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Brightness discrimination in the harbor seal (*Phoca vitulina*)

Christine Scholtyssek [a], Almut Kelber [b], Guido Dehnhardt [a,*]

[a] *General Zoology & Neurobiology, University of Bochum, ND 6/33, D-44780 Bochum, Germany*
[b] *Vision Group, Department of Cell and Organism Biology—Zoology, Lund University, S-22362 Lund, Sweden*

Abstract

The brightness discrimination ability of a male harbor seal was investigated at an ambient illumination of 0.9 lx. The visual stimuli consisted of circular gray discs that were presented on a black background on a TFT monitor. Eight standard intensities were tested against sets of lower comparison intensities. In accordance with Weber's law we observed a constant gain of the just noticeable intensity difference with increasing intensity of the standard stimulus. The calculated Weber fraction is 0.14. This result indicates that the brightness discrimination ability of the harbor seal is comparable to that of humans.
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1. Introduction

Marine mammals experience extreme low light levels while foraging at night (Hobson, 1966), but, as light even in clear ocean waters rapidly attenuates with depth (Warrant & Locket, 2004), also when diving during the day. While toothed whales compensated for poor visibility by evolving an active sonar system, this auditory specialization could not be demonstrated in the pinniped species studied so far. It has been suggested that in contrast to the fully aquatic Odontocetes it would have been a disadvantage for the amphibious pinnipeds to fully adapt their auditory system for underwater functioning (Schusterman, Kastak, Levenson, & Reichmuth, 2000; Schusterman, Kastak, Levenson, Reichmuth Katsak, & Southall, 2004). Instead, pinnipeds refined all their sensory channels in order to receive a high amount of multimodal information from their environment (Schusterman et al., 2004) which allows successful foraging and navigation. Experiments on underwater sound localization, for example, revealed that harbor seals possess a remarkably small minimum

audible angle that qualifies the auditory system to be of importance for prey detection (Bodson, Miersch, Mauck, & Dehnhardt, 2006). Furthermore, pinnipeds modified their vibrissae to function as a hydrodynamic receptor system that is assumed to be important for prey detection and navigation (Dehnhardt, Mauck, & Bleckmann, 1998b; Dehnhardt, Mauck, Hanke, & Bleckmann, 2001). Since vision is partially limited by water turbidity (Weiffen, Moeller, Mauck, & Dehnhardt, 2006), it is unclear, to what extend pinnipeds rely on visual information during foraging. The high degree of adaptation of the pinniped eye to their arrhythmic and amphibious lifestyle, however, argues for the significance of this sensory modality.

Pinnipeds adapted their visual system to function in dim light by increasing the sensitivity of the eye. On the one hand, light-sensitivity is based on the relatively big size of the pinniped eye. Big eyes allow for large pupillary dilatation which increases the amount of light focused on the retina (Jamieson & Fisher, 1971; Levenson & Schusterman, 1997; Walls, 1942; Warrant & Locket, 2004). On the other hand, the retina of the pinniped eye is densely populated with highly light-sensitive rods and almost completely subordinated by a tapetum lucidum which increases the probability of photon detection by the photoreceptors

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* Corresponding author. Fax: +49 221 97750604.
  E-mail address: dehnhardt@marine-science-center.de (G. Dehnhardt).

(Jamieson & Fisher, 1971; Walls, 1942; Peichl & Moutairou, 1998). An adaptation to the rapid changes in ambient illumination during diving is the high flexibility of the pupil. It allows for a fast adaptation to changing light levels and thus retrains the activity of the photoreceptors (Levenson & Schusterman, 1997, 1999).

The pinniped visual system does not only have to deal with a wide range of ambient brightness, but also with the different optical densities of water and air. Terrestrial mammals are hyperopic underwater, which is a consequence of the loss of the refractive power of the cornea that has approximately the same refractive index as water. In order to compensate for this, pinnipeds evolved spherical lenses (Johnson, 1893; Walls, 1942) and are therefore emmetropic under water (Hanke, Dehnhardt, Schaeffel, & Hanke, 2006). In air, however, the possession of a spherical lens leads to myopia, since light is additionally refracted by the corneal surface. Refractive measurements of the eye of harbor seals (*Phoca vitulina*) confirm myopia in air (Hanke et al., 2006). Nevertheless, it is assumed that harbor seals compensate for myopia in air by constricting the pupil to a small vertical slit which causes a stenopaic effect. This effect in turn leads to sharp vision over a wide range of distances (Walls, 1942). For other pinniped species, like the California sea lion (*Zalophus californianus*), emmetropia in air is generated by a flattened corneal window located in the central part of the cornea (Hanke et al., 2006; Johnson, 1893; Walls, 1942).

A psychophysical investigation by Schusterman and Balliet (1970) on the visual acuity of a harbor seal and a California sea lion confirmed sharp vision for pinnipeds under water. Their results indicate that the spatial resolution of the pinniped eye is comparable to that of terrestrial mammals, such as the cat, that have sharp vision. The visual acuity of the harbor seal in air still needs to be investigated, but an experiment with a Steller sea lion (*Eumetopias jubatus*) indicates a high resolving power of the pinniped eye in air (Schusterman & Balliet, 1971). However, the visual stimuli used to determine visual acuity consisted of high contrast gratings whereas in nature much lower contrasts between objects and background exist. Hendley (1948) demonstrated that the visual acuity of humans depends on the contrast between object and background. He showed that increasing the contrast above threshold improves the identification of details to some extend. Thus, in order to evaluate which details of a natural scene pinnipeds are able to resolve, data on their visual acuity per se are not sufficient, but have to be considered with respect to their brightness discrimination ability. The ability to detect small contrasts is not only important for spatial resolution, but also for the detection of movements and the identification of movement directions e.g. of prey (Buser & Imbert, 1992). Furthermore, knowledge about the brightness discrimination ability is important for the elimination of intensity cues in experiments dealing with color vision—a characteristic of the pinniped visual system that is not well investigated yet.

Very little is known about brightness discrimination in general. Psychophysical studies on humans adapted to the respective light level showed that their brightness discrimination threshold decreases with increasing light intensity. At high luminance values this decline becomes smaller until it reaches a relatively steady value (Craik, 1938; Hecht, Peskin, & Patt, 1938; Steinhardt, 1936). As demonstrated by Craik (1938), this relation only holds when the intensity of the reference stimulus matches the intensity the subjects are adapted to. Craik (1938) showed that the difference threshold does not solely depend on the state of adaptation, but also on the test or reference luminance to which the eye responds. The difference threshold is lowest when test and the background intensity the subjects were adapted to coincide, but raises drastically when the background intensity largely exceeds the test intensity and vice versa.

For pinnipeds and other mammals, the relation between the state of adaptation and brightness discrimination threshold still needs to be investigated. Furthermore we know little about the mechanisms that influence the capability to detect brightness contrasts, especially at high ambient illumination. At low ambient illumination, contrast vision depends on the number of photons that are detected by the photoreceptors. Thus improving the sensitivity of an eye enhances the ability to detect contrasts at low light levels (Land & Nilsson, 2002; Warrant & Locket, 2004). According to this it is likely that pinnipeds possess a high sensitivity for brightness contrasts in dim light.

To date, the only experiment dealing with brightness discrimination in pinnipeds was accomplished by Busch and Dücker (1987) with two species of fur seals (*Arctocephalus pusillus* and *Arctocephalus australis*). In their experiment, the animals had to discriminate between different shades of gray in a two alternative forced choice task. Unfortunately, Busch and Dücker did not have the possibility to control the level of ambient illumination during their experiments. Therefore, their results are not representative for an adaptation to a defined ambient illumination.

In the present study, the brightness discrimination ability of a harbor seal was investigated. Since it cannot be excluded that the brightness discrimination threshold of pinnipeds, like that of humans, depends on the state of adaptation, all experiments were accomplished at a constant ambient illumination.

2. Materials and methods

2.1. Subject

The experimental animal 'Luca' was a 4-year-old male harbor seal. The subject was kept together with eight other seals at the Marine Science Center (MSC, Zoo Cologne, Germany) since 2003. As Luca previously served as a subject in a study on visual size discrimination (Anais Bodson, unpublished data), he was experienced in performing visual discrimination tests. The results indicated that Luca is normal sighted. In the present study, the animal received approximately 80–90% of its daily diet (2–4 kg of herring and sprat) during experimental sessions. Tests were carried out twice per day on 5–6 days per week.

2.2. Apparatus

All experiments were performed in air in a dark chamber (3 m deep, 2 m wide, 2 m high) provided with an illumination box (1 m × 1 m) at the ceiling (Fig. 1). This illumination box contained 60 white LEDs (Conrad, Telux LED TLWW 7600; spectral distribution: 400–800 nm) and was powered by an adjustable constant current source (Voltcraft, type 3610). It served to produce a constant and equally distributed illumination of 0.9 lx (measured with a light meter, MS-1300, Voltcraft) in the area surrounding the experimental apparatus. This is equivalent to a luminance level of 0.5 cd/m^2 (measured with a luminance meter, SL-110, Minolta). This luminance value corresponds to the lower range of human mesopic vision (van Hateren & Snippe, 2006). The adaptation to the lower mesopic range facilitates the use of the brightness discrimination data in color vision experiments that will be accomplished in a subsequent study at the same ambient illumination.
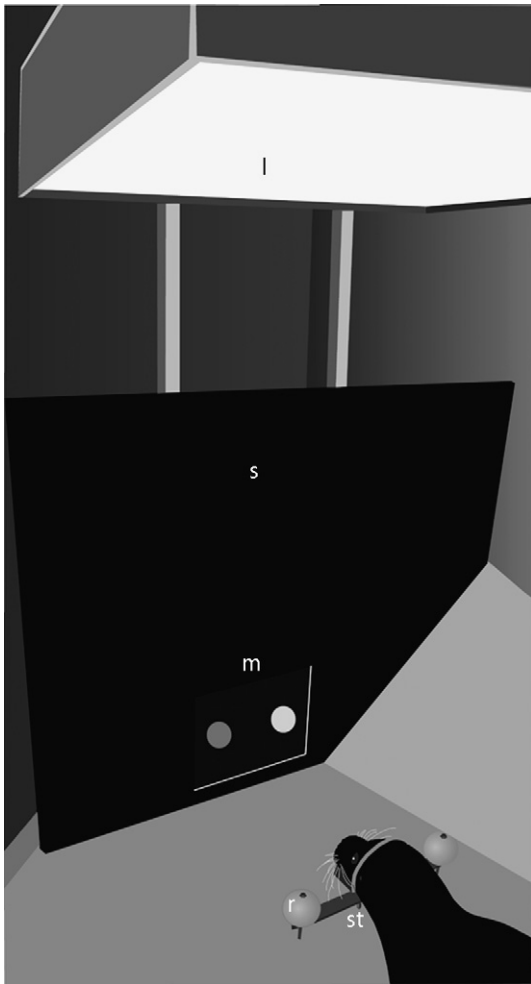

Fig. 1. Experimental apparatus: The stimulus pairs were presented on a 18 inch sized TFT monitor (m), placed behind an adequately sized window cut into a black screen (s). The screen served for the experimenter to hide from the animal's view in order to prevent any unintentional cueing. The animal stationed in front of the monitor by placing its head in a hoop fitting the seals head circumference and touching a small plastic ball located at the anterior part of the hoop station (st) with its lower jaw. Two response targets (r) are connected to the hoop station. The area surrounding the experimental apparatus is illuminated by a one square meter sized illumination box (l).

The stimuli were presented on an 18 inch TFT monitor (Eizo, FelxScan L 685) which was placed behind a correspondingly sized window cut into a 90 cm high and 110 cm wide black screen. The screen allowed the experimenter to hide from the seal's sight in order to avoid any unintentional cueing. The experimenter could observe the animal's behavior through a one-way mirror that was placed outside of the animal's field of view.

As the brightness contrast of a TFT monitor varies with the seal's perspective, an animal station guaranteed that the seal looked at the stimuli always from the same position. This station consisted of a metal hoop exactly fitting the girth of the seal's head and was installed at a distance of 50 cm from the center of the monitor. It was mounted to a steel-plate (10 cm long, 4 cm wide, 7 cm high) which was fixed to the floor, with its longitudinal axis perpendicular to the monitor. At the side of the plate facing the monitor there was a little plastic ball serving as a jaw station for the animal. The seal was trained to push its head into the hoop and to press the tip of its lower jaw to the jaw station. This guaranteed that the optical axis of the animal was perpendicularly oriented to the monitor. At a distance of 10 cm a response target was mounted to each side of the hoop station. The seal could easily reach the response targets after pulling its head from the hoop station.

2.3. Stimuli

The stimulus pairs presented on the monitor were generated in Power-Point (Microsoft). Each stimulus pair consisted of two circular gray discs each of 6.3° in width, separated by 16° (center to center) on a black background. The two discs differed in intensity which was achieved by varying the transparency of a white circular disc on a black background. This procedure guaranteed that the spectral distribution and thus the color of all shades of gray was identical. Therefore the different shades of gray were only characterized by the total amount of photons emitted. All stimuli, featuring the range of luminance they can be assigned to, are listed in Table 1. A luminance meter (Minolta, type SL-110) was used to measure the luminance of all standard stimuli (marked bold in Table 1), whereas the relative intensity of the stimuli was measured using a spectrometer (Ocean Optics, USB 2000). Due to the relative intensity calibration of the spectrometer, absolute intensity measurements could not be accomplished. For this reason a conversion of the measured raw data into radiometric units has been set aside and all intensities are given as the sum of counts detected by the spectrometer (i.e. the integral over the total emission spectrum of a stimulus).

Due to an inhomogeneous illumination of the TFT monitor, an intensity calibration has been conducted, guaranteeing that the intensity of each particular shade of gray remained the same, irregardless at which monitor side the stimulus was presented.

As the intensity within one stimulus disc varied by a maximum of 2%, only contrasts between standard stimulus and comparison stimulus exceeding 2% were used (see Table 1).

2.4. Pretest

In order to define intensity steps that are fine enough to determine a discrimination threshold, a pretest was conducted. Eight stimuli with a transparency ranging from 20 to 60% (Luminance 16–4 cd/m^2) were chosen for the pretest. These are marked bold in Table 1. In one session just one of the eight shades of gray was presented in a randomized order four times against the other seven shades of gray, while the seal always had to indicate the position of the brighter stimulus. In this pretest the animal could significantly discriminate all eight stimuli from each other.

2.5. Procedure

In the actual experiment, all of the stimuli used in the pretest, except stimulus No. 30, were used as standard stimuli. For every standard stimulus, the next darker stimulus that the animal could discriminate in 90–100% from the

Table 1
30-part series of gray stimuli: The stimuli used for the pretest are marked bold and were used as standard stimuli in the experiment (except stimulus No. 30)

No. stimulus	Luminace [cd/m^2]	No. stimulus	Luminace [cd/m^2]
1	16	**16**	7
2		17	
3		18	
4	14	19	
5		20	
6		**21**	6
7	12	22	
8		23	
9	10	24	
10		25	
11		**26**	5
12	9	27	
13		28	
14		29	
15		**30**	

All standard stimuli are provided with their luminance values.

standard stimuli in the pretest was determined. Within this range the brighter stimuli (standard stimuli) were tested in smaller intensity steps against darker shades of gray (comparison stimuli) (Table 1).

Over the whole experiment, 64 sessions were run. One session consisted of 32–50 trials. In each session, one of the eight standard stimuli was tested between four and eight times against the selected set of darker comparison stimuli. The position of the positive stimulus was determined using a pseudo random sequence according to the criterion of Gellermann (1933).

Before each stimulus presentation, the black background was presented on the monitor. As soon as the animal stationed properly in front of the monitor, the first stimulus pair was presented. The animal indicated the position of the brighter stimulus by pulling its head out of the hoop station and touching the corresponding response target with its snout. A correct choice was signaled by blowing a whistle that functioned as secondary reinforcer. Subsequently the animal was reinforced with a piece of cut herring. In case of an incorrect choice, no reinforcement was applied.

As soon as the animal had made its choice, the black background was presented again, and the next trial was started after the animal had taken up its position in front of the monitor.

2.6. Analysis

The absolute brightness discrimination threshold was defined as the intensity difference between standard and comparison disc at which the test animal performed 75% correct choices. Its exact value was calculated from the psychometric functions by linear interpolation. The level of significance was calculated using a chi square test with a probability value of 5%.

In order to facilitate the comparison of the results with data of other species, the difference thresholds for all standard stimuli were calculated as Weber fractions (C, Eq. (1)) and Michelson Contrast (MC, Eq. (2)). The Michelson Contrast is defined as the smallest intensity contrast the animal still could detect.

$$C = \Delta I / I_{ST} \tag{1}$$
$$MC = \Delta I / (I_{ST} + I_{75}) \tag{2}$$

with ΔI the just noticeable intensity difference, I_{ST} the intensity of the standard stimulus, and I_{75} the intensity the animal could discriminate from the intensity of the standard stimulus at 75% correct choices.

3. Results

The experimental animal learned the discrimination task fast and performed reliably throughout the experiment. For all standard stimuli at least one comparison stimulus was found that the seal did not discriminate reliably, i.e. his performance was lower than the calculated level of significance (68.6% correct choices, $p < 0.05$).

In order to describe the brightness discrimination ability for every single standard intensity that has been tested, separated calculations of the Weber fractions and Michelson Contrasts (see Eqs. (1) and (2)) have been accomplished. The values of the Weber fractions as well as those of the Michelson Contrasts are consistent, ranging from 0.13 to 0.16 and 0.07 to 0.08, respectively, except for standard stimulus No. 7 (see Fig. 2a). This is equivalent to an intensity difference between standard and comparison stimulus of 13–16%. For standard stimulus No. 7 a lower Weber fraction of 0.09 (Michelson Contrast 0.045) was determined. A replication of the brightness discrimination experiment with this standard stimulus yielded the same results. An explanation for the divergent difference threshold obtained for standard stimulus No. 7 might be that this stimulus was more intense than calculated for the monitor calibration. We therefore tested standard stimulus No. 7 against a set of comparison stimuli that were more intense (brighter) than this standard stimulus, and expected to obtain a higher value of the Weber fraction, if stimulus No. 7 was more intense than predicted by the monitor calibration. However, since the Weber fraction of 0.1 determined in this additional experiment corresponds closely to that obtained in the original test (0.09), a mistake in the monitor calibration can be excluded. Effects by the motivational status of the animal can also be excluded, since the different standard intensities were testes randomly over the whole experiment.

When the Weber fractions (mean: 0.14) and Michelson Contrasts (mean: 0.07) are regarded as a function of the standard intensity (I_{ST}) (Fig. 2a), higher and lower values are equally distributed among different standard intensities. The shape of the function suggests that the single Weber fractions are distributed around a constant value, which would be in line with Weber's law.

Weber's law states that the relation between the intensity of the standard stimulus (I_{ST}) and the just noticeable intensity difference (ΔI) is constant as long as the standard
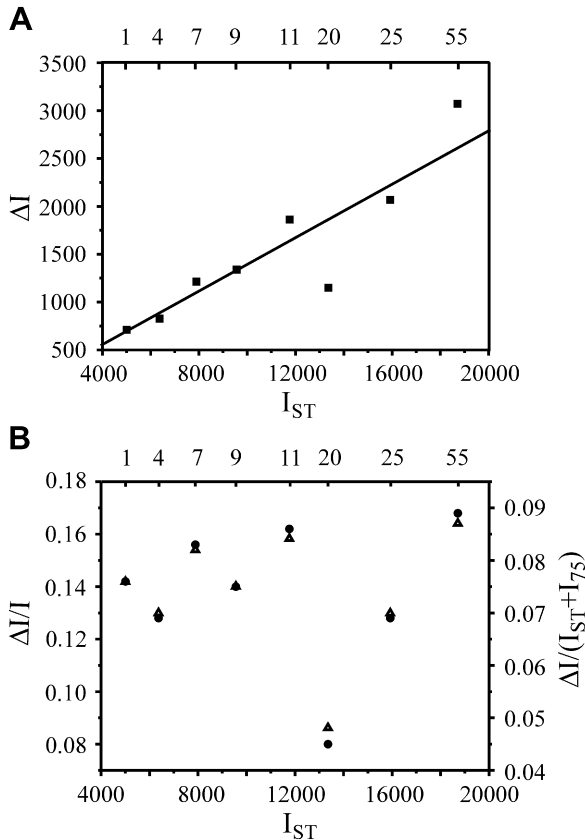
A

B

Fig. 2. (A) The brightness discrimination threshold calculated for every standard stimulus is drawn as a function of the intensity of the standard stimuli (I_{ST}). Left ordinate: Weber fraction ($\Delta I / I$) (▲). Right ordinate: Michelson Contrast ($\Delta I / (I_{ST} + I_{75})$) (●). Upper abscissa: Number of the stimuli. Higher and lower Weber fractions and Michelson Contrasts appear to be equally distributed among all standard intensities. The form of the function suggests that the single determined thresholds are distributed around a constant value, which would be in line with Weber's law. (B) The intensity difference (ΔI) between comparison stimulus and standard stimulus that the animal could just discriminate is drawn as a function of the intensity of the standard stimuli. The best fit to the data is a straight line through zero ($r = 0.9$), which indicates a proportional relationship between ΔI and I_{ST} as it is defined by Weber's law.

intensity is not close to the detection threshold. In order to test for the applicability of Weber's law to the results of the harbor seal, the just noticeable intensity difference was plotted as a function of stimulus magnitude (Fig. 2b). The best fit to the data is a straight line through zero described by the function:

$$\Delta I = 0.14 \, I_{ST}$$

Thus, the results of the harbor seal can be described as a proportional relationship between ΔI and I_{ST} as indicated by Weber's law. The proportional factor is equivalent to the Weber fraction and has the same value as the mean of the Weber fractions of 0.14.

4. Discussion

In the present study we determined a mean Weber fraction of 0.14 for the brightness discrimination ability of a

harbor seal. The constant illumination of the experimental apparatus assured that the animal was adapted to a luminance level that results in mesopic vision in humans. The experiment was accomplished with eight different standard stimuli, and, in accordance with Weber's law, a constant gain of the just noticeable intensity difference with increasing intensity of the standard stimulus was found. Compared to the mean Weber fraction, the deviation of Weber fractions calculated for different standard stimuli was very low. Only the Weber fraction calculated for standard stimulus No. 7 appeared to be conspicuously small. We could show that the low Weber fraction for this stimulus can neither be explained by the motivational status of the animal, nor by a miscalculation of the intensities of this standard stimulus. The reason of the deviating threshold obtained for stimulus No. 7 remains unclear.

To date, the only other pinniped species that have been tested for brightness discrimination are the South African fur seal (*Arctocephalus pusillus*) and the South American fur seal (*Artocephalus australis*) (Busch & Dücker, 1987). They were tested with a series of 28 shades of gray at illumination levels that fluctuated between less than 500 and 900 lx. Griebel and Schmid (1997) calculated the Weber fraction from the data of Busch and Dücker to be approximately 0.3 for both species, which implies that the brightness discrimination ability of the fur seal is approximately half as good as that of the harbor seal. However, a closer examination of the results of Busch and Dücker (1987) reveals an interesting phenomenon. In comparison to our results the Weber fraction of each standard stimulus deviates drastically from the mean Weber fraction. Plotting the mean Weber fractions obtained for the different standard stimuli as a function of stimulus magnitude (Fig. 3) reveals a distinct stimulus magnitude at which the bright-
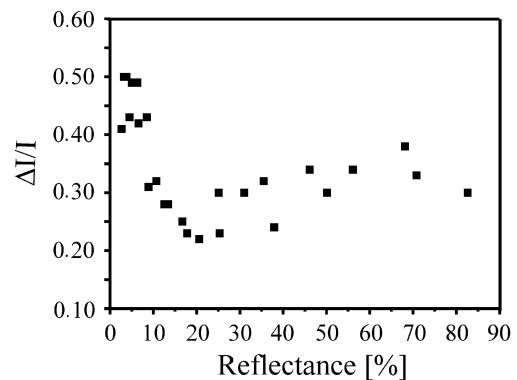

Fig. 3. The mean Weber fractions for every standard stimulus for five fur seals (Busch & Dücker, 1987) plotted as a function of stimulus reflectance. The values were recalculated from the published data. The separate calculated Weber fractions diverge drastically from the mean Weber fraction of 0.34 (threshold criterion 80%). The lowest difference threshold can be observed for a stimulus reflectance of 20%. Beyond this point of maximal brightness discrimination ability, an increase of the discrimination threshold for increasing as well as decreasing stimulus reflectance becomes apparent, whereas the increase is more distinct and more rapid for the latter one.

ness discrimination ability reaches a maximum. The best brightness discrimination ability is found for a stimulus reflectance of 20% and is described by a Weber fraction of 0.22. Beyond this point of maximum sensitivity for brightness contrast, discrimination ability decreases with increasing as well as decreasing stimulus reflectance, though the decline is more distinct and more rapid for the latter. The same phenomenon occurs when the results of the five subjects are treated separately.

A similar relationship between brightness discrimination threshold and intensity of the standard stimulus was already described by Craik (1938). He tested the influence of the stimulus intensity on the brightness discrimination ability of human subjects that were adapted to a certain background luminance. He could demonstrate that the ability to detect brightness contrasts decreases for test intensities that are lower and higher than the background intensity. Similar to the function drawn for the fur seals, the decline of brightness discrimination ability is more distinct for intensities that are lower than the background intensity the subjects were adapted to. But contrary to the fur seals, brightness discrimination in humans is only affected when the standard intensity is approximately a thousandfold higher or lower than the background intensity (Craik, 1938). Nevertheless, the results of Craik offer a basis for the interpretation of the function drawn from the data of Busch and Dücker. The point of the lowest brightness discrimination ability might indicate the mean luminance the fur seals were adapted to during the experiments. This would be equivalent to the luminance of a gray stimulus with a reflectance of 20%. The brightness discrimination ability at higher and lower stimulus luminosities decreases similar to the findings of Craik (1938), but already for smaller deviations of the standard intensity from the "adaptation" intensity.

With respect to the different threshold criterion applied by Busch and Dücker (80% correct choices, compared to

75% as in the present study), the Weber fraction indicating the point of best brightness discrimination should be even lower than 0.22, approximately around 0.19. This value is closer to the one obtained for the harbor seal and suggests a similar sensitivity to brightness contrasts in harbor seals and fur seals.

Besides the fur seal and the harbor seal, only few mammals have been tested with respect to their brightness discrimination threshold to date (Table 2). The results are difficult to compare due to differences in methodology as well as the different levels of ambient illumination in these experiments. The only herbivore marine mammal that has been tested is the West Indian manatee (*Trichechus manatus*) (Griebel & Schmid, 1997). Its brightness discrimination threshold at a constant illumination level of 150 lx is described by a Weber fraction of 0.3. Under the same experimental conditions Griebel and Schmid (1997) determined a Weber fraction of 0.11 for human subjects. An earlier experiment of Cornsweet and Pinsker (1965) yielded similar results for humans. They determined the brightness discrimination ability for subjects adapted to various levels of luminance. Their results show a minimum Weber fraction of 0.14 when the subjects were dark-adapted. Geisbauer, Griebel, Schmid, and Timney (2004) found Weber fractions of 0.45 and 0.42 for two Haflinger horses (*Equus caballus*) tested at a constant illumination level of 560 lx. The only representatives of terrestrial carnivores that have been tested to date are dogs (*Canis lupus familiaris*) (Pretterer, Bubna-Littitz, Windischbauer, Gabler, & Griebel, 2004). The results indicate a Weber fraction of 0.22 for the German Shepherd and 0.27 for the Belgium Shepherd. An earlier investigation on the brightness discrimination ability in two young fox terriers (Stone, 1921) revealed a lower difference threshold for these dogs. Unfortunately, only one standard intensity was tested by Stone (1921), but the results he obtained were consistent for the two subjects (Weber fractions of 0.12 and 0.10,

Table 2
Brightness discrimination thresholds in mammals

Species	Method	Ambient illumination	Threshold ($\Delta I/I$)	Reference
Dog (*Canis lupus familiaris*)	Discrimination between gray cards in a two alternative forced choice task	500 lx	0.25	Pretterer et al. (2004)
	Discrimination between two illuminated screens in a two alternative forced choice task	~1 Td	0.11	Stone (1921)
American fur seal (*Arctocephalus pusillus*) South African fur seal (*Arctocephalus australis*)	Discrimination between gray cards in a two alternative forced choice task	<500–900 lx	~0.3	Busch and Dücker (1987)
Harbor seal (*Phoca vitulina*)	Discrimination between gray stimuli presented on a TFT monitor in a two alternative forced choice task	0.9 lx	0.14	Present study
West Indian manatee (*Trichechus manatus*)	Discrimination between gray cards in a two alternative forced choice task	70 lx	0.3	Griebel and Schmid (1997)
Horse (*Equus caballus*)	Discrimination between gray cards in a two alternative forced choice task	580 lx	0.45, 0.42	Geisbauer et al. (2004)
Human (*Homo sapiens sapiens*)	Discrimination between gray cards in a two alternative forced choice task	Dark adapted	0.14	Cornsweet and Pinsker (1965)
	Discrimination between two circular disks of different intensity that were projected on the retina	70 lx	0.11	Griebel and Schmid (1997)

respectively). Chausseil and Löhmer (1986) could not determine difference thresholds in their study on brightness discrimination with the Kinkajou (*Potos flavus*, Procyonidae) because their 20-part series of grays was not fine enough.

Like pinnipeds, dogs, horses, and manatees are arrhythmic species with visual systems adapted to both, scotopic and photopic vision. Geisbauer et al. (2004) hypothesized that these visual generalists tend to have a much higher brightness discrimination threshold than completely diurnal species such as humans. Our results for the harbor seal argue against this hypothesis since the brightness discrimination threshold of this arrhythmic species compares more to the one obtained for human subjects and less to those obtained for dogs, horses and the manatee. Furthermore, the relatively high brightness discrimination threshold found for the dog by Pretterer et al. (2004) appears to be a consequence of the experimental methods. The dogs had to discriminate between stimuli of different intensities that were separated by 1.1 m. This large distance between the stimuli could have impeded the choice of the subjects and might have had affected the threshold. Thus, as described for the fur seals, the brightness discrimination ability of the dogs tested by Pretterer et al. (2004) may have been underestimated while the lower values obtained by Stone (1921) are more realistic.

As contrast is known to be a critical parameter for movement perception (Buser & Imbert, 1992), in carnivores low brightness discrimination thresholds might therefore facilitate the detection of movements and the movement direction of prey. It would not be surprising if carnivores in general possessed quite low brightness discrimination thresholds in the range shown here for the harbor seal. In contrast to carnivores, movement detection and thus the detection of small contrasts might be less important for herbivore species like manatees and horses. This is reflected in the relatively high Weber fractions obtained for the manatee and the horse. However, in order to prove a correlation between brightness discrimination ability, circadian activity, nutrition or optical properties of the natural environment, further species have to be tested.

The knowledge about the brightness discrimination ability of a species is also important for the elimination of brightness cues in color vision experiments. Since the retina of pinnipeds and cetaceans is only equipped with the MWS/LWS-cone type (Peichl & Moutairou, 1998; Peichl, Behrmann, & Kröger, 2001), color vision seems unlikely in these groups. Psychophysical experiments with the Bering Sea spotted seal (*Phoca largha*), the California sea lion and the Bottlenose dolphin (*Tursiops truncatus*), however, suggest the existence of some color vision in the blue-green range of the spectrum (Busch & Dücker, 1987; Griebel & Schmid, 1992, 1999; Wartzok & McCormick, 1978). In the experiments with the fur seals and the California sea lion, the animals had to discriminate colored stimuli against a series of gray stimuli in a simultaneous two alter-

native forced choice task. It was assumed that at least one of the gray stimuli and the colored stimulus would be equal in subjective brightness, so that the experimental animal would not be able to discriminate the color from gray if it used brightness as the relevant cue. Since the animals successfully discriminated the colored stimulus from all shades of gray, it has been judged as color discrimination. However, as in accordance with the results obtained by Wartzok and McCormick (1978) for *Phoca largha* our data show that the brightness discrimination threshold of the harbor seal is remarkably small, it is possible that in studies on color vision the sensitivity of pinnipeds for brightness differences has been generally underestimated. Thus it is questionable whether the discrimination required during the color vision experiments with fur seals (Busch & Dücker, 1987) and the California sea lion (Griebel & Schmid, 1992) was based on brightness rather than on chromatic cues. In order to exclude this, it is necessary to determine the brightness discrimination threshold of the experimental animals, then to test for the point of equal subjective brightness of the colored and the gray stimuli, and to test whether the animal is able to discriminate when color contrast is the only visual cue, the animal can rely upon (Kelber, Vorobyev, & Osorio, 2003).

5. Ecological implications

Harbor seals possess good visual acuity in clear water (Schusterman & Balliet, 1970; Weiffen et al., 2006). Weiffen et al. (2006) however described a remarkable decline of the visual acuity of the harbor seal with increasing water turbidity. This effect already emerges at moderate turbidity levels that are much lower than those found e.g. in the North Sea. Thus, the low brightness discrimination threshold of the harbor seal measured in the present study does not necessarily compensate for the reduced visual acuity in turbid water. This suggests that the visual system fails to serve as a long distance sensory system for prey detection under water. Therefore, Weiffen et al. (2006) assumed that in turbid waters seals use visual information mainly during the last stage of prey pursuit. During that stage, the low brightness discrimination threshold should facilitate visual identification of prey as well as the movements and movement directions of prey, even in dim light. Descriptions of foraging strategies of harbor seals feeding on benthic prey support the assumption that vision is utilized for prey capture (Bowen, Tully, Boness, Bulheier, & Marshall, 2002). For long distance prey detection acoustic cues as well as hydrodynamic cues that are perceived via the vibrissae are assumed to be of great importance for pinnipeds (Dehnhardt et al., 2001; Bodson et al., 2006). The visual acuity of the harbor seal in air is currently tested in our lab, and preliminary results indicate that the spatial resolving power at illumination levels above 50 cd/m^2 is comparable to that measured in clear water (Frederike Hanke, personal communication). High visual acuity in air and a low brightness discrimination threshold imply

that harbor seals perceive detailed and instantaneous information about their aerial environment. This qualifies the visual system to play a decisive role for orientation above the water surface.

Acknowledgments

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