

Brightness discrimination in the dog

Gabriele Pretterer

Institute for Physiology, Veterinary University Vienna,
Vienna, Austria

Hermann Bubna-Littitz

Institute for Physiology, Veterinary University Vienna,
Vienna, Austria



Gerhard Windischbauer

Institute for Medical Physics and Biostatistics, Veterinary
University Vienna, Vienna, Austria



Cornelia Gabler

Institute for Medical Physics and Biostatistics, Veterinary
University Vienna, Vienna, Austria

Ulrike Griebel

The University of Memphis, Department of Biology,
Memphis, TN, USA



Almost nothing is known about brightness discrimination in animals and how this ability relates to their lifestyles. As arrhythmic visual generalists, three dogs, a German shepherd and two Belgian shepherds, were tested on their ability to discriminate brightness using a series of 30 shades of grey varying from white to black. The dogs were trained to discriminate between different shades of grey in a simultaneous two-choice situation. Weber's law can be correlated to their ability to discriminate brightness differences with a calculated Weber fraction of 0.22 for the German shepherd and 0.27 for the Belgian shepherds. Thus brightness discrimination in dogs is about 2 times worse than in humans, a diurnal species.

Keywords: dog, *Canis familiaris*, brightness discrimination

Introduction

Almost nothing is known about brightness discrimination in animals and how this ability relates to their lifestyles. To date, studies on brightness discrimination involve only a handful of species: humans (Cornsweet & Pinsker, 1965; Griebel & Schmid, 1997), two species of fur seals (Busch & Dücker, 1987), the West Indian manatee (Griebel & Schmid, 1997), and the coatis (Chausseil & Löhmer, 1986). From such a small sample, we have no foundation to draw conclusions about differences between diurnal, arrhythmic, and nocturnal species. This represents a major gap in our understanding of vision.

This work reports results on a canid species, the dog, an arrhythmic animal, active during both day and night. The dog is thus a visual generalist who uses vision in a wide range of ambient light levels. The visual system of the dog has been subject to various investigations in the past (for a review, see Miller & Murphy, 1995).

Interestingly, however, we know less about the visual abilities of domestic dogs than we do about certain wild species of wolves and monkeys and domestic species such as cats and laboratory rats. Data about the visual capacities of dogs are valuable, not only because they add to our knowledge of comparative sensory functions, but also because they could have practical applications because working dogs are used in a variety of different tasks where vision is neces-

sary. Thus, for a retriever to do his job, he needs visually to track and mentally mark the places where birds fall. The job done by sheepherding dogs depends on their ability to detect small movements of members of a herd to keep the flock together. Sheepherding dogs also need their eyes to pick up the hand or arm signals of the master indicating which direction to go first, and where to move the flock. And, of course, guide dogs must serve as surrogate eyes for their charges. However, what we as humans can expect of dogs will depend in great measure on their sensory abilities.

Several behavioral investigations have shown that visual cues are very important for canids in interactions between conspecifics as well as during hunting (Osterholm, 1964; Fox, 1971; Lehner, 1978; Wells & Lehner, 1978). Canids seem to be visual generalists that are able to operate under a wide range of photic conditions. A superiorly located reflective tapetum lucidum probably enhances the view of a usually darker ground and the inferiorly located tapetum nigrum may reduce scattering light from the bright sky (Wen, Sturman, & Shek, 1985; Lesiuk & Braekevelt, 1983; Burns, Bellhorn, Impellizzeri, Aguirre, & Laties, 1988).

Canid retinas predominantly contain rods. Peichl (1991) reports that cones make up only 3% of all photoreceptors in dog and wolf retinas. In the central portion of the retina, they are more numerous and amount to 20% of all receptors, whereas in regions outward from the area centralis, the cone/rod ratio decreases (Koch & Rubin, 1972;

Parry, 1953; Allgoewer, 1991; Peichl, 1991). Human retinas contain about 5% cones and are also distributed differently than in the canids. Rods are completely absent in the central foveal pit and increase in numbers toward the periphery of the retina (Curcio & Hendrickson, 1991).

The presence of cones in the canid retina suggests the possibility of color vision. Although early behavioral studies on dog color vision produced ambiguous results (reviewed by Rosengreen, 1969), both recent behavioral studies (Coile, 1982; Neitz, Geist, & Jacobs, 1989) and visual-evoked potential studies (Aguirre, 1978; Odom, Bromberg, & Dawson, 1983) have demonstrated that dogs possess dichromatic color vision, with two classes of cone pigments, having spectral peaks at 429 nm and 555 nm.

Electroretinographic studies have confirmed these findings. Parry, Tansley, and Thompson (1953) found a maximal spectral sensitivity of the cones at 580 nm and 430 nm in the dog, and Jacobs, Deegan, Crognale, and Fenwick (1993), using electroretinogram flicker photometry, showed that four species of canids (dog, Island grey fox, red fox, and Arctic fox) have a long-wavelength sensitive cone with a peak sensitivity at 555 nm and a short-wavelength sensitive cone with a peak sensitivity of about 430 nm, a pattern suggesting that all canids might have a very similar dichromatic color vision system. A study from molecular genetics also supports these findings (Yokoyama & Radlwimmer, 1998). Scotopic sensitivity has a peak around 507 nm (Scheibner & Schmid, 1969; Kemp & Jacobson, 1992; Parkes, Aguirre, Rockes, & Liebman, 1982; Jacobs et al., 1993).

Arey and Gore (1942) showed that the retina of the dog contains about 150,000 ganglion cells. The optic chiasm has a crossover of about 75% in the dog, consistent with good binocular vision. The monocular field of view in the average dog is approximately 135–150°, and the binocular field is estimated to be about 30–60° (Sherman & Wilson, 1975). Visual acuity was tested behaviorally in a medium-sized, mixed-breed dog by Neuhaus and Regenfuss (1967). The threshold (minimum separable) was found to be at 4'50" (6.3 cycles/deg) at an illumination level of 37 lux. Several studies using visually evoked potential measurements have been conducted with various results. In two beagles, an average threshold of 4.62 cycles/deg was reported (Bromberg & Dawson, 1980), whereas another electrophysiological study measuring retinal and cortical field potentials found much lower thresholds of 11.61 cycles/deg (about 2'40") and 12.59 cycles/deg (about 2'35") for three beagles and one mixed-breed dog, respectively (Odom et al., 1983). A more recent study with three beagles found thresholds between 7.0 to 9.5 cycles/deg (about 4'19" to 3'10") (Murphy, Mutti, Zadnik, & Ver Hoeve, 1997).

Peichl (1992) has shown that several breeds of dogs as well as the wolf have a more or less pronounced "visual streak" of high ganglion cell density, extending from the central area into both temporal and nasal retina. The temporal resolution of the cones in dogs (70–80 Hz) seems to

be a little higher than in humans (50–60 Hz), whereas the critical flicker fusion frequency of the rods seems to be similar to humans (about 20 Hz) (Aguirre, 1978; Wadenton, 1956; Coile, Pollitz, & Smith, 1989).

One feature of the visual system that has not been studied is the brightness discrimination ability of the dog. Orbeli (1908) claimed that dogs are able to differentiate perfectly among closely related shades of grey that are indistinguishable to the human eye (Duke-Elder, 1958), but this claim has not been investigated formally. In general, only very few species have been tested on their ability to discriminate brightness, so the basis for comparison is still very small.

In our study, brightness discrimination in German and Belgian shepherd dogs was examined in a simultaneous two-choice situation. The tests were designed to show how much two steps of grey had to differ in their relative reflection to be discriminated by the animals and how this difference in relative reflection varied from bright to dark stimuli.

Materials and methods

Subjects

The experiments were conducted with three dogs of the Austrian police dog section at their housing and training facility in Strebersdorf, Vienna. Ajax, a male German shepherd, was aged 1.5 years at the beginning of the experiments. Astar, a male Belgian shepherd (Malinois), was aged 3 years, and Robby, another male Belgian shepherd (Malinois) was aged 1.5 years when the experiments started. None of the three experimental animals was used for police work during the time of the experiments. Before the start of the experiments, the eyes of all three dogs were thoroughly examined (including slit-lamp microscopy and indirect ophthalmoscopy) by a veterinarian eye specialist (Professor I. Walde, Institute for Surgery and Ophthalmology, Veterinary University Vienna) and were found to be in perfect condition. The experimental animals were maintained and treated according to the ABS/ASAB Guidelines for the Treatment of Animals in Behavioral Research and Teaching.

The experiments were carried out in an indoor facility under artificial light conditions. Each dog was trained and tested separately. The training and test sessions were carried out twice a day for each dog. The first session started in the morning and was carried out until noon, whereas the afternoon sessions started about 1 p.m. and usually lasted until the evening.

Little food balls were used as reinforcement. They were formed from a mixture of meat, innards, flakes, and pol-lard, the usual daily diet. The dogs were fed only during the experimental sessions and got their full daily food ratio during that time. When they did not receive all of it during the trials, the rest was fed to them right after the session.

Stimuli and apparatus

In the brightness discrimination task, the dogs had to discriminate two grey targets of differing brightness in a two-fold 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 to plastic plates (30 x 30 cm) and covered with a dull nonreflecting varnish. The spectral reflectance of the grey plates was measured using a spectrophotometer (MCS 230; Zeiss, Germany) to ensure that the spectral distribution of the reflected light was the same in the spectral range from 350–800 nm. The relative lightness of the grey plates was measured (Bacher-On-Line-Densimeter), the values expressed in photographic density (D), and converted into relative reflection ($R(\%) = 100 \times 10^{-D}$). Table 1 gives the density, the relative reflection values, and the cd/m^2 (human photometric units) of all grey targets from white to black (1–30).

The tests were conducted in an indoor facility in a specially prepared experimental room without windows. The

room (see Figure 1) was 7.2-m long and 4.10-m wide. The walls and partitions were white, and the room was illuminated with eight fluorescent tubes (Philips TLD 58 W/950 De Luxe 90) with a daylight-equivalent emission spectrum. The ambient light directly in front of the stimulus plates was measured with a Minolta Chroma-Meter XY-1; the constant illumination level was at 600 lx (human photometric units).

The stimulus plates were presented to the dogs in two identical plexiglass boxes (34.7 x 32.2 x 0.8 cm) with a handle on top to facilitate the change of the stimulus boxes. These boxes were inserted into two frames with nonreflecting front screens that were fixed to the front doors of two plywood boxes (60 x 60 x 60 cm). The front doors of the plywood boxes were hinged on top and could be pushed in easily by the dogs with their snouts and also stayed in an open position to make it possible for the dogs to get to their reward. Inside the feeding dish with the food was in a depression so that the opening of the door would not push the dish backward. The front doors could be bolted with a bar. The boxes were placed at the back wall of the room at a distance of 1.1 m from each other.

| Nr. | R(%) | D | cd/m^2 |
|-----|------|------|------------------------|
| 1 | 89.1 | 0.05 | 170.2 |
| 2 | 75.9 | 0.12 | 145.0 |
| 3 | 55.0 | 0.26 | 105.0 |
| 4 | 46.8 | 0.33 | 89.4 |
| 5 | 37.2 | 0.43 | 71.0 |
| 6 | 33.9 | 0.47 | 64.7 |
| 7 | 30.9 | 0.51 | 59.0 |
| 8 | 26.9 | 0.57 | 51.4 |
| 9 | 23.4 | 0.63 | 44.7 |
| 10 | 21.4 | 0.67 | 40.9 |
| 11 | 19.1 | 0.72 | 36.5 |
| 12 | 17.4 | 0.76 | 33.2 |
| 13 | 16.2 | 0.79 | 30.9 |
| 14 | 15.1 | 0.82 | 28.8 |
| 15 | 13.8 | 0.86 | 26.4 |
| 16 | 13.2 | 0.88 | 25.2 |
| 17 | 12.6 | 0.90 | 24.1 |
| 18 | 11.5 | 0.94 | 22.0 |
| 19 | 10.2 | 0.99 | 19.5 |
| 20 | 9.1 | 1.04 | 17.4 |
| 21 | 8.7 | 1.06 | 16.6 |
| 22 | 8.3 | 1.08 | 15.9 |
| 23 | 7.9 | 1.10 | 15.1 |
| 24 | 7.4 | 1.13 | 14.1 |
| 25 | 7.1 | 1.15 | 13.6 |
| 26 | 6.6 | 1.18 | 12.6 |
| 27 | 6.0 | 1.22 | 11.5 |
| 28 | 5.8 | 1.24 | 11.1 |
| 29 | 5.4 | 1.27 | 10.3 |
| 30 | 3.5 | 1.46 | 6.7 |



Table 1. Thirty-part series of grey stimuli. For each shade, the values of density (D), relative reflection (R), and cd/m^2 are given.

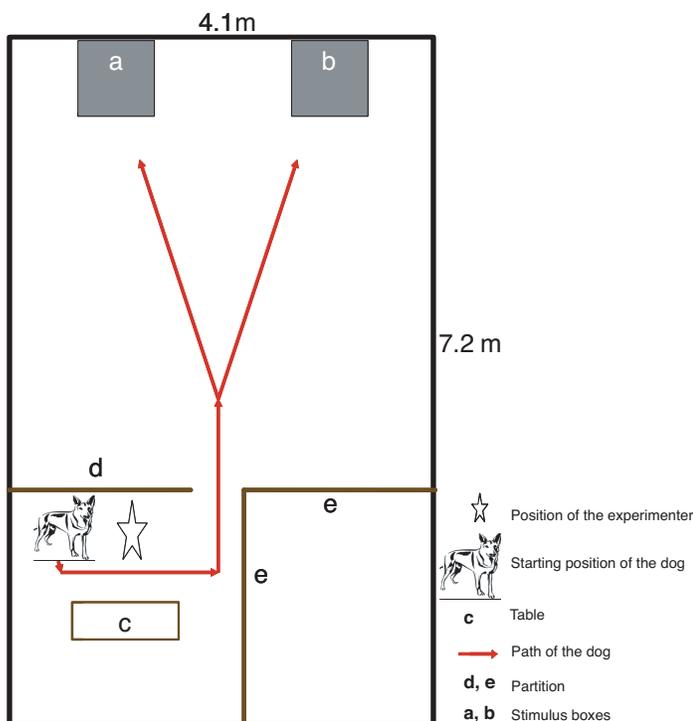


Figure 1. Experimental setup.

Procedure

Because dogs react even to subtle facial expressions or gestures, even subconscious ones, any kind of cueing from the experimenter had to be avoided. The procedure was as follows (see Figure 1).

The dogs were stationed behind a partition (d) during the exchange of the stimulus boxes, so they could not see the changing of the stimuli. To avoid acoustical cueing, both stimulus boxes were taken out of the frames after each trial, whether they stayed in the same position or not.

After the positioning of the stimuli, the experimenter went behind the partition and called the dog's name followed by the word "test", commanding the dog to walk from its starting position (see Figure 1) around the table (c) and then straight into the experimental room to make its choice. Thus the experimenter could not subconsciously influence the direction in which the dog would walk by manipulating the collar. The experimenter could, however, watch the choice of the dog through a small slit in the wall of the partition (15 x 2.5 cm). When the dog made a correct choice, the front door of the stimulus box would open and the dog could eat the food reward. Then it was called back to the adjacent room. With an incorrect choice, a whistle was blown and the dog came back to the adjacent room.

One test session consisted of a maximum of 31 trials. Each animal had two test sessions per day. After each trial, the stimulus boxes were changed and the food replaced. To avoid cueing by odors, both boxes contained food in all experiments, but only the positive stimulus box could be

opened. The dogs never touched the stimulus box itself, but only the plexiglass screen of the front door of the stimulus box, a precaution that also excluded chemical cueing. After 10 trials, there was a break of 10 min before continuing the session. During these breaks, the experimenter went outside with the dog and played with it. Before the next dog started the session, the plexiglass fronts of the stimulus boxes were cleaned with alcohol (70%) to avoid olfactory cues.

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 5 times on each side and did not remain at one position more than 2 times in a row, unless the animal made a wrong choice. In this case, the positive stimulus stayed in the same position until the animal chose correctly, a common procedure to discourage side preferences.

Experiment

In the experiment, the dogs had to discriminate two grey targets in a two-fold simultaneous-choice situation.

Training

In the training, the dogs first learned the discrimination of the brightest (G1) grey versus a dark grey (G20). The animals had to choose the brighter grey as the positive stimulus. During the training (as well as during the tests), a non-correction procedure was used. The number of trials per training was limited to 31. At the beginning, the whistle was not used as a secondary reinforcer, but later it became necessary because after an incorrect choice, the dogs stayed in the room and tried to push in the door of the stimulus boxes by force. After the introduction of the whistle, they stopped this behavior immediately.

When the performance reached the level of over 90% in 31 consecutive trials (28 correct choices in 31 trials), the next grey, which was six steps brighter (G 14), was presented with G1. When they passed the 90% level again, the next grey (G7) was presented until they again reached more than 90% in 31 trials. Then the test was started.

Test

To minimize the number of trials, the tests followed a closed sequential statistical plan for an error probability of $\alpha \leq 0.05$ (Bauer, Scheiber, & Wohlzogen, 1986). Thus the number of trials tested for each combination of greys was not constant. The maximal number of trials per session was 31. When they finished one combination before reaching 31 trials, the next combination was tested. During one session not more than two new combinations of greys were presented to the dog. After the combination G1 X G7, G6 to G2 was tested with G1. After completing the series with G1 as the standard, this step-by-step approximation to the threshold was repeated for every grey shade of the 30-part series. When a threshold was reached, the last dis-

crimable combination and the threshold combination were tested again. In case the repetition yielded a different outcome, the test was repeated again above and below the threshold until there were two tests in a row that yielded the same results. This last session was taken to determine the threshold.

Results

The experiments were conducted between September and December 1998 (6 days a week). In the initial training phase, Ajax learned to use the mechanism of the boxes in 1 training session, Astar in 2, and Robby, who was initially afraid of the boxes, in 5 sessions. For the training of the discrimination grey against grey, starting with the combination G1 X G20, then going down to G1 X G7, Ajax had 12, Astar 17, and Robby 15 training sessions.

The threshold of relative reflection for a choice frequency of 75% for every shade of grey was linearly interpolated for the three dogs.

To compare the results for the dogs with the data for other species, the relative difference threshold or Weber fraction was calculated. Weber's law states that the difference between two stimuli that is just noticeable depends on the magnitude of the starting stimulus. The greater the magnitude of the starting stimulus, the greater the just noticeable difference ($\Delta I/I = k$, where I is the intensity of the starting stimulus, ΔI 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- or very high-stimulus intensities, but neither very high nor very low intensities were used in this experiment. The Weber fraction was calculated for each threshold $\Delta R^*/R$, where ΔR^* is the difference in the relative reflectance between the distinguishable greys (see Table 2). Table 2 shows an example for the calculation of the Weber fraction for the dog Ajax. The mean Weber fraction for Ajax was 0.22 and for Astar and Robby, 0.27.

Figure 2 shows the dependence of the difference threshold [$\Delta R^*(\%)$] on the magnitude of the stimulus

| Grey no. | Density D | Relative reflection. R % | Difference in relative reflection between adjacent greys, Δr (%) | No. of discriminated grey | Difference in relative reflection between two discriminated greys, ΔR (%) | Calculated threshold for each grey in relative reflection, $\Delta R^*(\%)$ | Weber fraction for each threshold $\Delta R^*/R$ |
|----------|-----------|--------------------------|--|---------------------------|---|---|--|
| 1 | 0.05 | 89.1 | 13.2 | 3 | 34.1 | 23.65 | 0.27 |
| 2 | 0.12 | 75.9 | 20.9 | 3 | 20.9 | x | |
| 3 | 0.26 | 55.0 | 8.2 | 4 | 8.2 | x | |
| 4 | 0.33 | 46.8 | 9.6 | 5 | 9.6 | x | |
| 5 | 0.43 | 37.2 | 3.3 | 6 | 3.3 | x | |
| 6 | 0.47 | 33.9 | 3.0 | 7 | 3.0 | x | |
| 7 | 0.51 | 30.9 | 4.0 | 8 | 4.0 | x | |
| 8 | 0.57 | 26.9 | 3.5 | 10 | 5.5 | 4.50 | 0.17 |
| 9 | 0.63 | 23.4 | 2.0 | 10 | 2.0 | x | |
| 10 | 0.67 | 21.4 | 2.3 | 12 | 4.0 | 3.36 | 0.16 |
| 11 | 0.72 | 19.1 | 1.7 | 13 | 2.9 | 2.22 | 0.12 |
| 12 | 0.76 | 17.4 | 1.2 | 15 | 3.6 | 3.29 | 0.19 |
| 13 | 0.79 | 16.2 | 1.1 | 17 | 3.6 | 3.39 | 0.21 |
| 14 | 0.82 | 15.1 | 1.3 | 18 | 3.6 | 3.32 | 0.22 |
| 15 | 0.86 | 13.8 | 0.6 | 19 | 3.6 | 3.02 | 0.22 |
| 16 | 0.88 | 13.2 | 0.6 | 20 | 4.1 | 3.72 | 0.28 |
| 17 | 0.90 | 12.6 | 1.1 | 21 | 3.9 | 3.78 | 0.30 |
| 18 | 0.94 | 11.5 | 1.3 | 23 | 3.6 | 3.41 | 0.30 |
| 19 | 0.99 | 10.2 | 1.1 | 23 | 2.3 | 2.22 | 0.22 |
| 20 | 1.04 | 9.1 | 0.4 | 25 | 2.0 | 1.92 | 0.21 |
| 21 | 1.06 | 8.7 | 0.4 | 25 | 1.6 | 1.50 | 0.17 |
| 22 | 1.08 | 8.3 | 0.4 | 27 | 2.3 | 2.14 | 0.26 |
| 23 | 1.10 | 7.9 | 0.5 | 27 | 1.9 | 1.70 | 0.22 |
| 24 | 1.13 | 7.4 | 0.3 | 28 | 1.6 | 1.52 | 0.21 |
| 25 | 1.15 | 7.1 | 0.5 | 29 | 1.7 | 1.60 | 0.23 |
| 26 | 1.18 | 6.6 | 0.6 | 29 | 1.2 | 1.03 | 0.16 |
| 27 | 1.22 | 6.0 | 0.2 | 30 | 2.5 | 1.53 | 0.26 |
| 28 | 1.24 | 5.8 | 0.4 | | | | |
| 29 | 1.27 | 5.4 | 1.9 | | | | |
| 30 | 1.46 | 3.5 | - | | | | |
| | | | | | | | Mean Weber-fraction 0.22 |

Table 2. Example for the calculation of the Weber fraction for the dog Ajax. x indicates that the threshold could not be calculated here because the animal could discriminate the adjacent grey.

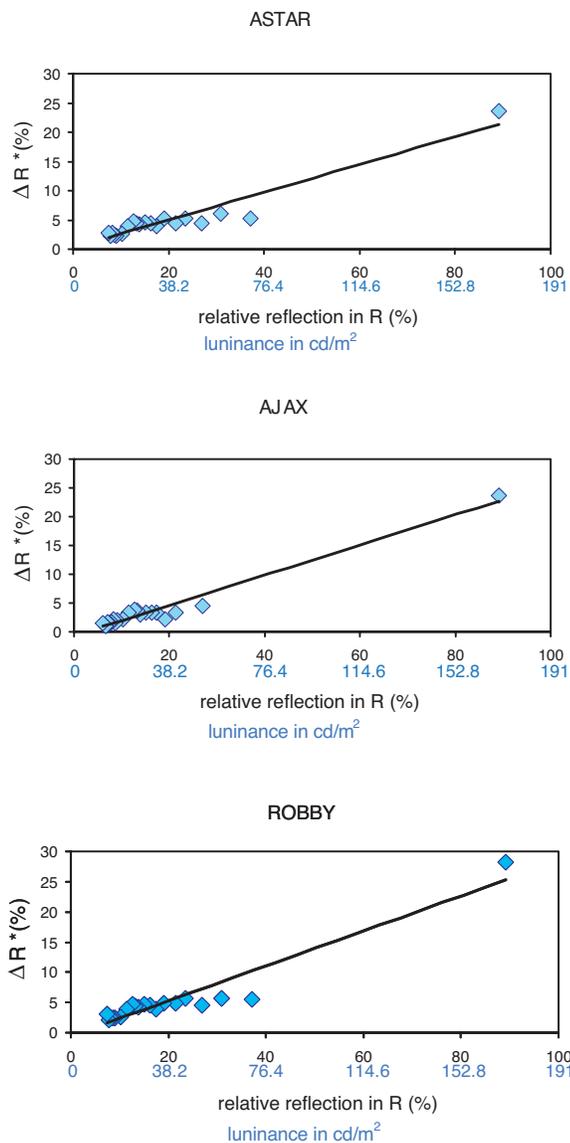


Figure 2. The amount of relative reflection ΔR^* by which two greys had to differ in order for the subjects to distinguish between them, as a function of the relative reflection R (%) of the brighter grey. The data fall approximately on a straight line, indicating that the threshold intensity difference ΔR^* is proportional to the intensity R , in agreement with Weber's law. Ajax: $y = 0.26x - 0.66$, $r = 0.98$; Astar: $y = 0.24x + 0.27$, $r = 0.95$; and Robby: $y = 0.29x - 0.55$, $r = 0.95$.

R (%). The best fit to the data is a straight line, indicating that the threshold intensity difference (= difference in relative reflection) [ΔR^* (%)] is directly proportional to the intensity (relative reflection) R (%).

Figure 3 shows the Weber fractions for each threshold for Ajax, Astar, and Robby ($\Delta R^*/R$) for each of the grey stimuli of the 30-part series [given in relative reflection, R (%) as well as cd/m^2]. Interestingly, Ajax, the German shepherd, is consistently at least one step better than the two Belgian shepherds.

Discussion

The difference in relative reflection that the dogs could discriminate varied with the absolute brightness of the stimuli according to the Weber fraction, which was 0.22 for Ajax, and 0.27 for Astar and Robby. Because the method and the stimuli we used were the same ones that were used by Griebel and Schmid (1997) in replicating the human thresholds of Cornsweet and Pinsker (1965), we are confident that the methods we employed with the dogs are valid. The German shepherd, Ajax, was generally one-to-two-steps better in discriminating the greys than the two Belgian shepherds Astar and Robby, who had almost identical results. Ajax could discriminate two adjacent greys in the bright range of the grey scale without problems up to G8 (26.9 % relative reflection), whereas the two Belgian shepherds started to have difficulties by G5 (37.2 % relative reflection). As shown in Table 2, the dogs could discriminate much smaller brightness differences in the dark range of the grey scale, which is also in accordance with Weber's law. The lowest single threshold in difference in relative reflection that the dogs could discriminate was 1.03% for Ajax, 2.33% for Astar, and 2.03% for Robby.

So far very few species have been investigated with respect to brightness discrimination ability, and in the few studies available, different evaluation methods have been used, which complicates the comparison of the data. Two species of fur seals, *Arctocephalus pusillus* and *Arctocephalus australis*, have been tested with a series of 28 greys (Busch & Dücker, 1987). The results for both species were very similar. Griebel and Schmid (1997) calculated the Weber fraction from the data of Busch and Dücker (1987) to be around 0.30. Griebel and Schmid (1997) conducted a brightness discrimination test in the West Indian manatee (*Trichechus manatus*) and found a Weber fraction of 0.35. They also tested two human observers under the same experimental conditions as the manatees, and calculated a Weber fraction of 0.11. The results of the human subjects agree well with the earlier results obtained by Cornsweet and Pinsker (1965), who found a Weber fraction of 0.14 in humans. Chausseil and Löhmer (1986) could not determine thresholds in their study on brightness discrimination with nocturnal coatis, because their 20-part series of greys was not a fine enough scale.

Ambient light conditions varied considerably in these studies. Whereas the manatees and the human subjects (Griebel & Schmid, 1997) were tested under constant ambient light levels of 150 lux, the fur seals (Busch & Dücker, 1987) were tested in an outdoor facility under high but varying light levels, probably yielding photopic conditions. The reason we cannot be absolutely sure about the degrees of photopic adaptation is that many animals, especially arrhythmic ones such as seals and sea lions, have highly flexible pupils that can drastically reduce the amount of light reaching the retina. In pinnipeds and cetaceans, the shapes of the photopic spectral sensitivity functions suggest that

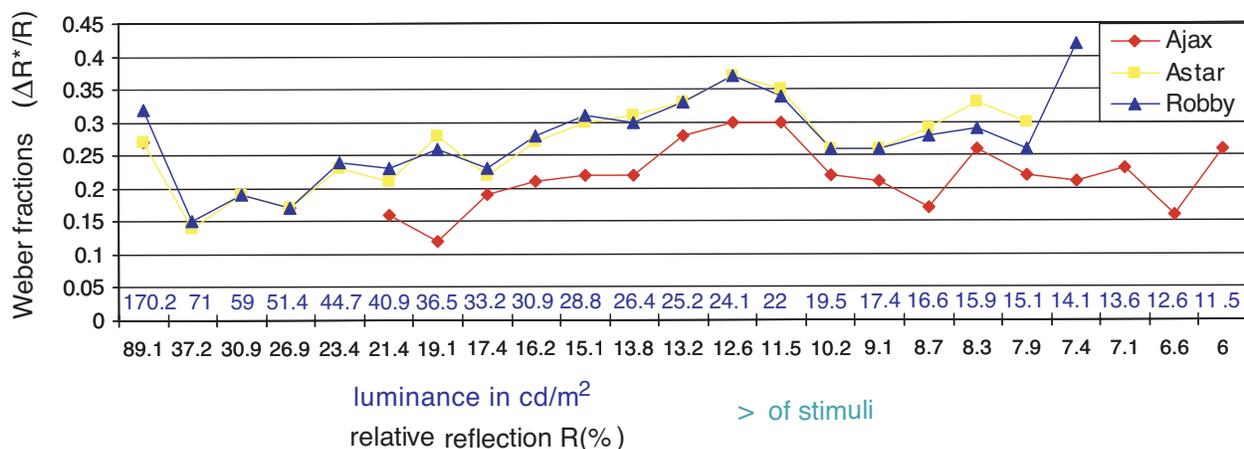


Figure 3. Weber fractions for each threshold for Ajax, Astar, and Robby ($\Delta R^*/R$) for each stimulus of the 30-part series (values are given in relative reflection R [%] and in cd/m^2).

rods contribute to spectral sensitivity even under ambient daylight conditions. This is probably achieved by constricting the pupil to a small slit aperture, thus maintaining a level of retinal illumination where both rods and cones can function (Crognale, Levenson, Ponganis, Deegan, & Jacobs, 1998; Griebel & Schmid, 2002). Manatees might use a similar mechanism.

We assume that the human subjects in Griebel and Schmid's study probably predominantly used the cone system. Cornsweet and Pinsker (1965) measured their subjects under dark adaptation, yielding the same Weber fraction as the later study by Griebel and Schmid (1997) under photopic conditions, 0.14 and 0.11, respectively. The three dogs in the current study were tested in ambient light levels of 600 lux, suggesting that the cones were predominantly involved in the discrimination.

Compared with these species, dogs seem to be in the middle range, but closer to the fur seals and manatees than to the humans. Like fur seals and manatees, dogs and other canid species are active during the day as well as during the night (Buehler, 1974; Lloyd, 1980). Their visual systems seem to be well adapted to both scotopic and photopic conditions. Thus dogs seem to be visual generalists, who also make extensive use of smell, just as manatees and fur seals probably compensate for visual deficiencies with their highly sensitive vibrissae. The brightness discrimination ability in humans, a diurnal species, seems to be about 2 times better than in the dog. Unfortunately, we do not have the comparison with a truly nocturnal species, because thresholds with nocturnal coatis could not be determined. Thus it is too early to draw any general conclusions regarding ecological correlates of brightness discrimination and lifestyle.

We know a great deal about how different species differ in color vision, acuity, and other capabilities of the visual system, but we know almost nothing about how species differ in brightness discrimination abilities. Hopefully, this study will inspire further investigations.

Acknowledgments

We are indebted to the Department of the Interior, the police dog section, Vienna, and to Colonel T. Diethart for permitting us to test the dogs and use the facility. This study was supported with a research grant by the Veterinary University of Vienna.

Commercial relationships: none.

Corresponding author: Ulrike Griebel.

Email: ugriebel@memphis.edu.

Address: The University of Memphis, Dept. of Biology, 103 Ellington Hall, 3700 Walker Avenue, Memphis, TN 38152.

References

- Aguirre, G. (1978). Retinal degeneration in the dog: Rod dysplasia. *Experimental Eye Research*, 26, 233-253. [PubMed]
- Allgoewer, I. (1991). Zur mikroskopischen Anatomie der Pars optica der Haussäugetiere und einiger Nager. Dissertation, Ludwig-Maximillan-Universität München.
- Arey, L. B., & Gore, M. (1942). The numerical relationships between the ganglion cells of the retina and the fibres in the optic nerve of the dog. *Journal of Comparative Neurology*, 77, 609-617.
- Bauer, P., Scheiber, V., & Wohlzogen, F. (1986). *Biometrie. Sequentielle statistische Verfahren*. Stuttgart: Gustav Fischer.
- Bromberg, N. M., & Dawson, W. W. (1980). Preliminary measures of canine visual spatial resolution with electrophysiological techniques. *Transactions of the American College of Veterinary Ophthalmological Society*, 11, 120-125.
- Buehler, L. E. (1974). *Wild dogs of the world*. London: Constable.

- Burns M. S., Bellhorn, R. W., Impellizzeri, C. W., Aguirre, G. D., & Laties, A. M. (1988). Development of hereditary tapetal degeneration in the beagle dog. *Current Eye Research*, 7, 103-114. [PubMed]
- Busch, H., & Dücker, G. (1987). Das visuelle Leistungsvermögen der Seebären (*Arctocephalus pusillus* und *Arctocephalus australis*). *Zoologischer Anzeiger*, 219, 197-224.
- Chausseil, M., & Löhmer, R. (1986). Untersuchungen über das Helligkeitssehen beim Wickelbären. *Zeitschrift für Säugetierkunde*, 51, 274-281.
- Coile, D. C. (1982). A determination of critical flicker fusion as a function of light intensity in dogs using conditional suppression. Master's thesis, Florida State University, Tallahassee, FL.
- Coile, D. C., Pollitz, C. H., & Smith, J. C. (1989). Behavioral determination of critical flicker fusion in dogs. *Physiology and Behavior*, 45, 1087-1092. [PubMed]
- Cornsweet, T. N., & Pinsker, H. M. (1965). Luminance discrimination of brief flashes under various conditions of adaptation. *Journal of Physiology*, 175, 294-310. [PubMed]
- Crognale, M. A., Levenson, D., Ponganis, P. J., Deegan, J. F., & Jacobs, G. H. (1998). Cone spectral sensitivity in the harbor seal (*Phoca vitulina*) and implications for color vision. *Canadian Journal of Zoology*, 76, 2114-2118.
- Curcio, C. A., & Hendrickson, A. E. (1991). Organization and development of the primate photoreceptor mosaic. *Progress in Retinal Research*, 10, 89-120.
- Duke-Elder, S. (1958). *System of ophthalmology. Vol. 1. The eye in evolution*. St. Louis: C.V. Mosby Co.
- Fox, M. W. (1971). Behavior of the wolves, dogs, and related canids. London: Jonathan Cape.
- Gellerman, L. W. (1933). Chance orders of alternating stimuli in visual discrimination experiments. *Journal of Genetic Psychology*, 42, 206-208.
- Griebel, U., & Schmid, A. (1997). Brightness discrimination ability in the West Indian manatee (*Trichechus manatus*). *Journal of Experimental Biology*, 200, 1587-1592. [PubMed]
- Griebel, U., & Schmid, A. (2002). Spectral sensitivity and color vision in the bottlenose dolphin (*Tursiops truncatus*). *Marine and Freshwater Behaviour and Physiology*, 35, 129-137.
- Jacobs, G. H., Deegan, J. F., Crognale, M. A., & Fenwick, J. A. (1993). Photopigments of dogs and foxes and their implications for canid vision. *Visual Neuroscience*, 10, 173-180. [PubMed]
- Kemp, C. M., & Jacobson, S. G. (1992). Rhodopsin levels in the central retinas of normal miniature poodles and those with progressive rod-cone degeneration. *Experimental Eye Research*, 54, 947-956. [PubMed]
- Koch, S. A., & Rubin, L. R. (1972). Distribution of cones in the retina of the normal dog. *American Journal of Veterinary Research*, 33, 361-363. [PubMed]
- Lehner, P. N. (1978). Coyote communication. In M. Bekoff (Ed.), *Coyotes: Biology, behavior and management* (pp. 128-162). New York: Academic Press.
- Lesiuk, T. P., & Braekevelt, C. R. (1983). Fine structure of the canine tapetum lucidum. *Journal of Anatomy*, 136, 157-164. [PubMed]
- Lloyd, H. G. (1980). *The red fox*. London: B.T. Balsford Ltd.
- Miller, P. E., & Murphy, C. J. (1995). Vision in dogs. *Journal of the American Veterinary Medical Association*, 207, 1623-1634. [PubMed]
- Murphy, C. J., Mutti, D. O., Zadnik, K., & Ver Hoeve, J. (1997). Effect of optical defocus on visual acuity in dogs. *American Journal of Veterinary Research*, 58, 414-418. [PubMed]
- Neitz, J., Geist, T., & Jacobs, G. (1989). Color vision in the dog. *Visual Neuroscience*, 3, 119-125. [PubMed]
- Neuhaus, W., & Regenfuss, E. (1967). Über die Sehschärfe des Haushundes bei verschiedenen Helligkeiten. *Zeitschrift für Vergleichende Physiologie*, 57, 137-146.
- Odom, J. V., Bromberg, N. M., & Dawson, W. W. (1983). Canine visual acuity: Retinal and cortical field potentials evoked by pattern stimulation. *American Journal of Physiology*, 245, R637-R641. [PubMed]
- Osterholm, H. (1964). The significance of distance receptors in the feeding behavior of the fox. *Vulpes vulpes L. Acta Zoologica Fennica*, 106, 3-31.
- Orbeli, L. A. (1908). Conditioned reflexes resulting from optical stimulation of the dog. Dissertation, St. Petersburg (in Russian).
- Parkes, J. H., Aguirre, G., Rockes, J. H., & Liebman, P. A. (1982). Progressive rod-cone degeneration in the dog: Characterization of the visual pigment. *Investigative Ophthalmology and Visual Science*, 23, 674-678. [PubMed]
- Parry, H. B. (1953). Degeneration of the dog retina. I. Structure and development of the retina of the normal dog. *British Journal of Ophthalmology*, 37, 385-404. [PubMed]
- Parry, H. B., Tansley, K., & Thompson, L. C. (1953). The electroretinogram of the dog. *Journal of Physiology*, 120, 28-40. [PubMed]
- Peichl, L. (1991). Catecholaminergic amacrine cells in the dog and wolf retina. *Visual Neuroscience*, 7, 575-587. [PubMed]

- Peichl, L. (1992). Topography of ganglion cells in the dog and wolf retina. *Journal of Comparative Neurology*, 324, 603-620. [[PubMed](#)]
- Rosengreen, A. (1969). Experiments in color discrimination in dogs. *Acta Zoologica Fennica*, 121, 3-19.
- Scheibner, H., & Schmidt, B. (1969). Zum Begriff der elektroretinographischen Ergebnissen am Hund. *Albrecht von Graefes Archiv für klinische und experimentelle Ophthalmologie*, 177, 124-135. [[PubMed](#)]
- Sherman, S. M., & Wilson, J. R. (1975). Behavioral and morphological evidence for binocular competition in the postnatal development of the dog's visual system. *Journal of Comparative Neurology*, 161, 183-195. [[PubMed](#)]
- Wadenstein, L. (1956). The use of flicker electroretinography in the human eye: Observations on clinical cases. *Acta Ophthalmologica*, 34, 311-340.
- Wells, M. C., & Lehner, P. N. (1978). The relative importance of the distance senses in coyote predatory behavior. *Animal Behavior*, 26, 251-258.
- Wen, G. Y., Sturman, J. A., & Shek, J. W. (1985). A comparative study of the tapetum, retina, and skull of the ferret, dog, and cat. *Laboratory Animal Science*, 35, 200-210. [[PubMed](#)]
- Yokoyama, S., & Radlwimmer, F. B. (1998). The "five-sites" rule and the evolution of red and green color vision in mammals. *Molecular Biology and Evolution*, 15, 560-567. [[PubMed](#)]