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ORIGINAL PAPER

Symmetry perception in bamboo sharks (*Chiloscyllium griseum*) and Malawi cichlids (*Pseudotropheus* sp.)

V. Schluessel · O. Beil · T. Weber · H. Bleckmann

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Abstract Several species have been shown to perceive symmetry as a measure of superior genetic quality, useful for assessing potential mates or mediating other visual activities such as the selection of food sources. The current study assessed whether *Pseudotropheus* sp. and *Chiloscyllium griseum*, two fish species from distantly related groups, possess symmetry perception. In alternative two choice experiments, individuals were tested for spontaneous preferences and trained to discriminate between abstract symmetrical and asymmetrical stimulus pairs. Pair discriminations were followed by extensive categorization experiments. Transfer tests elucidated whether bilaterally symmetrical and rotationally symmetrical stimuli could be distinguished. Sharks were also tested for the degree of dissimilarity between two symbols that could still be detected. While sharks showed both a spontaneous preference for symmetry as well as remarkable discrimination abilities by succeeding in all of the presented tasks, cichlids showed no spontaneous preference, had difficulties in discriminating between symbols and performed poorly in the categorization experiments. Sharks distinguished between bilaterally and rotationally symmetrical stimuli and easily differentiated between a four-armed cross (all arms 90° apart) and a cross where one of the arms was only 45° spaced from the one next to it. Performance did not decline when the separation was extended to 70°, but was significantly reduced at an 80° separation. Results indicate that the ability for symmetry perception varies across fish species and individuals, whereby some can detect even subtle differences in this respect.

Keywords Behaviour · Teleost · Elasmobranch · Cognition · Learning · Visual discrimination

Introduction

Symmetry plays an integral part in the natural world (from chemical compounds to entire organisms) as well as man-made environments, arts and artefacts. The term symmetry refers to a correspondence in size, shape and relative position of parts on opposite sides of a dividing line, median plane or about a centre or axis. Symmetry perception has been documented in both vertebrates and invertebrates, including mammals (e.g. Corballis and Roldan 1975; Rensch 1957; von Fersen et al. 1992; Evans et al. 2000; Waitt and Little 2006), birds (e.g. Delius and Habers 1978; Delius and Nowak 1982; Møller 1992; Swaddle and Cuthill 1994; Swaddle and Pruett-Jones 2012; Swaddle and Johnson 2007; Mascalzoni et al. 2012), fish (Morris 1998; Merry and Morris 2001; Mazzi et al. 2003; Morris et al. 2006) and insects (Giurfa et al. 1996, 1999; Møller and Sorci 1998; Plowright et al. 2011). Several types of symmetry exist; most animals are bilaterally symmetrical with respect to the sagittal plane (as in humans) or radially symmetrical, whereby the degree of symmetry varies in all organisms and individuals.

Fluctuating asymmetries, i.e. small, random variations from perfect bilateral symmetry, are caused by developmental disruptions due to environmental and genetic stresses (Swaddle et al. 1994; Graham et al. 2010). Being a measure of the 'deviation from perfection', asymmetry is

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therefore used by organisms as a measure of genetic quality and plays an integral role in behaviours associated with it (Leung and Forbes 1996). In fish, one example is mate choice by female swordtails, which prefer symmetrically over asymmetrically striped males (Merry and Morris 2001). However, symmetry perception also appears to influence other visually mediated activities such as foraging, e.g. bumble bees preferentially visit symmetrical over asymmetrical flowers (Rodríguez et al. 2004). It has further been suggested that symmetry detection is beneficial for prey-searching behaviour as it simultaneously increases conspicuousness of desirable, palatable (but potentially camouflaged) prey (as in great tits; Menne and Curio 1978) and of unpalatable species displaying antipredator warning patterns (Forsman and Merilaita 1999, 2003; Forsman and Herrström 2004). Specifically, bilateral symmetry has been implicated in being an indicator for superior phenotypic and genotypic quality, with many species displaying preferences for highly symmetrical features (Bornstein et al. 1981; von Fersen et al. 1992; Swaddle and Cuthill 1994; Morales and Pashler 1999; Morris 1998; Rodríguez et al. 2004; Little and Jones 2006). An alternative hypothesis claims though that symmetry preferences may be sensory biases instead of being detectors for genetic quality, i.e. they may be by-products of visual information processing (Enquist and Arak 1994). While some organisms may possess a preference for either symmetry or asymmetry, others may not (Swaddle 1999a, b; Clara et al. 2007; Forsman and Herrström 2004).

In fish, symmetry perception has only been tested in the context of sexual selection, whereby females usually prefer males displaying the most symmetrical phenotypic features. Cortez swordtails prefer males displaying an equal number of vertical stripes on either side (Morris and Casey 1998; Merry and Morris 2001), while female three-spined sticklebacks show a significant preference for males featuring symmetrically arranged pectoral fins (Mazzi et al. 2003, 2004). Rensch (1957, 1958) and Tigges (1962), however, showed that several fish species including the cichlid *Cichlasoma biocellatum* prefer irregular over regular stimuli.

This study investigated whether a teleost (*Pseudotropheus* sp.) and a shark (*Chiloscyllium griseum*) can distinguish symmetry from asymmetry independent of a specific biological context (such as mating behaviour). The two species belong to two very distantly related groups of fish; while elasmobranchs have existed for roughly 450 Mio years, modern teleosts only evolved about 220 million years ago. Performance on single stimulus pairs was tested, followed by complex categorization experiments once individuals had solved the former successfully. Sharks and cichlids are both bilaterally symmetrical organisms, and fluctuating asymmetries in various bodily features could act as indicators for the lack of genetic quality. In cichlids, including *Pseudotropheus*, vision is an important sensory system and specifically relevant to females when choosing a mate (Kellogg 1997; Seehausen and van Alphen 1998). Males are often brightly coloured (McElroy et al. 1991), displaying mating patterns that can be intensified within minutes (Nelisson 1991). Some of these visible markings or patterns may be symmetrical; there may even be ‘invisible’ ultraviolet light or polarized reflective patterns, both of which could bear symmetry information. Several coral reef fish use ultraviolet light for facial pattern recognition in conspecific (Siebeck 2004; Siebeck et al. 2010), and *Pseudotropheus zebra* is indeed sensitive to UV wavelengths (Carleton et al. 2000). Generally, UV light detection seems to be particularly important for communication between individuals (Carleton et al. 2000; Jordan et al. 2003, 2004). Whether cichlids display or use symmetrical facial or body pattern for mating or communication purposes is not known. Polarized light signalling for communication purposes has already been observed in cephalopods (Mäthger et al. 2009) and has been suggested to play a part in the behaviour of fish, such as the damselfish *Chromis viridis* (Mussi et al. 2005). As rock-dwelling cichlids such as *Pseudotropheus* are predominately herbivorous, grazing on algae, symmetry perception is unlikely to play a role in feeding. Overall, considering their bilaterally symmetrical body shapes, their clear water habitats, the importance of the visual system in general and its role in communication specifically, cichlids were expected to perceive symmetry as well as other teleosts, such as sticklebacks or swordtails.

Sharks are also known to use vision for a range of activities (Hueter et al. 2004), and similar to *Pseudotropheus*, *C. griseum* frequents clear water habitats such as rocky inshore environments and lagoons (Compagno 2001). While adult bamboo sharks are mostly unpatterned, juveniles display a range of saddle marks and transverse bands (Compagno 2001). As there are no conspicuous symmetrical visual markings in adults and probably no role of symmetry in foraging (as *C. griseum* is an opportunistic benthic feeder), it was assumed that sharks would have a lesser need for symmetry perception than cichlids. Nonetheless, sharks are also bilaterally symmetrical animals and deviations from perfect symmetry may still signal decreased genetic quality. Based on the biology of both species and previous experiments assessing cognitive abilities of these two genera (Fuss et al. 2014a; Gierszewski et al. 2013; Schluessel and Bleckmann 2012; Schluessel et al. 2012, 2014), it was therefore hypothesized that both species may not necessarily have a spontaneous preference for either sym- or asymmetry but can at least learn to distinguish between them and categorize them.

To test these abilities, several stimulus pairs each consisting of a symmetrical and an asymmetrical symbol had to be distinguished. Following successful completion, categorization experiments were conducted. Categorization is the ability of an animal to combine distinguishable events, objects or items into discrete mental units which are then treated equivalently (Mervis and Rosch 1981). The animal recognizes similarities among these events, objects and items and constructs categories that are based on shared features (Spinozzi 1996). This ability can be used for a range of behaviours including the identification of new objects, solving of problems, communication of ideas and obtaining environmental information (Spinozzi 1996). It is therefore one of the most basic ways to organize knowledge (Smith and Medin 1981). By testing individuals for their ability to categorize symmetrical from asymmetrical symbols, the risk that individual stimulus pairs were only distinguished based on single elementary features, such as edges, lines or the arrangement of light and dark segments, was eliminated. In categorization experiments, each individual was confronted with a completely new pair of stimuli on each trial, thereby making it impossible to chose correctly based on any other feature than symmetry. Transfer tests served to determine whether bilateral symmetry could be distinguished from rotational symmetry, and in a final step, it was tested to what degree symmetry can be perceived.

Materials and methods

Subjects

Cichlids Subjects were twelve naïve rock-dwelling Malawi cichlids of the genus *Pseudotropheus* that were obtained from a commercial aquarist shop. Individuals were bred in captivity, ranged between 8 and 10 cm in total length and were easily recognized by phenotypic characteristics. Cichlids were individually housed in 50-L aquaria (0.6 m × 0.3 m × 0.3 m), filled with aerated and filtered water and kept at a temperature of 25–26 °C. Four fish died at different stages during the experiments. *Sharks* Eight (2 males, 6 females) juvenile grey bamboo sharks (*C. griseum*), ranging between 20 and 25 cm in total length and born in captivity, were obtained from various Zoos. Individuals were kept in a 3,000-L aquarium system filled with aerated, filtered salt water at 25–26 °C. Conductivity was kept at 50 µS. Food (vegetarian pellets, Granugreen Sera®, Germany for the cichlids and small pieces of squid, fish or shrimp for the sharks) was only provided during experimental trials. There was a natural light/dark cycle.

Apparatus

Cichlids

Each fish was kept in an aquarium that served both as a holding as well as an experimental tank (Fig. 1). Walls and floor of each tank consisted of light grey PVC, while the front was made of white frosted plastic. A partition was inserted into the middle of the tank separating a back from a front compartment. The back compartment contained a pump and filter system (Duetto Cobra DJC 50) as well as a heating element. The water temperature was kept at 25–26 °C. The grey partitioning was fitted in the centre with a small grey guillotine door and controlled remotely by a hand-operated device. In the absence of testing, the door was always kept open and fish could move freely between compartments. Just prior to training, the door was closed, restricting the fish to the back compartment. On the inside of each aquarium front, two food holders were installed (Fig. 1), consisting of two small pieces of plastic pipe (5 cm long) which were attached to the wall with suckers. Into each pipe a hose filled with food was inserted. On the other end, the hose was connected to a syringe through which the food delivery was controlled remotely. With the help of markers (lines), the front compartment was further divided into a right and left compartment. Parallel to the front wall, a line indicated a 3-cm wide area, which together with the right and left division created two areas into which the fish had to swim in order for its stimulus choice to be valid. Stimuli (black outline on a light grey coloured background) were projected onto the plexiglass front of the tank just below the food holders, using an LCD projector (ES 521 Optoma, DLP®, China) which was located in front of the tank and connected to a notebook (Fig. 2). Markings on the plexiglass guaranteed a projection onto the same fixed spot in each session. The projection of stimulus fields was positioned at the height level of the guillotine door to ensure that individuals could immediately see the stimuli when exiting the guillotine door.

Sharks

Experiments were carried out in a set-up similar to the one described for each cichlid, with the exception that there was only one tank (100 cm × 50 cm × 50 cm, still divided in two compartments), which did not serve as housing tank. Sharks were kept in a separate aquarium system and individuals were transferred to the experimental tank about 10 min prior to each experiment. Frequent water changes ensured that water parameters remained the same between the two environments. A light grey guillotine door confined

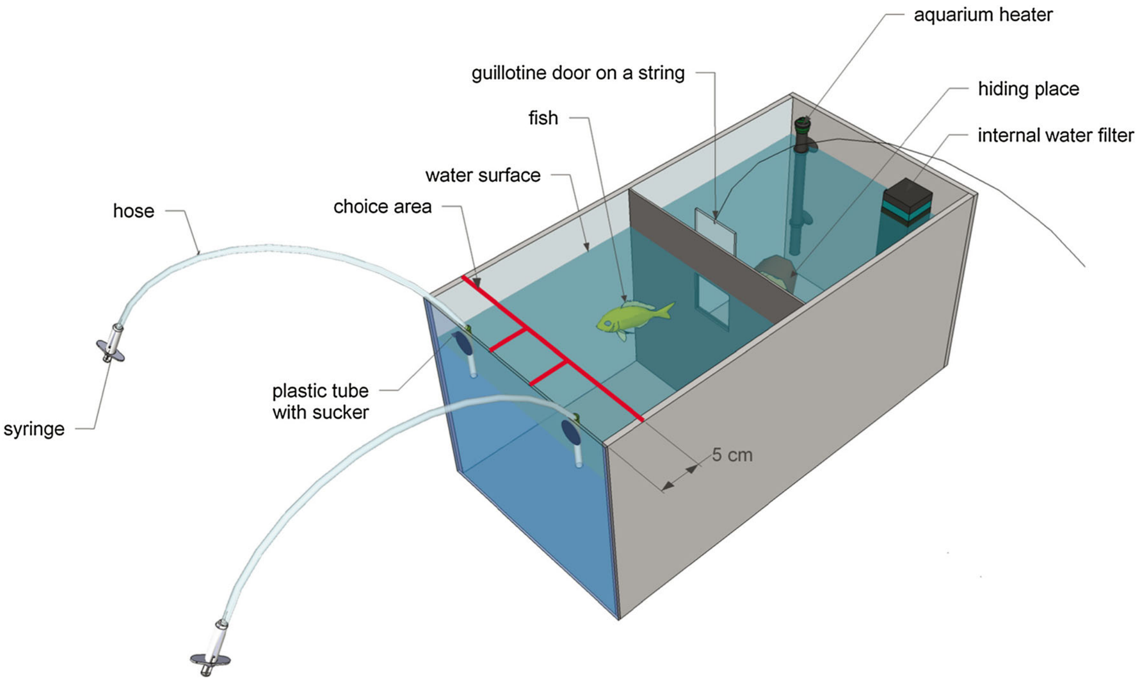


Fig. 1 Experimental apparatus, showing the two compartments, separated by a partition featuring a guillotine door. Immediately below the two food holders into which feeding tubes were inserted, the two stimuli were projected. Choice areas are indicated by *red lines* [reproduced from Gierszewski et al. (2013)] (color figure online)

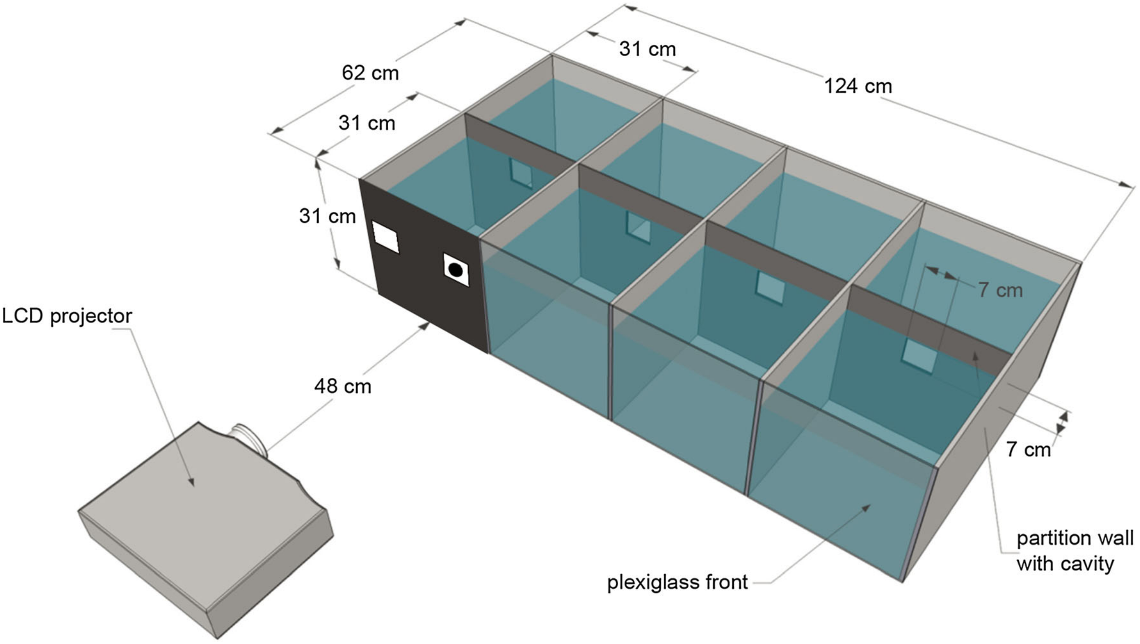


Fig. 2 Top view of the decision areas (*red square*) on the *right and left side* of the front wall **a** for cichlids and **b** for sharks. Trial time was measured from the time the individual passed through the guillotine door with its nose, until crossing the line in front of the stimulus on either side [reproduced from Gierszewski et al. (2013)] (color figure online)

the starting compartment (SC; equivalent to the 'housing' compartment for the cichlids), in which sharks were placed before each trial. The door was controlled manually by using a cable pull. As opposed to the cichlids, which usually swam in the upper parts of the water column, sharks were swimming on the bottom for most of the time;

therefore, the guillotine door was still located in the middle of the partitioning but on the floor. The experimental compartment was confined by the partition containing the guillotine door and a milk-coloured wall onto which stimuli were projected. On the milk-coloured wall, a small divider (transparent Perspex) separated a left from a right side. The 2D symbols were bluish-green coloured and displayed on a light grey coloured background. According to Hart et al. (2011), the maximum absorbance (λ_{max}) of cone visual pigments in the very closely related shark species *Chiloscyllium punctatum* was around 532 nm, in the visible light range for blue to green. For projections, a LED projector situated at a distance of about 1.0 m from the screen was used and stimuli were projected at a height of 3 cm above the bottom. Just above both stimuli, feeders were installed which allowed food to be dropped into the set-up manually using a cable pull at the experimenter's discretion. Both feeders were baited with small pieces of sepia, redfish or shrimp. Between trials, sharks were gently guided back into the SC, where they remained for up to 90 s before the next trial started.

Experimental procedure

Experiments were conducted during daylight hours; there was a natural light/dark cycle. Fish had to discriminate between a positive and a negative stimulus. Sessions were conducted daily, always at the same time. Each session consisted of ten trials (these were termed 'regular' trials to distinguish them from 'transfer test' trials which are explained in the "Transfer test" section); both feeders were baited in each trial (to prevent olfactory cues guiding the fish) and always simultaneously re-baited to prevent unintentional cuing by the experimenter. At the beginning of each trial, the fish was placed in the SC (housing compartment for the cichlids, from now on only referred to as SC). Stimuli were projected onto the milk-coloured front. For each trial, the position of the positive stimulus was randomly determined prior to the experiments (five times on each side); however, no stimulus was shown more than twice in a row on the same side. Four rotational schemes were used, so as to alter the succession of the stimuli shown on a particular side between sessions. The guillotine door was opened and the fish allowed was to enter the front compartment. Once the door was opened, the fish had to make a choice within 2 min, otherwise the trial was terminated. A choice was recorded as soon as the fish crossed over the decision line as indicated by markers. A correct choice was rewarded with food. Immediately following an incorrect choice or after consuming the food, the fish was ushered back into the SC. Intertrial time was 60 s for cichlids and 90 s for sharks. Training ended when the learning criterion was reached which was established at performing successfully in at least seven out of ten trials (≥ 70 % correct choices) in three consecutive sessions ($\chi^2(1) \leq 0.05$). For each session, the average trial time and the percentage of correct choices were recorded. Trial time was defined as the time it took the fish to swim through the guillotine door and cross the line in front of the food holders. Time was recorded using a stopwatch. Pumps and heating elements were removed from the back compartment where cichlids were kept prior to the experiments. To test for unintentional cues given by the experimenter, control trials with blank screens were randomly interspersed with regular trials as well as trials in which the experimenter did not know the location of the positive stimulus herself.

Pretraining

Prior to training, fish had to get used to the apparatus and to feeding from the pipettes/food holders. Sharks were allowed to habituate to the tank and the experimental set-up by swimming freely throughout the entire set-up for up to 20 min at a time for several days. The guillotine door was open, feeders were in place and fish were only fed at the feeders. In a second step, the door was closed and only opened when sharks/cichlids pressed against it/waited in front of it. After fish had learned to swim through the raised door and approach the food holders while the projector (no stimulus) was on, training started.

Training

Discriminations

All experiments were conducted as two alternative choice experiments. Individuals had to distinguish between two symbols (always a symmetrical and an asymmetrical), forming a stimulus pair. In total, there were six experiments, each featuring a different stimulus pair. In five of these, two symbols (in form of a symmetrical positive (rewarded) and an asymmetrical negative stimulus) had to be discriminated. In the remaining one, the fish were tested for a spontaneous symmetry or asymmetry preference (Fig. 3d), i.e. there was no positive or negative stimulus and every choice was rewarded. In the five discrimination experiments, the positive stimulus was either the square (experiments 1 and 2) or the symmetrical symbol (experiments 3, 5 and 6). Experiment 4 tested for spontaneous preferences; there were five sessions (fifty trials per fish). The six experiments were conducted in the following order: (1) square versus 'blank' (Fig. 3a), (2) square versus circle (Fig. 3b), (3) Sym1 versus Asym1 (Fig. 3c), (4) Sym2 versus Asym2 (spontaneous preference testing, Fig. 3d) (5) Sym3 versus Asym3 (Fig. 3e) and (6) Sym4 versus Asym4 (Fig. 3f). Apart from the stimulus pairs used

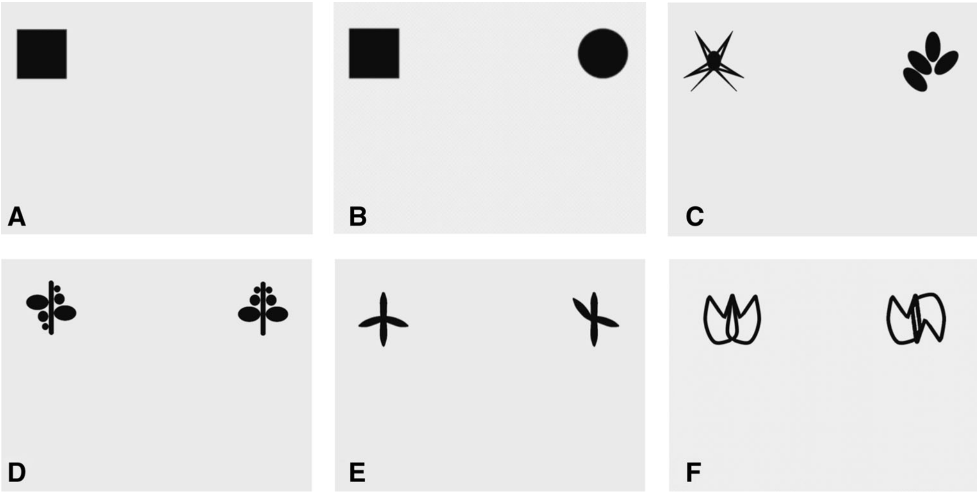


Fig. 3 Experimental stimuli for the cichlids shown in form of a PowerPoint slide presented to each individual (sharks were presented with the same stimuli; however, these were projected onto the bottom part of the screen and were *blue* instead of *black*). **a** and **b** give the positive and negative stimulus for the two form discrimination experiments 1 and 2 (*square* vs. *blank* and *square* vs. *circle*), **c** for experiment 3 (*Sym1*/*Asym1*), **d** for the spontaneous preference experiment 4 (*Sym2*/*Asym2*), and **e**–**f** for the two remaining symmetry/asymmetry discriminations in experiments 5 (*Sym3*/*Asym3*) and 6 (*Sym4*/*Asym4*) (color figure online)

in experiments 1, 2 and 3, both symbols within a pair were always of the same size (area) and colour and only varied with respect to symmetry. All symbols were constructed using the program PAINT.NET. Some symbols were taken (and modified) from a previous study on insects (Giurfa et al. 1996). Experiments 1 and 2 were conducted to check whether individuals were capable of performing simple visual discriminations (as it was known from previous experiments that the two species could distinguish these symbols) and to test for general motivation of individuals. Experiments 3, 5 and 6 tested for the ability to distinguish symmetry from asymmetry, whereby the two stimuli in experiment 3 varied not only in symmetry but also in size and area. Stimulus pairs 5 and 6 only varied with respect to symmetry.

Categorization 1 and 2

Following the discrimination experiments (of which at least the first two and one other had to be successful), individuals underwent three categorization experiments. In the first (categorization 1), thirty stimulus pairs (each consisting of a symmetrical and an asymmetrical symbol) were designed and a different pair shown on each trial (Fig. 4a, each box represents a pair (two symbols) shown in one trial; the symmetrical symbol is on the left, the asymmetrical on the right). This implied that for the first 30 trials, all stimulus pairs were completely new to the fish; after that, pairs were recycled but shown in a random order so that every pair only came up once every thirty trials. Both symbols within a pair (Fig. 4a) were always of the same area and colour and only varied with respect to symmetry. The symbols from different stimulus pairs varied in as many aspects as possible, to avoid conditioning to anything else than symmetry. After the learning criterion was reached and the first set of transfer tests were completed (see section below), another 30 stimulus pairs were designed (categorization 2; Fig. 4b) and a new stimulus pair was again shown on each of the first 30 trials; afterwards pairs were recycled. Once the learning criterion was reached, a second set of transfer tests ($n = 10$) was conducted (see below).

Transfer tests

Transfer tests trials elucidated whether fish could spontaneously (without prior training) distinguish between unknown bilaterally symmetrical and rotationally symmetrical stimuli. As they were unrewarded, they also served as a control to determine whether baiting had any unwanted effect on the stimulus selection process. After fish reached the learning criterion in the first and second categorization experiment, first an 80 % rewarding scheme was introduced. From then on, food was only provided in a maximum of eight (out of ten) correct trials; prior to each session, it was randomly determined which trials remained unrewarded (regardless of choice). This served to prepare the fish for the subsequent introduction of the unrewarded transfer test trials, i.e. by keeping the fish from realizing that only choices in transfer trials were unrewarded and therefore not worth participating in. If performance during the 80 % rewarding scheme remained unaffected, transfer

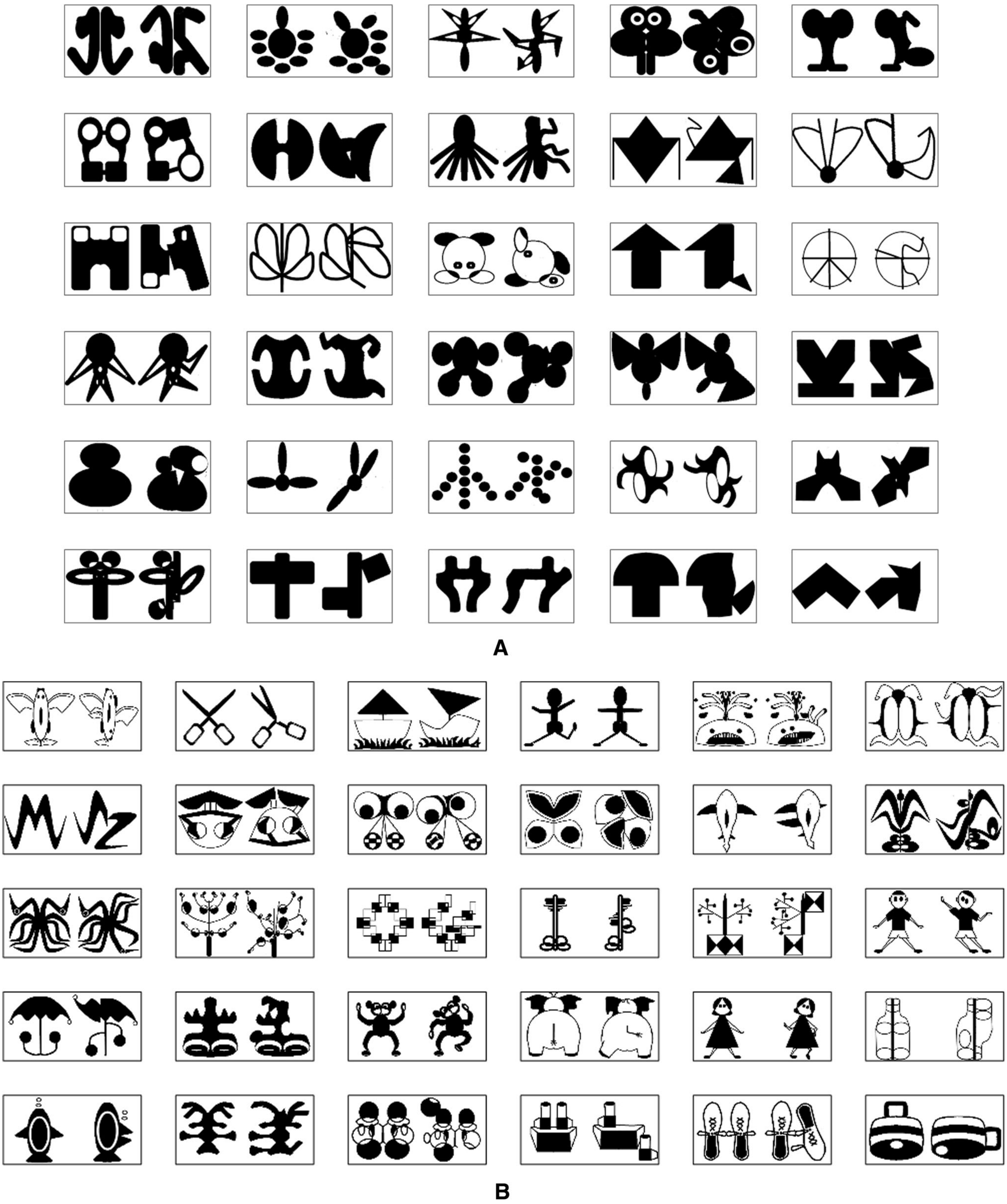


Fig. 4 Stimulus pairs shown during the regular trials in the categorization experiments **a** categorization 1 and **b** categorization 2. The symmetrical symbol on the *left* was always the positive stimulus. The here presented stimuli are not drawn to scale. The two symbols were arranged on the PowerPoint slides the same way as the positive and negative symbols presented in Fig. 3

trials started ($n = 10$ per type and individual; Fig. 5). Two transfer trials were randomly interspersed with the ten 'regular' trials within a session. While bilaterally symmetrical and asymmetrical stimuli were shown in the regular trials, bilaterally symmetrical and rotationally symmetrical stimuli were presented in the transfer tests.

Categorization 3

After the second set of transfer tests, categorization 3 started. In this experiment, the 60 stimulus pairs from categorization 1 and 2 (120 symbols in total) were separated and the 60 bilaterally symmetrical stimuli randomly mixed with the 60 asymmetrical stimuli (Fig. 6). A new symbol combination was shown on each trial, implying that for the first 60 trials no symbol occurred more than once. After the first 60 trials, symbols were recycled in new combinations. In this experiment, symbols within a pair varied in area, colour and symmetry; however, as individuals were presented with a new pair of symbols on each trial, there was no defining mutual symbol feature between correct choices other than that of bilateral symmetry.

Symmetry detection threshold

In this last task, fish had to distinguish between a symmetrical four-armed cross (all arms 90° apart) and an asymmetrical cross where one of the arms (right) was only 45° spaced from the one next to it (Fig. 7a). The positive, rewarded stimulus was the regular spaced four-armed cross. After fish reached the learning criterion, two transfer tests (20 per individual) were conducted. Transfer tests were randomly interspersed with regular trials; again there were 1–2 transfer trials per session. Prior to transfer trials, an 80 % rewarding scheme was introduced. During the transfer trials, the negative stimulus featured a 70° arm separation ($n = 10$ per individual) or an 80° separation ($n = 10$ per individual; Fig. 7b).

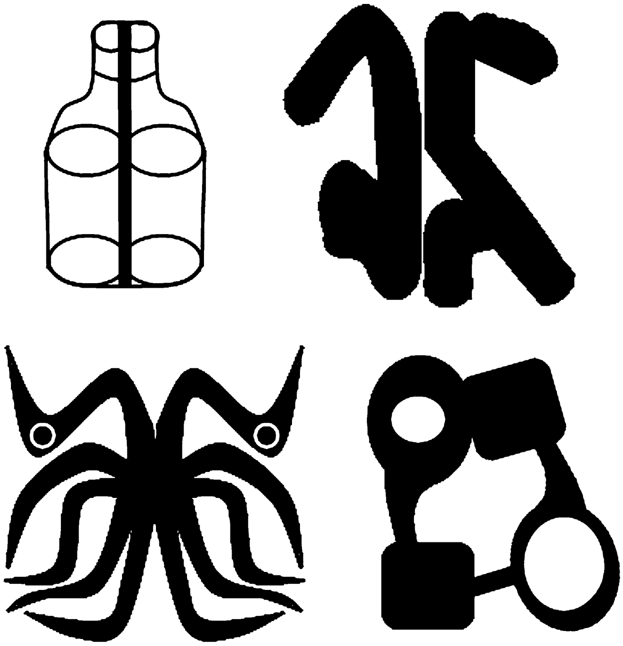


Fig. 6 Two representative stimulus pairs shown during the third categorization experiment. *Symbols* were randomly taken from the 60 symmetrical and 60 asymmetrical symbols used in categorization 1 and 2 and randomly mixed. The bilaterally symmetrical symbol on the left was always the positive stimulus

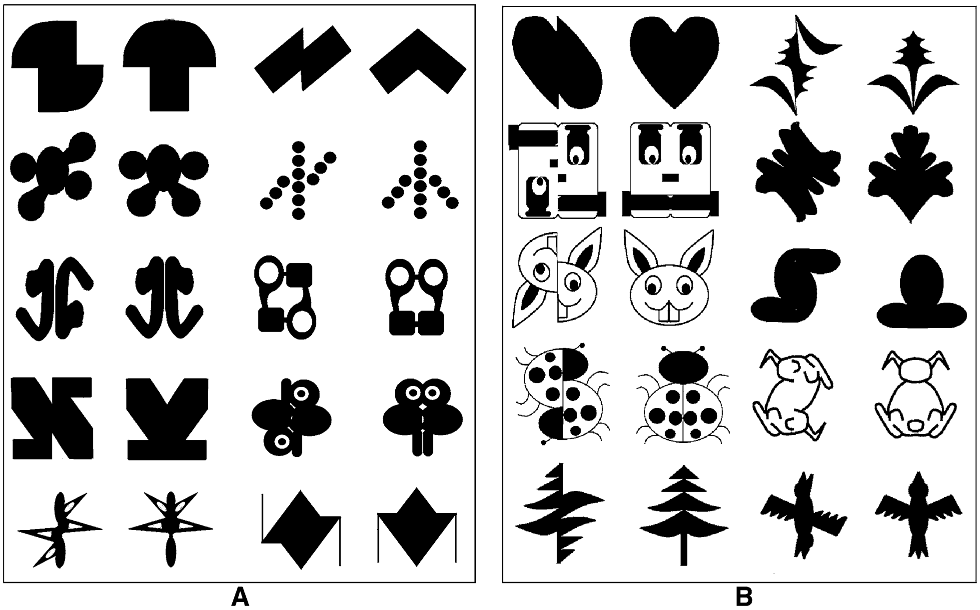


Fig. 5 Stimulus pairs shown during the transfer trials in the categorization experiments **a** transfer 1 and **b** transfer 2. The bilaterally symmetrical symbol on the *right* was always the positive stimulus

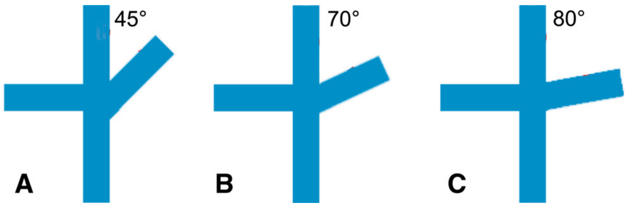


Fig. 7 Negative stimuli shown during the last discrimination experiment (*Sym5*/*Asym5*). The bilaterally symmetrical symbol (regular cross, 90° arm separation) was the positive stimulus. **a** The negative stimulus during the regular trials (45°), **b** the negative stimulus during transfer 1 trials (70°) and **c** the negative stimulus during transfer 2 trials (80°)

Data analysis

All sessions were recorded by a webcam (Logitech Webcam C210). The learning criterion was established to be $\geq$70.0 % correct choices on three consecutive sessions. The probability of achieving this by chance is less than 0.05 % (χ^2 test, $p < 0.05$). The following statistical tests were used for each individual fish (the criterion of statistical significance was $p < 0.05$): A sign and binomial test was run to determine whether those fish who did not reach the learning criterion within 40 sessions chose the positive (rewarded) stimulus significantly more often than the negative (unrewarded) stimulus. Chi square tests (χ^2) were performed to test whether individual fish chose the positive stimulus significantly more often than the negative one during transfer test trials. The 95 % confidence intervals (CI) are given. A Mann–Whitney *U* test or *t* test was used to assess differences in the average trial time between regular trials and transfer trials. A Mann–Whitney *U* test was also applied to determine whether the average trial times differed significantly between discriminations for each individual as well as for the group. For all tests, a $p \leq 0.05$ was considered significant.

Table 1 outlines the different experiments and their respective purpose.

Results

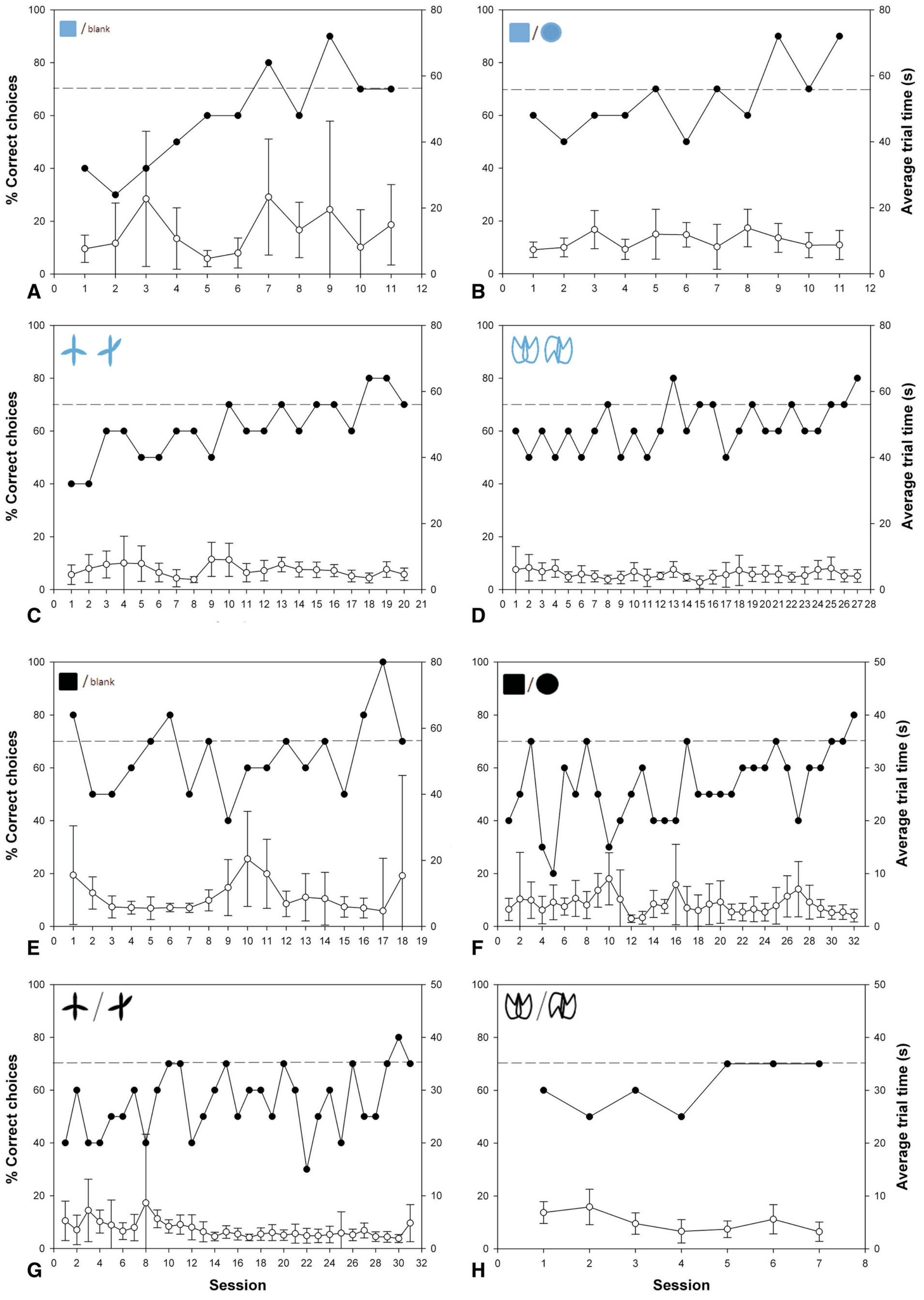
In the following, results will be presented for each experiment in chronological order, both for individuals and as group averages for sharks and cichlids. Representative learning curves (showing results for the two geometric symbol discriminations and for two of the symmetry/asymmetry discriminations) are shown in Fig. 8a, b, for a shark and a cichlid respectively.

Discrimination of simple geometric symbols (experiments 1 and 2)

These two discriminations (Fig. 3a, b) were only performed to test the general performance and motivation

Table 1 Chronological overview of the different experimental procedures used within this study

Procedure	Symbols	Purpose
Pretraining	No symbols	Get animals acquainted with the set-up, feeding, etc.
Training		
Single pair discriminations		
Experiment 1	One stimulus pair: square versus blank	Test motivation level and learning ability
Experiment 2	One stimulus pair: square versus circle	Test motivation level and learning ability
Experiment 3	One stimulus pair: Sym1 versus Asym1	Test discrimination ability
Experiment 4	One stimulus pair: Sym2 versus Asym2	Spontaneous preference testing
Experiment 5	One stimulus pair: Sym3 versus Asym3	Test discrimination ability
Experiment 6	One stimulus pair: Sym4 versus Asym4	Test discrimination ability
Categorization 1	New stimulus pair (a symmetrical vs. an asymmetrical symbol) on each trial for the first 30 trials, then recycling of old stimulus pairs in a new order	Test for abstraction and categorization ability of symmetrical and asymmetrical symbols
Transfer test 1	10 new stimulus pairs (a bilaterally symmetrical vs. a rotationally symmetrical symbol)	Determine if bilaterally and rotationally symmetrical symbols can be distinguished
Categorization 2	New stimulus pair (a symmetrical vs. an asymmetrical symbol) on each trial for the first 30 trials, then recycling of old stimulus pairs in a new order	Test for abstraction and categorization ability
Transfer test 2	10 new stimulus pairs (a bilaterally symmetrical vs. a rotationally symmetrical symbol)	Test if bilaterally and rotationally symmetrical symbols can be distinguished
Categorization 3	Random combinations of the 60 symmetrical and the 60 asymmetrical symbols used previously, a new combination was shown on each trial	Test for abstraction and categorization ability
Symmetry detection threshold	A cross (90°) versus a cross with one 70° or 80° bend arm	Determine the degree of symbol dissimilarity that can still be detected


A
/ blank
B
/
C
D
E
/ blank
F
/
G
/
H
/
% Correct choices
Average trial time (s)
Session
0
20
40
60
80
100
0
10
20
30
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50
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◀**Fig. 8** Representative learning curve for a shark (**a–d**) and a cichlid (**e–h**) during the two stages of the visual form discrimination (**a**, **b** and **e**, **f**) and the symmetry/asymmetry discrimination (**c**, **d** and **g**, **h**) experiments. *Open circles* give the average trial time (s) ± standard deviation, *closed circles* the percentage of correct choices. **a** and **e** *square* versus '*blank*' B and **f** *square* versus *circle*, **c** and **g** *Sym2* versus *Asym2* (experiment 4), **d** and **h** *Sym3* versus *Asym3* (experiment 5). The *dashed line* gives the 70 % threshold

levels of individuals. Prior experiments had already shown that both species can successfully discriminate simple geometric symbols (Fuss et al. 2014a; Schluessel et al. 2012; Gierszewski et al. 2013). Therefore, these two experiments were used to determine the ability of each individual to perform in visual discrimination experiments and helped to eliminate the possibility that a poor performance of an individual in the symmetry experiments could be based on motivational-, set-up- or experimenter-related issues.

All cichlids and sharks learned to discriminate a square from a 'blank' in less than 30 sessions (Fig. 9). There was great intraspecific variation; cichlids needed between 3 and 30 sessions, with an average of 12 sessions. Sharks showed a less widely spaced range, needing between 11 and 22 sessions, with an average of 18 sessions. While all sharks distinguished a square from a circle, one cichlid did not learn the task even after 43 sessions (Fig. 9). Performance in cichlids ranged from 5 to 46 sessions with an average of 29 sessions, which was much higher than in the previous task, while sharks performed much better than when distinguishing a square from a blank, needing on average only 10 sessions.

Surprisingly, the average trial time (Fig. 9) decreased in the cichlids in the second experiment ($n = 12$; $U = 11$; $p = 0.01$) despite fish needing more sessions to perform the task ($n = 12$; $U = 24$; $p = 0.019$) than in the first. In the sharks, the results of the Mann–Whitney U tests show that there were no significant differences between the average trial time the sharks needed within the first and second discrimination task ($n = 8$; $U = 27$; $p = 0.65$; Fig. 9). There was, however, also a significant difference in the number of sessions needed ($n = 8$; $U = 5$; $p = 0.003$).

Symmetry 1 versus asymmetry 1 (experiment 3)

As in the previous task, all sharks learned to distinguish the symbols of the first stimulus pair on average within about 21 sessions, while five cichlids did not learn to solve the task even within 40 sessions (Fig. 10). One individual died after 18 sessions. Cichlids ($n = 5$) needed between 7 and 27 sessions with an average of 18 sessions, while sharks ($n = 8$) needed between 16 and 26 sessions, with an average of 21 sessions. Compared to the previous task, trial time decreased even further in the cichlids, despite there being a completely novel task, but stayed about the same in the sharks (Fig. 10).

Spontaneous preference (experiment 4)

When cichlids were given the choice between a bilaterally symmetrical and an asymmetrical symbol (both rewarded), none of the cichlids (but one) showed a significant preference for either one (average: $n = 350$; $\chi^2 = 0.05$, $df = 1$, $p = 0.83$). Out of 350 trials (50 trials per fish, 7 fish), the symmetrical symbol was chosen 173 times, while the asymmetrical one was chosen 177 times (for individuals: $\chi^2 = 0.00$–2.88, $df = 1$, $p = 0.09$–1). The sharks, however, chose the symmetrical symbol significantly more often, i.e. 235 times out of 350 trials (50 trials per shark, 7 sharks), than the asymmetrical one (115 times; for individuals: $\chi^2 = 3.92$–11.52, $df = 1$, $p = 0.05$–0.001).

Symmetry 3 and 4 versus asymmetry 3 and 4 (experiments 5 and 6)

While all sharks distinguished a symmetrical from an asymmetrical cross on average within 25 sessions, only four cichlids learned to solve the task, needing 32, 52, 48 and 18 sessions, respectively (Fig. 10). Results were similar for the third symmetry pair 'blossom'; here, only three out of nine cichlids solved the task, while six did not (Fig. 10). These three cichlids needed much fewer sessions than in the previous task, though, on average 10. All sharks learned the new stimulus pair on average within 23 sessions (Fig. 10). There was no significant difference between the trial times for these two experiments for the cichlids ($n = 4$; $U = 11$; $p = 1$) and the sharks ($n = 8$; $U = 31$; $p = 0.96$). There was also no significant difference between the number of sessions (25 vs. 23) sharks needed to solve the two tasks ($n = 8$; $U = 24.5$; $p = 0.44$).

Categorization 1

In both categorization experiments, a new, unknown stimulus pair was presented to the individuals on each trial (Fig. 4a). After the first 30 trials, stimulus pairs were recycled; the order in which pairs were shown though was altered, and on average, there were 30 trials between repetitions of pairs. While sharks mastered the task much faster than any of the previous discriminations, needing on average nine sessions and a trial time of 3.64 s, only two out of eight cichlids performed well in this experiment, needing on average 11.5 sessions to reach the learning criterion (Table 2).

As neither of the two cichlids that reached the learning criterion was able to subsequently maintain a performance above criterion, they were excluded from transfer tests, categorization 2 and 3 experiments. Instead, several simple discrimination tests were performed to disclose, whether cichlids were generally not performing well (e.g. due to illness, absence of hunger) or only experiment related. Among others, experiment number one was repeated, in which cichlids were re-shown the stimulus pair ‘square’ versus ‘blank’. All animals were able to reach the learning criterion again within 8.5 ± 8.55 sessions. The average trial time was 1.5 ± 0.47 s. Despite an overall poor performance in the symmetry-related discrimination tasks, individuals remained highly motivated throughout the experiments and participated in all trials.

Categorizations 2 and 3 (sharks only)

In the second categorization experiment (Fig. 4b), sharks mastered the task even faster than in the first categorization, needing on average only six sessions and an average trial time of 4.1 s (Table 3). In the third categorization task, in which symbols from mixed stimulus pairs were presented (Fig. 6), sharks also needed 6 sessions and on average 3.8 s (Table 3). Results of the Mann–Whitney *U* tests showed that there was no significant difference between the number of sessions needed to reach the learning criterion ($n = 8$; $U = 26.5$; $p = 0.57$) in the two categorization tests and between the trial times needed ($n = 8$; $U = 27$; $p = 0.65$; Table 3).

Transfer tests (sharks only)

One or two transfer tests were interspersed with ten regular trials per session ($n = 20$ transfer test trials in total per shark) in the first and second categorization experiment (for symbols, see Fig. 5). In the first transfer test, which was conducted during the first categorization experiment, sharks chose the bilaterally symmetrical symbol (82.5 %) significantly more often than the rotationally symmetrical one ($n = 80$; $\chi^2 = 33.8$; $df = 1$; $p < 0.001$; 95 % CI 76.4–88.6; Table 4). There was no significant difference between trial time in the regular trials compared to trial times in the transfer test trials ($n = 8$; $U = 20$; $p = 0.234$). In the second transfer test (for symbols, see Fig. 5), which was conducted during the second categorization experiment, sharks still chose the bilaterally symmetrical symbol (77.5 %) significantly more often than the rotationally symmetrical one ($n = 80$; $\chi^2 = 24.2$; $df = 1$; $p < 0.001$; 95 % CI 72.6–82.4). There was no significant difference between trial time in the regular trials compared to trial times in the transfer test trials ($n = 8$; $U = 31$; $p = 0.959$). Throughout the transfer phases, performance in the regular trials was maintained at $\geq$70 % in all sharks.

Symmetry detection threshold

In this last task, sharks had to distinguish between a symmetrical four-armed cross (all arms 90° apart, Sym5) and an asymmetrical cross where one of the arms was only 45° spaced from the one next to it (Asym5; Fig. 7a). The positive, rewarded stimulus was the former. Sharks reached the learning criterion on average within 7 sessions; the average trial time was 3.9 s (Table 5). Transfer tests were randomly interspersed with regular trials; there were 1–2 transfer trials per session. During the transfer trials, the negative stimulus featured a 70° arm separation (T1) and an 80° separation (T2; Fig. 7b). In the first transfer test (Table 5), sharks chose the positive stimulus 68 out of 80 times [85 % (95 % CI 81.3–88.7)], which was highly significant ($n = 80$; $\chi^2 = 39.2$; $df = 1$; $p < 0.001$; CI 81.3–88.7). In the second transfer test, sharks chose the positive stimulus only 33 out of 80 times [41.3 % (95 % CI 32.6–49.9)], which was not significantly often anymore ($n = 80$; $\chi^2 = 2.45$; $df = 1$; $p = 0.118$; CI 32.6–49.9). Throughout the transfer phases, performance in the regular trials was maintained at $\geq$70 % in all sharks.

Discussion

The results of the present study show that both cichlids and sharks can be trained to distinguish symmetrical from asymmetrical artificial stimuli, independent of a sexual- or prey-selection context. The study also demonstrated for the first time categorization abilities in sharks. All eight individuals developed an abstract concept of symmetry, as the novel stimuli that fish were exposed to on each trial during the categorization experiments where distinguished with ease. Whereas the sharks solved all tasks including the transfer tests without significant problems, cichlids took very long to master most tasks, did not master all tasks and were not capable of maintaining a performance above criterion in the first categorization experiment, which eliminated them from subsequent testing (categorization 2 and 3, the respective transfer tests and testing of the symmetry detection threshold (Sym5 vs. Asym5)). This result was rather surprising, since prior studies had shown cichlids to be capable of complex discrimination and categorization tasks in various contexts (Schluessel et al. 2012, 2014). Also, previous studies suggested that cichlids rely heavily on the visual system for a range of activities including choosing a partner according to visual features (Kellogg 1997; Seehausen and van Alphen 1998). Cichlids had therefore been expected to perform well in these experiments. Sharks had also previously been tested in simple discriminations of geometrical stimuli (Fuss et al. 2014a) and illusionary contours (Fuss et al. 2014b), which they had performed well in, but had not been assessed in any categorization experiments prior to this study.

Discrimination of geometric symbols

As expected, all individuals in both groups reached the learning criterion in the discrimination task ‘square versus blank’ and thereby proved suitable for the present study. Sharks needed about 17.5 sessions to reach the learning criterion, which is comparable to what Fuss et al. (2014a) found (18.3 sessions). They also learned the second task a lot quicker than the first (average: 9.5 sessions), possibly because the positive stimulus (square) remained the same and sharks were now used to the experimental procedure. Results were again comparable to those collected by Fuss et al. (average of 10.1 sessions). The cichlids needed on average 11.8 and 28.9 sessions for the two experiments, while they only needed 5.7 and 8.1 sessions for the same two tasks in a previous study (Schluessel et al. 2012). As there is usually great intraspecific variation, those differences could possibly be attributed to individual diversity. Nonetheless, all sharks and all but one cichlid successfully finished the second discrimination task.

Spontaneous preferences

In experiment 4 (Sym2/Asym2), it was tested whether cichlids and sharks possessed a spontaneous preference for either a symmetrical or an asymmetrical stimulus. In agreement with the results of the other symmetry experiments performed within this study (experiments 3, 5 and 6), the cichlids as a group showed no significant preference for either stimulus. The sharks, however, chose the symmetrical symbol significantly often. Despite this preference, sharks still needed on average between 21.3 and 23.5 sessions to reach the learning criterion in the other three symmetry discriminations. This was surprising; after all, in these experiments, the preferred symmetrical stimulus was the rewarded one and one could have therefore expected sharks to reach the criterion faster. Many species tested so far possess an innate or spontaneous preference for either symmetry or even asymmetry (e.g. bees: Rodríguez et al.

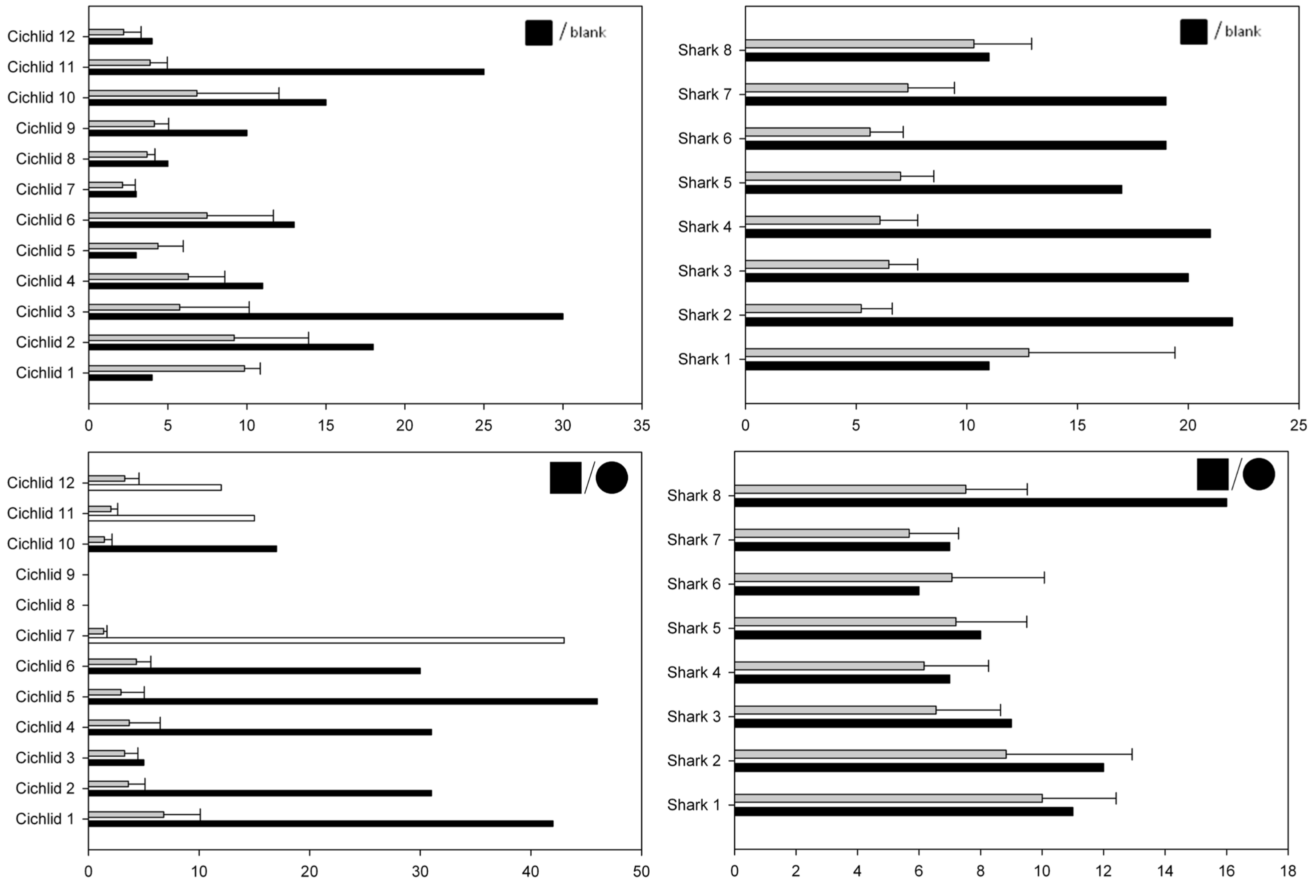

Fig. 9 Summary of the results obtained during the regular trials in experiments 1 (*square blank, top*) and 2 (*square circle, bottom*). The number of sessions (*black bars*) indicates how long each fish needed to reach the learning criterion (LC). *Grey bars* give the average trial time in seconds (±SD = standard deviation). A *blank* indicates the individual did not participate in the experiment, and a *white bar* indicates after what session the experiment was terminated without the LC being reached

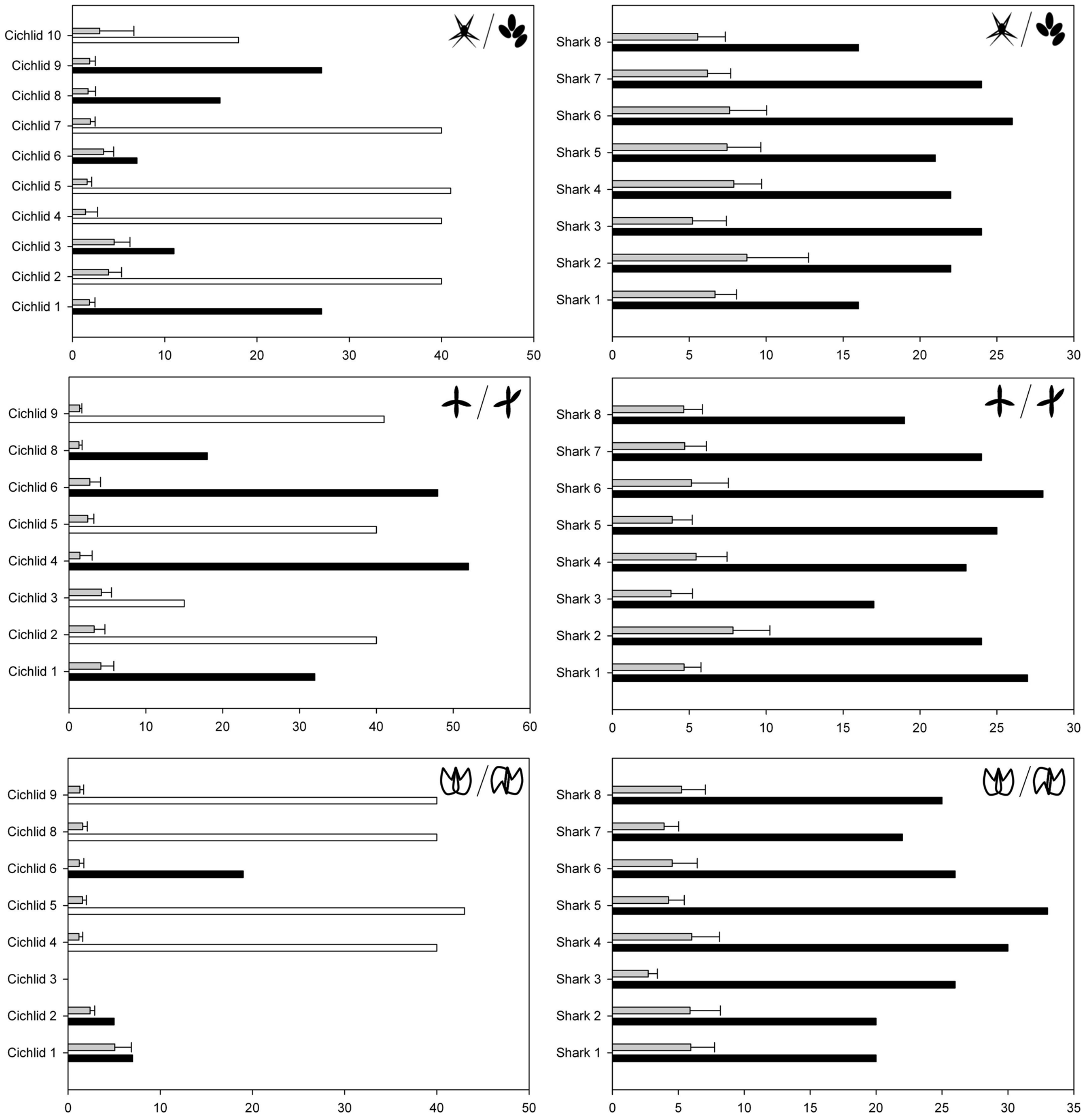

Fig. 10 Summary of the results obtained during the three single pair (*symmetry*) discrimination experiments 3 (*top*), 5 (*middle*) and 6 (*bottom*). The number of sessions (*black bars*) indicates how long each fish needed to reach the learning criterion (LC). *Grey bars* give the average trial time in seconds (±SD = standard deviation). A *blank* indicates the individual did not participate in the experiment, and a *white bar* indicates after what session the experiment was terminated without the LC being reached

2004; and jackdaws: Rensch 1958). Others, like starlings or crab spiders, show no initial preference (Swaddle et al. 2004; Wignall et al. 2006). In a study by Tigges (1962), cichlids (*Cichlasoma biocellatum*) showed a spontaneous preference for irregular over regular stimuli; however, stimuli varied in several aspects, not just in symmetry. Innate preferences were not tested for in the present study as individuals were experimentally naïve but had not been living in environments free of any (potentially) symmetrical stimuli, which theoretically could have biased subsequent choices. Also, experiment 3 (Sym1/Asym1) had been conducted prior to the spontaneous assessment, which

Table 2 Summary of the results obtained during the regular trials in the categorization experiment 1

Fish	Symbol	
	Categorization 1[a] 	
	Session #	Trial time (s)
Cichlid 5	/(40)	1.51 ± 0.43
Cichlid 6	/(41)	1.68 ± 0.65
Cichlid 8	/(30)	1.63 ± 0.54
Average	11.5	3.81
Shark 1	3	5.40 ± 2.19
Shark 2	7	4.24 ± 0.46
Shark 3	10	3.23 ± 0.99
Shark 4	10	5.56 ± 1.25
Shark 5	10	3.68 ± 0.63
Shark 6	12	3.87 ± 0.67
Shark 7	5	3.75 ± 0.75
Shark 8	14	3.44 ± 0.53
Average	8.88 ± 3.64	4.15 ± 0.88

The number of sessions indicates how long each fish needed to reach the learning criterion (LC). Average trial time is given in seconds (±SD = standard deviation). A backslash indicates the individual did not participate in the experiment or, with a number behind it, it indicates after what session the experiment was terminated without the LC being reached

[a] Only the symmetrical stimuli ($n = 30$) are shown here, for complete stimulus pairs please refer to Fig. 4a

Table 3 Summary of the results obtained during the regular trials in the categorization experiments 2 and 3

Fish	Symbol			
	Categorization 2 (30 new stimulus pairs)		Categorization 3 (mixed pairs from Cat. 1 & 2)	
	Session #	Trial time (s)	Session #	Trial time (s)
Shark 1	8	5.99 ± 1.53	5	5.05 ± 1.47
Shark 2	5	4.21 ± 0.60	5	4.17 ± 0.77
Shark 3	6	2.36 ± 0.47	8	3.61 ± 2.51
Shark 4	6	5.90 ± 1.45	6	6.61 ± 1.35
Shark 5	9	3.41 ± 0.63	5	2.80 ± 0.94
Shark 6	6	4.32 ± 0.71	8	2.81 ± 1.03
Shark 7	5	2.48 ± 0.66	6	2.32 ± 0.40
Shark 8	5	4.12 ± 0.87	3	3.18 ± 0.59
Average	6.25 ± 1.49	4.10 ± 1.36	5.75 ± 1.67	3.82 ± 1.42

The number of sessions indicates how long each fish needed to reach the learning criterion (LC). Average trial time is given in seconds (±SD = standard deviation)

Table 4 Summary of the transfer test results obtained during the first and second categorization

Fish	Symbol			
	Categorization 1 Transfer 1		Categorization 2 Transfer 2	
	Correct choices	Trial time (s)	Correct choices	Trial time (s)
Shark 1	7	4.54	8	6.57
Shark 2	9	4.36	9	3.29
Shark 3	9	2.36	7	2.43
Shark 4	9	4.70	8	5.87
Shark 5	9	2.51	8	2.59
Shark 6	8	1.93	7	4.18
Shark 7	7	2.51	7	1.92
Shark 8	8	2.21	8	4.06
Average	66/80	3.140 ± 1.17	62/80	3.866 ± 1.66

The numbers indicate correct choices out of 10 trials per individual, i.e. 80 trials in total

could have also affected performance. The fact that cichlids showed no spontaneous preference supports the data obtained in the other experiments. In order for there to have been a preference, fish would have had to perceive a distinct difference between the two symbols presented, and consequentially, one would have expected individuals to distinguish subsequent stimulus pairs more easily. This was the case in the sharks, which showed a preference (indicating successful discrimination) and also successfully mastered all tasks.

Symmetry discriminations

In general, cichlids seemed to have great difficulty distinguishing between symbols based on symmetry. For experiments 3, 5 and 6, cichlids as a group needed 17.6, 37.5 and 10.3 sessions, respectively, to reach the learning criterion; however, not all individuals solved all tasks. Results indicate that symmetry perception (at least if taken out of a specific context) may not play a principal role in the life of this species. Considering the results of previous

Table 5 Summary of the results obtained during the last discrimination experiment

Fish	Symbol			
	 (90°vs 45°)			
	Session #	Trial time (s)	Transfer 1 (90° vs. 70°)	Transfer 2 (90° vs. 80°)
Shark 1	8	5.72 ± 1.17	9	3
Shark 2	7	4.36 ± 1.09	8	5
Shark 3	5	2.02 ± 0.54	8	6
Shark 4	5	6.13 ± 1.39	8	3
Shark 5	8	3.31 ± 0.57	9	5
Shark 6	6	2.61 ± 0.38	8	3
Shark 7	5	3.20 ± 0.46	9	3
Shark 8	8	3.80 ± 0.67	9	5
Average	6.5 ± 1.41	3.89 ± 1.44	68 (85 %)	33 (41.25 %)

The number of sessions indicates how long each fish needed to reach the learning criterion (LC). Average trial time is given in seconds (±SD = standard deviation). In the last two columns (transfer tests), the numbers indicate correct choices (out of 10 per individual, i.e. 80 trials in total)

studies (Gierszewski et al. 2013; Schluessel et al. 2012) and the fact that some fish discriminated selected stimuli successfully, it seems unlikely that the overall poor performance can be attributed to low visual resolution.

Compared to the first two experiments, performance of sharks in the symmetry experiments (3, 5 and 6) was more homogenous; the individual spread was smaller, i.e. between 16 and 33 sessions were needed as opposed to 3–30 sessions. On average though, sharks needed more sessions in these experiments to reach the learning criterion than in the simple visual discrimination experiments 1 and 2. Symbols of the first stimulus pair (Sym1/Asym1, experiment 3) shown after the simple visual discrimination experiments varied from each other in several features other than just symmetry (e.g. size, area and colour) but were not faster discriminated than the following ones (experiments 5 and 6), which only varied in regard to symmetry.

While the cichlids that reached the learning criterion needed on average between 10 and 37.5 sessions (one should keep in mind though, that for the group as a subsample of the species, this average would be much higher as several individuals did not master the task in the time allotted) for the discriminations in the symmetry experiments and sharks between 21 and 25 sessions, pigeons in a similar task discriminated symmetrical from asymmetrical stimuli within 20 sessions (Delius and Habers 1978) or even faster (Delius and Nowak 1982). Starlings only needed about 15 sessions (Swaddle and Pruett-Jones 2012). As the present study only tested artificial stimuli, it cannot be excluded that symmetry may be important to cichlids in a more natural context. Nonetheless, it can be speculated that if it did play a significant role, performance should have been higher at least in some of the tasks. Some fish, like gobies and goldfish, have been suggested to focus their attention during visual discrimination tasks selectively onto specific parts of a stimulus such as top or bottom features (Herter 1929, 1930; Wyzisk 2005) or global versus local dimensions (Truppa et al. 2010). As the top and bottom parts of the positive and negative stimuli varied within most of the stimulus pairs in the present study, selective attention for these features should not have precluded successful discrimination by cichlids. In the categorizations, no top or bottom feature or any other feature (than symmetry) persisted throughout all symmetrical or all asymmetrical symbols of the different stimulus pairs. Accordingly, it would have been impossible for the cichlids to use any other feature but symmetry for successful stimulus distinction.

Categorizations

While object categorization has already been experimentally investigated in a wide variety of taxa, only two studies have investigated this phenomenon in teleosts (Schluessel et al. 2012, 2014) and none had previously looked at it in elasmobranchs. Whereas most cichlids and sharks needed well over 10 and most often over 20 or even 30 sessions to distinguish between any of the stimulus pairs shown in the first five experiments, both were much quicker during the categorization phase. The two successful cichlids needed 19 and 4 sessions for the first categorization, and the sharks as a group needed 8.9, 6.3 and six sessions, respectively, for the three categorizations (three sessions being the minimum to fulfil the learning criterion). Individuals grasped the symmetry concept very quickly once novel stimuli were shown on each trial. While performance in the sharks was consistent and levels above 70 % (in the regular trials) were maintained in each session throughout the transfer test phases, the two cichlids that managed to reach the learning criterion in the first categorization task did not maintain the required level of performance and were therefore excluded from further testing.

Sharks also performed well in the associated transfer tests. During these tests, sharks had to distinguish between bilaterally and rotationally symmetrical stimuli. Stimuli were new and each pair was only presented once. There was no reinforcement, and consequentially, there was no opportunity for learning. Results showed that sharks had somehow abstracted the general principle of the task and were able to apply the previously gained knowledge to these new situations. Individuals easily distinguished between the two types of stimuli, despite their complexity.

Transfer tests also served as controls, to ascertain that no unintentional cues were provided during the feeding process. Sharks' performance was also impressive in the third categorization, where symbols of pairs were mixed. Obviously, sharks were not looking at or comparing 'mental snapshots' anymore or utilized any other visual information apart from the symmetry content. The complexity of the symbols, specifically when presented in these random combinations, had in fact no impact on trial time or performance at all.

Similar to the sharks, cichlids in another study (Schluessel et al. 2012) also performed much better in categorization experiments than in any single stimulus pair discrimination. The reasons for this increase in performance are likely to be multifold. Individual sharks would have already had 'practice' by the time they performed in the categorizations and would have been familiar with the procedure. Most likely though, the sheer number of stimuli would have encouraged animals to search for common features forcing them to focus their attention onto the aspect of symmetry. In the single pair discriminations, the assembly of edges, curvatures and lines or the overall arrangement of the image could have aided individuals in distinguishing between positive and negative stimuli, apart from using the symmetry aspect. In the categorization experiments, however, this strategy would have not been feasible and in case such recognition mechanisms were previously applied, the shark would have now had to reorient. This may have been what prevented learning in the cichlids.

Being able to categorize even abstract concepts, such as symmetry, should provide an animal with essential information, a certain degree of flexibility and possibly an evolutionary advantage. As predators or prey may vary in a range of features including size, shape and colouring, it seems more than valuable to be able to tell objects or individuals apart by using general features these species may have in common or provide additional information. Categorization abilities would aid a faster and more efficient identification and thereby facilitate an appropriate response. In this study, abstract categories were chosen that may not have been immediately biologically relevant to *Pseudotropheus* or *Chiloscyllium*. In the former, symmetry detection may have indeed proceeded faster under more biologically relevant conditions. This, however, was not the aim of this study and had already been successfully assessed in other fish species.

Symmetry detection threshold

The last experiment tried to determine the degree of symbol dissimilarity that could still be detected. A symmetrical and an asymmetrical cross were presented. Sharks learned on average within 6.5 sessions to successfully distinguish between the two symbols. Subsequently, they entered into a series of transfer tests in which the asymmetrical stimulus was modified as to resemble the positive and rewarded symmetrical cross more closely. When the 'bend arm' was moved from a 45° angle to a 70° angle, sharks still chose the symmetrical stimulus significantly often. Once the arm was lowered to an 80° separation though (90° being equal to the symmetrical cross), sharks could not adequately distinguish between them anymore. This indicated that subtle deviations from perfection may not always be recognized and fluctuating asymmetries found in nature may only be detected or regarded as relevant if they exceed a certain degree. Again, if more biologically relevant stimuli had been used, the separation threshold could have been different. Considering the complexity of the symbols presented in the various categorization experiments, it is quite amazing to what extent sharks were able to differentiate between symmetrical and asymmetrical stimuli. One should mention that there is a small possibility that sharks discriminated the symbols in this experiment based on their different widths. The regular cross (90°) was slightly wider than the 45°, 70° or 80° cross version. In case of the 80° cross, which was the only one not reliably distinguished from the regular cross anymore, both the width as well as the symmetry aspect would have been very (most) similar to the original. Nonetheless, considering that sharks had just been trained for 10 months to pay close attention to symmetrical features and considering their quick and homogenous performance, it seems highly unlikely that they would have chosen the regular cross based on its broader width (instead of using symmetry), specifically without accompanying decreases in performance (number of sessions) or increases in trial time.

The fact that sharks possess a symmetry concept provides further evidence for the parallels and similarities between the mammalian (including human) and the fish visual systems and visual information processing. For example, just recently a review on illusionary contours in teleosts was published by Agrillo et al. (2013) and a study by Fuss et al. (2014b) tested perception of optical illusions in sharks. Both teleosts and elasmobranchs in fact fall for the same illusionary contours, e.g. Kanizsa figures, as mammals and other vertebrates. Interestingly though, sharks as well as goldfish (Wyzisk 2005) are not necessarily deceived by all optical illusions, including the Müller-Lyer illusion to which humans also have very varying reactions (Berry 1968; Segall et al. 1966). Cichlids may also be able to perceive symmetry in a different context to the one tested here.

Conclusions

This study provides first evidence for the ability of cichlids and sharks to distinguish between bilaterally symmetrical and asymmetrical symbols. Results suggest that *C. griseum* can distinguish between and categorize symmetrical stimuli and thereby form abstract concepts of symmetry (without a specific biological context). On the contrary, the inconsistent performance of *Pseudotropheus* suggests that symmetry perception (at least in the here presented experimental context) may not be of primary importance to this species and successful single pair discriminations could have been based on featural differences other than symmetry. Sharks furthermore distinguished between bilaterally and rotationally symmetrical stimuli. The recognition of symmetrical features may be important to both species for a range of contexts, none of which have been investigated so far. Results of the current study indicate, though, that sharks may have a greater need for symmetry perception than cichlids, as both individual and group performances of sharks were significantly better and more consistent than in the cichlids.

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