

Shape learning and discrimination in reef fish

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SUMMARY

Coral reef fish live in a complex world of colour and patterns. If they are to survive they need to be able to correctly identify the things they see (e.g. predators, prey) and act accordingly (e.g. flee, feed). This paper investigates whether discrimination is limited to ecologically relevant stimuli or is in fact more adaptable. Our work focuses on the reef damselfish *Pomacentrus amboinensis*. Within a day or two of capture the fish demonstrated an ability to associate an arbitrary stimulus with a food reward and to discriminate the reward stimulus from a distractor matched along various physical dimensions. In our initial experiments the reward was directly associated with the target. In the final experiment, however, the reward was separated from the target in both space and time, thereby eliminating a weakness applicable to the majority of food reward experiments involving fish; namely, the presence of olfactory cues emanating from the feeding tubes. All fish were not only able to solve this task but also showed anticipatory behaviour (also referred to as goal tracking). We conclude that freshly caught reef fish not only are able to quickly learn and discriminate between novel stimuli on the basis of shape but are also able to interpret stimuli as a predictor for the availability of food at a different time and place (anticipatory behaviour).

Key words: classical conditioning, goal tracking, reef fish.

INTRODUCTION

The intricate, 3-D world of coral reefs provides the backdrop for a large number of inhabitants that show high diversity in body shape and colour. Depending on their specific niche and life style, reef organisms have to classify other reef inhabitants into categories such as food items, potential predators, competitors or potential mates. As incorrect classification could, in the case of predator recognition, result in death, it is conceivable that in order to survive, maintain a territory and successfully reproduce, adult reef organisms have the ability to classify individual objects with a high degree of accuracy.

Different sensory modalities have different detection ranges. The useful range of a particular signal is determined by both intrinsic receptor sensitivity and signal disruption in the transmission medium (reef waters, in this case). Acoustic signals can be detected over large distances due to the fast speed of sound in water (5 times faster than in air); however, their directionality is rapidly lost due to multiple reflection and refraction boundaries (e.g. surface of water, 3-D reef structure). Olfactory cues are slow and become distorted by water movement, meaning that odour plumes have to be slavishly tracked to their source. Visual cues are fast and highly directional but are limited in range due to the absorption and scattering properties of water. This attenuation of light causes a blurring of edges and a loss of contrast, and is wavelength specific resulting in changes in colour signals with distance and depth (Jerlov, 1976). Despite these challenges, many aquatic animals have a very well developed visual sense (Lythgoe, 1972; Collin et al., 2003; Kröger and Katzir, 2008) including colour vision capabilities such as those described in stomatopods (Marshall et al., 1996) and damselfish (Siebeck et al., 2008). In the clear waters around coral reefs, visual signals may be visible

over many metres, making them ideal for fast intraspecific and interspecific communication.

It is well known that many organisms are able to use light to guide behaviour. But in some, more complex, organisms this ability has become highly refined to the point that they are creative with this information and, through experience, are able to mould behaviour around it. Pigeons and bees, for example, are well able to learn to associate food rewards with novel stimuli (Giurfa et al., 1997; Peissig et al., 2006). In the case of reef fish the question arises as to whether they too are able to adapt their behaviour. It need not necessarily be the case. As mentioned above, in the case of predators, wrong decisions can have lethal consequences. This would appear to offer no room for trial-and-error learning. It would also appear to confer every conceivable advantage for hard-wired, inherited discrimination abilities, such as have been described for juvenile cuttlefish (Langridge et al., 2007). The truth is that many complex organisms, including humans, strike a balance between inflexible but immediate, reflexive behaviour and flexible learnt behaviour. In the case of damselfish, Karplus and colleagues (Karplus et al., 2006) compared the behaviour of juvenile and adult damselfish (*Dascyllus marginatus*) and showed that only the latter have the ability to recognise predators, suggesting that, counter to earlier expectations, learning plays a role in something as fundamental as predator recognition. In practice it appears that learning plays a significant role in many different aspects of a fish's life, particularly in the lives of fish living in the highly diverse environments found in coral reefs (for reviews, see Kelley and Magurran, 2003; Brown et al., 2006).

Karplus and colleagues were also involved in an earlier study of image discrimination and conditioned responses using simple pictures and line drawings (Karplus et al., 1982). In this paper

the authors described how humbugs (*Dascyllus aruanus*) are able to distinguish between predators and non-predators on the basis of the shape of their mouths and the distance between their eyes. Their study could be seen as evidence for a degree of flexibility in the recognition process, although it might also reveal the use of simple facial metrics to assess the dangerousness of an approaching fish. So although the work does imply that fish are able to learn to discriminate between specific forms, it remains unclear to what extent this ability is tuned to the ecologically relevant stimuli they used. A truly flexible visual processing system should, in principle, be able to learn any arbitrary association between form and behaviour. Previous work in our own lab on colour discrimination suggests that coral reef fish are able to associate arbitrary colours with a food reward (Siebeck et al., 2008). Other work has revealed that minnows *Phoxinus phoxinus* are able to form associations between food and simple 2-D objects (Schaller, 1926), and that goldfish *Carassius auratus* can likewise form associations with horizontal and vertical gratings (Ingle, 1965; Ohnishi, 1991). Early work on shape discrimination in animals, including fish, concentrated on their ability to discriminate between either different 2-D objects (mostly triangles and circles) or different orientations of the same object (for a review, see Sutherland, 1961). Unfortunately, in most cases, the brightness and size of the stimuli were not well controlled. This is a problem because it has since been demonstrated that goldfish trained to stimuli containing pattern and colour information use the most salient cue available [e.g. shape or colour (see Ohnishi, 1991)].

The focus of this paper is on shape discrimination and the question of whether fish are able to process shape as well as they can process more basic colour and brightness information. There is already some recent evidence to suggest that they can. In a study conducted in parallel with our own, Wyzisk and Neymeyer (Wyzisk and Neymeyer, 2007) asked whether fish perceive different 2-D objects in terms of a set of oriented edges or in terms of overall shape. They discovered that goldfish can see illusory objects (Kaniza triangle and square), and after an exhaustive series of control studies they concluded that fish were not using local cues to perform this discrimination.

Here, we tested whether freshly caught coral reef fish can also learn to discriminate between different abstract 3-D objects, 2-D shapes and complex patterns. In a series of four experiments, the number of possible cues available to the fish was successively reduced, thus making the stimuli more similar, in order to test whether fish discriminate on the basis of simple cues such as length

or size, or more abstract concepts such as overall shape. In a final experiment, we tested the ability of fish to discriminate between complex geometrical shapes of matched brightness and introduced a new training and testing protocol that served to exclude concerns about the potential use of olfactory cues which could be levelled at our own, earlier studies (Siebeck et al., 2008) as well as those of others including Wyzisk and Neumeyer (Wyzisk and Neumeyer, 2007).

MATERIALS AND METHODS

Fish

Ambon damselfish, *Pomacentrus amboinensis* Bleeker 1868, were collected with hand nets while on SCUBA around Lizard Island, Australia. Throughout experimentation, the fish were maintained in individual aquaria (30 cm×40 cm×30 cm) exposed to natural sunlight, given a PVC tube for shelter and supplied with fresh seawater (flow-through system). Aquaria were cleaned and fish were fed daily as part of the experiments. Following the experiments all fish were released onto the reef where they had been caught. One group of fish ($N=10$, group 1) was used for experiments 1–4 and a different group of fish ($N=8$, group 2) was tested in experiment 5, during a second field trip.

Training

Method 1

For experiments 1–3 the fish were trained following the methods outlined previously (Siebeck et al., 2008). Briefly, the fish were initially trained to feed off a feeding apparatus (tube attached to a syringe containing a paste made from fish flakes and water). The rewarded stimulus was then attached to this apparatus, and the fish had to tap (bite or push) the rewarded stimulus (not the tube) 10 times before a food reward was given. This was achieved by applying pressure to the syringe, which resulted in the expulsion of a small amount of food from the tube (Fig. 1).

Method 2

For experiments 4 and 5 the training method was further developed. Principally, food delivery was separated from the stimuli so that no olfactory cues were present while the fish were making their choices. The feeding tube was only inserted into the aquarium and a food reward released once the fish had made a correct choice.

The new training method added several learning steps to the previous method as the fish had to get used to the presence of a plastic board, which was used to present the stimuli. In experiment 4 the reward stimulus was drawn directly onto the board while in

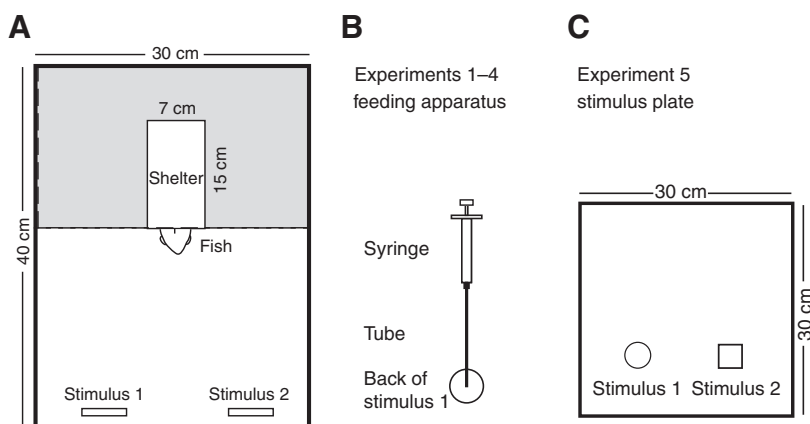


Fig. 1. Schematic diagram of experimental set up. (A) Aquarium showing the position of the shelter and the position at which the stimuli were presented. (B) In experiments 1–4, a feeding apparatus was used with which food could be released from the end of a tube at the back of each stimulus. (C) In experiment 5, a plate containing both stimuli was inserted into the aquarium during each trial, and the fish were rewarded at a random position in the grey shaded area shown in A.

experiment 5 the reward stimulus was a laminated printout (1.5 cm×1.5 cm) that could be attached to the board with hook-and-loop fasteners (Fig. 1).

Testing procedure

In order to be able to discount a side preference from the selection results the stimuli were presented in random positions counterbalanced across each testing session. The only constraint on the randomisation process was that the stimuli never appeared in the same position more than twice in a row. If a fish took more than 2 min to complete the task, the board was removed and the next fish was tested.

In experiments 1–3 stimuli were held in position until the fish made its choice. In experiment 4, the two stimuli (reward and distracter) were drawn on the front and back of the board in reversed positions so that the positions of the stimuli could be controlled by presenting a particular side of the board. In experiment 5, two printed laminated stimuli were attached to the board. For each trial, the stimuli were randomly chosen from six replicate stimuli thus preventing the fish from using any cues specific to a particular replicate.

In all experiments, the stimuli were removed from the aquarium following correct completion of the task and a food reward or a timeout (2 min). Fish were tested twice a day and made between 4 and 10 choices in each session. In experiments 1–4, correct completion involved tapping the correct stimulus 10 times consecutively, while in experiment 5 a single tap on the correct stimulus was rewarded. This was done because results from experiments 1–4 had shown poor first choice behaviour while results from previous experiments, using simple colour stimuli (Siebeck et al., 2008), showed first choices to be a good predictor of overall performance. We wanted to test whether this poor first choice behaviour experienced here but not in previous experiments was an artefact of the testing procedure and if the fish would change their behaviour and still solve the task when forced to do so with one choice only.

Stimuli

General

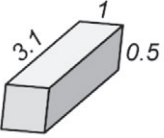
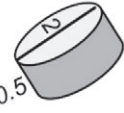
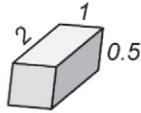
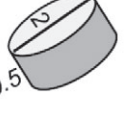
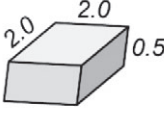
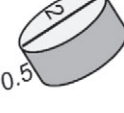
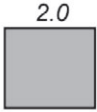
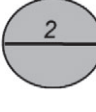




The aim of the first part of the study (experiments 1–4) was to test what kind of information reef fish use to discriminate between two simple abstract objects, a disc and a bar. In a series of experiments, we limited the available cues (edge length, dimensions, tactile differences of curved *versus* straight edges) step by step until only 2-D shape information was available. In the second part (experiment 5), we tested whether the fish were able to discriminate between more complex 2-D stimuli that differed in shape only.

Part 1 (experiments 1–4)

Ten specimens of *Pomacentrus amboinensis* were trained on 3-D discs (0.5 cm thick, 2 cm in diameter) using method 1 (see Table 1). All objects were made of latex, were dark brown in colour (natural latex colour), and were created with the help of a plaster mould. All objects were presented against the white background of one of the sides of the aquarium. Three sets of objects were tested, long bars (volume matched, experiment 1), short bars (diameter matched in one dimension, experiment 2) and squares (diameter matched in both dimensions, experiment 3).

Following the completion of experiments 1–3, the same group of fish were trained on 2-D circles and tested against 2-D squares (see Table 1). Both objects were drawn on a white plastic board using blue paint (Optimacryl, Schmincke, Erkrath, Germany).

Table 1. Summary of stimuli used

Experiment	Shapes (cm)	Matched
1	 	Surface area and thickness
2	 	Length and thickness
3	 	Width, length and thickness
4	 	Width and length
5	   	Diameter and surface area of black <i>versus</i> white zones

3-D stimuli were used in experiments 1–3, where the volume (experiment 1), the width (experiment 2) or the diameter (experiment 3) was equal for the two stimuli. 2-D painted stimuli (equal diameter) were used in experiment 4 and laminated printouts (2-D) were used in experiment 5 (equal black and white area).

Part 2 (experiment 5)

A new set of eight fish were trained on one of four objects: single circle, two concentric circles, windmill with four blades or windmill with eight blades (see Table 1). Fish trained on single circles were tested against the windmill with four blades and *vice versa*, and fish trained on the two concentric circles were tested against the windmill with eight blades and *vice versa*. In each case, the black and white components of each pattern were matched in surface area.

RESULTS

Learning

All fish acclimatised to their aquaria within 24 h of being in captivity. During the 24 h their behaviour changed from hiding at the far end of their shelter tube, irrespective of the presence of an observer, to freely swimming around the aquaria when no observer was present and looking at the observer from within their shelter tubes when an observer approached.

While the fish learned at different rates, all fish (group 1) were able to complete the initial task of tapping the rewarded target 10 times consecutively within 10 to 12 trials (3–4 days; see Figs 2 and 3). Five fish fed from the feeding tube within a day of being captured, while the other five fish took between 2 and 3 days to reach this

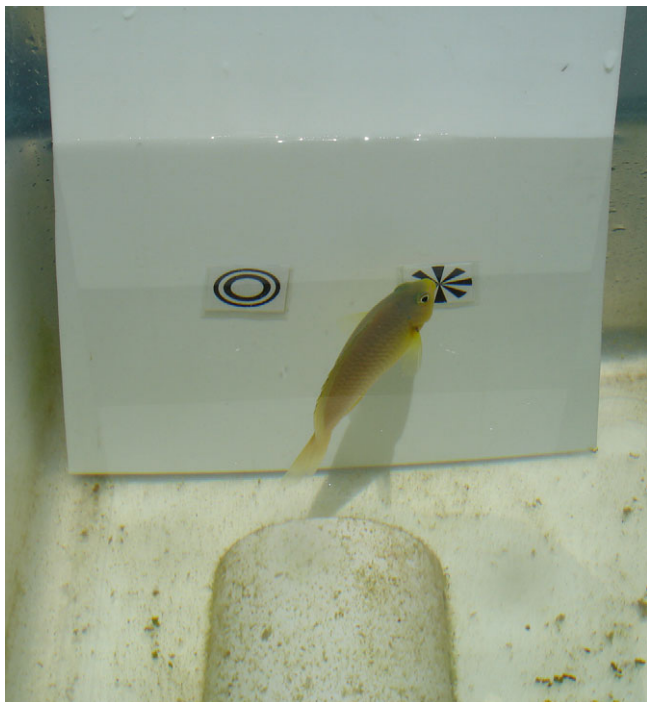


Fig. 2. Photograph of a fish during experiment 5.

same level of performance. The latter five fish compensated for this initial slowness by readily learning to tap the target first 5 and then 10 times.

Experiment 1: circle versus long bar (3D objects)

No side bias was found towards the right or left presentation side (all paired *t*-tests, $P > 0.05$) so that all fish could be included in the analysis. All fish were able to tell the difference between the circle (rewarded stimulus) and the distracter (long bar, same volume as circle; Fisher's Exact test, $P < 0.01$ for all fish). When the first and last three trials were compared, 3 out of 10 fish significantly improved their performance during the course of the experiment (Fisher's Exact test, $P < 0.05$).

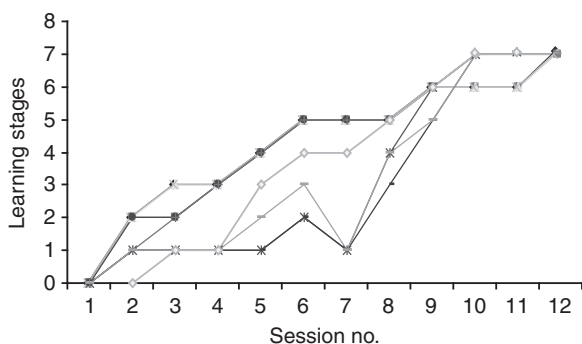


Fig. 3. Learning curve experiment 1. Learning stages: 0, capture; 1, feed for the first time in captivity; 2, feed from tube near shelter; 3, feed from tube anywhere in tank; 4, tap tube once before food is released; 5, 6 and 7, tap at least twice, 5 times and 10 times before food is released, respectively. Different symbols and traces represent different fish.

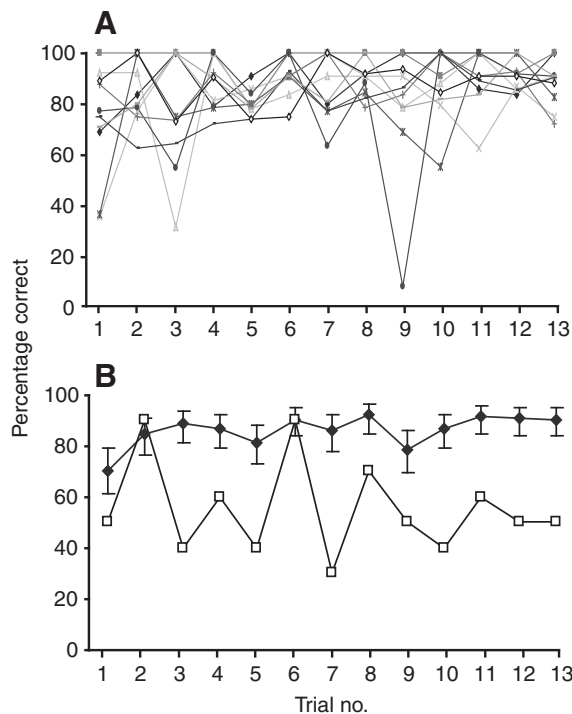


Fig. 4. Results from experiment 1. (A) Individual traces represent the behaviour of all 10 individual fish. (B) Average number of correct taps (100 choices per data point) over all fish (filled diamonds) and percentage of total number of correct first taps (open squares).

On average, the fish achieved a level of 70% correct (lower 95% confidence interval, CI: 61; upper 95% CI: 79) in the first trial and improved to 90% correct (84; 95) in the last trial when all taps were taken into account (Fig. 4). When only the first tap in each trial was analysed, the performance was much worse (Fig. 4). The overall percentage correct for first taps was 43% (33; 52). No significance difference was found from chance when only first taps were analysed (Fisher's Exact test, $P = 0.21$).

Experiment 2: circle versus short bar (3D objects)

No side bias was found and the results of all fish could be included. On average, the fish were able to distinguish between the two objects [78% correct (70; 86); Fisher's Exact test,

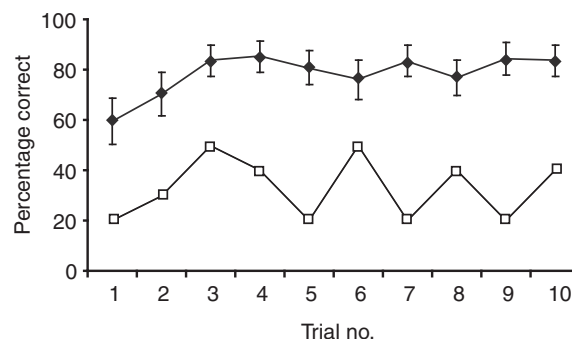


Fig. 5. Results from experiment 2. Filled diamonds, average number of correct taps (100 choices per data point) over all fish; open squares, percentage of total number of correct first taps.

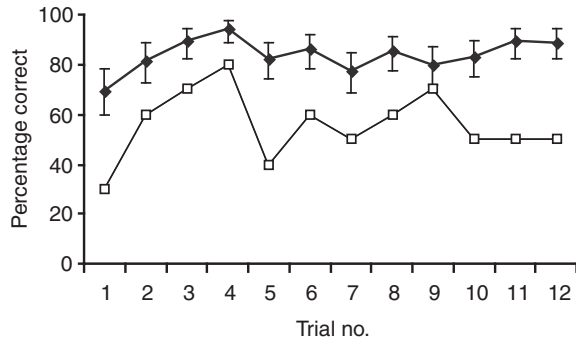


Fig. 6. Results from experiment 3. Filled diamonds, average number of correct taps (100 choices per data point) over all fish; open squares, percentage of total number of correct first taps.

$P < 0.001$; Fig. 5]. When the responses of the last three trials are combined and analysed, all but one fish (fish 7) appeared to be able to tell the difference between the circle (rewarded stimulus) and the distracter (short bar, same length as circle diameter; Fisher's Exact test, $P < 0.01$ for nine fish, $P = 0.08$ for fish 7). However, close examination of the raw data showed that this fish maintained a high level of accuracy ($> 80\%$ correct) following initial learning of the task and only dropped to 55% correct in the very last trial.

Comparing the first and last three trials, 6 out of 10 fish significantly improved their performance during the course of the experiment (Fisher's Exact test, $P < 0.05$); the other four fish also appeared to improve their performance but the improvement was not statistically reliable.

On average, the fish achieved a level of 60% correct (50; 79) in the first trial and improved to 84% correct (75; 90) in the last trial when all taps were taken into account (Fig. 5). When only the first tap in each trial was analysed, the performance was much worse (Fig. 5). The overall percentage correct for first taps was 33% (24; 43). In fact, if only the first tap of each trial was taken into consideration, the fish selected the distracter significantly more often than the target (Fisher's Exact test, $P < 0.01$).

Experiment 3: circle versus square (3D objects)

No side bias was found and the results of all fish could be included. On average, the fish were able to distinguish between the two objects

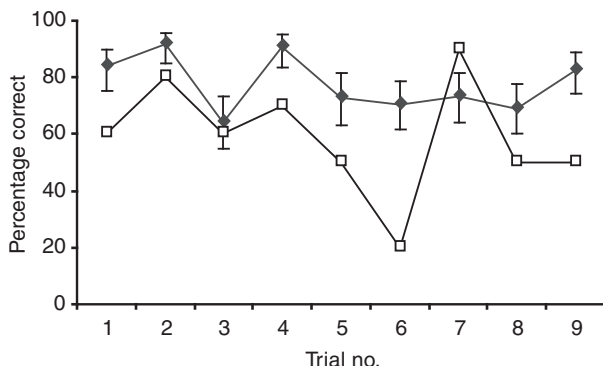


Fig. 7. Results from experiment 4. Filled diamonds, average number of correct taps (100 choices per data point) over all fish; open squares, percentage of total number of correct first taps.

[83% correct (76; 91)]. When the responses of the last three trials were combined and analysed, all fish were able to tell the difference between the circle (rewarded stimulus) and the distracter (square bar, same diameter as circle; Fisher's Exact test, $P < 0.05$ for all; Fig. 6).

Overall, when the first and last three trials were compared, there was no significant improvement of the performance ($P > 0.05$). Interestingly, 2 out of 10 fish significantly reduced their performance during the course of the experiment (Fisher's Exact test, $P < 0.05$) while the remaining fish showed no difference in performance ($P > 0.05$).

On average, the fish achieved a level of 70% correct (60; 79) in the first trial and improved to 89% correct (82; 96) in the last trial when all taps were taken into account (Fig. 6). When only the first tap in each trial was analysed, the performance was much worse (Fig. 6). The overall percentage correct for first taps was 46% (37; 56). The results for the first taps only were not significantly different from chance (Fisher's Exact test, $P = 0.4$).

Experiment 4: circle and square (painted shapes)

No side bias was found and the results of all fish could be included. On average, the fish were able to distinguish between the two objects [78% correct (69; 85); Fig. 7]. When the responses of the last three trials were combined and analysed, 6 out of 10 fish were able to tell the difference between the circle (rewarded stimulus) and the distracter (square, same diameter as circle; Fisher's Exact test, $P < 0.05$ for six fish and $P > 0.05$ for four fish). Overall, when the first and last three trials were compared, there was no significant improvement of the performance ($P > 0.05$). On average, the fish achieved a level of 84% correct (75; 90) in the first trial and dropped slightly to 82% correct (74; 89) in the last trial when all taps were taken into account (Fig. 7).

When only the first tap in each trial was analysed, the performance was much worse (Fig. 7). The overall percentage correct for first taps was 59% (49; 68). The overall results for the first taps only were not significantly different from chance (Fisher's Exact test, $P = 0.15$).

One of the surprising results to come out of the first three experiments was the poor performance based on first choice tap. In some ways this reinforced the utility of requiring multiple taps, but also raised the question of whether touch was required to solve the task. By introducing flat, 2-D shapes this fourth experiment removed any useful tactile information and verified that the fish are able to perform discrimination on the basis of visual appearance alone.

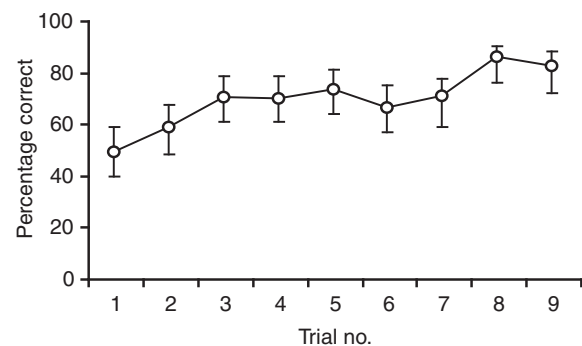


Fig. 8. Results from experiment 5 in which fish were required to tap the correct stimulus once. Averages for all eight fish are shown (80 choices per data point).

Experiment 5: circle versus propeller (printed shapes)

No side bias was found and the results of all fish could be included. Overall, the fish learned to distinguish between the circle and windmill shapes [last three sessions: 80% correct (71; 87); Fig. 8]. When the responses of the last three trials were combined and analysed, 7 out of 8 fish were able to tell the difference between the circle and the distracter, irrespective of the object they were trained to (Fisher's Exact test, $P < 0.05$ for six fish and $P = 0.055$ for one fish). Overall, when the first and last three trials were compared, the fish showed significant improvement in performance ($P < 0.0001$). When the performance of individual fish was analysed, two fish achieved significant improvement in their performance ($P < 0.001$). On average, the fish achieved a level of 49% correct (40; 59) in the first session and increased to 83% correct (74; 89) in the last session (Fig. 8).

DISCUSSION

Our results show that adult reef fish rapidly learn to discriminate between abstract 2-D and 3-D stimuli. Throughout the experimental series, the conditions (location of reward) as well as the stimuli the fish had to discriminate between changed. All fish adapted to the new conditions quickly and learned each task rapidly. When the stimulus and the reward were separated in time and space fish showed anticipatory behaviour following the completion of their task. This type of behaviour is best known for mammals, but has recently also been found in the cod *Gadus morhua* (Nilsson et al., 2008). This suggests that the ability to learn and interpret novel stimuli as signals plays an important role in the life of reef fish.

In each experiment, all fish learned the required task within 10 to 12 training sessions, which is comparable with what was found in previous experiments with reef fish (Siebeck et al., 2008) and the red split fin *Xenotoca eiseni* (Sovrano and Bisazza, 2008) but much faster than with the goldfish *Carassius auratus* (Wyzik and Neumeier, 2007). Experiments 1–4 were designed in such a way that the number of cues available for performing stimulus discrimination was reduced successively until only shape information remained. In particular, the fourth experiment confirmed that the image of a shape was sufficient for the fish to discriminate between the shapes accurately and reliably. This eliminated the possibility that the fish were using tactile cues provided by the straight and curved edges of the test stimuli.

In experiment 5 we moved to geometric patterns, so as to increase difficulty and remove any remaining spurious differences in luminance between the stimuli. By choosing flat stimuli with equal areas of dark and light, average stimulus luminance remained constant. In addition, by assigning fish to different shapes it was possible to confirm that the target had been learned, rather than it being innately preferred for some reason.

Another motivation of the final experiment was to better understand why first taps were often a poor indicator of final selection in the first four experiments. Far from being evidence for the need to physically explore the two stimuli we, as observers, had the impression that the first taps were often aggressive moves aimed at an intruder, or inquisitive gestures checking whether the novel stimulus was also a source of food – both of which imply correct target identification. By switching to a single tap response we were able to shorten testing times and force the fish to select only the food reward stimulus, as a false tap resulted in termination of the trial. In most previous studies overall tapping is generally used as this is seen to allow the fish to correct a wrong choice [this is referred to as the 'correction method' (e.g. Mackintosh and Southerland, 1963; Wyzik and Neumeier, 2007)]. Unfortunately none of these

studies provide data on first and subsequent choices and so it is unclear whether the behaviour we found is particular to the procedure or species. In the 'non-correction' method used in experiment 5 (see also Sovrano and Bisazza, 2008), the fish only have one chance to get it right. This method has the disadvantage that if the fish do not understand the task, position bias may develop (for a review, see Sutherland, 1961). On the other hand, if the fish are able to solve the task under these conditions our results show that it can speed up the testing procedure. It also brings into sharper relief the true quality of their discrimination abilities. As the fish must now make a single correct choice, it tends to ignore novel, non-reward stimuli which it might otherwise approach, not through error but as part of defensive posturing or out of simple curiosity.

The final experiment also introduced another significant improvement to the training and testing protocols. Conditioning experiments with fish commonly associate the distracter and rewarded stimuli with a loaded feeding apparatus and thus with the smell of food (Neumeier, 1984; Neumeier, 1992; Siebeck et al., 2008). This configuration is essential during the learning part of any classical conditioning experiment, at least until the fish have formed an association between the stimulus and the food. However, there is a major drawback of this method. It is possible that food may leak from the submerged feeding tube, influencing the fish's behaviour through either visible or olfactory cues. In the first four experiments of this study we tried to reduce this possibility by timing out a trial after 2 min to prevent excessive wetting and uncontrolled release of food. The method developed in experiment 5 avoids this problem entirely by separating the food reward from the stimulus, meaning that no food was present in the aquarium when the fish selected a target stimulus. Only after the rewarded stimulus was correctly identified did the fish receive their reward, and in a completely separate part of the aquarium. In this way we could be sure that there were no olfactory cues associated with either stimulus and that the fish were making their choices purely on the basis of their visual abilities. Besides the physical separation of the target and reward, the fish also had to cope with an increased time delay between target identification and reward. This delay has previously been shown to be critical for successful conditioning (Thorndike, 1911). If the delay is too long, the strength of the association between target and reward remains weak (Costa and Boaxes, 2007). However, the authors showed that a strong association can still be achieved if the delay is short initially and then increased over the course of the experiment. Our results confirm this finding, as none of the fish (initially trained with close association between stimulus and reward) had problems tapping a stimulus on one end of the aquarium before swimming to the other end to receive their food reward. In fact, after tapping a target they quickly turned around and swam to the other end of the aquarium in anticipation of their food reward. This kind of anticipatory behaviour has recently been described for the cod *Gadus morhua* (Nilsson et al., 2008) but had previously only been found in humans and other mammals (Moore, 2004). Birds (Brown and Jenkins, 1968) and cuttlefish (Cole and Adamo, 2005), on the other hand, tend to treat the stimulus as if it is the food reward itself [auto-shaping (Brown and Jenkins, 1968)] rather than as a signal that a food reward will be available in a different location.

In the fish's natural habitat, an obvious determinant of their survival and fitness is their ability to recognise objects such as food or predators, but another important determinant is their ability to recognise predictors associated with these stimuli. Some fish species have specialised in stirring up invertebrates buried in the sand and the probability of finding food items for an observer may increase

if the situation is recognised and a position close to these species is selected. Such associations have been described for temperate fish (Matsumoto and Kohda, 2001) and are often observed between goatfish and wrasses, or even divers and wrasses on coral reefs (U.E.S., personal observation). Within just minutes of observing a diver catching fish, some labrid species start to follow the diver around and capture any organisms that are trying to escape from the diver's net. These wrasses thus not only are showing anticipatory behaviour but also can transfer their knowledge to new situations by associating the diver's presence with an increased likelihood of capturing prey. Instead of biting the diver (sign-tracking) they anticipate fleeing prey (goal-tracking, or anticipatory behaviour).

In summary, freshly caught reef fish are able to efficiently learn and perform visual discrimination tasks, whether they involve the discrimination of colour (Siebeck et al., 2008) or that of simple and complex shapes (present study). Reef fish also show a capacity for advanced learning as demonstrated by their anticipatory behaviour. This opens up possibilities for further tests of their colour vision abilities (e.g. colour processing) as well as of their object, shape and pattern discrimination abilities. Both of these lines of investigation are interesting in terms of understanding the cognitive abilities of reef fish and comprehending how reef fish perceive their environment.

What we can conclude from these studies is that fish can discriminate between a range of stimuli on the basis of their physical shape, and that this discrimination ability is not simply determined by basic properties such as width, surface area or aspect ratio. What we can also say is that simple shapes drawn on a flat surface can also be discriminated and that the choice of reward stimulus is unimportant as it can be learned. What we have shown here falls short of a demonstration of fully fledged object recognition, as the fish are always afforded the view of the reward stimulus that they had during training. Future experiments will be required to ascertain whether fish can generalise recognition across changes in viewing direction.

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