World in Motion:
Perception and Discrimination of Movement in Juvenile Grey Bamboo Sharks (*Chiloscyllium griseum*)

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Abstract - The aim of the present study was to test juvenile grey bamboo sharks (*Chiloscyllium griseum*) for their ability to perceive and discriminate simple and complex motion patterns. Experiments were carried out as two-alternative forced choice experiments; choosing the designated positive stimulus was rewarded with food. Individuals were first trained to differentiate between two videos of circles moving at different velocities surrounded by squared reference frames. All tasks were successfully mastered within 3–30 training sessions. Transfer tests revealed whether the training stimulus was still successfully detected if velocity or direction of movement were changed. In a second task, individuals were presented with more complex motion patterns in form of videos of different organisms such as eel vs. trout, eagle vs. bat and dolphin vs. shark. A series of transfer tests elucidated whether sharks could still recognize these stimuli when shown (a) without a reference frame, (b) from a different perspective (front or sideways), (c) enlarged or downsized or (d) as point displays (PDs). Results were rather surprising, as sharks discriminated easily between circles moving in different directions as well as between differently moving organisms but failed in two out of three experiments to apply the acquired information to new situations as provided by transfer tests. Nonetheless, PD videos of 'eel' and 'trout' were recognized by all sharks (N = 7), suggesting that the ability to spontaneously recognize an organism based on its biological motion alone is present in elasmobranchs.

Keywords – Cognition, Learning, Biological motion, Point light display, Elasmobranchs, Vision

For a wide range of behaviors most fish rely largely on vision (e.g., Brown, Laland & Krause, 2011; Fritsches, Marshall, & Warrant, 2003; Guthrie, 1986; Siebeck, Parker, Sprenger, Mäthger, & Wallis, 2010), many of which also involve movement. However, most previous studies dealing with visual cognitive abilities in fish investigated only stationary stimuli (e.g., Arthur & Levin, 2001; Colwill, Raymond, Ferreira, & Escudero, 2005; Darmaillacq, Dickel, Rahmani, & Shashar, 2011; Frech, Vogtsberger, & Neumeyer, 2012; Gierszewski, Bleckmann, & Schluessel, 2013; Schluessel, Fricke, & Bleckmann, 2012; Siebeck, Litherland, & Wallis, 2009; Sovrano & Bisazza, 2008), while few included the presentation of moving objects (e.g., Baldauf, Kullmann, Thünken, Winter, & Bakker, 2009; Gori, Agrillo, Dadda, & Bisazza, 2014; Nakayasu & Watanabe, 2014; Schluessel, Kortekamp, Cortes, Klein, & Bleckmann, 2015; Shashar, Rosenthal, Caras, Manor, & Katzir, 2005). In a recent study by Schluessel et al. (2015), *Dascyllus aruanus* and *Pseudotropheus zebra* distinguished successfully between two circles moving at different velocities and amplitudes, moving dot patterns as well as moving objects. Zebrafish (*Danio rerio*) and guppies (*Poecilia reticulata*) were tested for their ability to perceive true and

illusionary movements (Gori et al., 2014). Individuals showed significant innate preferences for moving geometric stimuli compared to stationary ones (Gori et al., 2014). Zebrafish larvae were found to perceive Fourier and non-Fourier motion and oriented themselves in the direction of movement, with object brightness influencing their decision (Orger, Smear, Anstis, & Baier, 2000). Baldauf et al. (2009) used full-video displays and photos of mating partners and showed significant preferences for movement in Nigerian red krib (*Pelvicachromis taeniatus*).

In case of elasmobranchs, several studies have already shown the significance of the visual system for a range of behaviors, including orientation and predation (e.g., Fuss, Bleckmann, & Schluessel, 2014a; Seamone, Blaine, & Higham, 2014; Strong, 1996). Sharks can visually distinguish between a variety of two-dimensional stimuli, ranging from geometric symbols to images of organisms (for a review see Schluessel, 2015). As in most teleost studies, all experimental stimuli were stationary, neglecting aspects such as movement and/ or changes in perspective of moving organisms. However, considering ecology and lifestyle of bamboo sharks, the ability to detect and recognize movement and to correctly identify an organism from a new perspective seems crucial for survival as predators, prey, or con-specifics not only vary in size, shape and coloring, but move around, sometimes rapidly, often changing their position in space or approach angle.

Visual sensory information is perceived and processed differently across human and non-human species. To some extent, this is due to evolutionary differences in the vertebrate eye itself such as spatial or temporal sampling or resolving power (e.g., mammals: Coimbra, Hart, Collin, & Manger, 2013; Hughes, 1977; Mengual, García, Segovia, & Pertusa, 2015; birds: Coimbra, Nolan, Collin, & Hart, 2012; Fite & Rosenfield-Wessels, 1975; Hodos & Leibowitz, 1977; elasmobranchs: Hueter, 1990; Lisney & Collin, 2007, 2008; Ryan, Hart, Collin, & Hemmi, 2016; Ryan, Hemmi, Collin, & Hart, 2017; Theiss, Collin, & Hart, 2010), cone monochromacy or multichromacy (for review see Osorio & Vorobyev, 2008; see also Bedore et al., 2013; Hart, Lisney, Marshall, & Collin, 2004; Hart, Theiss, Harahush, & Collin, 2011; Van-Eyk, Siebeck, Champ, Marshall, & Hart, 2011), photoreceptor topography (Collin, 1999, 2008), the composition of the dioptric system (Collin & Collin, 2001; Hueter et al., 2001; Sivak, 1990) or other adaptive ocular specializations. Moreover, there are differences in the neural processing of visual information in the brain. For instance, the pallial cortex of mammals devotes large areas to visual processing (reviewed by Grill-Spector & Malach, 2004; Logothetis & Sheinberg, 1996), whereas fish lack a cortex. Even though fish possess a dorsal pallium, which may take care of some of the information that is processed by cortical areas in mammals (Rodriguez, Broglio, Durán, Gómez, & Salas, 2006), fish are thought to deal with the majority of visual information in the optic tectum of the midbrain (e.g., Ebbesson, 1970; Smeets, 1983; Wullimann & Meyer, 1990).

Following extensive testing of biological motion perception in adult humans, Johansson (1973) defined "biological movement" as a type of visually induced stimulus allowing for the perception, detection and distinction of characteristic movements even when these were abstracted and presented without any figural information. In his pioneering study, the movement of a human body was reduced to a few light spots, marking the position of essential joints on dark clothing – known as Point Light Displays (PLD). Only the perception of movement remained observable, while external factors such as physical properties (e.g., size or weight) or outer appearance (e.g., gender, clothing or haircut) were eliminated. Subsequent studies were performed on adults and children (Kuhlmeier, Troje, & Lee, 2010; Pavlova, Krähgeloh-Mann, Birbaumer, & Sokolov, 2002), and people of different cultures (Pica, Jackson, Blake, & Troje, 2011). Based on PLDs, humans can recognize and distinguish friends and family (Cutting & Kozlowski, 1977), gender (Beardsworth & Buckner, 1981; Cutting & Kozlowski, 1977; Kozlowski & Cutting, 1977), emotions such as fear, anger, grief, joy, disgust or surprise (Dittrich, 1993; Dittrich, Troscianko, Lea, & Morgan, 1996), interactions in couples (Dittrich, 1993) as well as other aspects (reviewed in Nakayama, 1985; Troje, 2008).

Besides humans, various non-human species including mammals (primates: Brown, Kaplan, Rogers, & Vallortigara, 2010; Parron, Deruelle, & Fagot, 2007; Siegel & Andersen, 1988; Tomonaga, 2001; Vangeneugden, Vancleef, Jaeggli, VanGool, & Vogels, 2010; rats: Foley et al., 2012; MacKinnon, Troje, & Dringenberg, 2010; cats: Blake, 1993; dolphins: Herman, Morrel-Samuels, & Pack, 1990) and

birds (e.g., Dittrich & Lea, 1993; Dittrich, Lea, Barrett, & Gurr, 1998; Ortega, Stoppa, Güntürkün, & Troje, 2009; Regolin, Tommasi, & Vallortigara, 2000; Troje & Aust, 2013; Vallortigara, Regolin, & Marconato, 2005; Vallortigara & Regolin, 2006; Zylinski & Osorio, 2013) have also been tested for their ability to recognize and distinguish biological motion patterns. Most species distinguished successfully between simple and complex biological and non-biological motion patterns; however, few were able to transfer or generalize their previously gained knowledge (e.g., MacKinnon et al., 2010; Vangeneugden et al., 2010). A study on medaka fish (*Oryzias latipes*; Nakayasu & Watanabe, 2014) looked at the perception of biological motion stimuli and tested if movements such as those created by conspecifics also induced shoaling behavior when expressed as a PLD. The study concluded that shoaling was successfully induced by presenting the familiar movement cues of conspecifics but was less pronounced or inhibited if movements deviated from these. It gave the first indication that fish perceive and process biological motion. Cichlids were unable to identify a familiar training stimulus based on its PD alone, despite individuals successfully discriminating between two PDs and PLDs after a short period of training (Schluessel et al., 2015). This showed that biological motions presented in the form of PLDs could be distinguished but the transfer of learned information to a new situation failed. New research shows though, that cichlids can in fact perform this transfer test, indicating that while not all individuals may be able to do so, a general ability to recognize familiar organisms when shown in form of a PD exists (V. Schluessel, unpublished). Neri (2012) found spontaneous preferences for moving images of conspecifics over photos in zebrafish (*Danio rerio*). However, despite visual characteristics of shape and movement appearing to be clearly associated, single or isolated characteristics were insufficient to recognize conspecifics.

In the present study, juvenile bamboo sharks were tested for their ability to distinguish between various types of movement and moving objects. Sharks were presented with videos displaying a stationary circle against a moving circle as well as videos of two circles moving at different velocities and in different directions. Following successful training, sharks learned to distinguish between more complex motion patterns, i.e., videos of dot patterns and moving organisms. Lastly, sharks were tested for their ability to generalize and transfer the learned information by showing them altered training stimuli (enlarged or size-reduced), point displays (PDs) and/or new perspectives of known organisms (e.g., eel, trout, eagle, bat, dolphin or shark).

General Methods

Participants

Twelve experimentally experienced juvenile bamboo sharks (TL: 25 – 35 cm), captive bred at the Vienna Aquarium, were kept in aquaria filled with aerated, filtered salt water [conductance: about 50 mS (ca. 1.0217 kg/dm3)] at 24 – 25°C, providing constant environmental conditions (conductivity, temperature, and pH). There was a 10 hr light:14 hr dark cycle; experiments were conducted during the day. Food (small pieces of squid, fish, or shrimps) was provided only during the experimental sessions. Individuals were identified based on unique phenotypic characteristics.

Apparatus and Materials

Experiments were conducted in a rectangular glass aquarium (1.00 x 0.5 x 0.5 m), containing a grey PVC partition featuring a small, hand operated guillotine door in the middle of the tank, separating a back compartment (starting compartment, SC) from a front compartment (decision area, DC; Figure 1). To prevent unintentional cueing or potentially disturbing external influences, the lateral walls, the floor as well as the rear side were covered with blue opaque adhesive film. Two grey PVC partitions were provided inside the SC for guidance. In the front, a milky colored plastic screen allowed stimuli presentation via a LED projector. Attached to the front screen, a divider separated a left from a right area, thereby allowing for unambiguous decision-making in response to the presented stimuli. All stimuli were

projected at a height of 3 cm above the ground, as sharks were usually swimming close to the bottom. Feeders were installed just above each stimulus, which allowed food to be released into the setup manually at the experimenter's discretion. To make a choice, sharks had to cross a virtual decision line about 10 cm in front of the stimuli. To exclude unintentional cueing, both feeders were baited during all trials. Moreover, the water in the maze was stirred after every trial to preclude any olfactory cues after a reward was given. Videos and PDs were generated using the 3D animation software "Autodesk Maya 2015".
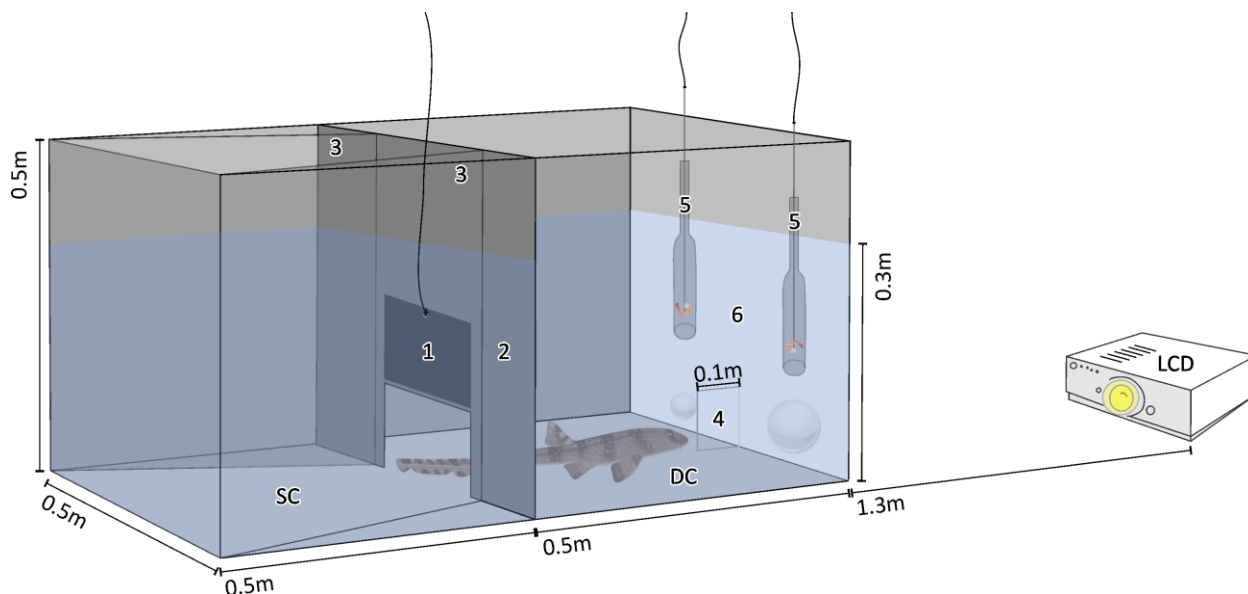

Figure 1. The experimental setup: The rectangular setup consisted of a starting compartment (SC), a decision area (DC) and a frosted screen for projections, featuring a divider allowing for unambiguous choice-making (left and right). For projections, a LCD projector was used. 1: guillotine door with cable pull, 2: PVC partition featuring guillotine door, 3: PVC side fences for guidance, 4: divider to separate a left from a right division, 5: feeders, 6: frosted screen for projection (modified from Fuss and Schluessel, in press).

General Design and Procedure

Training followed a schedule outlined previously (Fuss, Bleckmann, & Schluessel, 2014b). As all individuals had already participated in previous experiments on visual discrimination, they were used to the setup, the training procedure (two-alternative forced choice experiments) and feeding. Each experiment consisted of training and a subsequent transfer test phase. Training consisted of ten 'regular' trials per session (Figure 2A-C). Before each training, the sharks were manually caught and transferred from their home tank into the experimental setup.

During regular trials, the two stimuli to be discriminated were displayed simultaneously (one in each division) and switched randomly between the left and the right side of the screen (Figure 1, 2A-C). Both objects within a stimulus pair were uniformly black colored and had a size of about 5 x 5 cm. Choosing the designated positive stimulus (from now on symbolized by *) was rewarded with food; choosing the alternative stimulus resulted in the disappearance of both stimuli and a black screen. After each trial, sharks were gently guided back into the starting compartment (Figure 1). Training was completed as soon as the learning criterion of ≥ 70% correct choices in three consecutive training sessions was reached. If a shark did not reach the criterion within 30 training sessions, the next experiment commenced.
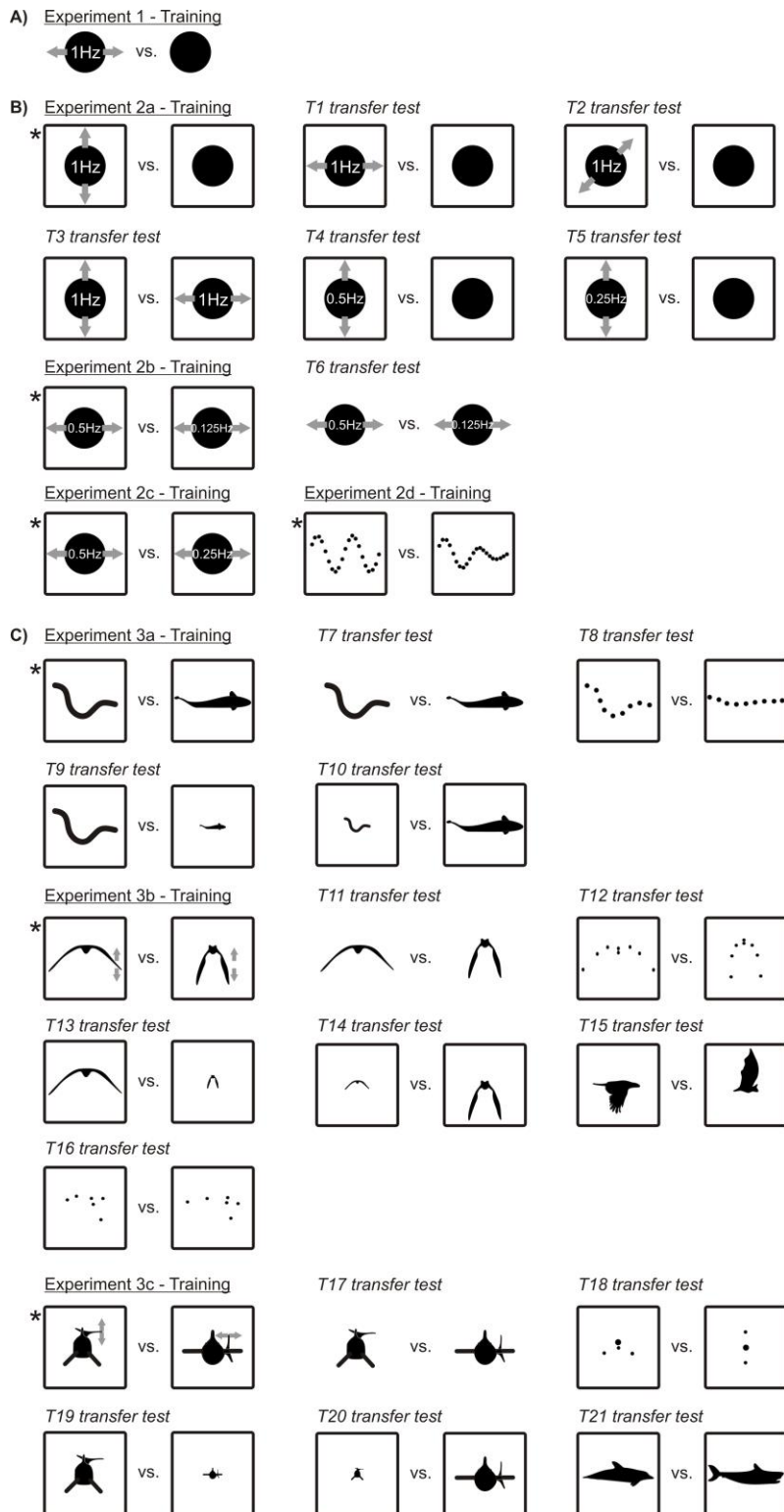
Figure 2. Stimuli presented during regular training trials and during the transfer test trials in Experiment 1, Experiments 2A – 3, and Experiments 3 A – C. Positive, rewarded training stimuli are indicated by an asterisk.

In transfer trials (Experiments 2A, 2B and 3A – C), sharks had to perform under altered conditions. There were no transfer tests for experiments 1 and 2C – D. Up to two transfer trials (in random combinations) were interspersed randomly with the ten regular trials within one session (resulting in 12 trials per session). These two trials were separated by at least two regular trials from each other. Each type of transfer test was presented a total of 20 times to every individual. Transfer trials remained unrewarded to prevent any kind of learning with respect to the new situation. Prior to the first transfer test, but following completion of training, a 'reduced-rewarding scheme' in the regular trials was introduced, i.e., only a maximum of eight regular trials (out of ten) was rewarded (random and pre-experimental selection) irrespective of choice. This served to prepare sharks for the upcoming implementation of unrewarded transfer trials (so as to keep the animals from realizing that only transfer trials were unrewarded and therefore not worth participating in). This 80% rewarding scheme was maintained throughout the remainder of the phase. Transfer tests were analyzed separately from regular trials. It is important to note that despite successfully mastering a task some individuals still developed significant side preferences. Reaching the learning criterion and developing a significant side preference were therefore not mutually exclusive.

Data analysis

The percentage of correct choices, the percentage of right and left choices, and the average trial time were recorded for each session for each individual. The learning criterion was established to be $\geq$ 70% correct choices in three consecutive training sessions (χ^2 (1) $p \leq 0.05$). With respect to the training paradigm used, Chi square tests were calculated (by using the absolute numbers of decisions) for each individual to determine whether individuals significantly preferred the designated positive stimulus during transfer test trials. For all tests, $p \leq 0.05$ was considered significant, and p is reported throughout for these Chi square tests.

Experiment 1 (Moving circle* vs. Stationary Circle, without a Reference Frame)

Methods

Five individuals were trained to differentiate the video of a stationary circle from the video of a horizontally moving circle; the latter was defined as the positive, rewarded stimulus. There was no reference frame surrounding the stimuli in the video presentations. There were no transfer tests.

Results

Only one individual (Shark 10) reached the learning criterion within the allocated 30 training sessions (Figure 3). Although Shark 4 did not reach criterion, it chose the positive, rewarded stimulus significantly more often than the alternative one ($p = 0.043$, Table 1). Sharks needed on average between 9.56 ± 6.59 s and 15.64 ± 15.60 s to make a decision. At the end of experiment 1, Sharks 10, 11, 12 and 13 stopped cooperating and were excluded from further experiments.
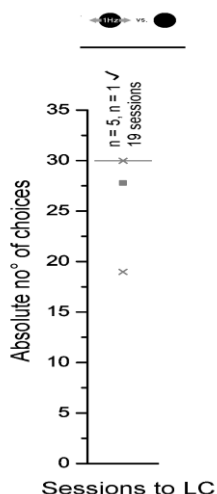
Figure 3. Group results of Experiment 1 – moving circle vs. stationary circle. The training stimuli are shown on top. The number of sessions needed to reach the learning criterion (LC; marked in grey) is shown as a boxplot. Additionally, the number of participating individuals and the number of successful individuals (indicated by a checkmark) are given.

Table 1

Results for sharks that did not meet or maintain the pre-established learning criterion.

| Subject | Experiment | Training sessions | Chi² test with Yates' correction on successful trials | | | The 95% exact confidence interval extends from… |
			[%] of correct choices	*P* value	χ^2 (1)	
Shark 4	1	(30)	56.0 ± 16.10	0.043*	4.083	0.502 to 0.617
Shark 11	1	(30)	49.6 ± 11.80	0.525	0.403	0.422 to 0.538
Shark 12	1	(30)	51.3 ± 14.00	0.686	0.163	0.455 to 0.571
Shark 13	1	(30)	46.0 ± 12.76	0.174	1.763	0.403 to 0.518
Shark 2	2A	21 #	64.0 ± 14.77	≤ 0.001***	22.963	0.583 to 0.694
Shark 1	3C	7 #	57.0 ± 10.55	0.018*	5.603	0.512 to 0.627
Shark 2	3C	4 #	61.0 ± 9.95	≤ 0.001***	14.083	0.552 to 0.665
Shark 3	3C	(30)	58.0 ± 8.87	0.007**	7.363	0.522 to 0.636
Shark 4	3C	(30)	55.67 ± 11.04	0.057	3.63	0.498 to 0.614
Shark 5	3C	(30)	57.67 ± 8.17	0.002**	10.417	0.519 to 0.633

Note. $p \leq 0.05$*, $p \leq 0.01$**, $p \leq 0.001$***; (30) = Shark did not reach the learning criterion within the allocated 30 training sessions; # Shark reached the learning criterion within the allocated 30 training sessions, but performance dropped to chance level during the following sessions. Sharks 1 and 2 did not participate in the transfer test phases.

Experiment 2 (Moving circle* vs. Stationary Circle, with a Reference Frame)

Experiment 2A

Methods. Experiment 2A was a repetition of experiment 1, but included reference frames (Figure 2B). The frequency of the moving circle was 1 Hz; it was presented with a stationary stimulus. Five different types of transfer test were conducted (T1 – T5). In T1 – T2 and T4 – T5, the movement of the moving circle was altered in regards to velocity or direction. In T3, the stationary stimulus was exchanged for a horizontally moving circle.

Results. All sharks (N = 5) reached the learning criterion within the allocated 30 sessions (Figure 4). Although, Shark 2 reached the learning criterion, performance dropped to chance level during the following sessions. Thus, Shark 2 did not participate in the transfer tests. Nevertheless, it chose the

positive, rewarded stimulus significantly more often than the alternative one ($p \leq 0.001$, Table 1). Sharks needed between 2.82 ± 1.28 s and 8.17 ± 3.01 s to make a decision.

T1 (horizontal movement, frequency 1 Hz vs. stationary circle). All individuals (N = 4) significantly preferred the horizontally moving stimulus (now moving in a different direction) over the stationary alternative ($p = 0.044$ to ≤ 0.001, Figure 4).

T2 (diagonal movement, frequency 1 Hz vs. stationary circle). All sharks (N = 4) significantly preferred the diagonally moving circle (now moving in a different direction) over the stationary alternative ($p = 0.014$ to ≤ 0.001, Figure 4).

T3 (vertically moving circle (frequency: 1 Hz) vs. horizontally moving circle (frequency: 1 Hz). All individuals significantly preferred the vertically moving circle (as learned during training) over a horizontally moving alternative ($p = 0.044$ to ≤ 0.001, Figure 4).

T4 (vertically moving circle (frequency: 0.5 Hz) vs. stationary circle). All individuals (N = 4) significantly preferred the slowly moving circle over the stationary alternative ($p = 0.014$ to ≤ 0.001, Figure 4).

T5 (vertically moving circle (frequency: 0.25 Hz) vs. stationary circle). Three individuals chose according to chance level between both stimuli ($p = 0.264$ to 0.823); only Shark 3 chose the very slowly moving circle significantly more often than the stationary alternative ($p = 0.004$, Figure 4).
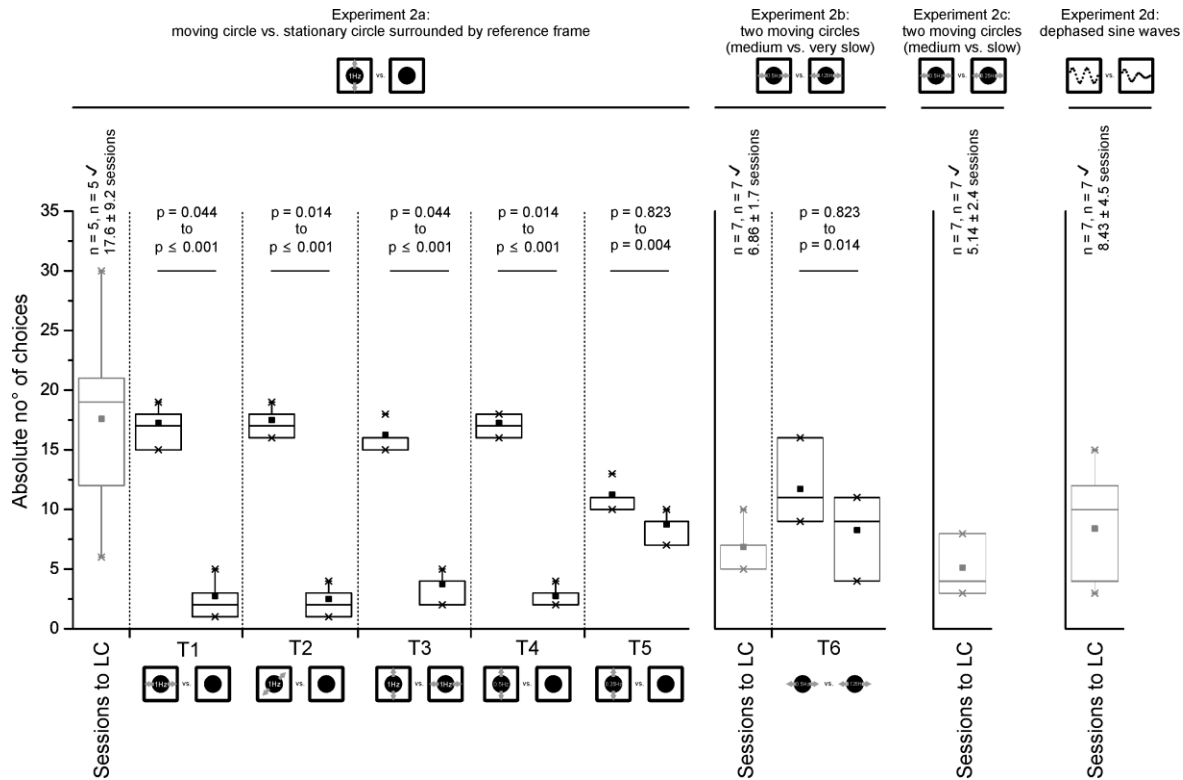

Figure 4. Group results of experiment 2A -– D. Training stimuli are shown on top. The average number of sessions needed to reach the learning criterion (LC; marked in grey) is shown as a boxplot. The number of participating individuals and the number of successful individuals (indicated by a checkmark) are provided for each experiment. The results of the T1 to T6 trials (marked in black) are also shown as boxplots. Additionally, the range of *p*-values for all participating individuals is provided.

Experiment 2b

Methods. During training, a horizontally moving circle* with a medium frequency (0.5 Hz) was presented against a horizontally moving circle* with a very slow frequency (0.125 Hz) (Figure 2B). During the only type of transfer test (T6) the same stimuli were presented but without a reference frame.

Results. Seven sharks reached the learning criterion within five to ten training sessions (Figure 4). Sharks needed between 3.09 ± 0.38 s and 6.00 ± 2.33 s to make a decision. Only Sharks 6 and 7 significantly preferred the faster moving circle over the slower one in the T6 trials, the others chose according to chance level ($p = 0.502$ to 0.823, Figure 4).

Experiment 2C

Methods. During training, a horizontally moving circle* with a medium frequency (0.5 Hz) was presented against a horizontally moving circle* with a slow frequency (0.25 Hz) (Figure 2B).

Results. Seven sharks reached the learning criterion within three to eight training sessions (Figure 4). Sharks needed between 2.43 ± 0.13 s and 5.32 ± 2.59 s to make a decision.

Experiment 2D

Methods. During training, videos of two dephased sine waves were shown (Figure 2B).

Results. Seven sharks reached the learning criterion within three to 15 training sessions (Figure 4). Sharks needed between 2.37 ± 0.47 s and 5.82 ± 2.56 s to make a decision.

Experiment 3 (Differentiation of Moving Organisms)

Methods (Experiments 3A – 3C)

Following these simple movement discriminations, sharks (N = 7) were presented with more complex motion patterns in form of different organisms: eel vs. trout, eagle vs. bat, dolphin vs. shark (Experiments 3a-c; Figure 2C). A series of 15 different transfer tests (T7 to T21; Figure 2C) examined whether sharks could still recognize these movement patterns (a) without a reference frame, (b) when enlarged or size reduced, (c) from a different perspective (front or sideways) or (d) in form of point displays (PDs).

During T7, T11 and T17, the respective training stimuli were presented without the reference frame.

In T8, T12 and T18 trials determined whether sharks recognized the movement patterns of the organisms shown during training when presented in form of PDs, thereby reducing the information content about the organism to the movement alone.

In T9, T13 and T19 transfer tests it was determined whether sharks recognized the trained positive stimulus when enlarged compared to the trained alternative stimulus (size ratio: 3:1).

In T10, T14 and T20 trials it was investigated whether sharks recognized the trained positive stimulus when scaled down compared to the trained alternative stimulus (size ratio: 1:3).

In the T15 and T21 transfer tests it was examined whether shark recognized the trained positive stimulus when being presented from a new, unfamiliar perspective (front or sideways).

In the T16 trials it was determined whether sharks recognized the familiar organisms presented during training when shown both from a new, unfamiliar perspective (sideways) and in form of a PD reducing the information content about the organism to the movement alone.

Results

  Experiment 3A (eel* vs. trout). Seven sharks reached the learning criterion within four to twelve training sessions (Figure 5). Sharks needed between 3.15 ± 0.31 s and 7.55 ± 5.19 s to make a decision.

  In the T7 trials, only Sharks 6 and 7 significantly preferred the eel, the others chose randomly between the two stimuli or developed side preferences (Figure 5).

  In the T8 trials, all individuals chose the eel shown as a PD significantly more often than the alternative ($p = 0.044 \leq 0.001$, Figure 5).

  In the T9 trials all individuals significantly preferred the enlarged eel over the trout ($p = 0.014$ to ≤ 0.001, Figure 5).

  In the T10 trials all but one shark (Shark 1) chose the size-reduced eel over the negative alternative ($p = 0.044$ to ≤ 0.001, Figure 5).
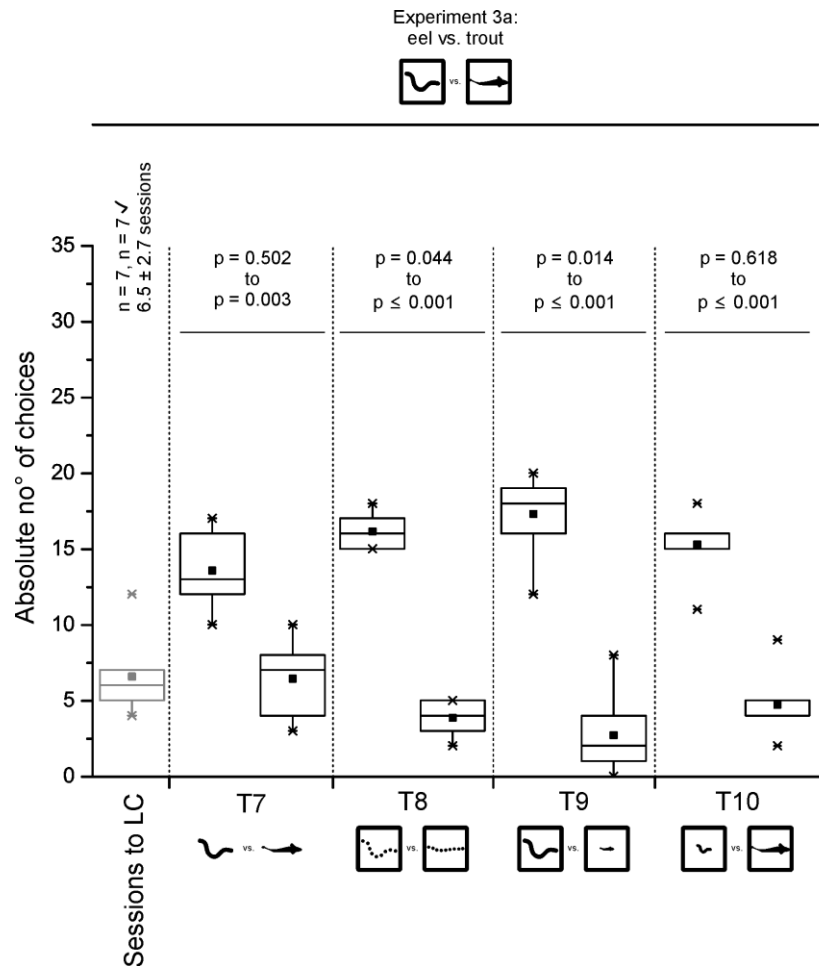

Figure 5. Group results for Experiment 3A – eel* vs. trout: training stimuli are shown on top. The average number of sessions needed to reach the learning criterion (LC; marked in grey) is shown as boxplots. The number of participating individuals and the number of successful individuals (indicated by a checkmark) are provided. The results of T7 to T10 trials (marked in black) are also shown as boxplots. Additionally, the range of *p*-values of all participating individuals is provided.

  Experiment 3B (eagle* vs. bat). Six out of seven sharks reached the learning criterion within three to ten training sessions and participated in transfer tests (Figure 6). Unfortunately, Shark 6 died just before the beginning of experiment 3B. Sharks needed 2.13 ± 0.08 s to 4.31 ± 2.48 s to make a decision.

In the T11 trials (no reference frame), Shark 5 significantly preferred the eagle and Shark 4 preferred the eagle but not to a significant level. Four individuals chose according to chance or developed side preferences.

In the T12 trials, all individuals chose randomly between both stimuli shown in PD form or developed side preferences ($p = 0.824$ to 0.260).

In the T13 trials (Figure 6), four individuals significantly preferred the enlarged eagle over the bat ($p = 0.044$ to ≤ 0.001). Two individuals chose according to chance.

In the T14 trials, Sharks 2 and 4 significantly preferred the scaled down eagle over the alternative stimulus ($p = 0.044$ to ≤ 0.001). Sharks 1 and 7 preferred the eagle but not to a significant level. Sharks 3 and 5 chose according to chance.

In the T15 trials, no individual (N = 6) chose the eagle when presented from a new perspective (sideways) significantly often. Sharks 4 and 5 showed a non-significant preference for the eagle.

In the T16 trials (new perspective and PD presentation), five out of six sharks chose according to chance or developed side preferences ($p = 0.502$ to 0.120). Sharks 2 and 5 showed a non-significant preference for the eagle. Shark 3 significantly preferred the alternative stimulus (bat; $p = 0.044$).
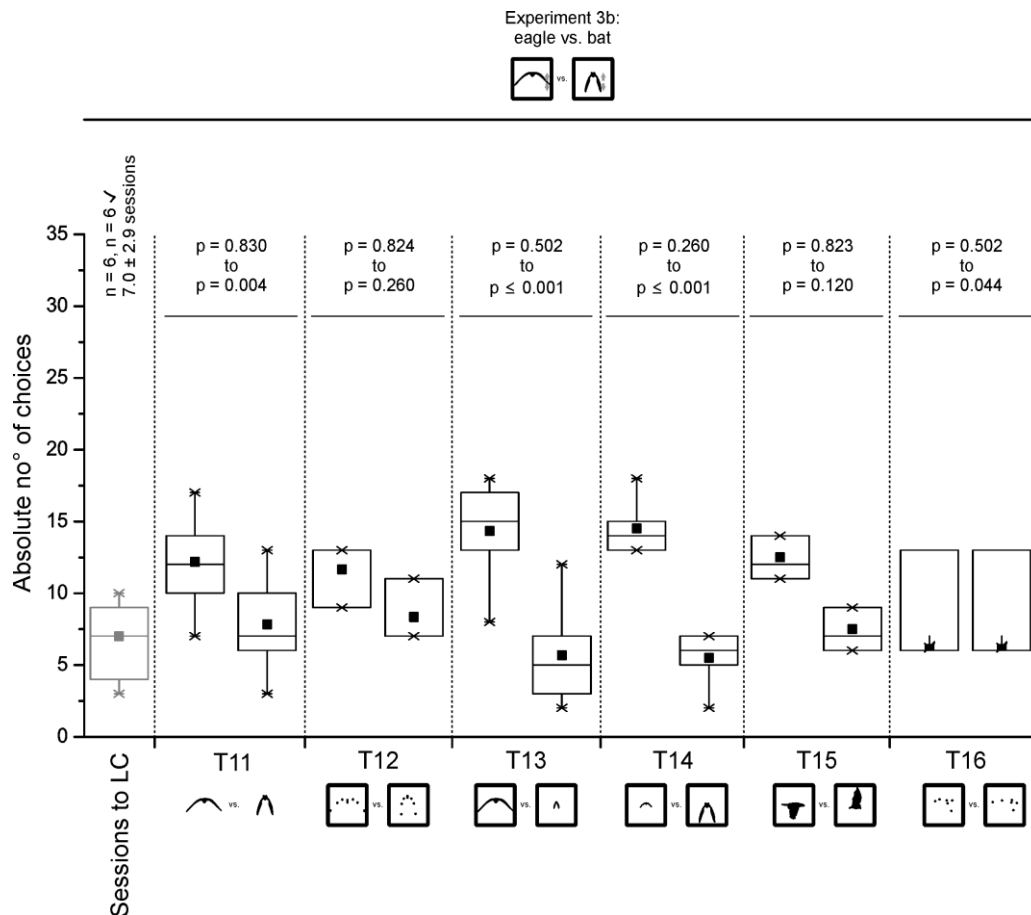

Figure 6. Group results of experiment 3B – eagle vs. bat: training stimuli are shown on top. The average number of training sessions needed to reach the learning criterion (LC; marked in grey) is shown as boxplots. The number of participating individuals and the number of successful individuals (indicated by a checkmark) are provided. The results of T11 to T16 trials (marked in black) are also shown as boxplots. Additionally, the range of *p*-values of all participating individuals is provided.

Experiment 3C (dolphin* vs. shark). Three out of six sharks reached the learning criterion within four to seven training sessions, but only Shark 7 was able to maintain a high performance of $\leq 70\%$ correct choices in subsequent sessions (Figure 7). Sharks 1 and 2 reached the learning criterion within 30

training sessions, but as performance dropped to chance level during the following sessions, they did not participate in any transfer trials. Sharks 1, 2, 3 and 5 chose the positive stimulus significantly more often than the alternative one ($p = 0.018$ to ≤ 0.001; Table 1). Sharks needed on average between 5.32 ± 4.39 s and 7.10 ± 2.26 s to make a decision.

In the T17 to T21 trials (Figure 7), the only participating shark (Shark 7) chose according to chance ($p = 0.823$ to 0.264), regardless of the presence or absence of a reference frame (T17), using PDs (T18), enlarged or scaled down stimuli (T19 and T20), or when stimuli were shown from a new perspective (T21).
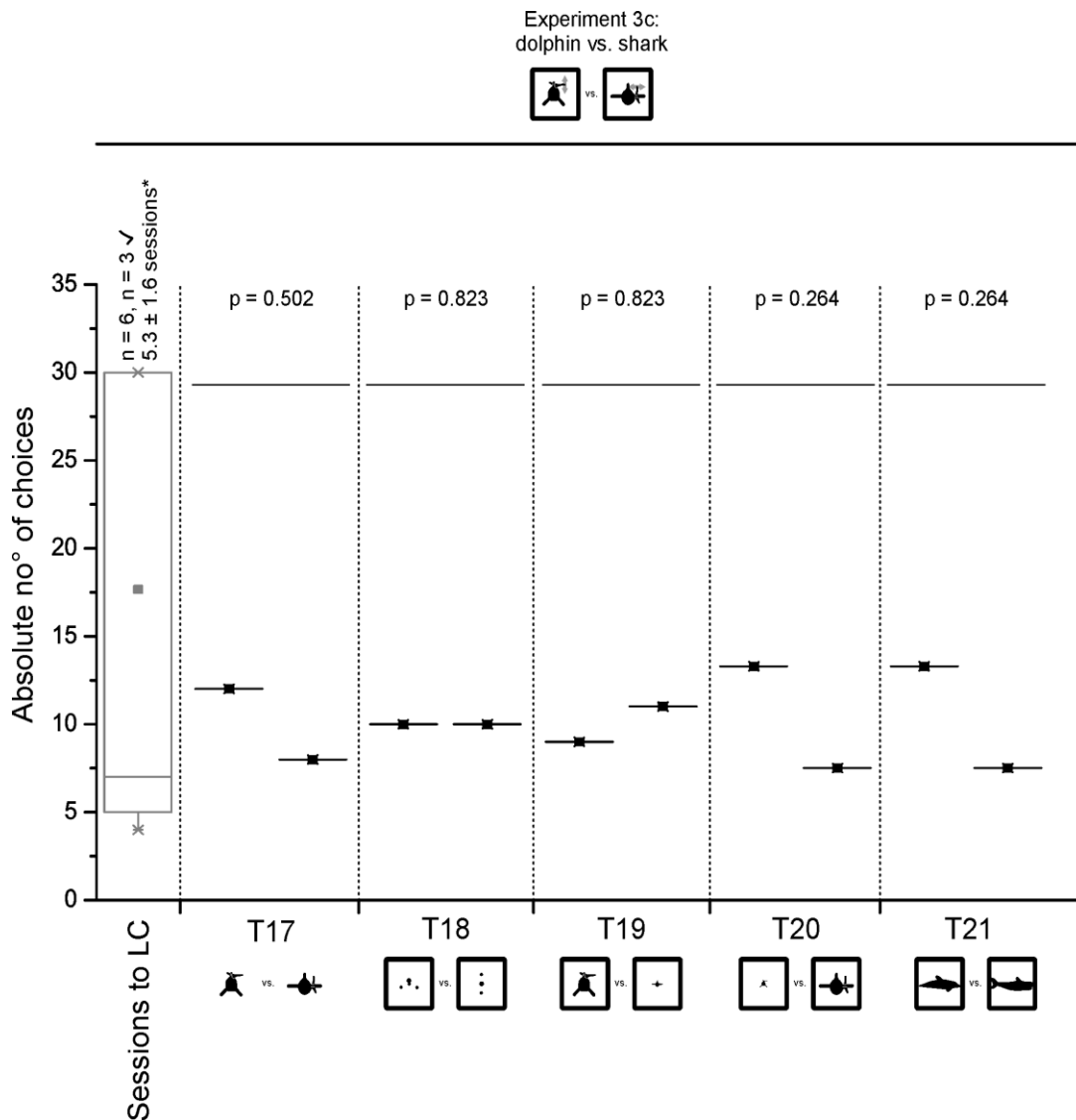

Figure 7. Group results for experiment 3C – dolphin vs. shark: training stimuli are shown on top. The average number of sessions needed to reach the learning criterion (LC; marked in grey) is shown as boxplots. The number of participating individuals and the number of successful individuals (indicated by a checkmark) are given. The results of T17 to T21 trials (marked in black) are also shown as boxplots. Additionally, the range of *p*-values of all participating individuals is provided. * Note, that 3 of 6 individuals reached the learning criterion but only one shark maintained performance above threshold and participated in transfer test trials.

Discussion

Juvenile bamboo sharks successfully discriminated videos displaying either simple (i.e., stationary and/or moving circles) or more complex (i.e., movement of different organisms) motion patterns. Surprisingly though, sharks initially failed the most basic experiment, i.e., to discriminate between a stationary circle from a horizontally moving circle (Table 1). A squared reference frame was introduced around each stimulus during the following experiments. This reference frame intended to place more emphasis on the 'movement' portion of the stimulus and indeed facilitated training and learning in subsequent experiments.

Simple Motion Patterns

Sharks were able to discriminate vertically, horizontally or diagonally moving circles at different velocities from stationary circles, from one another (horizontally vs. vertically) or from slower moving alternatives (Figures 3, 4). Sharks appeared to be confused (e.g., as seen from decreased swimming speeds, indecision and hesitancy or interrupted trials) when being presented with a slowly moving circle (horizontal movement, 0.25 Hz) against a stationary circle (T5, Figure 4). However, they discriminated a horizontally moving circle with a medium velocity (0.5 Hz) against a slow (0.25 Hz, Experiment 2C) or a very slow (0.125 Hz, experiment 2B) moving circle (Figure 4). These findings resemble results obtained for both cichlids and damselfish (Schluessel et al., 2015), whose discrimination performance decreased if velocity and amplitude were separately or simultaneously reduced. In contrast to the cichlids though, sharks succeeded in discriminating these stimuli only when presented in combination with a reference frame (T6, Figure 4). Whereas sharks discriminated two dephased sine waves on average within eight training sessions, cichlids needed seven and damselfish 24 sessions.

Compared to the average training trial times in the first experiment, sharks performed considerably faster in subsequent experiments and did not even slow down when presented with complex motion patterns of different organisms (experiments 3A – C). Simultaneously, performance in later experiments was much better than in experiment one. The reason for this seems to be the lack of reference frames in the first experiment, rather than experiment 1 being harder than subsequent ones. The fact that performance and trial time both increased when stimuli were surrounded by reference frames (experiments 2 to 3) clearly showed that this measure helped to draw the sharks' attention more precisely to the actual discriminating criterion (i.e., 'movement').

Psychophysical studies on humans show that associations between factors such as size, shape or orientation of lines and movements require focused attention on elements in the visual field (Julesz, 1984; Treisman & Gelade, 1980; Treisman, Sykes, & Gelade, 1977). It was observed that the time required for finding a unique item increases with the number of items in the display. The search time for a unique item appeared to be faster when all items differed by two or more attributes (e.g., color, shape or movement). Based on these observations, two sequential processes involved in mammalian visual perception were suggested, i.e., preattentive and attentive processes (Julesz, 1984; Treisman & Gelade, 1980; Treisman et al., 1977). A preattentive process is concerned with the simple detection of objects and rapidly scans an object's global texture or features. It mainly deals with properties of individual elements in a scene (e.g., color, orientation size or direction of movement) and emphasizes grouping of items that are required to distinguish between figural elements and for example background. At this stage of mammalian visual processing complex differences and relationships between properties are not detected ('bottom-up processing'; Treisman, 1986. This initial, preattentive grouping of single or very few features is followed by attentive processes that successively select, highlight and identify the individual elements of an object or a scene ('top-down processing'; Julesz, 1984; Treisman & Gelade, 1980; Treisman et al., 1977). Thus, in mammals, some perceptions are produced by preattentive scanning, whereas others require focal attention.

Although, these experiments were performed on mammals, it might be worthwhile to consider these findings for non-mammalian species as well. Previous studies on juvenile grey bamboo sharks using

different optical illusions revealed that sharks most likely applied complementing visual mechanisms such as perceptual grouping and local focal attention of a few features of a scene (Fuss, Bleckmann & Schluessel, 2014c; Fuss & Schluessel, in press). It is likely, that sharks (preattentively) identified the basic features of the presented stimuli ('black circles' and 'movement'), but – speculatively –failed to associate both elements, as distinction of the presented stimuli (or single features of these stimuli) was not strong enough when presented without a frame of reference. There are also important differences in the neural processing of information in the brain of mammals and non-mammalian species. For instance, the pallial cortex of mammals devotes large areas to the processing of visual information (for review see Grill-Spector & Malach, 2004; Logothetis & Sheinberg, 1996), whereas fish (lacking a cortex but possessing a dorsal pallium) are thought to perform the vast majority of visual processing in the optic tectum of the midbrain (e.g., Ebbesson, 1970; Smeets, 1983; Wulliman & Meyer, 1990). Furthermore, perceptual mechanisms that enable animals to perceive figures or shapes instead of lines, curves or circles are often thought to be subject to cognitive functions, which are closely related to areas of the dorsal pallium, i.e., the mammalian neocortex or their equivalent areas in the pallium of birds and possibly even fishes (e.g., Agrillo, Petrazzini, & Dadda, 2013; Berryhill & Olson, 2008; Hampton & Shettleworth, 1996; Kandel, Schwartz, Jessell, 2000; Mishkin 1978; Murray & Mishkin, 1984; Shapiro & Olton, 1994; Squire & Zola-Morgan, 1988). There is increasing evidence that at least some learning and memory mechanisms are homologous to those identified in mammals and birds (Broglio, Rodriguez, & Salas, 2003). These functional similarities in cognitive processes and their neural bases of fish and land vertebrates (mammals, birds, reptiles), are consistent with the idea of a common basic pattern of behavior and brain organization (Broglio et al., 2003; Salas, Broglio, & Rodríguez, 2003; Salas et al., 2006).

Complex Motion Patterns

All sharks learned to discriminate complex motion patterns of eel and trout ("swimming", lateral view, Experiment 3A, Figure 5) as well as eagle and bat ("flying", front view, Experiment 3B, Figure 6) when surrounded by a squared reference frame within three to twelve training sessions. While all individuals successfully transferred their previously gained knowledge to presentations of eels and trout shown in form of PDs or as resized versions of these stimuli, five of seven sharks failed to succeed to do the same in the transfer task where stimuli were shown without a reference frame. Cichlids distinguished easily between videos of eel and trout, but only one of five damselfish reached the learning criterion and both species were unsuccessful in recognizing the positive training stimulus when displayed in the form of a PD during transfer tests (Schluessel et al., 2015).

Considering the results in the eel-trout experiment, sharks performed surprisingly poorly in all transfer tests conducted in the subsequent eagle vs. bat experiment. Even though this may seem reasonable at first glance, as neither eagle nor bat are aquatic organisms, it is unlikely that this unfamiliarity caused the poor performance. Despite the fact that eagles and bats are terrestrial organisms and that sharks would have had no prior experience encountering either of them, the sharks should have still been able to differentiate between them based on individual movement as they did in the eel-trout task. Many other tasks that sharks were previously trained in (reviewed in Schluessel, 2015) used very artificial or unfamiliar stimuli, i.e., sharks had no prior knowledge of what these stimuli actually 'were', but did not deter sharks from successfully differentiating between them. It seems more likely, that during training, sharks learned to differentiate between eagle and bat based on selected figural cues instead of movement, which were then unavailable or insufficient for successful differentiation in the PD trials. In addition, only three of seven sharks learned to distinguish between the aquatic organisms dolphin vs. shark when presented in front view ("swimming", Experiment 3B, Figure 7) and only one individual maintained a high performance in the sessions after reaching the learning criterion. Unfortunately, it also failed to succeed in any transfer trials. At this point, it is also not clear what caused this. However, the four sharks that did not reach the learning criterion still chose the correct stimulus significantly often, indicating at least some kind of learning (Table 1).

Ryan et al. (2017) measured temporal resolution, contrast sensitivity and spatial resolving power electrophysiologically in five species of shark, including the closely related species *Chiloscyllium punctatum* (brown-banded bamboo shark). *Chiloscyllium punctatum*, a tropical species, was found to possess a higher temporal resolving power than the assessed temperate shark species, all five species possessed very high contrast sensitivity (higher than almost any other animal species tested so far) and *C. punctatum* had a comparatively low spatial resolving power compared to other sharks and fish species. Of the parameters tested, visual contrast information may provide the most relevant information to this species (Ryan et al. 2017). A major task of the brain is to construct successive frames of reference for visual perception and the control of movement: (1) a retinotopic frame of reference, (2) a head-centered frame of reference, and (3) a body-centered frame of reference (Kandel et al., 2000; Wurtz, 2008). These three frames of reference need to be (virtually) associated and updated immediately any time the head, body or the observed scene moves (Kandel et al., 2000; Wurtz, 2008). These virtual, 'visual' frames of reference were not only found in mammals, but also in teleosts (Baier, 2000; Bilotta & Saszik, 2001; Portugues & Engert, 2009). For example, Baier (2000) observed different optokinetic behaviors in (mutant) zebrafish (*Danio rerio*) that turned out to be capable of high-level motion processing, previously thought to be restricted to animals with a visual cortex.

Bamboo sharks move their whole body, including the head, while swimming. Thus, their "visual" frames of reference have to adapt permanently to reconcile a stable visual image. The smaller or less pronounced the differences in movement patterns between two encountered stimuli are, the closer the individual has to observe both stimuli and the more the shark's perception is affected by its own movements. This could possibly also help to explain, why bamboo sharks failed to succeed in experiments in which stimuli were presented without the squared reference frame. In this setting, movements were possibly not distinct enough to be perceived and discriminated appropriately, despite high visual acuity regarding stationary objects (Fuss et al., 2014b, c, Fuss & Schluessel, in press; Schluessel, Beil, Weber, & Bleckmann, 2014; Schluessel & Duengen, 2015). Bamboo sharks naturally live in visually well-structured environments such as coral reefs (Riede, 2004; Weigmann, 2016). Thus, bamboo sharks probably rarely experience "pure" or "isolated" motion without some kind of reference structure or system (as displayed in Experiment 1, Experiment 2B, T6 and Experiment 3, T7, T11, T17) resulting in a visual system that may be better adapted to detect relative movements of organisms (e.g., prey, predators or conspecifics) against a fixed background. To account for this the squared reference frame was introduced during training. Present results show that sharks are indeed able to discriminate simple and complex motion patterns under these conditions.

In conclusion, bamboo sharks perceived and discriminated a variety of motion patterns presented as either moving circles or moving organisms as long as they were comparatively set within a squared frame of reference each. In selected tasks, sharks were able to transfer previously gained knowledge to resized stimuli or stimuli shown in the form of a PD (eel vs. trout), but failed to accomplish this in others (e.g., eagle vs. bat). Sharks also did not easily recognize organisms shown from new perspectives or as 'isolated' movement patterns without a reference system.

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for the care and use of animals were followed. This article does not contain any studies with human participants performed by any of the authors.

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