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Something worth remembering: visual discrimination in sharks

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Abstract This study investigated memory retention capabilities of juvenile gray bamboo sharks (*Chiloscyllium griseum*) using two-alternative forced-choice experiments. The sharks had previously been trained in a range of visual discrimination tasks, such as distinguishing between squares, triangles and lines, and their corresponding optical illusions (i.e., the Kanizsa figures or Müller–Lyer illusions), and in the present study, we tested them for memory retention. Despite the absence of reinforcement, sharks remembered the learned information for a period of up to 50 weeks, after which testing was terminated. In fish, as in other vertebrates, memory windows vary in duration depending on species and task; while it may seem beneficial to retain some information for a long time or even indefinitely, other information may be forgotten more easily to retain flexibility and save energy. The results of this study indicate that sharks are capable of long-term memory within the framework of selected cognitive skills. These could aid sharks in activities such as food retrieval, predator avoidance, mate choice or habitat selection and therefore be worth being remembered for extended periods of time. As in other cognitive tasks, intraspecific differences reflected the behavioral breadth of the species.

Keywords Elasmobranch · *Chiloscyllium griseum* · Visual memory · Memory retention · Visual discrimination · Optical illusion

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Introduction

As in humans, memory windows in fishes vary between species and tasks (Brown 2001), with more relevant or potentially life-saving skills being retained for longer periods of time than memories of lesser value (Warburton 2003). For example, food patch profitability and availability of prey may change over time (e.g., daily or seasonally) and therefore only need to be remembered temporarily (Warburton 2003). While it may be advantageous to forget certain behaviors quickly, the anecdotal 'one-second memory of the goldfish' is truly fictional and previous studies have already shown that memory windows in fish usually range from days to months. Rainbow fish (*Melanotaenia duboulayi*) remembered an escape response for 11 months (Brown 2001), Atlantic cod (*Gadus morhua*) retained associations of time-separated events for more than 3 months (Nilsson et al. 2008a, b) and hook avoidance reactions in carp and salmon even lasted for over a year (Tarrant 1964; Beukema 1970). Information on successful feeding interactions was only remembered for a few weeks by bluegill sunfish (*Lepomis macrochirus*, Dugatkin and Wilson 1992). In fifteen-spined sticklebacks, newly acquired foraging skills were forgotten after only 8 days (Croy and Hughes 1991), while they lasted up to 3 months in rainbow trout (*Oncorhynchus mykiss*) (Ware 1971). There have also been many studies on spatial memory retention in fishes (Bshary et al. 2002; Odling-Smee and Braithwaite 2003; Odling-Smee et al. 2008). Gobies for example retained information on tide pool locations for up to 40 days (Aronson 1951, 1971; Goldsmith 1914), while *Amphiprion bicinctus* and female cardinalfish (*Apogon notatus*) retained landmark and homing information for over 6 months (Fricke 1974;

Fukumori et al. 2009). Memory windows ranging from three to 7 months using acoustic and visual stimuli have been demonstrated in paradise fish (*Macropodus opercularis*, Csányi et al. 1989), cod (*G. morhua*, Nilsson et al. 2008a, b, 2010), several species of trout (*Salvelinus fontinalis*, *Salmo clarki*, *Salmo gairdneri*, Bryan and Larkin 1972) and two species of sticklebacks (i.e., *Spinachia spinachia* and *Gasterosteus aculeatus*, Mackney and Hughes 1995; Tlusty et al. 2008; Zion et al. 2011). Across vertebrate taxa, the rate at which animals remember the learned information often decreases exponentially with time (adult and juvenile humans, cats and birds; for review see White 2001). More recently acquired information is usually the most important and therefore the best remembered (starlings, Cuthill et al. 1990).

Few studies have investigated memory retention capabilities in elasmobranchs. Clark (1959) reported that lemon sharks (*Negaprion brevirostris*) retained memory of how to obtain food in a classical conditioning paradigm for up to 10 weeks; however, this was only based on a single observation. Recently, Port Jackson sharks (*Heterodontus portusjacksoni*) associated an underwater LED light or stream of air bubbles with a food reward and remembered these associations for at least 24 h, and up to 40 days (Guttridge and Brown 2014). Schluessel and Bleckmann (2012) assessed retention capabilities of gray bamboo sharks (*Chiloscyllium griseum*) in two spatial learning tasks and found animals to remember the learned information in the absence of reinforcement for a period of up to 6 weeks, after which experiments were terminated, precluding further assessment. Kimber et al. (2014) used electroreceptive foraging in the cat shark (*Scyliorhinus canicula*) to test learning and memory abilities. Sharks easily associated artificial electric stimuli with a food reward and rewarded cat sharks showed more interest in the electrodes than unrewarded ones, to which they quickly habituated. However, none of the learned and habituated behaviors were remembered after a 3-week interval without reinforcement. Forgetting in this case may provide an advantage for an opportunistic benthic predator living in a variable environment (Kimber et al. 2014) as was also suggested by Warburton (2003).

In the present study, juvenile gray bamboo sharks (*C. griseum*) trained in discrimination tasks on illusory contours (Fuss et al. 2014b) were subjected to various training breaks (up to 50 weeks) in order to test individual memory retention capabilities. Discrimination skills are integral to such diverse behaviors as recognition of predators or prey, conspecifics and heterospecifics, finding shelter and establishing territories and were therefore predicted to be retained by sharks even after long periods of time.

Materials and methods

Animals and housing facilities

Eight juvenile bamboo sharks (*C. griseum*; four male, four female, TL 30–40 cm) were kept in aquaria ($1 \times 0.5 \times 0.5$ m) connected to each other and to the experimental setup, providing constant environmental conditions (conductivity, temperature and pH). The system was filled with aerated, filtered saltwater (conductance: about 50 mS $\triangleq \beta \approx 1.0217$ kg/dm^3) at $26 \pm 2°$ C. Food (small pieces of squid, fishes or shrimp) was only available during the experimental training. Experiments were conducted during daylight hours; there was a 12-h light:12-h dark cycle. Individuals were identified by phenotypic characteristics.

Setup

Experiments were performed by using the same octagonal experimental basin as well as the same setup as outlined in Fuss et al. (2014a; Fig. 1).
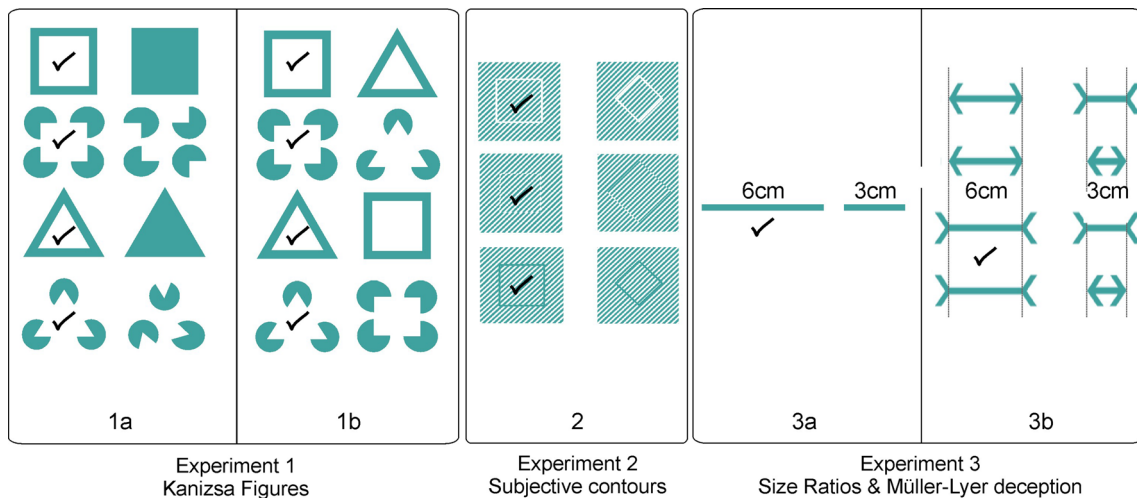
Training

The original behavioral experiments (Fuss et al. 2014b) consisted of three experiments (Fig. 2): Experiment 1 (Kanizsa figures), Experiment 2 (subjective contours) and Experiment 3 (size ratios and Müller–Lyer deception). The memory retention test followed the same procedure as the previous learning experiments (Fuss et al. 2014b) and will therefore only be briefly described here. For the memory retention tests, individuals were only tested once after a single, individual-specific training break of up to 50 weeks.

Sharks were successively trained in three experiments (five sub-experiments, Fig. 2) for which each individual needed a different number of sessions. One experiment consisted of three phases: 1—acclimatization, 2—training and 3—transfer trials. During Phase 1, sharks became familiar with the experimental setup (Fig. 1) after which training (Phase 2) commenced. All experiments were conducted as two-alternative forced-choice experiments. At the beginning of each trial, the shark was placed in the starting compartment (Fig. 1). To start a trial, the shark had to push against the guillotine door with its nose. A choice was recorded as soon as the shark touched one of the two stimuli displayed on the frosted screen on the opposite end of the setup with its nose (Fig. 1). To reward sharks for a correct decision, feeders were installed just above the stimuli, allowing food to be dropped into the setup manually using a cable pull (Fig. 1). The two stimuli to be discriminated (Fig. 2) were displayed simultaneously (one

Fig. 1 Experimental setup located within the experimental basin, inside the white pavilion. The *keyhole-shaped* setup consisted of a starting compartment, a decision area and a frosted screen for projections, featuring a divider allowing for unambiguous choice-making (*left* and *right*). For the projections, a LED projector was used. Sharks were placed within the SC at the start of each trial. *1* feeders, *2* frosted screen for projection, *3* cable pulls to release feeders, *4a* guillotine door, *4b* cable pull to open guillotine door, *5* ceiling mounted fluorescent tubes (above pavilion roof)
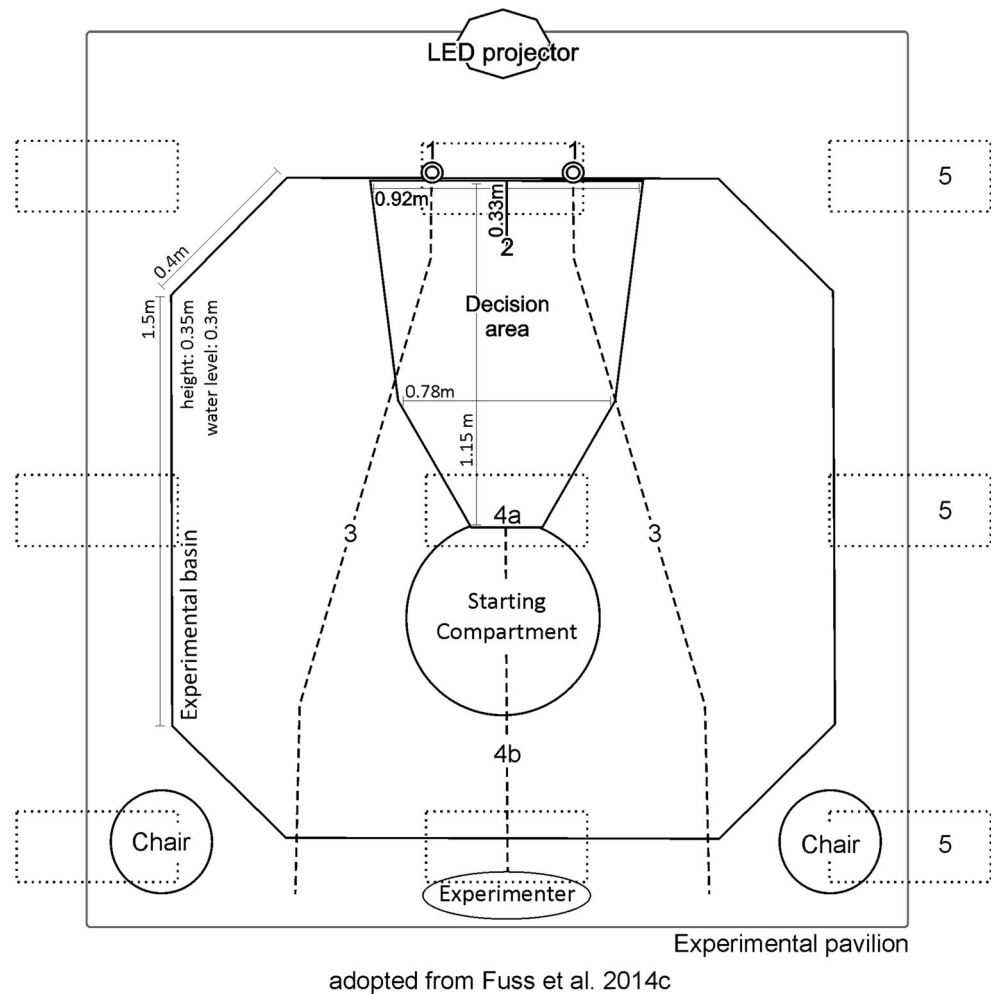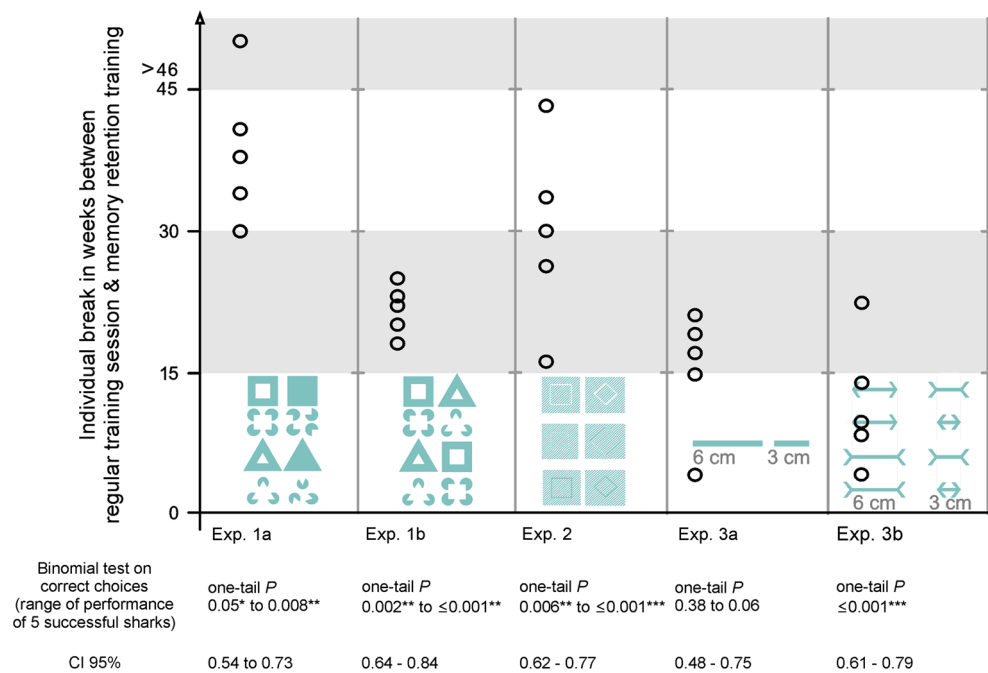

adopted from Fuss et al. 2014c

adopted from Fuss et al. 2014d

Fig. 2 Stimuli that were presented to each group during regular training for Experiments *1–3* and accordingly, the memory retention test. The positive, rewarded stimulus is indicated by a *checkmark*

Binomial test on correct choices (range of performance of 5 successful sharks)	Exp. 1a	Exp. 1b	Exp. 2	Exp. 3a	Exp. 3b
	one-tail *P* 0.05* to 0.008**	one-tail *P* 0.002** to ≤0.001**	one-tail *P* 0.006** to ≤0.001***	one-tail *P* 0.38 to 0.06	one-tail *P* ≤0.001***
CI 95%	0.54 to 0.73	0.64 - 0.84	0.62 - 0.77	0.48 - 0.75	0.61 - 0.79

in each division) and switched randomly between the left and the right side of the screen (Fig. 1) to avoid direction conditioning. Bluish green-colored stimuli used during all experiments were displayed on a light gray-colored background using an LED projector (Figs. 1, 2).

Training sessions consisted of ten trials. The training phase was completed for each individual as soon as it reached a learning criterion of 70 % correct choices in three consecutive sessions ($P \leq 0.05$, χ^2 tests, 1 *df*. There was no time limit during Phase 1 (acclimatization), but if an animal did not reach the criterion within 30 training sessions (Phase 2), it was excluded from further training. Following Phase 2, transfer tests were interspersed within regular training trials (Phase 3) during which the sharks had to perform under altered conditions (Fuss et al. 2014b). Transfer trials remained unrewarded to prevent any kind of learning with respect to the new situation. The same training schedule was repeated for all three experiments (five sub-experiments, Fig. 2).

Following the third and last experiments, training and testing ceased and sharks remained without reinforcement until the memory retention tests commenced. As adaptive training had been used (Fuss et al. 2014b), the length of this final training break differed for all individuals (Fig. 3). Similarly, the break periods following Experiments 1 and 2 varied for all individuals. Additionally, these breaks consisted of the days that each shark spent in subsequent experiments and of the days following the termination of all experiments, i.e., they contained days on which the sharks were trained in a different task (to the one they were

having a break from) and days on which no training occurred at all.

Eight sharks that had participated successfully in all three experiments reported in Fuss et al. (2014b) were subjected to one 90-min memory retention test session. Individuals were presented with five different stimulus sets in random order (Fig. 2). The memory retention test trials followed exactly the same procedure as the regular training trials described above (Fuss et al. 2014b).

During the 90-min session, between 82 and 92 trials were presented to each individual. The session was considered successful if a shark chose the positive (rewarded) stimuli significantly often over the negative ones (binomial test: one-tail $P \leq 0.05$). Two days before testing, sharks were food deprived to increase motivation.

Data analysis

The average trial time, the percentage of correct choices and the percentage of right and left choices were recorded for each individual. A binomial test as well as the 95 % confidence intervals of a proportion (both using the absolute numbers of decisions) was run to determine whether a shark chose the positive stimulus significantly often. Only sharks that chose positive stimuli significantly more often than negative stimuli (binomial test: one-tail $P \leq 0.05$) were included in further analysis. The results of the three original experiments (Fuss et al. 2014b) are listed for each of the five successful individuals in order to present the range in performance (binomial test: one-tail and 95 %

confidence interval of a proportion; both using the absolute numbers of decisions). Since all sharks had already demonstrated successful discrimination of the test stimuli (Fuss et al. 2014b), a one-tailed binomial test was chosen.

A Mann–Whitney U test was used to determine whether the average trial times differed significantly between the final trials described in Fuss et al. (2014b; after reaching the learning criterion) and the newly performed memory retention trials (using the same number of trials). This analysis was repeated for each individual. Additionally, Pearson's correlations were performed to establish correlations between (1) the sharks' performance and the length of the break period, (2) the trial time and the length of the break period and (3) the sharks' performance and the trial time during the memory retention tests (using the absolute number of correct decisions).

For all tests, a $P \leq 0.05$ was considered significant. Additionally, the Holm–Bonferroni procedure was applied to correct the level of significance for multiple comparisons to $P_{\alpha 1} \leq 0.01$.

Results

Eight sharks participated in the memory retention tests, but only five chose the positive stimuli significantly often (binomial test: one-tail $P \leq 0.05$, Table 1, Part 1) and can therefore be considered to have remembered the task. Three sharks were not able to reproduce what they had learned during training (binomial test: one-tail $P > 0.05$, Table 1, Part 1) and were therefore excluded from further analysis. The following section will only summarize individual results for the five successful sharks.

Considering all trials of all experiments combined, five individuals chose the positive stimuli significantly more often than the negative one (binomial test: one-tail $P \leq 0.001$, CI 95 % 0.56–0.81, Table 1, Part 1). Average training breaks ranged from 15.71 ± 8.77 to 32.57 ± 12.88 weeks (Table 1, Part 1). With respect to each of the three experiments, the results for each of the five successful individuals are listed to indicate the spread of performance: In all but one (sub-) experiment (Experiment 3a), the positive stimulus was chosen significantly often (Table 1, Part 2). There was no significant correlation between individual performance and length of the break period (Table 2).

The average trial time decreased significantly during the memory retention tests compared to the original trial times (Fuss et al. 2014b) for all but two sharks (Shark 5: no significant difference, Shark 7: significant increase, Table 1, Part 1). With respect to the three experiments, there was also a significant decrease in the average trial time for Experiments 1a, 1b (i.e., Kanizsa figures), 3a (i.e.,

size ratios) and 3b (i.e., Müller-Lyer illusion) for all individuals. The average trial times in Experiment 2 varied to a considerable degree across individuals (i.e., subjective contours, Table 1, Part 2). Moreover, there was no significant correlation between the average trial time during the memory retention test and the length of the break period or between the individual performance and the average trial time for any individual (Table 2).

Discussion

Given the complexity of the environment in which many fish live, the ability to learn and retain information increases the probability of success and may confer a selective advantage. Accordingly, remembering is an adaptive reflection of environmental demands (White 2001).

In the present study, the performance of eight individuals was evaluated within a single session of memory retention tests following the absence of reinforcement lasting 30–50 weeks (Exp. 1a), 18–25 weeks (Exp. 1b), 16–43 weeks (Exp. 2), 4–21 weeks (Exp. 3a) and 5–23 weeks (Exp. 3b). While three out of eight sharks were unable to maintain their previous performance in choosing the positive stimuli significantly more often over the negative ones (Fuss et al. 2014b), five sharks performed significantly above chance (binomial test: one-tail $P \leq 0.05$, Table 1; Fig. 3). These results fall within the range of results obtained in earlier studies on teleosts using various acoustic and visual stimuli (memory windows of 3–7 months; Csányi et al. 1989; Nilsson et al. 2008a, b, 2010; Bryan and Larkin 1972; Mackney and Hughes 1995; Tlusty et al. 2008; Zion et al. 2011). Similar results were also obtained for turtles (food acquisition task: memory windows of up to 24 months; Davis and Burghardt 2012) and corvid birds (recovering of food from caches: memory windows of up to 9 months; Kamil and Balda 1985, 1990). Potentially, sharks could have even remembered the tasks for longer periods; this was not tested but appears to be reasonable, as there was no (negative) correlation between break duration and individual performance.

Remarkably, sharks remembered three distinct sets of stimuli, which—during training—had been presented separately over a period of 12 months and which they had never seen intermixed prior to the memory retention test. As mentioned before, there was no significant correlation between the sharks' performance and the duration of the break period for any shark (Table 2). Thus, sharks remembered all tasks equally well (except for Experiment 3a, Table 1, Part 2), instead of preferentially remembering the task they had most recently been trained in last (i.e., the task with the shortest break period). White (2001)

Table 1 Results of the memory retention tests—binomial test and 95 % confidence interval of a proportion to compare performance and Mann–Whitney U test to compare the time needed to solve trials during the memory retention tests and the corresponding last two regular training trials per experiment for every individual as well as the range of results of the successful individuals for each experiment ($n = 5$)

Part 1: Results of the memory retention tests, individual results

Subject	Mean break length	Successful trials	Absolute no. of trials	Binomial test	95 % Confidence interval of a proportion	Mann–Whitney U test
Shark 1	24.28 ± 11.37	67	92	<0.001***·#	0.63–0.81	<0.001***·#
Shark 2	20.14 ± 9.34	63	92	<0.001***·#	0.58–0.76	0.002**·#
Shark 3[a]	21.28 ± 12.76	58	82	<0.001***·#	0.61–0.79	0.006**·#
Shark 4	15.71 ± 8.77	62	92	<0.001***·#	0.59–0.77	<0.001***·#
Shark 5	32.57 ± 12.88	61	92	0.001**·#	0.56–0.76	0.19
Shark 6	30.17 ± 14.54	52	92	0.13	0.46–0.66	0.59
Shark 7	13.25 ± 7.14	42	92	0.23	0.36–0.56	<0.001***·#
Shark 8	16.43 ± 9.02	50	92	0.24	0.44–0.64	0.15

Part 2: Results of memory retention tests per experiment, range of results of successful individuals ($n = 5$)

Experiment	Mean break length $\bar{x}$ ($n = 5$)	Successful trials Σ ($n = 5$)	Absolute no. of trials Σ ($n = 5$)	Binomial test 1-tail P value	95 % Confidence interval of a proportion Based on Σ ($n = 5$)	Mann–Whitney U test
Experiment 1a	38.61 ± 7.60	64	100	0.05*–0.008**·#	0.54–0.73	0.032*–0.007**
Experiment 1b	21.64 ± 2.70	67	90	0.002**–≤0.001***·#	0.64–0.84	0.034*–0.001***
Experiment 2	29.73 ± 9.52	78	110	0.006–≤0.001***·#	0.62–0.77	0.46–0.01**·#
Experiment 3a	15.25 ± 6.65	71	100	0.38–0.06	0.48–0.75	0.016*–0.005***·#
Experiment 3b	12.42 ± 7.34	31	50	≤0.001***·#	0.61–0.79	0.05*–0.008**

$P \leq 0.05$ * significant, $P \leq 0.01$ ** significant, $P \leq 0.001$ *** significant; level of significance according to *Holm–Bonferroni* correction ($n = 8$): $P\alpha1 \leq 0.01$ # → significant

[a] Due to the 90-min time limit and decreasing motivation, Shark 3 participated only in 82 trials (i.e., only 1 session of Experiment 1b) instead of 92 trials (i.e., two sessions of Experiment 1a, b, 2, 3b, one session of Experiment 3a)

Table 2 Pearson's correlation to test for a correlation between the sharks' performance and the length of the break period as well as the trial time during the memory retention tests and the length of the break period

Subject	Correlation between performance and break length: Pearson's correlation coefficient (2-tailed test of significance)	Correlation between average trial time and break length: Pearson's correlation coefficient (2-tailed test of significance)	Correlation between Performance and average trial time: Pearson's correlation coefficient (2-tailed test of significance)
Shark 1	0.38 ($P = 0.56$)	−0.58 ($P = 0.30$)	−0.51 ($P = 0.38$)
Shark 2	0.11 ($P = 0.85$)	−0.45 ($P = 0.45$)	0.78 ($P = 0.12$)
Shark 3	−0.25 ($P = 0.69$)	0.37 ($P = 0.54$)	0.32 ($P = 0.60$)
Shark 4	0.49 ($P = 0.40$)	−0.28 ($P = 0.64$)	0.62 ($P = 0.27$)
Shark 5	0.10 ($P = 0.78$)	−0.31 ($P = 0.61$)	0.30 ($P = 0.62$)

Pearson's correlation coefficient: values close to +1 or −1 reveal the two variables are highly related; +1 = highly positive correlation, −1 = highly negative correlation; 2-tailed test of significance: $P \leq 0.05 \rightarrow$ significant; level of significance according to *Holm–Bonferroni* correction ($n = 5$): $P\alpha1 \leq 0.01$ [#]$\rightarrow$ significant

discussed that 'forgetting minimizes proactive interference from prior memories and facilitates the discrimination of recency. Normally, its adaptive utility stems from its primary characteristic—namely diminution in accuracy with increasing temporal distance' (macaques, pigeons: White 2001; for review see Kraemer and Golding 1997). For up to 12 months, sharks obtained food exclusively after making a positive decision (during the original training). Committing such a long-lasting type of food retrieval to long-term memory storage seems beneficial. Nonetheless, following termination of the experiments sharks had only been fed in their aquarium tanks for weeks, which could have been sufficient time for forgetting. Assuming that an individual's memory capacity reflects a trade-off between costs and benefits (insects: Burns et al. 2011; teleosts: Brown et al. 2004; invertebrates and vertebrates: Dukas 1999), sharks must have treated this specific memory as 'valuable' enough to be retained for an extended period of time. Generally, memories of minor importance may be forgotten rapidly while critical memories appear to be maintained or even stored indefinitely (invertebrates and vertebrates: Dukas 1999). Also, quite unexpectedly, the average trial time decreased significantly during the memory retention tests (Table 1); there was no significant correlation between the trial time and the length of the respective break period, nor between the sharks' performance and the average trial time (Table 2).

Results obtained in the study by Fuss et al. (2014b) did not provide information on whether sharks had actually committed the learned information to long-term memory storage or whether they had just relied on visual working memory. In a study on humans, Schneiders et al. (2011) determined that information (visual and acoustic stimuli using adaptive *n*-back paradigms) is only transferred into long-term storage if the task has actually been learned, while simple task repetition to an extent below the level of learning is not. Moreover, they reported specific training effects for adaptive training (Schneiders et al. 2011; Kelley 1969). Across the extensive evolutionary gap between mammals and elasmobranchs, learning represents a basic need for species' survival and has been found in invertebrates and vertebrates alike, starting with simple organisms such as the amoeba-like cell *Physarum polycephalum* (Saigusa et al. 2008). Memory functions are potentially costly as constantly changing environments require continual adaptations including appropriate modifications and improvements of behavior with respect to all experiences (in both invertebrates and vertebrates; Dukas 1999; Burns et al. 2011). Sharks in this study were trained over a period of at least 16 weeks per experiment (adaptive training for about 1 year in total before the memory retention tests commenced). Considering the duration of training and the results of the present study, it can be concluded that the learned information was committed to long-term memory storage, which allowed the sharks to successfully access it whenever needed.

Once a new task has been learned, it may be consolidated and transferred from short-term into long-term memory (in both invertebrates (e.g., *Drosophila* sp., crickets, mollusks) and vertebrates (e.g., primates, rats, birds): e.g., Dudai 1989; Goelet et al. 1986; Fuster 1995; McClelland et al. 1995; Tully 1996). However, most information in long-term memory is inactive. To facilitate further learning, there seems to be a mechanism of silencing of presently irrelevant memories (Dukas 1999). Accordingly, sharks were able to proceed from one experiment to the next and perform successfully in it, while the information on the previous experiment seemed to have been stored and possibly silenced in the long-term memory. This is supported by the fact that no significant correlation between the sharks' performance and the length of the break period for any shark was found. The precise mechanism of silencing inactive memories is barely known (Dukas 1999).

As opposed to keeping and silencing old memories, while still being able to form new ones, other mechanisms can become effective. For example, the storage of old memories could prevent the acquisition of new information (proactive interference), or new information could overwrite older memories (retroactive interference) (reviewed by Spear and Riccio 1994; Dukas 1999). This could possibly be one of the several explanations why three sharks did not retain the previously acquired discrimination ability. Although these sharks were able to learn to distinguish new sets of stimuli during training (Fuss et al. 2014b), this new information could have overwritten recall of earlier experiments. The problem of interference has already been examined in insects and several vertebrates (Stanton 1983; Lewis 1986; Woodward and Laverty 1992; Clayton and Krebs 1994; Goulson et al. 1997; Gegear and Laverty 1998). However, if that were the case in those three particular sharks, at least the memory of the last experiment would be expected to have remained.

Lastly, different brain areas process and store different kinds of information (Chittka and Niven 2009), and memory capacity is influenced by the stimulus modality used during the stimulus presentation (De Haan et al. 2000). It is safe to assume that brain regions perform parallel tasks simultaneously by using different neural circuits. Thus, any visual task activates several parallel processes. Other cognition experiments on the neural basis of visual recognition memory in macaque monkeys revealed the interconnections during perceptual processing followed by the encoding, storage and retrieval of its neural representation (e.g., Mishkin 1978; Murray and Mishkin 1984; Squire and Zola-Morgan 1985; Berryhill and Olson 2008). The sharks' different capabilities regarding the memory retention of visual discrimination tasks (five sharks retained the discrimination tasks successfully, three did not) highlight not only the behavioral variability, but may be another example of the variability in neural and/or perceptual processing found among individuals trained in the same procedure and using the same training schedule.

Cognitive functions, including memory, are known to be closely related to cortical and, especially, neocortical processes in mammals and probably representative homologous areas in birds and possibly even fishes. For example, in birds and mammals, the hippocampus is an integral structure for memory processing, storage and retrieval (e.g., Mahut et al. 1982; Zola-Morgan et al. 1991) and involved in memory interferences (Shapiro and Olton 1994; Hampton and Shettleworth 1996). Currently, it is completely unknown how and where in the brain elasmobranchs process, store and retrieve memories. More extensive behavioral but also neuroanatomical studies are needed to place the present results into context and identify both the relevant mechanisms involved in remembering and forgetting as well as the corresponding neural substrates.

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