

## BRIGHTNESS DISCRIMINATION ABILITY IN THE WEST INDIAN MANATEE (*TRICHECHUS MANATUS*)

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### Summary

Two manatees were tested on their ability to discriminate brightness using a series of 30 shades of grey varying from white to black. The animals were trained to discriminate between different shades of grey in a twofold simultaneous-choice situation. Their ability to discern brightness

differences correlates with Weber's law, and the calculated Weber fraction is 0.35.

Key words: *Trichechus manatus*, manatee, Sirenia, brightness discrimination, visual sensitivity, vision.

### Introduction

Marine mammals present a unique opportunity to study the course of evolutionary development of sensory processes in their adaptation from a terrestrial to an underwater environment. Sirenians are the only group of marine mammals that have evolved to exploit the benthic macrophytes of the sea margin. Their sensory adaptations to the aquatic environment and to their herbivorous lifestyle are therefore of special interest. Nevertheless, we know very little about their visual and tactile senses or about the senses involved in orientation, navigation and taste. Only recently, as habitat degradation and direct human effects have put them on the verge of extinction, has interest focused on these unusual grazing animals.

The West Indian manatee *Trichechus manatus* inhabits the rivers and coastal zones of the southeastern United States, the Caribbean area and northeastern South America. We are interested in how these animals perceive their environment visually. Sirenian vision was considered to be very poor by most early investigators because of the small size of the eyes, the paucity of retinal ganglion cells and the apparent absence of an accommodation mechanism (Dexler and Freund, 1906; Petit and Rochon-Duvigneaud, 1929; Walls, 1942; Rochon-Duvigneaud, 1943; Duke-Elder, 1958; Ronald *et al.* 1978; Piggins *et al.* 1983; West *et al.* 1991). Behavioural observations of visually guided behaviour of the manatee suggest otherwise (Hartman, 1979; Gerstein, 1994).

The manatee eye is small (approximately 1.9 cm in diameter) compared with its body size and is nearly spherical. The shape of the lens is also nearly spherical and seems to suit the aquatic environment. The optic nerve appears thin. Reports on ocular refraction in sirenians are not quite unanimous. Piggins *et al.* (1983) reported low hyperopia to emmetropia in water and found no astigmatism in *Trichechus inunquius*, Petit and Rochon-Duvigneaud (1929) found that the dugong eye (*Dugong dugong*) appears emmetropic in air and hyperopic under water, and Dexler and Freund (1906) reported that the

dugong is myopic in air and hyperopic under water. There appears to be no accommodation mechanism (Walls, 1942; West *et al.* 1991). The size of the binocular visual field was estimated to be 15° (Piggins *et al.* 1983). Extraction of the visual pigment from *Trichechus inunquius* yielded a pigment based on retinol with a maximal absorption at approximately 505 nm (Piggins *et al.* 1983).

A detailed study on the fine structure of the retina (Cohen *et al.* 1982) showed that the manatee (*T. manatus*) retina has both rod-like and cone-like photoreceptors and also two types of cone cells, which raises the possibility that the manatee has colour vision. A recent behavioural investigation (Griebel and Schmid, 1996) demonstrated the ability of the manatee to discriminate colours. These results suggest a dichromatic colour vision system with two photoreceptor types, one having maximum sensitivity in the blue part of the spectrum and one in the green part. These results agree very well with the earlier morphological findings (Cohen *et al.* 1982).

Another measure of the efficiency of the visual system is the ability to discriminate brightness differences. This study investigates the ability of the manatee to discern greys from a 30-part series varying in brightness from white to black. We tested by how much two steps of greys had to differ in their relative reflection to be discriminated by the animals and how this relative reflection varied from bright to dark stimuli.

### Materials and methods

#### Subjects

The subjects were two female sea cows (*Trichechus manatus*) living in an aquarium in the zoo at Nürnberg (Germany). Cara was 2 years old and Nona was 1 year old. Cara had already participated in a colour vision study, so she was not an experimentally naive animal like Nona. The pool temperature during experiments was 25°C.

The training and test sessions were carried out at 08:00h because at this time the manatees were very active. The first step in training the animals was to determine which food items they preferred. Various fruits, vegetables and biscuits were offered. It turned out that their favourite foods were egg-plants, zucchinis and cucumbers. The vegetables were cut into little pieces and used as rewards.

Because there was only one pool, it was impossible to separate Cara and Nona from the other manatees during the experiments. Thus, as soon as an experimental animal was chosen, none of the other animals was fed any more. They quickly ceased to expect food and seldom bothered Cara and Nona during their sessions. The two females performed the tests in parallel, but they would wait for their turn to do each trial and thus did not interfere with each other.

#### *Stimuli and apparatus*

The manatees had to discriminate two grey targets of differing brightness in a twofold simultaneous-choice situation.

The grey stimuli consisted of a series of 30 shades of grey. The grey plates were produced by exposing photographic paper in an arithmetic series of exposure times resulting in shades from white to black. The photographic papers were fixed on plastic plates (30 cm×30 cm) and covered with a dull non-reflecting varnish. The relative intensities of the grey plates were measured (using a Bacher on-line densitometer), the values expressed in photographic density ( $D$ ) and converted into relative reflection ( $R$ , reflected intensity/incident intensity, as a percentage) ( $R=100\times 10^{-D}$ ). Table 1 gives the density and relative reflection values of all grey targets from white to black (1–30).

The distribution of the spectral reflection of the grey plates was measured using a spectrophotometer (MCS 230, Zeiss) to ensure that the spectral distribution of the reflected light was the same over the entire spectral range (300–700 nm).

The stimulus plates for the tests were presented to the animal in two identical acrylic boxes (31 cm×31 cm front side, depth 1.3 cm) with a 1.5 cm wide grey frame on the non-reflecting front screen and a handle on the back for holding.

The tests were conducted in an indoor facility. The manatee pool was illuminated using plant lamps (Osram HQI, 250 W) with a daylight-equivalent emission spectrum. The ambient light in front of the stimuli was measured using a Minolta Chroma-Meter XY-1, which showed a constant illumination level of 150 lx. This means that the experimental animals were light-adapted.

#### *Procedure*

The stimulus boxes were presented directly at the edge of the manatee pool. The manatee was trained to position itself in front of the experimenter in a position perpendicular to the edge of the pool with its head out of the water, looking with both eyes at the experimenter. The targets were then presented to the animal at a distance of 30 cm from each other and equally far from the animal at the edge of the pool. The manatee made its choice by moving to one of the targets and touching it with

Table 1. *Thirty-part series of grey stimuli*

Number	$R$ (%)	$D$	
1	89.1	0.05	
2	75.9	0.12	
3	55.0	0.26	
4	46.8	0.33	
5	37.2	0.43	
6	33.9	0.47	
7	30.9	0.51	
8	26.9	0.57	
9	23.4	0.63	
10	21.4	0.67	
11	19.1	0.72	
12	17.4	0.76	
13	16.2	0.79	
14	15.1	0.82	
15	13.8	0.86	
16	13.2	0.88	
17	12.6	0.90	
18	11.5	0.94	
19	10.2	0.99	
20	9.1	1.04	
21	8.7	1.06	
22	8.3	1.08	
23	7.9	1.10	
24	7.4	1.13	
25	7.1	1.15	
26	6.6	1.18	
27	6.0	1.22	
28	5.8	1.24	
29	5.4	1.27	
30	3.5	1.46	

For each shade, the values of density ( $D$ ) and relative reflection ( $R$ ) are given.

its snout. The brighter grey was always the positive stimulus and the darker grey the negative stimulus. At a correct choice, the experimenter blew a whistle, the targets were removed and the animal received a piece of vegetable as a reward. During the training period, in the case of a wrong choice, the animal received no food reward, the targets were removed and, after an intertrial interval of 30 s, the next trial started. During the tests, the animals were always rewarded with food, but in the case of a wrong choice the whistle was not blown.

To ensure that the subjects were not being cued by the experimenter, experimentally naive people who were uninformed about the nature of the discrimination task were asked to present the stimuli to the manatee at regular intervals. Ten different people acted as experimenters.

A test session usually consisted of 20–30 trials per day for Cara and 10–20 trials per day for Nona, depending on the cooperation of the animals, which was fairly constant. When an animal did not reach the lower limit (20 or 10 trials in one session), the same discrimination task was presented again in the next session. There was only one session each day, in the morning, and only one combination of grey shades was tested

in each session. The chance level of performance in a two-choice discrimination is 50 %, and the criterion level for the threshold was set at 75 %.

*Training*

In the initial training, the manatees learned to touch the stimulus plates with their snout when they were presented. In the next step, they learned to discriminate a white stimulus (G1, see Table 2) from a dark shade of grey. When they reached a performance level of 80% in one session, the brightness of the dark stimulus was increased step by step in each succeeding session until the animals reached a level of correct choices of 80 % in the stimulus combination G1 × G8. Then the test was started.

*Test*

In initial tests, G1 was paired with G8. The brightness of the darker grey was increased step by step with each succeeding session until the adjacent grey shade was reached or until the performance of the manatees dropped below 75 % of correct choices. After G1, this step-by-step approximation to the threshold was repeated for every grey shade of the 30-part series. The position of the positive stimulus was changed according to the criteria of Gellerman (1933). During a series of 10 trials, the positive stimulus appeared five times on each side and did not stay at one position more than twice.

To be able to compare the results for the manatee directly with those for humans, two people were tested with the same stimuli and under the same conditions as the manatees at a constant illumination level of 150lx.

**Results**

The experiments started in February 1995 and were completed in October 1995. Cara performed 1575 experimental trials and Nona 1224 trials.

In the training period, Cara reached the criterion of 80 % for the pairing G1 × G15 in one session with 21 trials (81 % correct choices) and for the pairing G1 × G8 in 30 trials (80 % correct choices). Nona took a little longer, possibly because she was an experimentally naive animal. She reached the criterion of 80 % in the third session after 45 trials with the pairing G1 × G25, in the fourth session after 61 trials with the pairing G1 × G15, and in the first session after 20 trials with the pairing G1 × G8 (95 % correct choices).

At the beginning of the test series, several sessions for certain pairings of grey shades were repeated with each manatee (see Table 2; repeated sessions are indicated by bold symbols) to test whether the performance level of the animals would increase, which it did not. The manatees showed no signs of variation in motivation; their performance was highly reliable.

Table 2 shows the results of the brightness discrimination test for the animals Cara and Nona. The only pairing in which the manatees discriminated two adjacent greys was with G1 × G2. Both animals had almost identical thresholds (performance

Table 2. Results of the brightness discrimination test of a 30-part series of greys for the manatees Cara and Nona

		Cara																													
Grey no.		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
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		Nona																													
Grey no.		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1		⊕	+	+	+				+	+																					
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A + symbol indicates a session in which the animal discriminated the two greys with a performance level above 75 % correct choices). A – symbol indicates a session in which the performance of the animal was below 75 % correct choices.

One session with Cara consisted of 20–30 trials. Sessions with Nona consisted of 15–20 trials, but in the vicinity of the threshold she also had to perform at least 20 trials per session.

Bold symbols indicate repeated sessions; ⊕ indicates the only pairing where the animals were able to discriminate two adjacent steps of greys (G1 × G2).

level below 75 %): there was only one shade of grey where Nona showed a different threshold from that of Cara, which was the pairing G4 × G8 for Nona and G4 × G7 for Cara.

The threshold of relative reflection for a choice frequency of 75 % for every grey shade was linearly interpolated for both animals, and the mean threshold for Cara and Nona is given in Table 3. The threshold for grey 1 could not be calculated because the animals discriminated the adjacent grey 2.

In order to compare our data with those for other species, we calculated the relative difference threshold, the so-called Weber fraction. Weber’s law states that the difference between

Table 3. *Thirty-part series of grey stimuli*

Grey no.	Density, $D$	Relative reflection, $R$ (%)	Difference in relative reflection between adjacent greys, $\Delta r$ (%)	No. of discriminated grey	Difference in relative reflection between two discriminated greys, $\Delta R$ (%)	Calculated threshold for each grey in relative reflection, $\Delta R$ (%)†	Mean threshold for bright, medium and dark greys in relative reflection‡	Weber fraction for each threshold, $\Delta R^*/R$
1	0.05	89.1	13.2	2	13.2	—		—
2	0.12	75.9	20.9	4	29.1	27.3	} Grey 2–8 Mean=16.4	0.36
3	0.26	55.0	8.2	6	21.1	19.8		0.36
4*	0.33	46.8	9.6	8 (9)	19.9 (23.4)	20.4		0.44
5	0.43	37.2	3.3	9	13.8	12.7		0.34
6	0.47	33.9	3.0	10	12.5	11.5		0.34
7	0.51	30.9	4.0	12	13.5	12.9		0.42
8	0.57	26.9	3.5	13	10.7	10.2		0.38
9	0.63	23.4	2.0	13	7.2	6.6	} Grey 9–15 Mean=5.3	0.28
10	0.67	21.4	2.3	14	6.3	6.0		0.28
11	0.72	19.1	1.7	15	5.3	4.7		0.25
12	0.76	17.4	1.2	17	4.8	4.4		0.25
13	0.79	16.2	1.1	18	4.7	4.5		0.28
14	0.82	15.1	1.3	20	6.0	6.0		0.40
15	0.86	13.8	0.6	21	5.1	5.0		0.36
16	0.88	13.2	0.6	22	4.9	4.8	} Grey 16–22 Mean=3.8	0.36
17	0.90	12.6	1.1	23	4.7	4.5		0.36
18	0.94	11.5	1.3	24	4.1	4.0		0.35
19	0.99	10.2	1.1	26	3.6	3.4		0.33
20	1.04	9.1	0.4	27	3.1	2.8		0.31
21	1.06	8.7	0.4	28	2.9	2.9		0.33
22	1.08	8.3	0.4	30	4.8	4.0		0.48
23	1.10	7.9	0.5	—	—	—		—
24	1.13	7.4	0.3	—	—	—		Mean=0.35
25	1.15	7.1	0.5	—	—	—		—
26	1.18	6.6	0.6	—	—	—		—
27	1.22	6.0	0.2	—	—	—		—
28	1.24	5.8	0.4	—	—	—		—
29	1.27	5.4	1.9	—	—	—		—
30	1.46	3.5	—	—	—	—		—

†Calculated threshold (mean for Cara and Nona) for each grey in relative reflection,  $\Delta R^*$ , for a choice frequency of 75 %.

‡Mean thresholds for the bright (greys 2–8), medium (greys 9–15) and dark (greys 16–22) ranges of the grey scale in relative reflection.

For grey 4\*, the numbers for Nona are given in parentheses.

two stimuli that is just noticeable depends on the magnitude of the starting stimulus. In general, it is found that the greater the magnitude of the starting stimulus, the greater is the just noticeable difference ( $\Delta I/I=k$ , where  $I$  is the intensity,  $\Delta I$  is the absolute intensity difference threshold and  $k$  is the relative difference threshold, i.e. the Weber fraction). Weber's law does not apply to very low and very high stimulus intensities. The Weber fraction was calculated for each threshold ( $\Delta R^*/R$ , where  $\Delta R$  is the difference in the relative reflectance between the distinguishable greys) (Table 3) and the mean Weber fraction was 0.35. Fig. 1 shows the dependence of the difference threshold ( $\Delta R^*$ ) on the magnitude of the stimulus  $R$ . The best fit to the data is a straight line,  $y=-0.63+0.38x$ , indicating that the threshold intensity difference (i.e. the difference in relative reflection) ( $\Delta R^*$ ) is directly proportional to the intensity (or relative reflection)  $R$ .

Thus, the difference in relative reflection that was

discriminated varied with the absolute brightness of the stimuli according to the Weber fraction. When we divide the series of greys into three ranges of brightness (Table 3), one from grey 2 to grey 8, one from grey 9 to grey 15, and one from grey 16 to grey 22, we find that, in the bright range, the mean threshold was 16.4 %, in the medium range 5.3 %, and in the dark range 3.8 %. The lowest single threshold was in the dark range at 2.8 %.

The two human observers could discriminate most of the grey levels. One person could not discriminate the pairings G20  $\times$  G21 and G28  $\times$  G29, and both were unable to discriminate the pairings G5  $\times$  G6, G22  $\times$  G23, G23  $\times$  G24, G25  $\times$  G26 and G27  $\times$  G28. The smallest difference in relative reflection that the human observers could still discern was 0.4 %. From the few thresholds that could be determined, the Weber fraction was calculated to be 0.11. This means that,

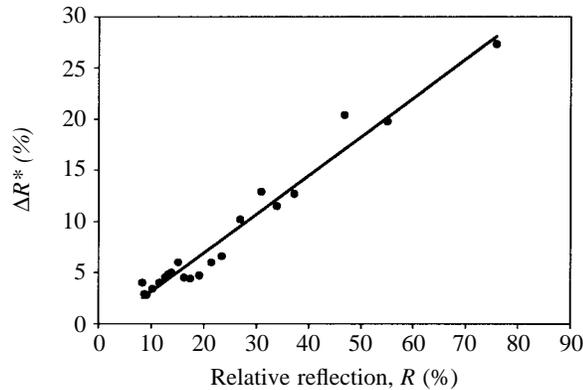


Fig. 1. The percentage relative reflection ( $\Delta R^*$ ) by which two greys had to differ in order for the subjects to distinguish between them as a function of the relative reflection ( $R$ ) of the brighter grey. The data fall approximately on a straight line ( $y = -0.63 + 0.38x$ ), indicating that the threshold intensity difference ( $\Delta R^*$ ) is proportional to the intensity ( $R$ ), in agreement with Weber's law.

with the same brightness discrimination task, humans are three times better in their resolution of greys than are manatees.

### Discussion

The difference in relative reflection that was discriminated by the manatees varied with the absolute brightness of the stimuli according to the Weber fraction, which is 0.35. In the bright range, the mean threshold is 16.4%, in the medium range 5.3% and in the dark range 3.8%. The lowest single threshold the manatees reached was in the very dark range at 2.8%. Very few species have been investigated with respect to their brightness discrimination ability. Another problem is that, in the few studies available, different evaluation methods have been used and the Weber fraction has not been calculated, which complicates comparisons between the data.

Busch and Dücker (1987) have tested two species of fur seals, *Arctocephalus pusillus* and *Arctocephalus australis*, with a series of 28 greys. The results for both species were very similar. The fur seals discerned a 17.1% difference in relative reflection in the bright range, 4.3% in the medium range and 2.1% in the dark range. We calculated the Weber fraction from the data of Busch and Dücker (1987) to be 0.34. All values for the fur seals should be considered to be somewhat higher than the calculated ones, because in that study 79% was used as the criterion level, so the Weber fraction comparable with the criterion for the manatees would be approximately 0.30. Even taking this into account, it seems quite surprising that the brightness discrimination abilities of the fur seals and the manatees do not differ very much. It would seem quite reasonable that a fish-hunting predator would need a much better brightness discrimination ability than a placid herbivore.

Both manatees and fur seals are active during both day and night; their activity is essentially arrhythmic. Absolute thresholds of sensitivity for fur seals are not known, but it is

very likely that they use also vision during the night for hunting with the aid of an extensive tapetum lucidum (Walls, 1942). In manatees, the existence of a tapetum lucidum is still a matter of discussion (Piggins *et al.* 1983). In the dark, both manatees and fur seals probably also make use of their highly sensitive vibrissae.

The results from the human observers showed that the smallest discernible difference in relative reflection was 0.4%, and the Weber fraction was calculated to be 0.11. This agrees very well with results from an experiment by Cornsweet and Pinsker (1965), in which human subjects were presented with two disks that were flashed simultaneously and briefly, and then asked which of the disks was brighter. The Weber fraction was determined to be 0.14 in this experiment. The slightly better results in our experiments might have been due to the fact that our human observers had more time to evaluate the stimuli. Thus, the brightness discrimination ability of humans is three times better than that of manatees and fur seals. Nevertheless, it seems that the capacity of the manatee eye has been underestimated because of its small size. We have found that manatees almost certainly have dichromatic colour vision (Griebel and Schmid, 1996), which is very common in mammals, and that their brightness discrimination ability compares very well with that of another group of marine mammals, the fur seals. The next step will be to study the visual acuity and spectral sensitivity of the manatee eye.

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