

RESEARCH ARTICLE

Behavioural evidence for colour vision in an elasmobranch

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SUMMARY

Little is known about the sensory abilities of elasmobranchs (sharks, skates and rays) compared with other fishes. Despite their role as apex predators in most marine and some freshwater habitats, interspecific variations in visual function are especially poorly studied. Of particular interest is whether they possess colour vision and, if so, the role(s) that colour may play in elasmobranch visual ecology. The recent discovery of three spectrally distinct cone types in three different species of ray suggests that at least some elasmobranchs have the potential for functional trichromatic colour vision. However, in order to confirm that these species possess colour vision, behavioural experiments are required. Here, we present evidence for the presence of colour vision in the giant shovelnose ray (*Glaucostegus typus*) through the use of a series of behavioural experiments based on visual discrimination tasks. Our results show that these rays are capable of discriminating coloured reward stimuli from other coloured (unrewarded) distracter stimuli of variable brightness with a success rate significantly different from chance. This study represents the first behavioural evidence for colour vision in any elasmobranch, using a paradigm that incorporates extensive controls for relative stimulus brightness. The ability to discriminate colours may have a strong selective advantage for animals living in an aquatic ecosystem, such as rays, as a means of filtering out surface-wave-induced flicker.

Key words: colour vision, colour discrimination, giant shovelnose ray, *Glaucostegus typus*.

INTRODUCTION

Elasmobranchs (sharks, skates and rays) are a subclass of the Chondrichthyes, which evolved over 400 million years ago during the Silurian period (Last and Stevens, 2009) and inhabit all major marine and some freshwater habitats (Gruber and Myrberg, 1977). Despite their status as apex predators, their visual capabilities and visual specialisations are poorly studied compared with those of other fishes, especially in regard to colour vision.

Colour vision, or the ability to discriminate objects based on differences in spectral reflectance independently of brightness, requires two or more spectrally distinct photoreceptor types. Microspectrophotometry (MSP) and electrophysiological recordings can be used to identify the neural basis for colour vision (i.e. spectrally distinct visual pigments and colour-opponent responses, respectively). However, the ability of an organism to discriminate colour, and more importantly to use this information, can only be shown conclusively *via* behavioural experiments. Behavioural experiments testing for colour vision that removed brightness as a confounding factor were first used almost a century ago by von Frisch (von Frisch, 1913; von Frisch, 1914). Subsequently, similar behavioural experiments have been used to investigate the presence and nature of colour vision in a range of vertebrate and invertebrate species (reviewed in Kelber et al., 2003).

Representatives from most of the major vertebrate groups (teleost fish, birds, reptiles, amphibians and mammals) have been shown to possess colour vision or are thought to have the ability to discriminate colour based on the presence of two or more spectral cone types (reviewed in Jacobs, 1981; Jacobs, 2004). Given that most elasmobranchs, with the possible exception of the skates

(Dowling and Ripps, 1970; Ripps and Dowling, 1991) and some deep-sea species, have duplex (rod and cone) retinas (reviewed in Hart et al., 2006) and that the genes coding for the five different major classes of vertebrate visual pigment proteins evolved prior to the divergence of the jawed and jawless vertebrate lineages (Collin et al., 2003), it would seem likely that at least some elasmobranchs should possess two or more cone types and colour vision. However, the evidence for the presence or absence of colour discrimination in sharks and rays remains equivocal.

The earliest behavioural experiments on sharks concentrated on demonstrating that sharks were capable of being conditioned to press a target in order to receive a food reward (Clark, 1959; Wright and Jackson, 1964; Aronson et al., 1967). From these studies, more complex behavioural experiments that examined shape recognition and colour vision were developed. In one of the first studies (Tester and Kato, 1966) that attempted to show colour vision in elasmobranchs, juvenile blacktip (*Carcharhinus melanopterus*) and grey (*C. menisorrhah*) sharks were tested on a two-choice discrimination task, in which the sharks learnt to pair an electric shock with a grey (negative) stimulus. Although the sharks were capable of discriminating some coloured stimuli from the grey control stimuli, colour vision could not be demonstrated conclusively as there was limited control of the relative brightness of the coloured and grey stimuli used.

Further experiments testing for colour vision have yielded conflicting results. The lemon shark, *Negaprion brevirostris*, was reported to have the potential for colour vision after physically restrained sharks were shown to respond to the substitution of a coloured adapting light with that of another colour by the extension

of their nictitating membrane (Gruber, 1975). However, the possibility remains that the sharks responded to differences in brightness rather than colour as only limited brightness controls were employed. In another experiment, free-swimming lemon sharks were trained to perform a two-choice colour discrimination task but were unable to discriminate the coloured target reliably despite more than 4000 trials [S. H. Gruber, unpublished data, cited in Cohen (Cohen, 1980)]. The difficulties in demonstrating colour vision in sharks using behavioural methods are reflected in the failure to obtain conclusive evidence of more than one spectral type of cone in the retina (Cohen and Gruber, 1977; Cohen, 1980; Sillman et al., 1996; Hart et al., 2011).

The evidence for more than one spectral cone type in the ray retina, however, is more convincing, with studies indicating the presence of more than one photopic cone-based mechanism (Govardovskii and Lychakov, 1977; Toyoda et al., 1978). Recently, data obtained using MSP have indicated the presence of up to three spectrally distinct cone pigments in the retina of the giant shovelnose ray, *Glaucostegus typus* [wavelength of maximum absorbance (λ_{\max})=477, 502 and 561 nm], the eastern shovelnose ray, *Aptychotrema rostrata* (λ_{\max} =459, 492 and 553 nm) (Hart et al., 2004), and the bluespotted maskray, *Neotrygon (Dasyatis) kuhlii* (λ_{\max} =476, 498 and 552 nm) (Theiss et al., 2007). These findings raise the possibility that rays have a potentially trichromatic colour vision system.

Here, for the first time, we show that giant shovelnose rays can perform alternative forced-choice discrimination tasks in which they are able to distinguish coloured reward stimuli from an extensive range of distracter stimuli of variable brightness.

MATERIALS AND METHODS

Animals

Two juvenile giant shovelnose rays [*Glaucostegus (Rhinobatos) typus*, Bennett 1830] were caught under permit (General Fisheries Permit 100541) using seine nets from the waters of North Stradbroke Island, Moreton Bay, Australia (27°35'S, 153°27'E) in 2010. Rays were young-of-the-year with total lengths ranging from 25 to 45 cm.

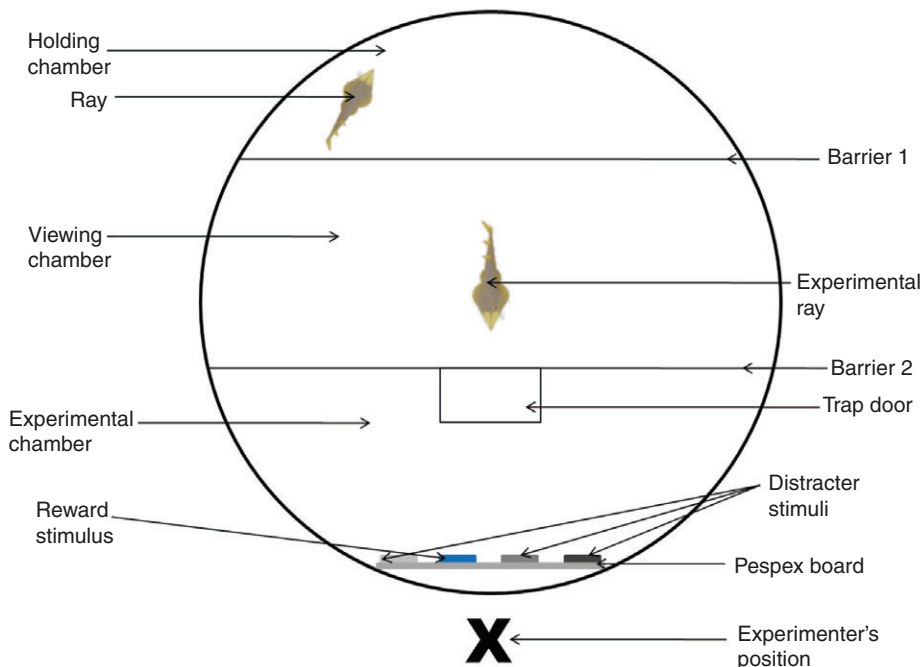


Fig. 1. The tank setup used for experiments in which Rays 1 and 2 completed the four-choice discrimination task. In this instance, the blue reward stimulus appeared in position 2 whilst three distracter stimuli of varying brightness appeared in positions 1, 3 and 4. The experimenter was always seated between the two stimuli and the feeder was hidden from sight. One ray was placed into the viewing chamber whilst the other animal remained in the holding chamber. The stimuli were placed an equal distance from the experimenter.

Housing and experimental setup

Animals were transferred to The University of Queensland, St Lucia, Australia, and housed and tested indoors in a 3 m diameter grey polythene tank containing 1200 l of recirculating artificial seawater (salinity 32–34 ppt; 23°C) to a depth of 40 cm. The tank was illuminated using overhead diffuse fluorescent strip lighting on a 12 h:12 h light:dark cycle. During testing, two barriers were introduced to the tank (Fig. 1). The first was an opaque barrier that was used to create a holding chamber to separate the remaining ray from the individual ray being tested. The second was made of a wide plastic mesh and formed a viewing chamber with a trap door to allow the ray being tested to view the test stimuli in the experimental chamber prior to commencement of each trial. Individual rays were identified using unique variations in skin colouration. All procedures were approved by The University of Queensland Animal Ethics Committee (SBMS/445/09/SBMS).

Feeding apparatus design

A feeding apparatus was constructed from acrylic plastic to enable the delivery of a controlled amount of food to each ray underwater. The feeder contained a wide-bore syringe that was used to deliver a food paste (comprised of mashed prawn and white bait) via a plastic tube to a reservoir in a ramp platform at the base of the feeder. In order to obtain food the rays had to swim over the ramp platform of the feeder.

Summary – experimental procedures

Our experiments were based upon the classical grey card paradigm of von Frisch (von Frisch, 1914). Rays were required to discriminate a coloured reward stimulus from a range of distracter stimuli of differing brightness. The basic idea is to render the potential cue of brightness as unreliable so that each task can only be solved if the animals can distinguish the stimuli on the basis of hue alone. We conducted experiments to test whether the animals could distinguish a single hue (blue) from a variety of distracters with a large range of brightness levels. The distracters were created to include stimuli brighter than, equal to and darker than the rewarded stimulus. The

expectation was that if the animals make their choice on the basis of hue, they should preferentially select the correct stimulus irrespective of whether it was displayed together with darker, brighter and/or equally bright distracters. If, however, the animals made their choices based on brightness, they should always select either the brightest or darkest of the stimuli in cases of brightness differences, or should not be able to tell the difference in cases of isoluminant stimuli.

The four-choice discrimination paradigm used to test for colour vision in *G. typus* was adapted from previous work on fishes (Neumeyer, 1984; Siebeck et al., 2008). Subsequent to establishing that this species could complete a two-choice task successfully based on prior experiments (not reported here), two rays completed a four-choice discrimination paradigm. Details of the two experiments are described below.

Stimuli

Stimuli were chosen based on the known spectral properties of the cone visual pigments of *G. typus* (Hart et al., 2004). For each cone type, the relative quantum catches (Q) for all coloured reward stimuli, distracter stimuli and the grey background of the Perspex board used in the experiments were calculated as the product of the spectral reflectance (S) of the coloured stimulus (Fig. 2A,B), the spectral sensitivity (R) of the cone type corrected for axial path length and the transmittance of the ocular media (Fig. 2C), and the irradiance (I) in the experimental arena (Fig. 2D) as per Eqn 1 (Vorobyev and Osorio, 1998; Kelber et al., 2003):

$$Q_i = \int_{400}^{700} I(\lambda) R_i(\lambda) S(\lambda) d\lambda. \quad (1)$$

Ocular media transmittance was obtained from a previous study (Siebeck and Marshall, 2001), while the spectral irradiance of the laboratory was measured using an Ocean Optics USB 4000 spectroradiometer (Ocean Optics, Dunedin, FL, USA).

Stimuli (21.5 × 13.5 cm) were printed on matte photographic paper (Epson, Sydney, NSW, Australia), using an Epson Stylus Photo 1290 inkjet printer, and neutral density filters, designed by printing greys

of differing brightness onto transparency films (Nobo, Acco Australia, Sydney, NSW, Australia), were applied to produce stimuli of the same hue but differing brightness. All stimuli were laminated using transparent plastic pouches (glossy laminating pouches, 125 μm thick, 216 × 303 mm; Fellowes, Itasca, IL, USA). The reflectance spectrum of each laminated stimulus and the grey background of the Perspex board was measured using an Ocean Optics USB 4000 spectroradiometer. Three blue reward stimuli and six distracter stimuli of varying brightness were created. Any reward colour that differed from the distracter stimuli could have been used for the experiments; however, the blue stimuli were chosen as the reward colours based on the calculated quantum catches (Fig. 3A). This was done specifically to ensure that a range of distracter stimuli of varying brightness were selected with some brighter, some darker and some similar to the reward stimuli. In particular, three distracter stimuli (2, 3 and 4) each matched one of the blue reward stimuli (light blue, medium blue and dark blue, respectively) in brightness, based on the sum of the quantum catches of the three cone types (Fig. 3B).

Multiple copies of all reward and distracter stimuli were printed and selected randomly for use in the experiment. This was done to control for the potential of experimental animals choosing the stimuli based on other factors (e.g. subtle differences in the stimuli due to printing artefacts, etc.).

Experiment 1 – blue reward stimulus versus six distracter stimuli of varying brightness

This experiment utilised a four-choice discrimination task in which the rays were required to select the blue stimulus as the reward, which they viewed against six different distracter stimuli of varying brightness. The use of variable distracter stimuli rendered relative brightness as an unreliable cue. Therefore, hue was the only reliable cue remaining for the rays to discriminate between the reward and distracter stimuli.

During testing, four stimuli (the blue reward and three distracter stimuli of variable brightness) were placed on a grey Perspex board (96 × 34 cm) an equal distance from one another and placed into the experimental arena prior to the commencement of each trial. The

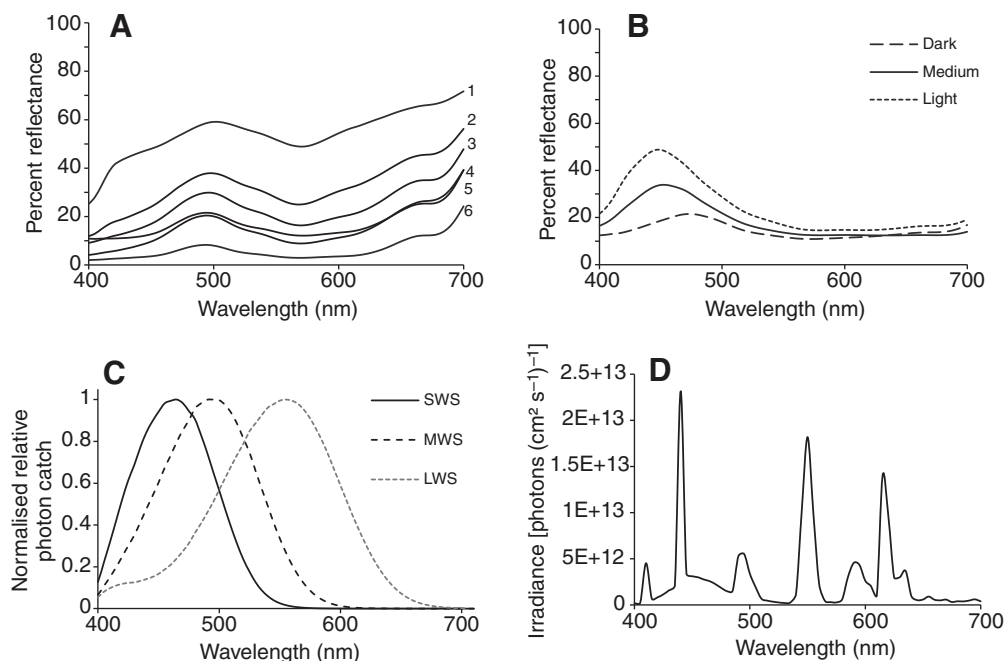


Fig. 2. (A) Spectral reflectance of the six distracter stimuli (1–6) used in both experiments. (B) The spectral reflectance of the three blue reward stimuli: medium blue was used in Experiments 1 and 2; light and dark blues were used in Experiment 2. (C) Spectral sensitivity (normalized relative photon catch) for the short wavelength sensitive (SWS), medium wavelength sensitive (MWS) and long wavelength sensitive (LWS) cone types of *Glaucostegus typus*. (D) The measured illumination (irradiance) of the experimental arena.

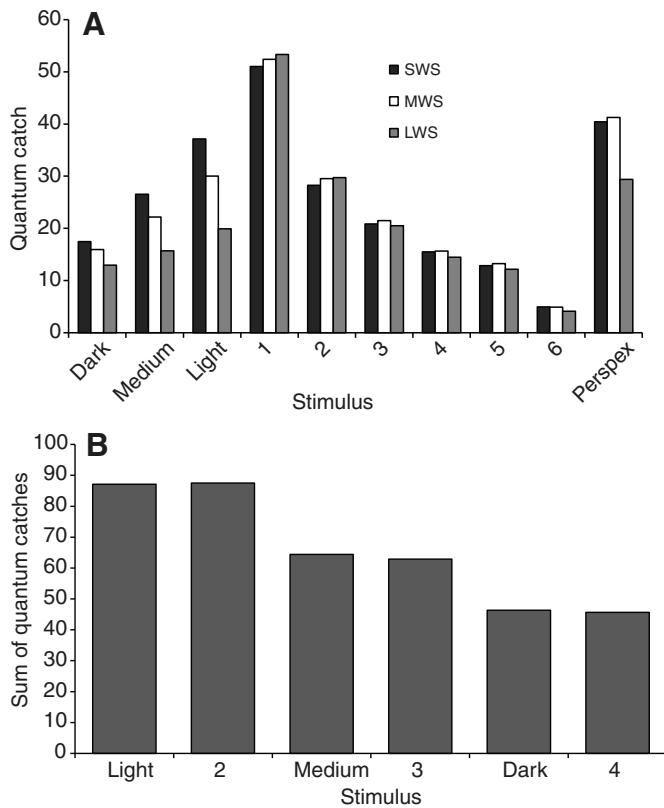


Fig. 3. (A) Relative quantum catches of the three blue reward stimuli (light, medium and dark), the six distracter stimuli (1–6) and the Perspex background used in Experiments 1 and 2 for the three different cone photoreceptor types (SWS, MWS and LWS) of *G. typus*. (B) Sum of the calculated quantum catches for the light, medium and dark blue reward stimuli and distracter stimuli 2, 3 and 4.

observer was positioned directly behind the Perspex board on the outside of the tank (Fig. 1). All trials were completed in an identical fashion with the position of the reward stimulus varied pseudo-randomly with the following constraints: it was never placed in the same position more than twice in a row and was presented in all four positions equally often. This was done to reduce the risk of introducing side bias and to control for possible natural side bias. The rays were required to physically touch the reward stimulus with their snout (as viewed by the observer) in order to receive a food reward. However, if they touched one of the three distracter stimuli, the trial was terminated and the ray did not receive a food reward. Upon completion of each trial the ray was returned to the viewing chamber in order for the next trial to commence. For each trial the rays' response was recorded as either correct or incorrect and the stimulus selected was recorded. At the end of the experiment the percentage of correct choices against each of the six distracter stimuli was calculated for both rays. The two rays completed a total of 32 trials (four sessions, eight trials per session) in which four stimuli (three distracters and one rewarded stimulus) were presented simultaneously, resulting in a one in four (25%) chance that the rays would select the reward stimulus based on chance. In any given trial, the blue reward stimulus was viewed together with three of the six distracter stimuli selected at random within the constraints that all distracter stimuli appeared equally often in all four positions over the course of the experiment (each distracter stimulus was viewed a total of four times in each of the four positions; $N=16$).

The distracter stimuli used in each trial were selected at random to ensure that brightness was an unreliable cue, i.e. that the rewarded stimulus was not consistently brighter or darker than the distracter stimuli. This task can only be solved if: (1) the animals are able to perceive hue and thus have colour vision or (2) the animals are able to learn and memorise the absolute brightness of the reward stimulus.

Experiment 2 – variable blue reward stimuli versus six distracter stimuli of varying brightness

This experiment utilised the same procedure as Experiment 1, with the exception that the six distracter stimuli were viewed against three blue reward stimuli of varying brightness. In this test the rays had to learn to generalise from the original blue and accept all blue stimuli as reward stimuli in order to complete the task correctly. The reward stimuli included the original blue reward stimulus (medium blue) and two novel blue reward stimuli (light and dark blue) that were viewed equally often in all four positions over the course of the experiment. For any given trial, a blue reward stimulus was randomly selected along with three of the six distracter stimuli and placed in one of the four marked positions on the Perspex board as described for Experiment 1. Both rays completed a total of 144 trials (18 sessions, eight trials per session) and viewed each of the blue reward stimuli against each of the distracter stimuli an equal number of times (each distracter stimulus was shown in each of the four positions twice for each reward stimulus; $N=8$). The numbers of correct and incorrect choices were recorded and a percentage of correct choices was calculated for each of the distracter stimuli against the three reward stimuli.

Analysis

Data obtained from the experiments were used to calculate binomial probabilities where $P(X=x)$ using Stat Trek Binomial Distribution calculator (<http://stattrek.com/Tables/Binomial.aspx>) in order to test whether the rays were capable of discriminating the reward stimuli from the distracter stimuli. The percentages of correct choices for all three reward stimuli against each of the six distracter stimuli were calculated. Confidence intervals were calculated assuming a binomial distribution.

RESULTS

Experiment 1

Both rays (rays 1 and 2) trained to the medium blue reward stimulus were able to distinguish the reward from all six distracter stimuli reliably ($P \leq 0.001$; Fig. 4). Ray 1 discriminated the reward from distracter stimulus 1 with a percentage of correct choices of 62.5% [95% confidence intervals (CI)=84.8, 35.4]; this value was 93.8% (95% CI=99.8, 69.8) for distracter stimuli 2 and 4, 100.0% (95% CI=100.0, 79.4) for distracter stimulus 3, 87.5% (95% CI=98.5, 61.7) for distracter stimulus 5 and 81.3% (95% CI=96.0, 54.4) for distracter stimulus 6. Ray 2 discriminated the reward stimulus from distracter stimulus 1 with a percentage of correct choices of 75.0% (95% CI=92.7, 47.6); this value was 81.3% (95% CI=96.0, 54.4) for distracter stimuli 2, 5 and 6, 93.8% (95% CI=99.8, 69.8) for distracter stimulus 3 and 87.5% (95% CI=98.5, 61.7) for distracter stimulus 4.

Experiment 2

Both rays reliably selected all three blue reward stimuli from all six distracter stimuli with P -values ≤ 0.004 (Fig. 5).

The original blue reward stimulus (medium blue) was discriminated by Ray 1 with a percentage of correct choices of 87.5%

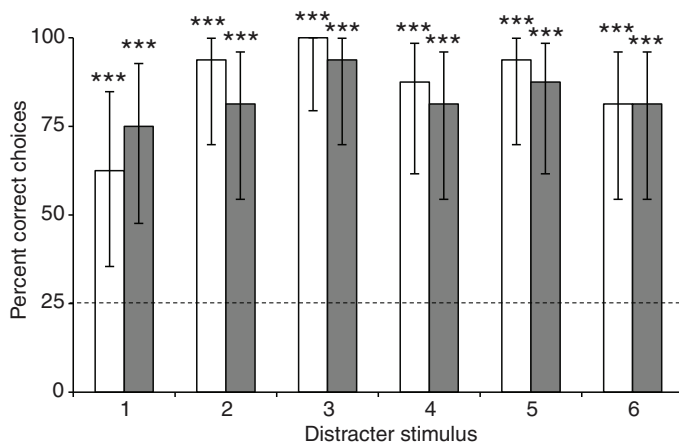


Fig. 4. Results for Experiment 1 showing the percentage of correct choices for the reward stimulus (medium blue) against the six distracter stimuli (1–6) for Ray 1 (white) and Ray 2 (grey). Dotted line represents 25% chance level. Error bars illustrate 95% confidence intervals (CI). *** $P < 0.001$ ($N = 16$).

(95% CI=99.7, 47.4) for all distracter stimuli (1–6), whereas the percentage of correct choices for Ray 2 was 100.0% (95% CI=100.0, 63.1) for distracter stimuli 1 and 4, 75.0% (95% CI=96.8, 34.9) for distracter stimuli 2 and 6, and 87.5% (95% CI=99.7, 47.4) for distracter stimuli 3 and 5.

The light blue reward stimulus was discriminated by Ray 1 with percentage of correct choices of 87.5% (95% CI=99.7, 47.4) for distracter stimulus 1, 100.0% (95% CI=100.0, 63.1) for distracter stimuli 2–5 and 75.0% (95% CI=96.8, 34.9) for distracter stimulus 6. Ray 2 discriminated the light blue reward stimulus from distracter stimuli 1, 3 and 5 with a percentage of correct choices of 75.0% (95% CI=96.8, 34.9); this value was 100.0% (95% CI=100.0, 63.1) for distracter stimulus 2 and 87.5% (95% CI=99.7, 47.4) for distracter stimuli 4 and 6.

The dark blue reward stimulus was discriminated from all distracter stimuli by Ray 1 with a percentage of correct choices of 75.0% (95% CI=96.8, 34.9) for distracter stimuli 1, 2, 4 and 6; 87.5% (95% CI=99.7, 47.4) for distracter stimulus 3; and 100.0% (95% CI=100.0, 63.1) for distracter stimulus 5. Ray 2 discriminated the dark blue reward stimulus from distracter stimuli 1–4 with a percentage of correct choices of 75.0% (95% CI=96.8, 34.7); for distracter stimuli 5 and 6, this value was 100.0% (95% CI=100.0, 63.1).

DISCUSSION

Shovelnose rays, *G. typus*, successfully performed a four-choice discrimination task, which confirms earlier work showing that elasmobranchs are capable of learning visual discrimination tasks (Clark, 1959; Clark, 1963; Wright and Jackson, 1964; Tester and Kato, 1966; Hodson, 2000). The rays were capable of discriminating coloured reward stimuli from differently coloured distracter stimuli that varied in relative brightness from trial to trial. Furthermore, rays were able to generalise from a specific reward stimulus (with a given brightness and hue) to a larger group of stimuli that were identical in hue but varied in brightness without additional training. We therefore conclude that the giant shovelnose ray has a functional colour visual system under photopic conditions.

In Experiment 1, rays were required to select the blue reward stimulus from all distracter stimuli that varied in brightness in order

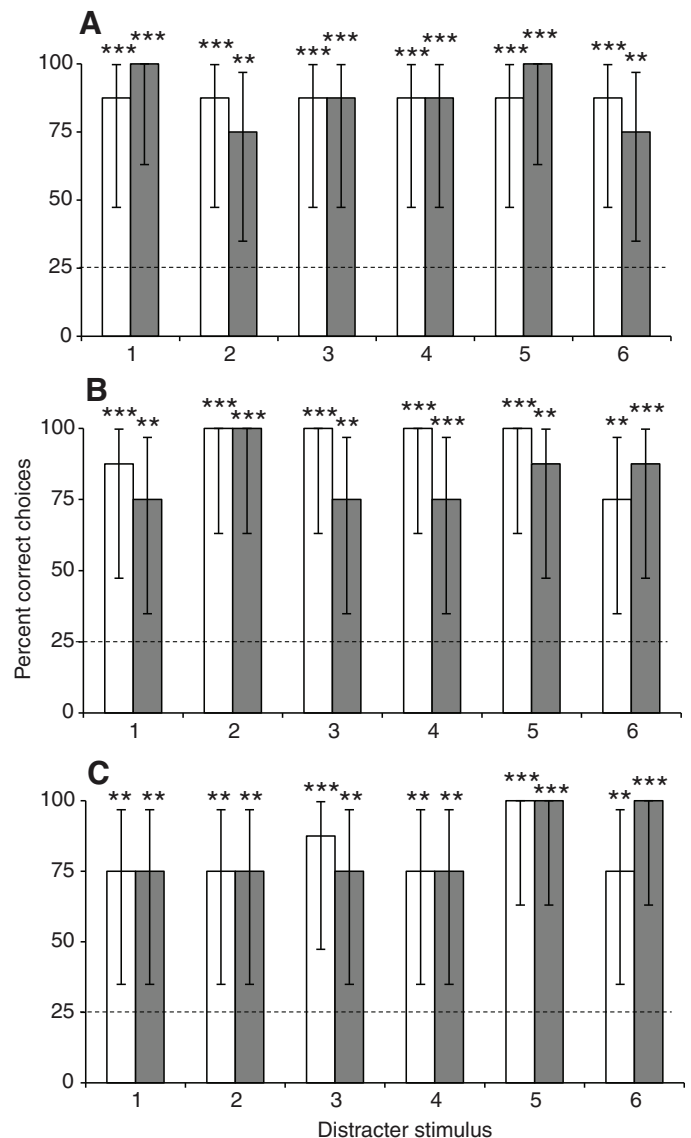


Fig. 5. Results for Experiment 2 showing the percentage of correct choices against the six distracter stimuli (1–6) for Ray 1 (white) and Ray 2 (grey) for (A) the original blue reward stimulus (medium blue), (B) the light blue reward stimulus and (C) the dark blue reward stimulus. Dotted line represents 25% chance level. Error bars illustrate 95% CI. ** $P < 0.01$; *** $P < 0.001$ ($N = 8$).

to demonstrate colour vision. Examination of the results demonstrates that the rays were capable of reliably distinguishing the reward stimulus from all distracter stimuli (1–6). In summary, the results from Experiment 1 demonstrate that the giant shovelnose ray was capable of selecting the reward stimulus over a range of distracter stimuli that varied in brightness. At this point we can conclude that giant shovelnose rays: (1) either learned the absolute brightness of the reward colour, or (2) were utilising at least two spectrally distinct cone types to discriminate between the stimuli and thus possess colour vision. In order to exclude the possibility that the rays had learned the absolute brightness of the reward stimulus, Experiment 2 was designed so that brightness was an unreliable cue for both the reward and the distracter stimuli.

In Experiment 2 when the brightness of both the blue reward stimulus and the distracter stimuli were varied, both rays reliably

discriminated all three blue reward stimuli (light, medium and dark) from all six distracter stimuli. These findings not only support the contention that rays have colour vision, but also demonstrate for the first time their ability to generalise from the learned reward colour to accept any blue irrespective of brightness as a reward stimulus.

General discussion

Previous reports indicating the potential for colour vision in rays measured the early receptor potential of the light-adapted retina of the common stingray, *Dasyatis pastinaca*, and found three peaks in spectral sensitivity at 476, 502 and 540 nm (Govardovskii and Lychakov, 1977). Moreover, colour-opponent responses were recorded from horizontal cells in the retina of the red stingray, *Dasyatis akajei* (Toyoda et al., 1978), and recent MSP studies have reported the presence of up to three spectrally distinct cone types in three ray species, including *G. typus* (Hart et al., 2004; Theiss et al., 2007). The results obtained from the present study suggest that *G. typus*, and most likely other rays with multiple cone types, are capable of discriminating a coloured reward stimulus from a range of different coloured distracter stimuli of varying brightness. Moreover, they were capable of learning to generalise from a single coloured reward stimulus to other reward stimuli of the same hue but of variable brightness. Together, these results provide support for the presence of colour vision in rays.

The appearance of colour vision very early on in vertebrate evolution, and its almost ubiquitous distribution throughout the vertebrate lineage, suggests that the ability to discriminate colour has a strong selective advantage in many aquatic ecosystems. Vision underwater is hampered to a great extent by the optical properties of water itself (Lythgoe, 1968). Of particular consequence for animals inhabiting shallow-water habitats are rapid variations in the intensity of the downwelling irradiance (i.e. 'flicker') produced when light passing through the water's surface is disrupted by surface waves and ripples (McFarland and Loew, 1983). It has been suggested that colour vision evolved in early aquatic vertebrates as a means of filtering out this surface-wave-induced flicker (Maximov, 2000). For a monochromatic visual system that is only able to detect changes in brightness, flickering illumination may make it challenging to detect prey or predators when viewed against the water's surface or the substrate. However, if the animal has photoreceptors that are maximally sensitive to different wavelengths of light and are connected to colour opponent neurons that can subtract the wavelength-independent variations in brightness caused by the surface flicker, it can generate a non-flickering image of any object that differs in spectral reflectance from the background against which it is viewed. This in turn may provide an increase in the distance at which potential prey or predators can be detected.

The giant shovelnose ray inhabits the shallow waters of the Indo-Pacific up to depths of 100 m (Last and Stevens, 2009) and occupies habitats similar to those of teleost fish (Losey et al., 2003; Siebeck et al., 2008) and invertebrates (Marshall et al., 1996) that are also known to utilise colour vision. Therefore, it is perhaps not surprising that this species also employs colour vision. Colour vision is unlikely to be useful for prey detection as *G. typus* is mostly benthic and feeds on invertebrates excavated from below the substrate. However, this species is often prey for large predatory sharks and colour vision may be useful for detecting potential predators at a distance that allows sufficient time to escape, which may not be possible with a monochromatic visual system. Colour vision generally increases the contrast and detectability of a number of objects in a number of contexts (McFarland and Loew, 1983). Although we are unsure of specific tasks that may require colour vision in these rays, their

colour sense may be useful for several requirements of general existence.

In conclusion, our results show that *G. typus* is capable of performing sophisticated visual discrimination tasks, making them ideal candidates for studying perception in a 'lower' vertebrate. They readily solved a four-choice discrimination task in which it was demonstrated that giant shovelnose rays have a functional colour vision system. This is the first conclusive behavioural evidence that any elasmobranch species possesses colour vision. Experiments are underway to investigate the dimensionality of colour vision of *G. typus* and establish whether this species has a trichromatic visual system based on the three cone types identified using MSP (Hart et al., 2004).

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