ORIGINAL PAPER

No rainbow for grey bamboo sharks: evidence for the absence of colour vision in sharks from behavioural discrimination experiments

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Abstract Despite convincing data collected by microspectrophotometry and molecular biology, rendering sharks colourblind cone monochromats, the question of whether sharks can perceive colour had not been finally resolved in the absence of any behavioural experiments compensating for the confounding factor of brightness. The present study tested the ability of juvenile grey bamboo sharks to perceive colour in an experimental design based on a paradigm established by Karl von Frisch using colours in combination with grey distractor stimuli of equal brightness. Results showed that contrasts but no colours could be discriminated. Blue and yellow stimuli were not distinguished from a grey distractor stimulus of equal brightness but could be distinguished from distractor stimuli of varying brightness. In addition, different grey stimuli were distinguished significantly above chance level from one another. In conclusion, the behavioural results support the previously collected physiological data on bamboo sharks, which mutually show that the grey bamboo shark, like several marine mammals, is a cone monochromate and colourblind.

Keywords Elasmobranch · Behaviour · Ray · Cognition · Colour vision

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Introduction

For many years, it was only a matter of speculation whether sharks and rays actually had colour vision or not. Quite early on, it was already found that most sharks and rays are not all-rod vertebrates but possess duplex (rods and cones) retinas (Gruber et al. 1963, 1991; Gruber 1975; Gruber and Cohen 1978; Hueter 1991) and therefore have the potential for colour vision, while all assessed skates (*Raja* sp.) and the Port Jackson shark (*Heterodontus portusjacksoni*) seem to possess all-rod retinas and are therefore colour blind (Dowling and Ripps 1970; Ripps and Dowling 1990; Schieber et al. 2012). However, despite this anatomical prerequisite for colour vision in most sharks and rays, analyses regarding different cone types, i.e. their spectral sensitivities and experiments addressing behavioural abilities remained lacking until recently—and with these, the evidence for the presence or absence of actual colour vision.

The elasmobranch eye follows the common vertebrate *Bauplan* and is generally well developed, despite the absence of structures such as double or twin cones (Hart et al. 2006, 2011). Discrimination of objects according to brightness in sharks is about the same as in humans, and sharks can detect light from all parts of our visible spectrum (Gruber and Cohen 1978). Colour vision, however, the ability to discriminate objects based on their reflectance differences irrespective of brightness, requires at least two or more spectrally distinct photoreceptors, i.e. cone types.

More recently, the colour vision question was finally solved for several species of batoids which were shown both physiologically (Hart et al. 2004; Theiss et al. 2007; Bedore et al. 2013) and behaviourally (Van-Eyk et al. 2011) to be able to perceive and discriminate colour using multiple cone visual pigments. For example, *Glaucostegus typus* has three spectrally distinct cone pigments, with

wavelengths of maximum absorbance (λ_{max}) at 477, 502 and 561 nm (Hart et al. 2004) and can discriminate between hues of blue and greys of similar brightness (Van-Eyk et al. 2011). *Urobatis jamaicensis* possesses cones with absorption maxima at 475, 533 and 562 nm (Bedore et al. 2013), *Neotrygon (Dasyatis) kuhlii* at 476, 498 and 522 nm (Theiss et al. 2007) and *Rhinoptera bonasus* at 470 and 551 nm (Bedore et al. 2013). The species assessed by Bedore et al. also showed some UV sensitivity, despite the absence of UV-specific cones.

Despite the fact that the shark retina contains cones in different species-specific densities (Hueter 1991) as for example arranged in form of a visual streak (Hueter 1988), Hart et al. (2011) collected a very robust data set using single-receptor microspectrophotometry (MSP) which showed that all previously assessed species of shark are cone monochromats with no spectrally distinct cone pigments; each shark only possesses one single long-wavelength-sensitive cone type. The wavelengths of maximum absorbance (λ_{max}) in shark rods were found at 484–518 nm and in cones at 532–561 nm (Hart et al. 2011). Theiss et al. (2012) also collected molecular data for the Wobbegong sharks *Orectolobus maulatus* and *O. ornatus* by isolating visual opsin genes. Only two opsin genes were found, i.e. a rod and a cone type, thereby supporting the data for cone monochromacy in sharks by Hart et al. (2011). Anatomical and molecular studies were not followed up by behavioural experiments, possibly due to being considered redundant considering the previous results. Very early research by Clark (1959, 1963) on visual discrimination abilities of sharks, which were conducted prior to the recent anatomical and molecular findings, led to the successful training of adult lemon sharks to press coloured visual targets to obtain food. Few others followed (e.g. Tester and Kato 1966; Aronson et al. 1967; Gruber 1975) but none of these early experiments sufficiently controlled for discrimination based on brightness instead of colour. Apart from the assessment of colour, there have been quite a few behavioural experiments on elasmobranch visual discrimination abilities (reviewed in Schluessel 2014) while vision in elasmobranchs has been reviewed by Lisney et al. (2012).

In the here presented experiments, the ability of grey bamboo sharks (*Chiloscyllium griseum*) to discriminate between coloured and grey stimuli of equal brightness as well as between additional grey distractor stimuli of varying brightness was tested. Despite the convincing MSP data, it cannot be excluded that different cone types with varying absorption maxima are still present in the shark retina in very small or very patchy distributions. Behavioural experiments, controlling adequately for the confounding brightness factor, would provide the last piece of the puzzle, as to whether sharks can see colour (instead of just brightness differences) or not. For this purpose,

experiments similar to those by von Frisch (1914) on the honeybee were replicated on sharks.

Materials and methods

Animals

Five juvenile bamboo sharks (*C. griseum*, one male, four female, TL: 25–40 cm) were kept in aquaria ($1 \times 0.5 \times 0.5$ m) connected to each other and to the experimental set-up, providing constant environmental conditions (conductivity, temperature and pH). The system was filled with aerated, filtered salt water [conductance: about 50 mS (ca. 1.0217 kg/dm³)] at 26 ± 2. Food (small pieces of squid, fish or shrimp) was only provided in form of rewards during the experimental training. Experiments were conducted during daylight hours; there was a 12-h light:12-h dark cycle. Individuals were identified by phenotypic characteristics. At the end of Experiment 2, two individuals died (unrelated to the experiment); accordingly, Experiment 3 was only performed on three individuals.

Set-up

Experiments were performed using a similar set-up to the one described by Fuss et al. (2014a, b; Fig. 1). The grey Polyvinylchloride set-up featured a starting compartment (SC, 0.51 m × 0.35 m), a decision area (113.5 m × 0.87 m × 0.35 m) and a frosted white screen for stimuli presentations (0.92 m × 0.35 m). The set-up itself was placed within an octagonal experimental basin (2.5 m × 2.5 m × 0.35 m) made out of transparent Perspex featuring a white covered floor (Fig. 1). During experiments, the basin was filled with water to a depth of about 0.3 m. To exclude uncontrolled cueing as well as other potentially disturbing external influences, the basin was surrounded by a white pavilion (3.0 m × 3.0 m × 2.5 m). Ceiling-mounted fluorescent tubes allowed an even illumination during the experiments (above pavilion roof; Osram L 18 W, Lumilux Cool White, Germany).

Sharks were placed in the SC before each trial. Independent of the type of trial/experiment the experimenter was always situated behind the SC. The guillotine door was controlled manually by using a cable pull. Two 15-cm-long dividers, attached to the frosted screen separated the front into four compartments, allowing for an unambiguous decision-making in response to the four stimuli displayed on the front screen using laminated colour cards (10 cm × 12 cm). Cards were fitted with Velcro dots, which were easily stuck to and removed from the front allowing quick reassembly between trials. As sharks were usually swimming close to the bottom,

Fig. 1 Overview of the experimental set-up (modified from Fuss et al. 2014a). *1* Food holders below which the stimulus cards were attached, *2* compartment divider, *3* overhead lighting (on both sides)
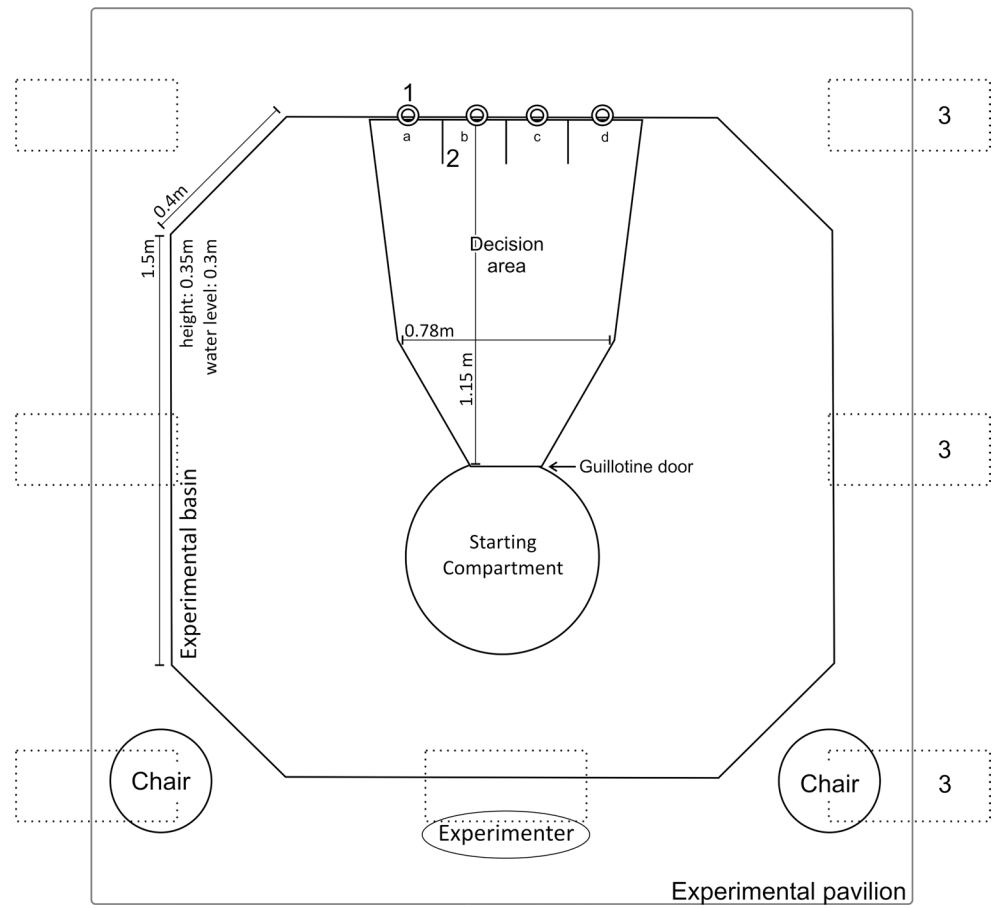
stimuli were presented at a height of 3 cm above the ground. To reward sharks for a correct decision, feeders were installed just above each stimulus, which allowed food to be dropped into the set-up manually using a cable pull from the experimenter's position at the opposite side of the experimental set-up. For a correct choice to be recorded by the experimenter, sharks had to press their nose against the wall just below/onto the positive stimulus. Selected sessions were videotaped. All feeders were baited during all trials to exclude unintentional cueing. Additionally, the water in the set-up was stirred after every trial to preclude any olfactory cues after a reward was given (which could have biased the shark's choice in subsequent trials).

Stimuli

Stimuli used for the discrimination tests were chosen by taking into account the spectral absorbance of rod and cone visual pigments in the closely related shark species *Chiloscyllium punctatum* (Hart et al. 2011). The quantum catch for the rod and cone photoreceptor, Q_i, when viewing a given stimulus was calculated after Kelber et al. (2003) as follows:

$$Q_i = \int_{400}^{700} R(\lambda)I(\lambda)S_i(\lambda)d\lambda$$

where R is the spectral reflectance of the provided stimuli (ranging 0–1, Fig. 2a, b), I is the normalized irradiance measured in the experimental set-up (ranging 0–1, Fig. 2c), and S_i is the normalized absorbance of receptor type i (ranging 0–1, Fig. 2d). Reflectance scans of the experimental stimuli were recorded using an Avantes Avaspec 2048 spectrophotometer connected to a deuterium–halogen light source (Avantes DHs) for illumination. The end of a bifurcated fibre-optic probe with unidirectional illumination and recording was inserted in a darkened pipette tip to exclude ambient light and to take measurements in a 45° angle at a fixed distance of 0.3 cm from the stimulus surface. Reflectance intensity was determined relative to a 98 % Spectralon white reference between 400 and 700 nm. Data were recorded with Avasoft 7.7 (Avantes) and imported into Microsoft Excel. Underwater downwelling irradiance was measured by placing an Avantes CC-UV/VIS cosine corrector at the position of the test fish's eye at a distance of 30 cm from the stimulus presentations (Fig. 2d). After conversion to illuminance the measured spectral irradiance was calculated to be equivalent to 67 lx, which lies

Fig. 2 Spectral reflectance of the stimuli used throughout the experiments, i.e. of **a** *blue*, *yellow* and *grey* 144 (all the same reflectance); **b** of all grey shades from 0 (*black*) to 240 (*white*) (the *line colouring* represents the respective grey shading). Blue and yellow were of equal brightness. Grey 144 was equal in brightness to *blue* and *yellow*. Grey 0 was equal to *black*, grey 240 equal to *white*. **c** Visual pigment templates for the rod (*grey line*) and cone (*black line*) type of *C. punctatum*. **d** Downwelling irradiance measured in the experimental set-up

in the lower photopic range (Kelber and Roth 2006). However, in the absence of data on the upper limits of mesopic vision in sharks a potential involvement of rod cells in colour discrimination cannot completely be ruled out for the rather dim experimental lighting conditions. Hence, spectral sensitivity curves for both the rod and cone receptors were determined from absorbance maxima for a vitamin A1-based visual pigment template (Hart et al. 2011) following equations given in Govardovskii et al. (2000).

In total, nine grey stimuli of varying brightness as well as one blue and one yellow stimulus were created according to the calculated quantum catches (Figs. 2a, b, 3a, b). Stimulus brightness was defined as the summed quantum catches of the cone and rod photoreceptors. Grey 140, blue and yellow were of similar brightness but differed in hue. Grey 0 was equal to black, grey 240 equal to white; numbers in between give the degree of shading in between.

Training

Before each trial, all feeders were baited and the water stirred. At the beginning of each trial the shark was placed in the SC. To start, the shark had to push against the guillotine door with its snout. A choice was recorded as soon as the shark touched the frosted screen in one of the four compartments with its snout. The four stimuli to be discriminated were displayed simultaneously (one in each division) and switched randomly between all four positions to prevent side biases and direction conditioning. Also, five alternating rotational schemes were used, so as to vary the succession of stimuli shown on a particular side between sessions. A correct choice was rewarded with food. There was an inter-trial interval (ITI) of 30 s. If a shark did not choose a stimulus within 2 min, the trial was aborted; three such trials would terminate a session. Training sessions were carried out 5–6 days per week; each session consisted of 12 trials (so that every stimulus card was shown three times per session at each of the four positions). Training was considered successful or completed as soon as a learning criterion of ≥70 % correct choices on three subsequent sessions was reached ($\chi2$ (1) ≤ 0.05; to prove statistical significance). If a shark did not reach the criterion within
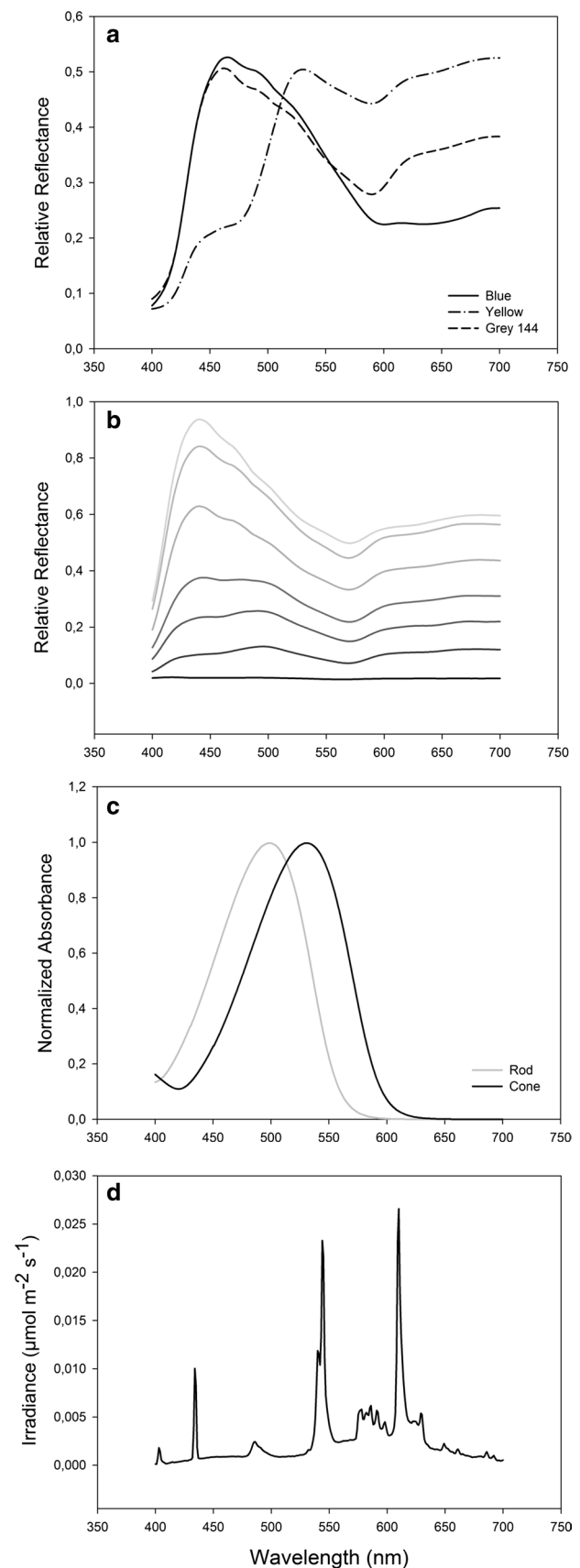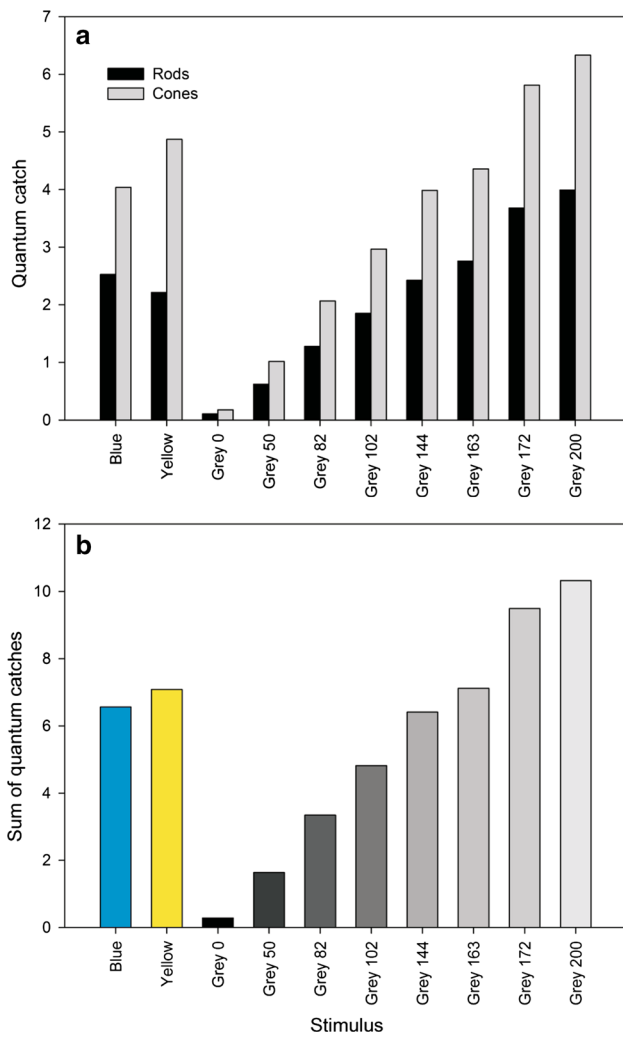
Fig. 3 a Relative excitation (quantum catches) of the rod (*grey bars*) and cone (*black bars*) photoreceptors of *C. punctatum* and **b** sum of quantum catches for each stimulus used throughout the experiments

30 training sessions, the experiment was terminated and the shark moved to the next task.

Discrimination of blue and grey

In Experiment 1a ($n = 5$), the following four stimuli were shown: blue, grey 144 (same brightness as blue), distractor grey 200 (lighter grey) and distractor grey 82 (darker grey) (Figs. 2, 3a). There were 30 sessions. In Experiment 1b, the same four stimuli were shown but both the blue stimulus and the grey 144 stimulus (same brightness) were rewarded.

Discrimination of yellow and grey

In Experiment 2 ($n = 5$), the following four stimuli were shown: yellow (same brightness as blue), grey 144 (same

brightness as blue), distractor grey 200 and distractor grey 82 (Figs. 2, 3a). There were 10 sessions.

Discrimination of four different shades of grey

In Experiment 3 ($n = 3$), the following four stimuli were shown: grey 144 (same brightness as previously blue or yellow), distractor grey 200, distractor grey 50 and distractor grey 163 (Fig. 2). There were up to 15 sessions. In transfer tests ($n = 10$ per individual; up to two per session), which were randomly interspersed with regular trials, sharks were presented with four new grey stimuli (grey 0, 102, 172, 240), none of which compared in brightness to the greys previously shown, including grey 144.

Data analysis

The average trial time, the percentage of choices for each stimulus card and the percentage of choices for each compartment were recorded for each session for each individual. To test for statistical significance of learning success, the learning criterion was established to be $\geq 70\,\%$ correct choices in three consecutive sessions ($\chi^2 (1) \leq 0.05$). Yates' Chi-square test including 95 % confidence intervals was used to determine if the rewarded stimuli were chosen significantly more often than the distractor stimuli. For all tests a $p \leq 0.05$ was considered significant and a $p \leq 0.001$ highly significant.

Results

Discrimination of blue and grey

None of the sharks ($n = 5$) reached the learning criterion in Experiment 1a. On average, the blue stimulus (positive stimulus rewarded) was chosen 570 times ($31.8 \pm 3.82\,\%$), the grey 144 stimulus (same brightness) 617 times ($34.4 \pm 2.45\,\%$) and the two distractor stimuli 305 times ($17.0 \pm 1.91\,\%$; grey 200) and 301 times ($16.8 \pm 2.01\,\%$; grey 82), respectively (Fig. 4a). The blue stimulus was not chosen significantly more often than grey 144 (Yates' $\chi^2 = 1.78$, $df = 1$, $p = 0.182$), but significantly more often than either grey 200 or grey 83 (both $p < 0.0001$). Blue and grey 144 together (66.2 %) were chosen significantly more often than the two remaining grey distractor stimuli ($n = 1793$; Yates' $\chi^2 = 187.6$, $df = 1$, $p < 0.001$).

In Experiment 1b, the blue stimulus (positive stimulus rewarded) was chosen $35.2 \pm 2.4\,\%$ of the time, the grey 144 stimulus (same brightness, also rewarded) $39.7 \pm 4.8\,\%$ of the time and the two distractor stimuli $12.5 \pm 3.8\,\%$ (grey 200) and $12.7 \pm 3.3\,\%$ (grey 82) of the time, respectively (Fig. 4b). Combined, the two rewarded
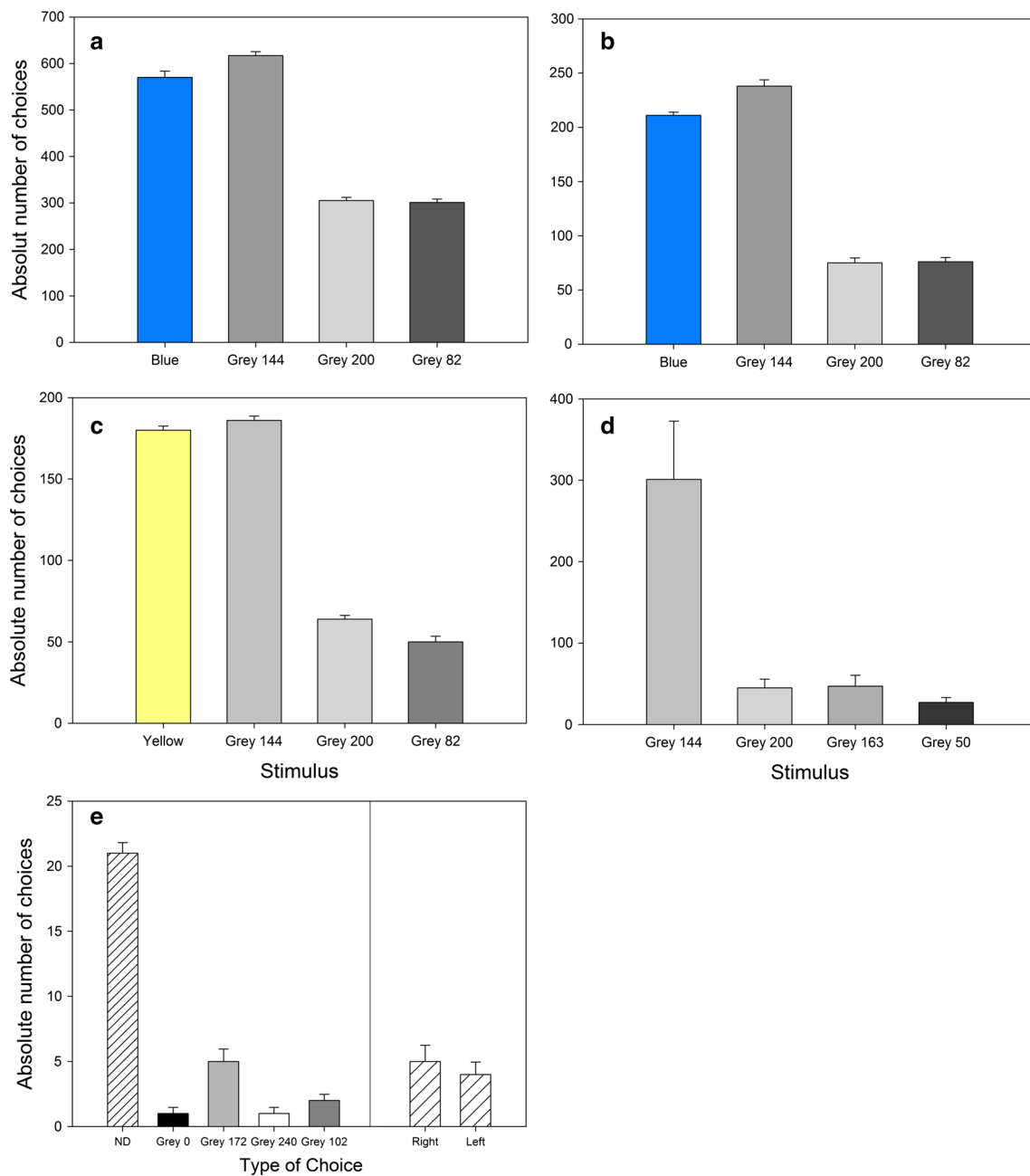
Fig. 4 Absolute number of choices of each stimulus for Experiment 1a (**a**), 1b (**b**), Experiment 2 (**c**), Experiment 3 (**d**) and transfer tests of Experiment 3 (**e**). In **e** ND = no decision; the remaining choices that were made are given as colour choices on the left, and as right and left choices on the right side of the diagram

stimuli were chosen 74.8 % of the time, i.e. they were chosen significantly more often than the two remaining ones ($n = 600$; Yates' $\chi^2 = 148.0$, $df = 1$, $p < 0.001$).

Discrimination of yellow and grey

None of the sharks ($n = 5$) reached the learning criterion; instead, yellow and grey 144 were chosen about equally often ($n = 366$; Yates' $\chi^2 = 0.068$, $df = 1$, $p = 0.754$)

(Fig. 4c). On average, the yellow stimulus was chosen 45 ± 2.5 % of the time, the grey stimulus (same brightness) 46.5 ± 2.7 % of the time and the two distractor stimuli 16 $\pm$ 2.3 % (grey 200) and 12.5 $\pm$ 3.5 % (grey 82) of the time, respectively. Combined, the yellow and the grey stimulus were chosen 91.5 % of the time, which was significantly more, than the choice of the two distractor stimuli ($n = 480$; Yates' $\chi^2 = 131.252$, $df = 1$, $p < 0.0001$).

Discrimination of four different shades of grey

All sharks ($n = 3$) chose the known grey stimulus (grey 144) featuring the same brightness as the blue or yellow colour previously shown significantly often over the other known (grey 200) and unknown (grey 50 and grey 163) stimuli ($n = 420$; Yates' $\chi^2 = 486.41$, $df = 3$, $p < 0.0001$) (Fig. 4d). On average, grey 144 was chosen 71.6 % of the time, grey 200 at 13.6 % of the time and the new grey 50 and grey 163 stimuli 10.7 % and 6.3 % of the time, respectively. There were no significant differences between the choices of grey 200, 50 and 163 ($n = 480$; Yates' $\chi^2 = 5.498$, $df = 2$, $p = 0.064$).

In the randomly interspersed transfer tests (in which sharks were not rewarded), sharks were presented with four new grey stimuli (greys 0, 102, 172 and 240), none of which matched the previously shown grey 144 (and the previously shown and rewarded colours) in brightness, so there was actually no 'correct' choice. In 21 out of the 30 transfer trial tests (ten per individual), sharks made no decision at all (Fig. 4e). They would leave the starting compartment, stop or swim around and then return to the starting compartment without having made a choice. Of the remaining nine trials, shark went four times to the far left and five times to the far right, thereby randomly choosing the stimuli shown in these positions. Also, of the nine remaining trials in which individuals chose, the grey 172, which most closely resembled grey 144 was chosen five times, whereas the remaining greys were only chosen once (grey 0 and grey 240) or twice (grey 102) (Fig. 4e).

Discussion

As expected from the available physiological data on *C. punctatum* and other sharks (Hart et al. 2011), the behavioural data collected here could not demonstrate colour vision in the grey bamboo shark (*C. griseum*). While all individuals completed all assigned tasks and showed high levels of motivation (as indicated by high levels of swimming and feeding), none could tell the presented colour stimuli apart from either a grey of equal brightness or another colour of equal brightness. Brightness differences on the other hand were easily perceived by all individuals.

Colour discrimination

During Experiments 1 and 2, the presented colours were chosen about equally often as the grey (grey 144), which was matching the respective colours in brightness. When only blue was rewarded (Experiment 1a), the success rate was slightly lower, than when both blue and grey were both rewarded (Experiment 1b). If the sharks could in fact not distinguish between blue and grey 144, they would have been only rewarded at a maximum of 50 % of what they would have perceived as the 'correct' stimulus. As expected, when both stimuli were rewarded the success rate increased from 66 to 75 %. This rate agrees with results obtained in previous visual discrimination experiments (two alternative forced choice) on grey bamboo sharks (Fuss et al. 2014a, b; Schluessel et al. 2014). Surprisingly, in this type of behavioural experiment both sharks and cichlids rarely achieve results >80 % (Fuss et al. 2014a, b; Schluessel et al. 2012; Schluessel et al. 2014). However, it needs to be remembered that it also took a while for the sharks to associate the blue/grey 144 with the food and therefore would have chosen at random within the first several sessions, lowering absolute choices within these categories. When the blue was substituted by a yellow stimulus of equal brightness, performance remained the same; again, there was no significant difference between the number of times yellow and grey144 were chosen by the group and by individual sharks.

While sharks in this study obviously did not discriminate between colours, they perceived differences in achromatic brightness between the different shades of grey.

Brightness discrimination

Results of Experiments 1 and 2 were confirmed in Experiment 3. Sharks continued choosing grey 144 over the remaining greys significantly often. In the transfer test trials, where no 'correct' choice was offered, individuals refrained from making a choice altogether in 21 out of 30 trials and chose the grey most similar to grey 144 in five out of the nine remaining trials. The other three grey choices were chosen only once or twice. This clearly indicates that sharks associated the specific brightness of grey 144 with being the correct choice instead of just using the provided grey shades as reference points and choosing the 'correct' grey shade based on features such as intermediate brightness.

Why are bamboo sharks colourblind?

Apart from confirming the physiological data, this outcome is interesting and even somewhat surprising from an ecological perspective. Bamboo sharks (*Chiloscyllium* sp.) are small benthic species that inhabit tropical shallow water environments including sea grass beds and coral reefs. Usually, fish species living in sun-lit regions possess multiple cone types (Marshall and Vorobyev 2003) and therefore also colour vision, which can be used for an entire range of behaviours related to mate choice and sexual displays, territorial defence, predator avoidance (e.g. camouflage, threat displays, mimicry) and individual or species recognition. It

is not well known, if bamboo sharks are diurnal or nocturnal; there are some indications that in the wild activity levels may be increased at night, but sharks can also frequently be seen to move around during the day (pers. observ.). Sharks kept in the lab are definitely much more active during the day than at night. Nonetheless, even if bamboo sharks were nocturnal this would not necessarily imply a loss of colour vision; with few exceptions, most nocturnal terrestrial animals still possess more than one cone type and can see colour. Whales and seals seem to have lost the ability for colour vision altogether, which may be related to their frequent excursions into great water depths (Peichl et al. 2001). A similar adaptation could possibly account for an absence of colour vision in a range of shark species, but seems unlikely for those living in such shallow, well-lit regions as the bamboo sharks. Perceiving colour for the sake of mate choice and sexual displays seems unneccessary, as to the human eye, bamboo sharks do not appear to be very colourful (despite the conspicuous saddle band patterns juveniles possess) but this may also be different from an elasmobranch point of view (Bedore et al. 2013). Bamboo sharks are also unlikely to rely on vision for foraging, as they are benthic predators that feed mainly on invertebrates hidden in the substrate. However, possessing colour vision could still be a worthwhile adaptation for various discrimination purposes related to the respective habitat and potential territories as well as for the detection and identification of predators. Shovelnose rays (*G. typus*), which are found in similar habitats and possess colour vision not only discriminated between a coloured reward and a range of grey distractor stimuli of varying brightness, but also generalized from a reward colour to other reward colours of the same hue but varying brightness (Van-Eyk et al. 2011). The latter was not tested in the present study, as sharks were not able to discriminate even a single hue from a grey of equivalent brightness. Also, no additional experiments were conducted using more diverse distractor stimuli; obviously, grey 144 was already similar enough in brightness to blue and yellow to prevent successful distinction.

Individuals of *C. griseum* were extremely motivated and eagerly participated in all tasks of the experiment. The sharks had not been naïve but had already participated previously in a range of behavioural experiments, in which they had shown impressive cognitive abilities in regards to learning, visual discrimination and categorization (Schluessel et al. 2014). It seems therefore unlikely, that the here collated results could be attributed to something other than the absence of colour vision.

Are all sharks colourblind?

Very little is known about the visual system of most of the 1185 extant elasmobranch species (White and Last 2012), as only very few species have been studied in detail. Considering, that there are well over 500 shark species known to date, displaying a wide range of ecological and behavioural adaptations, i.e. by inhabiting almost all marine and even some freshwater habitats, living at different depths and in waters of varying turbidity, it cannot be excluded that some shark species may in fact possess some form of colour vision despite all of the previously collected experimental evidence refuting this. Exceptions are often the rule, for example, all but one of the assessed shark species by Hart et al. (2011) possessed duplex retinas, only the Port Jackson shark did not. In the batoids, all assessed ray species were found to have two or even three cone types, while skates have none; they have all-rod retinas (Ripps and Dowling 1991; Hart et al. 2004; Theiss et al. 2007). Accordingly, it would not be too surprising if some unexamined shark species were to possess more than the one and only cone type found so far. Also, it cannot be completely ruled out that a rudimentary form of colour vision could also be achieved by comparison of signals from rods and cones instead of comparing signals from multiple cone types (Hart et al. 2011). The present experiments were conducted under illumination in the lower photopic range, which can be assumed to fall within the range of light levels bamboo sharks encounter in their natural habitat during the day. The chosen lighting conditions make rod-mediated vision rather unlikely but not impossible, as information for the upper limits of mesopic vision in elasmobranchs is lacking. Future studies should thus be conducted using a wide range of lighting conditions including illumination levels where both rods and cones are more clearly expected to contribute to vision. However, in the absence of further behavioural work it seems likely that at least the shark species assessed by Hart et al. (2011), which were found to be cone monochromats, are in fact incapable of colour vision.

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