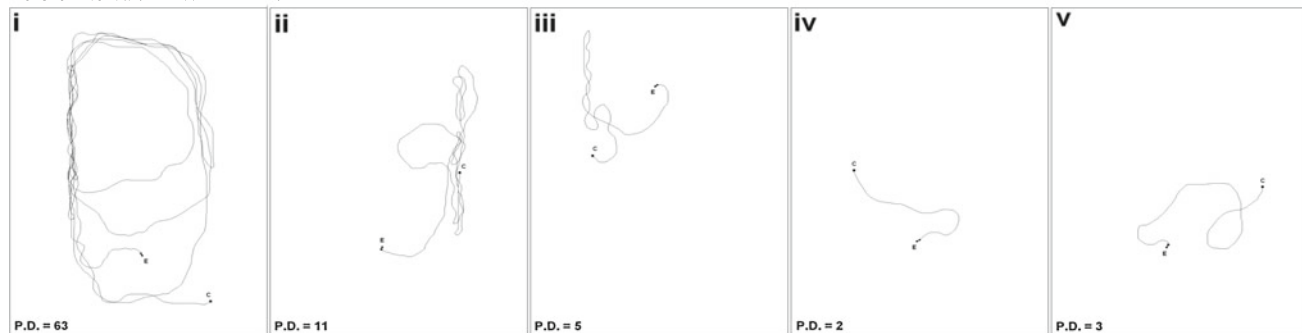


After interval: **REWARDED**

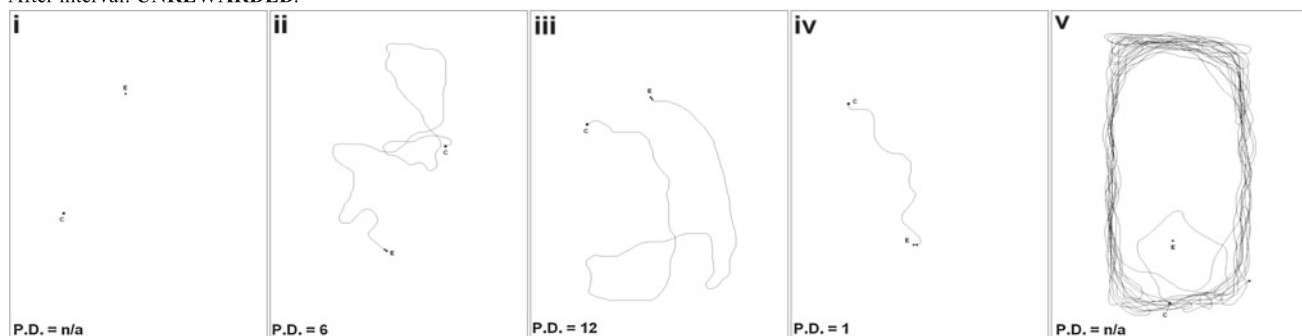


Catshark Blue 1501

Before interval: **REWARDED:**



After interval: **UNREWARDED:**



Catshark Green 230

Fig. 7 Examples of individual catshark search paths throughout experimental week (i–v) when rewarded and unrewarded. C = catshark start position; E = electrode position; P.D. = path directness (rounded figures)

Table 1 Results when comparing hierarchical response parameters between week before (1) and week after (2) a 3-week interval and interactions between reward (R) and not reward (N) and week 1 and 2

Behaviour parameter	Week 1 and 2				Interaction R/N and week 1/2			
	Effect ^a	SE	Stat ^b	<i>P</i>	Effect ^a	SE	Stat ^b	<i>P</i>
Passes within 5 cm	−0.117	0.149	0.78	0.44	0.169	0.260	0.65	0.52
Latency to 1st response	−0.487	0.245	1.99	0.05	0.582	0.387	1.90	0.21
Turn frequency	0.264	0.166	1.59	0.11	0.047	0.306	0.15	0.88
Bite frequency	0.038	0.163	0.23	0.82	0.119	0.273	0.44	0.66
Reward time (<i>df</i> = 139)	0.005	0.211	0.00 (<i>w</i>)	0.98	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>
Reward bite (<i>df</i> = 170)	0.037	0.115	0.32	0.75	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>
Path directness	0.020	0.079	0.06 (<i>SS</i>)	0.80	−0.091	0.065	2.18 (<i>SS</i>)	0.16

SE = standard error, *n/a* = model not well fitting due to lack of data, *df* = degrees of freedom

^a Estimate of effect (relative difference between means)

^b *t* statistic, unless otherwise stated (*w* = Wald; *SS* = sum of squares)

Discussion

All catsharks were of similar size and maturity, from the same geographic location, acclimatised to the study conditions for equal time periods and fed on equal, minimum rations. Previous experience and initial motivation to feed was therefore assumed to be standardised among experimental animals. Rewarded catsharks consistently foraged and ingested rewards suggesting the small size of rewards prevented satiation and ensured continued motivation to respond to feeding opportunities. Unrewarded catsharks also showed continued, but not increasing motivation to feed.

Water temperature varied with natural conditions during experimental procedures (18.22 °C ± 0.98 SD). However, this small level of variation has previously been shown to have little effect on electroreceptive behaviour (Kimber et al. 2009). All experimental animals were subjected to the same experimental conditions in stable, predator-free environments and the large sample size and powerful modelling provided the confidence that differences and trends observed were accountable to the experience and behavioural flexibility of the catsharks.

Reinforcement of the operant foraging response to an electric stimulus by rewarding with food clearly altered the behaviour of catsharks. As would be expected, rewarded catsharks showed more interest in the electrodes than the contrasting treatment, unrewarded catsharks, demonstrated by more passes by, turns towards and bites upon the electrodes. Crucially, rewarded catsharks exhibited a number of behavioural alterations that suggest they were learning how to obtain food. The number of times they passed within close proximity of the electrodes before responding to them and the time latency of first response decreased. The bite number and time after which they managed to acquire the food reward from the trap-door

compartment decreased. Therefore, they did not need to respond further, and consequently, the number of times they turned towards and bit the electrodes also decreased. Furthermore, the length of search path they employed to first respond to the electrodes also decreased (see Fig. 7 for clear examples of individual catshark search paths decreasing). Effectively, these results strongly suggest these catsharks were learning that when stimulated to forage, by rapidly locating the electrodes and biting them, food would appear in close proximity of the electrodes. Furthermore, the substantial changes in behaviour elicited by so few rewards (a maximum of ten per catshark, but often requiring just a few) demonstrate impressively rapid learning. Behavioural alterations improved the foraging efficiency of these catsharks over time and theoretically would have reduced energetic costs per unit food attained.

Conversely, in the contrasting treatment, unrewarded catsharks exhibited less interest in the electrodes and less behavioural adaptation; no change in the number of times they passed in close proximity of the electrodes; no change in latency to respond to the electrodes and no change in the length of their search paths. They did, however, markedly reduce the amount of times they turned towards and bit upon the electrodes throughout an experimental week (even more so than their rewarded counterparts), and even stopped biting altogether, which suggests they habituated to the electric stimulus since they did not obtain any food by biting it. Theoretically, such adaptations would also have reduced energetic and opportunity costs by reducing wasted effort. Figure 7 shows examples of typical search path sequences of unrewarded catsharks, with no apparent pattern or clearly habituating (eventually failing to respond to the electrodes and scent).

Whilst the results clearly demonstrate striking learning in the catsharks, according to classical cognition theory, there is a possibility that non-contingency might explain

some behavioural alterations (differences elicited by the food rather than being a consequence of the contingency between bites to the electrodes and subsequent food reward). A further control condition in which food is delivered non-contingently might help to address this question, ideally involving a yoked procedure whereby two catsharks in separate tanks are both offered concurrent rewards when one (the executive) responds to an Efield, regardless of the other, yoked catshark's responses (*sensu* Church 1964). Such a control would be a significant challenge in itself, especially considering the complex, hierarchical stimulus modality inherent when studying elasmobranch electroreceptive foraging behaviour. However, since the experiment was designed to involve operant conditioning under positive reinforcement and to investigate ability to learn to distinguish between anthropogenic Efields and prey bioelectric fields in the natural environment, the behavioural adaptations observed demonstrate significant learning nonetheless.

The average learning behavioural adaptations revealed by statistical analysis were exhibited by most, but not all catsharks. For example, 70 and 76 % of rewarded catsharks exhibited trends associated with learning, decreasing reward attainment bite time and bite number, respectively. Hence, 30 and 24 % did not exhibit such trends associated with learning. Therefore, learning ability apparently varied between individuals. However, both sexes exhibited similar behavioural adaptations. It is possible that differences between the adaptations of the sexes might become apparent if groups of catsharks were studied, rather than individuals, since sexual conflicts (specifically male harassment and female avoidance) have been demonstrated to affect foraging behaviour (Kimber et al. 2009).

The fact that none of the learned and habituated behaviours were continued after a 3-week interval and that behaviour levels were independent of whether rewards were offered before or after the interval suggests that the memory window for these elasmobranchs is less than 3 weeks. Having returned to the experimental arenas after the interval, the catsharks behaved as if they had not been subjected to the previous experimental sessions, regardless of whether rewarded or unrewarded. They then began to swiftly adapt their foraging behaviour over the subsequent experimental weeks accordingly.

Like many other marine predators, elasmobranchs often inhabit highly variable, shallow coastal waters (Compagno et al. 2005) and many are therefore opportunistic predators (Lyle 1983; Ellis et al. 1996; Laptikhovskiy et al. 2001). When considering populations of these elasmobranchs in their natural habitats, the impressive cognitive abilities demonstrated here make ecological sense. In essence, the sharks seem able to rapidly learn to improve their electroreceptive foraging efficiency towards profitable stimuli

(in terms of food gain) over short periods (and presumably within small spatial scales). Equally, within similar temporal and spatial limits, they can rapidly habituate to (or learn to ignore) non-profitable stimuli (i.e. no food gain). This swift flexibility would therefore allow, for example, the predators to focus their efforts on easily caught, edible or nutritious prey (Dill 1983; Stephens and Krebs 1986; Kaiser et al. 1992). Similarly, efforts towards inedible, nutrient lacking and difficult to catch prey could be reduced, which would permit focussing elsewhere and minimising missed opportunities. For example, greater modification of foraging behaviour has been demonstrated in crabs (Micheli 1997) and sticklebacks (Girvan and Braithwaite 1998) when encountering variable prey in less stable habitats. Greater adaptability, inferred from larger brain size, has also been suggested to enable success in novel, complex or variable environments in passerine birds (Maklakov et al. 2011), primates (Reader and MacDonald 2003) and marine mammals (Kuczaj et al. 2009).

The coastal zone is especially variable due to both natural and anthropogenic factors. In such an environment, therefore, remembering these electroreceptive foraging adaptations over longer temporal periods and larger spatial scales may not be of benefit (*sensu* Hirvonen et al. 1999). Possessing a memory window of less than 3 weeks for these skills is reasonable when considering prey diversity and distributions, in addition to physical habitat, may well change over relatively short time periods and over small distances. It would be interesting to determine exactly where this memory window lies in these benthic elasmobranchs. The results suggest it lies somewhere between 12 h (learned behaviour was obviously remembered between experimental sessions each day) and 3 weeks (the experimental interval period). Longer memories have been demonstrated in teleost fish inhabiting relatively stable environments (e.g. up to 6 months in trout: Bryan and Larkin 1972; 3 months in cod: Nilsson et al. 2008) compared to shorter memories in those inhabiting more variable environments (e.g. 3 h in paradise fish: Csanyi et al. 1989; from minutes to days in sticklebacks: Mackney and Hughes 1995; Hughes and Blight 1999).

Cognitive abilities are also likely to vary between elasmobranch species. For example, one may expect better memory windows in species inhabiting more stable habitats than more variable habitats (c.f. teleost fish; Odling-Smee and Braithwaite 2003). Inter-specific differences in visual learning have previously been observed between lemon and nurse (Clark 1959) and lemon and bull sharks (Wright and Jackson 1964). Variation in brain to body mass ratios and in the relative mass of the major brain divisions can be used to postulate the capacities of different species' senses and cognition (Demski and Northcutt 1996). *Scyliorhinus canicula* have average brain to body

mass ratios (Ridet et al. 1973) compared to higher and lower examples such as scalloped hammerheads (*Sphyrna lewini*) and Greenland sharks (*Somniosus microcephalus*), respectively (Northcutt 1978; Myagkov 1991). Interestingly, the former range widely throughout a number of markedly different coastal habitats, whilst the latter remain predominantly in cold, stable, deep arctic waters (Compagno et al. 2005).

In addition to ecological considerations, the results of this study also have important implications regarding growing interest in possible interactions between electro-receptive fish and anthropogenic sources of Efields in the coastal environment that are within the range detectable and attractive to elasmobranchs (such as subsea cables: Gill et al. 2005; Gill and Kimber 2005; Sutherland et al. 2008; Boehlert and Gill 2010). Given the results of this study, it appears that within small temporal and spatial scales, the sharks may be able to learn to ignore anthropogenic Efields and focus upon bioelectric fields by behavioural adaptation (assuming they can differentiate the sources; Kimber et al. 2011). However, they may well forget these adaptations over larger scales (e.g. when travelling between foraging areas) and respond to both types of Efield again. The balance between learning and forgetting would ultimately dictate long-term effects on individual success and ecological fitness.

In conclusion, we have measured rapid learning and habituation adaptation but relatively short memory in a fundamental behaviour for a model, benthic elasmobranch species. These cognitive abilities ideally suit a predator inhabiting a variable environment by improving foraging efficiency, but preventing missed opportunities, and support studies of other taxa that suggest relatively large brain size and behavioural adaptability correlates with habitat stability.

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