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HOW A HARBOR SEAL SEES THE NIGHT SKY

BJÖRN MAUCK
University of Bochum,
General Zoology & Neurobiology,
ND 6/33, D-44780 Bochum, Germany
E-mail: mauck@neurobiologie.ruhr-uni-bochum.de

DANIEL BROWN
WOLFHARD SCHLOSSER
University of Bochum,
Astronomical Institute, NA 7/67, D-44780 Bochum, Germany

FRANK SCHAEFFEL
University Eye Hospital Tübingen,
Section of Neurobiology of the Eye, Department II,
Calwerstr. 7/1, D-72076 Tübingen, Germany

GUIDO DEHNHARDT
University of Bochum,
General Zoology & Neurobiology,
ND 6/33, D-44780 Bochum, Germany

ABSTRACT

Astronavigation is a possible mechanism of offshore orientation in marine mammals. However, the basic prerequisite for astronavigation is to see enough stars of the night sky. This cannot be taken for granted in seals as, due to adaptations of their dioptric apparatus to the optical properties of water, seals are supposed to be myopic and astigmatic when out of the water under low light conditions. Using various real and artificial stars in a go/no-go response paradigm we therefore determined the minimum brightness at which a harbor seal (*Phoca vitulina*) can detect stars. The dark-adapted seal was trained to look through an empty tube ("seal telescope") and to retract its head only when a star appeared at the opposite aperture. The seal reliably detected Venus or Sirius becoming suddenly visible when the telescope was moved across the night sky. Detection thresholds were determined using artificial stars (parallel light identical to starlight coming from the universe) of predefined brightness generated by an optical system installed in front of the seal's telescope. The seal detected artificial stars down to 4.4 stellar magnitudes. Although these results cannot present evidence for astronavigation, they imply that seals should see enough stars to allow such orientation mechanisms.

Key words: harbor seal, *Phoca vitulina*, vision, orientation, astronavigation.

On open seas, orientation is a major problem. In the rather featureless marine environment, humans find it difficult to obtain information about their own position relative to their goal and, thus, the direction in which to move is not easily determined. Without other salient landmarks available, heavenly bodies like the sun, the moon, and the stars can be reliably used in celestial navigation.

For animals, evidence for celestial orientation has accumulated mainly for birds (*e.g.*, Kramer 1953, Sauer 1957, Moore 1978, Able 1990, Schmidt-König 1990, Phillips and Moore 1992, Mouritsen and Larsen 2001) and insects (*e.g.*, Gould 1980, Wehner and Lanfranconi 1981, Rossel 1993, Dickinson 1994). Here, celestial orientation means both determination of compass direction by the sun or the skylight polarization pattern and usage of star constellations or lodestars during night travel to keep direction (Emlen 1967*a*, *b*, 1975; Wiltschko and Wiltschko 1978; Wehner 1984; Able and Able 1990; Mouritsen and Larsen 2001). In animals, only determination of compass direction has been found up to now, while position fixing as latitude and longitude on a bi-coordinate grid, as has been suggested for magnetic orientation in sea turtles (Lohmann and Lohmann 1996), is yielded only from technical astronavigation applied by humans.

Celestial information could be especially advantageous for animals facing rather unstructured environments like the oceans. Various marine animal species are capable of long passages across featureless seas during migration, foraging trips, or even homing after experimental displacement (*e.g.*, Kenyon and Rice 1958, Herrnkind and Kanciruk 1978, Lockeyer and Brown 1981, Ridgway and Robinson 1985, Quinn 1994, Lohmann and Lohmann 1996, Papi and Luschi 1996). Although harbor seals are not considered an offshore species, they regularly travel distances up to 45 km from their haul-out sites on feeding trips of up to six days duration (Thompson and Miller 1990, see also Lésage *et al.* 2004 for a report on seasonal migration in harbor seals). Although rather inshore, the positions found in these studies nevertheless were certainly out of sight of terrestrial landmarks, at least at night. As the skies over many coastal marine habitats are often heavily overcast for days or weeks at a time, pinnipeds may use celestial information if available, although they cannot solely depend on it while orienting at night. However, many pinniped species hunt at night (Hobson 1966), probably feeding in response to nocturnal changes in the vertical distribution or schooling behavior of their prey (Trillmich and Mohren 1981, Croxall *et al.* 1985, Thompson *et al.* 1989). Thus, harbor seals should be able to navigate without salient terrestrial landmarks and star navigation is one possibility.

However, a prerequisite for celestial navigation is the perception of the respective stimuli. While the sun and the moon are sufficiently large ($\sim 32'$) and bright enough to be seen by many marine animals, evidence for the perception of polarized light only exists for some birds, insects, fishes, and marine invertebrates. Similarly, while the above cited behavioral evidence that some migrating birds use the night sky for navigation certainly proves that these animals can see the stars, detection of these comparable faint ($\leq 93.28 \times 10^{-9}$ W/m^2, *i.e.*, light flux of the brightest star, Sirius) and point-like ($\leq 0.04''$, *i.e.*, interferometrically determined diameter of the largest measured star, α Sco) light sources could be a problem for marine animal eyes adapted to the aquatic environment and not well-suited for aerial vision (*e.g.*, sea turtles, Ehrenfeld and Koch 1967, Akesson 1996, Lohmann and Lohmann 1996).

For pinnipeds there is some evidence for good daylight visual acuity both underwater and in air. Schusterman and Balliet (1970*b*) reported harbor seals and Steller sea lions to be capable of resolving gratings presented under water with grating periods subtending visual angles of $5'$ to $9'$. Both underwater and aerial visual acuity of a California sea lion was found to depend on luminance, but deterioration of visual resolution with decreasing light was much stronger in air than under water (Schusterman and Balliet 1971). In fact, anatomical examinations of marine mammal eyes demonstrated modifications which certainly can be attributed to the primary demand of underwater vision (Kröger and Kirschfeld 1993). Having roughly the same refractive index as sea water, the cornea and encased fluids of a marine mammal eye become optically ineffective under water and the refractive power is restricted to the lens. Similar to fishes, most pinnipeds and cetaceans evolved a large almost spherical lens (Walls 1942, Jamieson and Fisher 1972), resulting in emmetropia or slight hyperopia under water. Regaining its refractive power in air the cornea should produce severe myopia and—due to strong curvature differences probably improving ocular streamlining (Jamieson 1971)—and extreme astigmatism unknown in other mammals. Piggins (1970) found a significant difference between the refraction of the harp seal eye in air and under water, confirming the findings of Walls (1942) that the astigmatism is primarily corneal. This corneal astigmatism could be corrected for aerial daylight vision by a pupil forming a narrow vertical aperture (inverted drop form) parallel to the axis of least astigmatism (Johnson 1893).

Thus, while marine mammal visual resolving power might be sufficient under water and in air under bright illumination, they might suffer from myopia and astigmatism when above the water surface at night. It was therefore particularly unclear whether these animals see enough stars to allow for astronomical navigation. We therefore determined the seal's detection threshold for stars of different stellar magnitudes.

Methods

Test Animal

The test animal was a 4-yr-old male harbor seal named "Nick." Nick was also the subject in the study by Dehnhardt *et al.* (2001), but was experimentally naive concerning visual tasks. There was a routine food deprivation of about 10 hr between the last feeding in the early afternoon and the experiments during the night. To reduce light pollution and to be sure that the seal's eyes were dark adapted, experiments were performed in dark, mainly cloudless nights between midnight and 0300, when nearly all of the lights of the surrounding city quarters were off.

Test Apparatus and Experimental Procedure for Tests with Real Stars

The seal could observe the night sky through a telescope-like device consisting of a tube (length: 1 m, inner diameter 150 mm, angular field of view 8.578°, inner walls painted black, no lens system) installed on a carriage in the shallower part of the pool (Fig. 1). Traversing and turning the apparatus, the upper aperture of the tube moved across the sky. The seal could stick its head into the tube's lower aperture thereby tightening the tube with its neck against incoming light from below, which also avoided unintentional cueing by the experimenter. A sighting mechanism consisting of two crosshairs and a magnifying mirror enabled the experimenter to watch the segment of the sky at which the apparatus was aiming. A circle on the mirror allowed the experimenter to decide which celestial objects came into the seal's view. With both crosshairs aligned, all objects inside the circle were also visible to the seal.

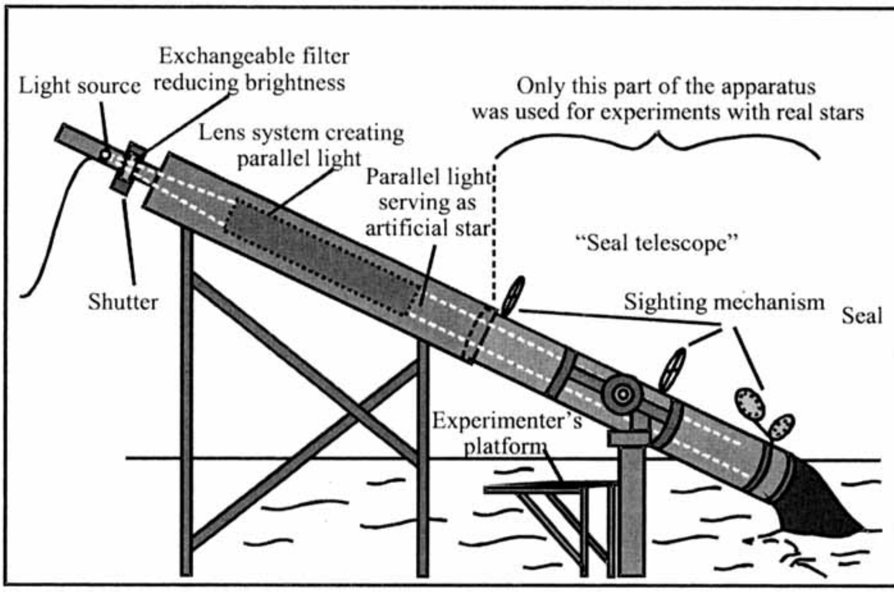

Figure 1. Schematic drawing of the experimental set-up. The lower part of the apparatus used for testing detection of real stars was modified for threshold determination by additional installation of an optical device for presentation of artificial stars (see Methods).

Experiments were performed using a go/no-go response paradigm. The experimenter started a trial by aligning the tube to a dark sky segment in the neighborhood of a test star and sent the seal to the tube's lower aperture. Now the tube was slowly traversed such that the upper aperture moved across the night sky. While moving the upper aperture in different ways and directions over the sky, care was taken that no other star than the one to be tested came into view. Due to the unavoidable light pollution of the city sky, only the bright stars of the night sky were visible in most of the nights used for testing. As far as available it was also helpful to use parts of the sky in the neighborhood of the star to be tested that were rather dark due to being partly occluded by clouds. The seal had to follow the movement of the apparatus with its head in the tube. The seal had to retract its head from the tube and press a response paddle as soon as a star appeared. In non-stimulus trials the tube was moved across a dark segment of the sky ("catch trials"); here, the seal had to remain in the tube for 10 s. Correct responses were rewarded by fish pieces. Typically, 30 trials were conducted per session. Depending on the weather and on the position of the stars to be tested, up to three sessions were conducted in clear dark nights. Stimulus trials and catch trials were balanced over a session. Sessions were composed according to pseudo-random schedules concerning the sequence of trials with and without stimulus.

Threshold Determination Using Artificial Stars

The seal's detection threshold in stellar magnitudes was determined using artificial stars of different brightness. The apparatus was modified for the generation of the kind of light reaching the earth from the stars by projecting a beam of parallel light through the tube's upper aperture (Fig. 1). For this purpose, a telescope (f = 159 cm) was installed upside down in front of the tube's upper aperture. The ocular optics were replaced by a light source with a reed switch and a filter ($\lambda = 480–680$ nm). Another filter with a miniature aperture between the light source and the telescope optics reduced the light source to pinhole size. The light's passage through the inverted telescope optics created a beam of parallel light identical to the starlight coming from the universe. Thus, to a human eye there was the impression of a real star at the upper end of the tube but no diffuse increase of brightness in the otherwise dark tube. Various gray filters could be placed between the light source and the telescope optics thereby dimming the light source in predefined steps. A small sheet of thin opaque metal could be placed in front of the gray filter thereby serving as a removable shutter in the light path.

The apparatus was fixed in a position in which it was comfortable for the seal to place its head in the tube. For a stimulus trial a gray filter corresponding to the stellar magnitude to be tested was placed in the apparatus. The path was shut by placing the metal sheet in front of the gray filter. Now the light source was switched on and the seal was sent to the tube. After 5–10 s (interval arbitrarily chosen) the metal sheet was removed. As soon as the artificial star appeared the seal had to retract its head from the tube and press the response paddle. During "catch trials" the light source remained switched off and thus no artificial star appeared when the shutter was opened. In these trials, the seal had to stay in the tube for a further 10 s. Again, correct responses were rewarded by fish pieces. 30 trials were typically conducted per session; up to three sessions could be conducted per night. Stimulus trials and catch trials were balanced over a session; sessions were composed according to pseudorandom schedules concerning the sequence of trials using different gray filters and of stimulus trials and catch trials.

Calibration of Artificial Stars

The brightness of the artificial stars was calibrated against real stars. The apparatus was installed on the roof of the Astronomical Institute, University of Bochum. Digital images of each artificial star were recorded using a 2,048 × 2,048 pixel AT200 Photometrics CCD Camera System with a filter (480 nm–680 nm) in front of a 50-mm Nikon lens. Comparison images of the night sky were taken of the region around Cassiopeia near the zenith, including the four stars α Cas (2.2 mag), β Cas (2.3 mag), δ Cas (2.7 mag) and ε Cas (3.4 mag) used for calibration. Before and after the observations we took calibration images ("bias") to determine the CCD camera's dark current (offset from zero current) which was subtracted from every recorded image.

The IRAF reduction-package for astronomical images (National Optical Astronomy Observatories, Tuscon, AZ) was used for data analysis. The flux of every star was determined using aperture photometry. The radius of the aperture was chosen to be six times the full-width-at-half-maximum of the star. Given the brightness of the background and the integration times of the images, individual flux values were determined for every artificial and the four calibration stars. Given the magnitudes of the four calibration stars, the measured flux values of the artificial stars were transformed into stellar magnitudes.

Results

Testing with Real Stars

The seal's detection of bright heavenly bodies was tested during 26 sessions. Venus, the brightest heavenly body besides the sun and the moon, can be regarded as

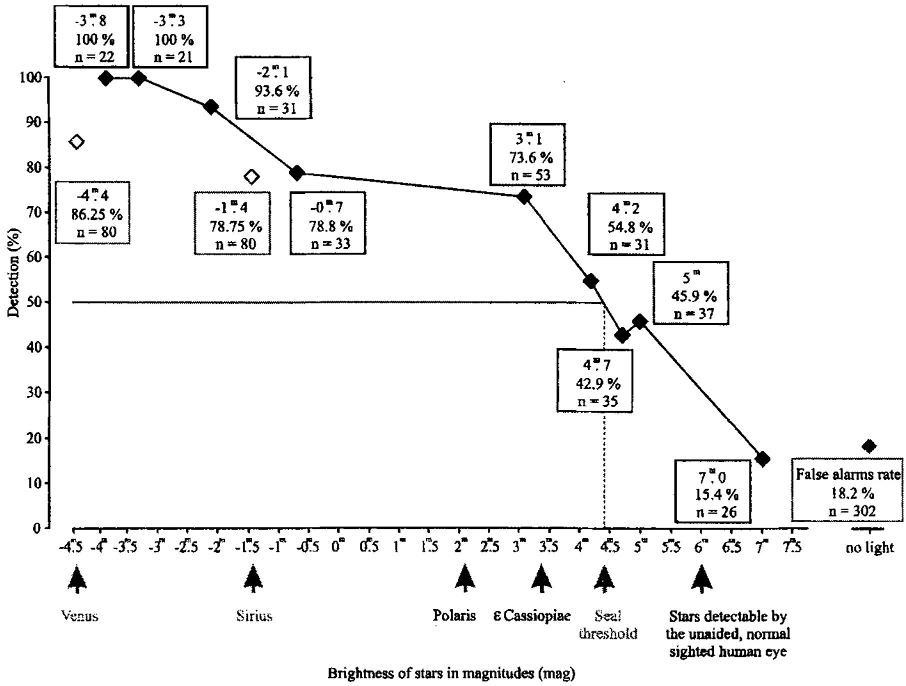

Figure 2. Detection of real and artificial stars of different brightness by our harbor seal. Detection (%) is plotted against brightness of stars (stellar magnitudes). Detections of Venus and Sirius (open gray diamonds); psychometric function for artificial stars (black diamonds); threshold value (defined as stimulus intensity the seal detected in 50% of presentations) determined as interpolation between the last value above threshold and the first value below threshold (stippled gray line); false-alarm rate (filled gray diamond).

a stimulus similar to a very bright star and was used as first stimulus. Sirius, the brightest star in the sky was used as second stimulus. However, as sessions were performed in nights of differing sky brightness, and sometimes stars were occluded by a thin layer of clouds, even these bright heavenly bodies did not represent stimuli of constant intensity. Nevertheless, detection rate for both Venus and Sirius was calculated from 80 stimulus presentation trials that were considered to be of comparable respective stimulus intensity due to similar experimental conditions. Detection rate for Venus (86.25%) and Sirius (78.75%) are plotted against star brightness in magnitudes in Figure 2 (open gray diamonds). Detection of both stimuli differed significantly from chance (χ^2 test, $P < 0.05$). As it was sometimes difficult to decide whether or not another star had come into the seal's view when the seal reacted during catch trials, a false-alarm rate was not determined here.

Determination of the Seal's Detection Threshold for Artificial Stars

Because stimulus intensities were not completely constant during experiments with real stars, absolute detection thresholds were determined using artificial stars as described above. Percentage of detections was calculated from at least 20 trials with every stellar magnitude to be tested, this way nine stimulus intensities were tested (*i.e.*, −3.8 mag, $n = 22$; −3.3 mag, $n = 21$; −2.1 mag, $n = 31$; −0.7 mag, $n = 33$; 3.1 mag, $n = 53$; 4.2 mag, $n = 31$; 4.7 mag, $n = 35$; 5 mag, $n = 37$; 7 mag, $n = 26$). False-alarm rate was determined as percentage of reactions without stimulus (*i.e.*, no light, $n = 302$, filled gray diamond in Fig. 2). Detection rate for each artificial star was plotted against stimulus intensity (stellar magnitudes) (Fig. 2, black diamonds) and detection threshold was determined by linear interpolation between the last stimulus intensity above and the first intensity below 50% detections (Fig. 2, stippled gray line). The seal's detection threshold for artificial stars was calculated to be 4.4 mag.

Discussion

Experiments with Venus and Sirius showed that our harbor seal could see these bright heavenly bodies. However, due to varying background brightness of the night sky and due to being sometimes partly occluded by high clouds, these "stars" in fact did not represent stimuli of constant intensity. Furthermore, it was sometimes difficult to decide whether or not another star had come into the seal's view when the seal reacted. Therefore, a false-alarm rate was not determined for these experiments and detection rate for Venus and Sirius might be contaminated by an undefined rate of spontaneous reactions. Results of these experiments therefore demonstrated the seal's capability to see some real stars, but had to be confirmed by tests with stimuli of reproducible and constant intensity. This was done in the experiments with artificial stars, which showed that our harbor seal detected the light emitted from celestial objects as faint as 4.4 stellar magnitudes.

The light coming from stars enters the earth's atmosphere in parallel rays and thus seems to come from infinity. The dioptric apparatus of a normal sighted human eye focuses these rays on the retina resulting in the impression of a miniature spot of light. Because all stars—except for the sun—are too far away and are therefore too small in diameter to be seen as objects of defined extension, our perception of a star's apparent size depends solely on the flux of light reaching the retina. Whether or not a star is seen thus depends mainly on its brightness against its background in the sky (Riggs 1965, Schaefer 1990, Garstang 2000).

Besides these environmental factors, detection of stars depends on the eye. For a typical normal-sighted human the zenith limiting magnitude is 6.05 mag against a sky of typical brightness (136 mμl), however, observations with magnitudes as faint as 8.9 mag were also reported (Schaefer 1990 and references therein). Both light sensitivity and the eye's visual resolution will be critical for detection of a star.

However, it is common experience that detection of stars is impaired by myopia which is easily simulated by observing the night sky through a magnifying glass. For harbor seals, Johnson (1893) studied the aerial refraction under cycloplegia and found 4 diopters of myopia in the vertical meridian and 13 diopters in the horizontal, resulting in 9 diopters of astigmatism, which should make well-focused retinal images of stars rather impossible. Piggins (1970) confirmed a strong myopia and corneal astigmatism for aerial vision in a refraction study under cycloplegia on a harp seal (*Pagophilus groenlandicus*), and Wilson (1970) found comparable results for a Weddell seal (*Leptonychotes weddellii*). Although aerial and underwater visual acuity of some pinniped species was found to be 5′–9′ under moderate illumination (Schusterman and Balliet 1970*a*, *b*, 1971; Busch and Dücker 1987), this seems to be grossly reduced by darkness, rendering the visual acuity of a sea lion at low light

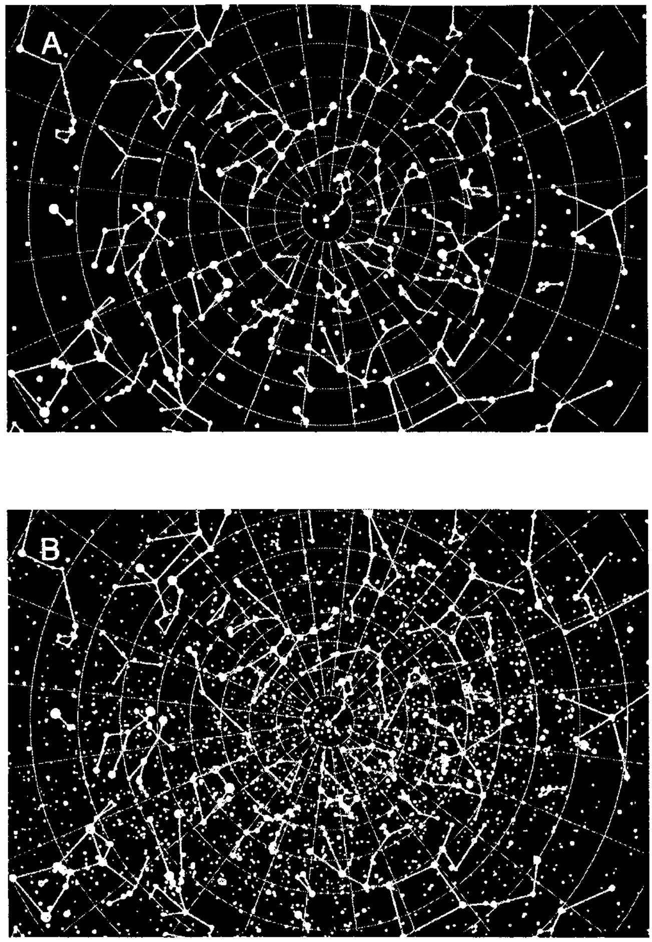

Figure 3. Schematic star chart of the central part of the northern night sky (star constellation figures and equatorial grid are included to allow orientation). (A) Stars that can be seen by a harbor seal given that stars down to a stellar magnitude of 4.4 mag can be detected. Stars are presented here as point-like light-sources, however, due to possibly being out of focus a seal might perceive the stars as blurry discs of different brightness. (B) Starry sky as seen by a normal-sighted human.

levels (10^{-4} ml) to less than that of a rat under moderate luminance (20′–36′, Schusterman and Balliet 1971). However, other studies on marine or amphibious animals shed some doubt on the earlier view of lacking accommodation to correct for the refractive loss of the cornea in water, resulting in either underwater hyperopia (assuming emmetropia in air) or aerial myopia (assuming emmetropia in water) (Howland and Sivak 1984, Murphy *et al.* 1990). There might be an unknown mechanism that compensates for aerial myopia and astigmatism under dark conditions and thus enabled our harbor seal to detect stars of the given magnitude. However, our present experiments were not intended to reveal such possible mechanisms, we rather wanted to know if seals see enough stars to allow astronavigation. We therefore propose that the question of aerial myopia and corneal astigmatism should be reexamined in seals. Corresponding experiments using photorefraction are currently being carried out in our lab.

The other important factor in detecting stars against a slightly darker night sky should be the eye having sufficient light sensitivity. Whereas differential thresholds of seals for the detection of light against backgrounds of various brightness have not been determined yet, Levenson and Schusterman (1999) determined dark adaptation rates and absolute light sensitivities in a comparative study with three seal species and humans. Their elephant seal reached a very fast complete dark adaptation and showed a significantly higher light sensitivity than a California sea lion and a harbor seal. However, even the shallow-diving pinnipeds showed a quicker dark adaptation rate and a higher light sensitivity than humans. This might enable seals to detect stars even if these spot-like light sources are not well-focused on the retina but imaged as blurry areas of light that would not be detected by a myopic eye of lower light sensitivity. However, even if stars were seen as blurry areas of light in the night sky which sometimes could not be separated from each other, the resulting light pattern would be characteristic and reliable, and thus well-suited for orientation.

Given that seals see stars down to a stellar magnitude of 4.4 mag, the stars of the northern night sky visible to a traveling seal are presented in Figure 3A. In contrast to that, normal-sighted humans see stars as faint as 6 stellar magnitudes resulting in a rather confusing night sky similar to that presented in Figure 3B. The present experiments were not intended to reveal the possible mechanisms of astronavigation and our psychophysical results clearly cannot show that seals actually use the starry sky for orientation, but they are an important empirical first step towards testing for celestial navigation. In fact, the question remains how the information inherent in the night sky could be used by seals. In the light of the present psychophysical results, we are currently preparing appropriate experiments to test the usage of star patterns for orientation.

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