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Rod-cone based color vision in seals under photopic conditions

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ABSTRACT

Marine mammals have lost the ability to express S-cone opsin, and possess only one type of M/L-cone in addition to numerous rods. As they are cone monochromats they should be color blind. However, early behavioral experiments with fur seals and sea lions indicated discrimination ability between many shades of grey and blue or green. On the other hand, most recent training experiments with harbor seals under "mesopic" conditions demonstrated rod based color blindness (Scholtyssek et al., 2015). In our experiments we trained two harbor seals (*Phoca vitulina*) and two South African fur seals (*Arctocephalus pusillus*) with surface colors under photopic conditions. The seals had to detect a triangle on grey background shown on one of three test fields while the other two test fields were homogeneously grey. In a first series of experiments we determined brightness detection. We found a luminance contrast of >3% sufficient for correctly choosing the triangle. In the tests for color vision the triangle was blue, green or yellow in grey surround. The results show that the animals could see the colored triangle despite minimal or zero brightness contrast. Thus, seals have color vision based on the contribution of cones and rods even in bright daylight.

1. Introduction

Mammals, with the exception of old-world primates, have in general two cone types and dichromatic color vision. Marine mammals, however, have lost their S-cones as known from immunocytochemical investigations of the retina (Peichl, Behrmann, & Kröger, 2001; Peichl & Moutairou, 1998) and molecular genetic studies of the opsin component of photopigments (Levenson et al., 2006; Newman & Robinson, 2005). Thus, pinnipeds are cone monochromats with only one M/L-cone type. In harbor seals only 1% of the photoreceptors are cones, whereas the vast majority consists of rods (Peichl & Moutairou, 1998). Maximal absorbance of rod rhodopsin in situ was found at 496 nm (Lavigne & Ronald, 1975), whereas the gene sequence predicted a value of 501 nm (Levenson et al., 2006). The gene sequence of cone opsin predicted maximal absorbance at 552 nm in harbor seals (Levenson et al., 2006). The same value was found by measuring the absorbance spectrum after expressing the LWS opsin supplied with 11-cis-retinal in mammalian cells (Newman & Robinson, 2005). For the South African fur seal (*Arctocephalus pusillus*) there are no data available. In another Otariid species, the sea lion (*Zalophus californianus*) maximal absorbances of rods and M/L cones were predicted at 501 and 560 nm, respectively (Levenson et al., 2006).

As color vision requires the comparison of the signals of at least two photoreceptor types (cones in vertebrates) marine mammals have been presumed color-blind. However, to prove the existence of color vision or color blindness behavioral experiments are necessary. There are two earlier studies which strongly indicate that fur seals and sea lions are able to discriminate blue and green from many finely tuned shades of grey (Busch & Dücker, 1987; Griebel & Schmid, 1992). Thus, there is a discrepancy between the results of cellular and molecular-genetic studies, and the behavioral data (Griebel & Peichl, 2003). As a solution it was proposed that the signals of M/L-cones are compared with signals of rods. Assuming that rods work at lower light levels, recent behavioral experiments have been performed under conditions which are mesopic for humans (Scholtyssek & Dehnhardt, 2013; Scholtyssek, Kelber, & Dehnhardt, 2008; Scholtyssek, Kelber, & Dehnhardt, 2015). The authors investigated the brightness discrimination ability of one harbor seal (*Phoca vitulina*) and one South African fur seal (*Arctocephalus pusillus*) in a first step. This is necessary because it has to be excluded that the animals discriminate on the basis of brightness instead of color. They found that harbor seals and fur seals were able to discriminate brightness differences of 14% and 8–10%, respectively. In subsequent tests for color vision harbor seals were unable to discriminate blue and green of equal brightness. Furthermore, one harbor seal responded to these colors as "equal" in a "same-different" task (Scholtyssek et al., 2015). Thus, under "mesopic" conditions seals behaved as if color blind.

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In our behavioral training experiments performed with two harbor seals (*Phoca vitulina*) and two fur seals (*Arctocephalus pusillus*) we worked under various natural daylight conditions outdoors between bright sunlight and overcast sky using surface colors. The animals had to perform an object detection task: they were trained on a triangle in grey surround on one test field, while the other two test fields were homogeneously grey. To be certain that color is not confounded by brightness cues, we tested at first grey triangles in grey surround and later blue, green, yellow and orange triangles again in grey surround. We found that the animals did not have problems in detecting the colored triangle even in situations with minimal or zero luminance contrast. Thus, under photopic illumination conditions and using an object-detection task seals show color vision.

2. Material and methods

2.1. Animals

Two harbor seals (male Fridolin, 9 years old, and female Angie, daughter of Fridolin, 1.5 years old) and two South African fur seals (male Otti, 8 years old and female Nabi, two years old; age data refer to the beginning of the experiment) were trained in Frankfurt Zoo between 2008 and 2014. The harbor seals were kept in an open air enclosure of 350 m^2 with a water basin of 400 m^3 and 10 × 18 m surface area. They lived in a group of 5 animals: one male, 3 females and 1 young. The enclosure of the fur seals had a size of 450 m^2, and a basin of 800 m^3 with a surface area of 8 × 30 m. The male Otti was kept with 5 females and 2 young males. The training experiments were in accordance with the EU directive for animal experiments.

2.2. Setup

The three test fields were presented on a vertically oriented dark grey plastic board (88 cm long, 36 cm height) standing on the land part of the enclosure (Fig. 1a). The test field folia (DIN A4) were inserted in three U-shaped frames (22 cm vertical, and 24.5 cm horizontal) from above and their position could be easily changed after each trial in random order. At a "target", a tennis ball attached to a stick, the animals could be stationed after each trial. Whereas the two harbor seals and the female fur seal were trained and tested on the enclosure visible to the visitors of the Zoo, fur seal male Otti was trained behind the scene (Fig. 1b). For him each of the three test fields was presented on a separate hanger next to each other on the fencing at a height of about 1 m. The target on which the animal was stationed after each trial was 3 m away. From this position the seal could not see the test fields while their position was changed.

2.3. Stimuli

To investigate the capacity for brightness detection we printed a grey triangle of variable brightness in grey surround of medium brightness. This was the positive stimulus rewarded with fish. The other two (negative) test fields showed a homogeneously grey field of the same size and brightness as the surround of the triangle (width: 21 cm, height: 15 cm). The grey steps were selected using CorelDRAW 11. The HSB color model was used, characterizing color by hue (H), saturation (S) and brightness (B). The grey fields had the values H/S/B = 0/0/60, the triangles H/S = 0/0, and B = 10, 25, 38, 49, 51, 57, 59, 61, 63, 65, 73, 80, 87 and 90. Using Adobe Photophop CS2 the edges of the triangles were slightly blurred (Gaussian blur 20 pixels) to prevent possible border contrast due to printing. The patterns were printed on Digital Color Printing

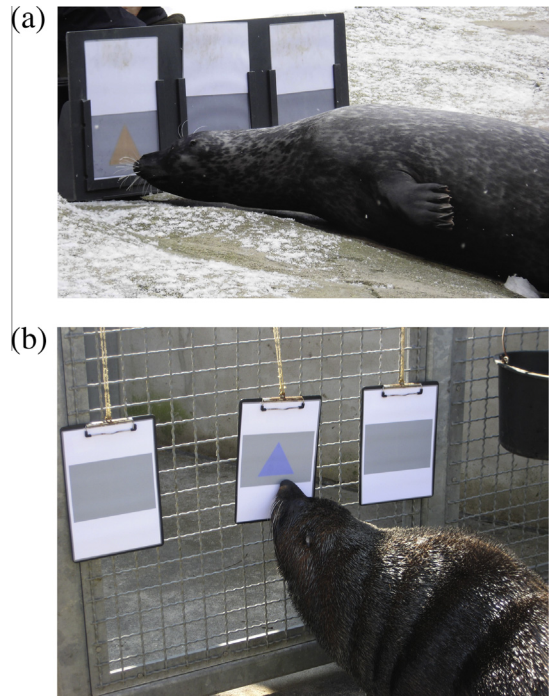

Fig. 1. (a) Harbor seal male Fridolin touching the folia presenting the triangle with his mouth. The other two test fields show a homogenously grey field, (b) fur seal Otti choosing the correct test field. The female Nabi was trained and tested with the same apparatus as the two harbor seals. Here the apparatus was standing higher up, ca. 30 cm above the ground.

paper (Claire fontaine 100 g/m^2) using an Epson Stylus Photo EX printer. To protect the prints, the folia were laminated (A4 Matt-Pouch, GBC9). This also reduced the fluorescence peak at 440 nm. In the tests for color vision the triangle was blue, green, yellow or orange, in grey surround. The CorelDRAW values of these colors were as follows. Blue: H/S/B = 240/100/60; green: H/S/B = 120/100/20, 30, 40, 45, 48, 50, 51, 52, 55, 60, 70, 80, 90, 100; yellow: H/S/B = 60/100/0, 10, 20, 30, 40, 45, 47, 48, 49, 50, 51, 52, 53, 55, 60, 70, 80, 90, 100; orange: H/S/B = 0/100/10, 15, 20, 25, 30, 35, 40, 45, 47, 48, 49, 50, 51, 52, 53, 54, 55, 60, 65, 70, 80, 85, 90, 100. The blue triangle was presented in grey surround of variable brightness, whereas for practical reasons the green, yellow, and orange triangles varied in brightness and were surrounded by constant grey (H/S/B = 0/0/60). The homogeneously grey test fields, used as negative stimuli, were equally bright as the grey surround of the triangle. The spectral reflectance of all grey steps and triangles were measured between 350 and 700 nm in steps of 1 nm using a spectroradiometer (Instrument Systems, Spectro 320). The spectra are shown in Fig. 2a. In addition, the luminance values Y were noted, given by the spectroradiometer. This photometric unit is based on the human V_λ-function. It was used because its λ_{max} (555 nm) is very close to that of the cone sensitivity function of harbor seals (552 nm) (Fig. 2b). Furthermore, it allows comparison with the results of other studies.

2.4. Illumination

Due to the specific conditions of a Zoological Garden the animals had to be trained outdoors under different weather conditions. As natural daylight is variable we measured the spectral radiance flux of the illumination at the beginning of the experiments. For practical reasons and because we did not find any difference in the results under direct sunlight or overcast sky we stopped these measurements after some time. In Fig. 2b some