Research

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Colour cues proved to be more informative for dogs than brightness

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The results of early studies on colour vision in dogs led to the conclusion that chromatic cues are unimportant for dogs during their normal activities. Nevertheless, the canine retina possesses two cone types which provide at least the potential for colour vision. Recently, experiments controlling for the brightness information in visual stimuli demonstrated that dogs have the ability to perform chromatic discrimination. Here, we show that for eight previously untrained dogs colour proved to be more informative than brightness when choosing between visual stimuli differing both in brightness and chromaticity. Although brightness could have been used by the dogs in our experiments (unlike previous studies), it was not. Our results demonstrate that under natural photopic lighting conditions colour information may be predominant even for animals that possess only two spectral types of cone photoreceptors.

1. Introduction

As in most mammals, the canine retina contains rod photoreceptors responsible for scotopic vision at low light levels, and cone photoreceptors responsible for the photopic (bright light) vision. Cones make a minor fraction of photoreceptors [1], with the highest packing density in the central portion of the retina, where their fraction comprises 20% of all photoreceptors [2]. The cones are represented by two spectral types: short- and long-wavelength-sensitive cones with maximum sensitivity of approximately 429 and 555 nm, respectively [3].

The existence of the two cone types provides the potential for two-dimensional colour perception that can be used by dogs in object recognition. However, it is not obvious whether this mechanism of visual information processing actually takes place and to what extent [3]. One could expect that colour recognition might not be essential for canids as they are active not only during the day, but also at dusk and during the night. In low light levels, only rods are active and thus dogs have to do without any chromatic information. Moreover, even in daylight it could be difficult for dichromatic animals to recognize visual objects by their surface colour under changing lighting conditions. As follows from theoretical considerations, low-dimensional colour vision exhibits a high degree of colour metamerism, thwarting colour constancy under changes in the spectral composition of the illuminant [4–6]. This apparently makes the assumption of the significance of colour recognition in dogs (and in dichromatic mammals in general) even less feasible.

When training animals to discriminate and recognize visual stimuli according to their colour, it is common to eliminate brightness as an additional cue that could be used by the animals when making their choice [7]. In order to make brightness of coloured stimuli an unreliable cue, the stimuli are either equalized in their brightness or the brightness is varied during the training [3,8]. The first method relies on assumptions (often groundless or completely incorrect) about the animal's luminous efficiency function (i.e. the spectral sensitivity function, which determines the brightness of the stimuli as seen by the animal) [9–11]. The second method is not only labour- and time-consuming; its main shortcoming is that animals are actually trained that brightness is an unreliable cue, even though they could use it when discriminating the stimuli. Although in more recent behavioural studies the ability to discriminate coloured visual stimuli was demonstrated in the dog [3,8], it is still not clear whether colour cues can
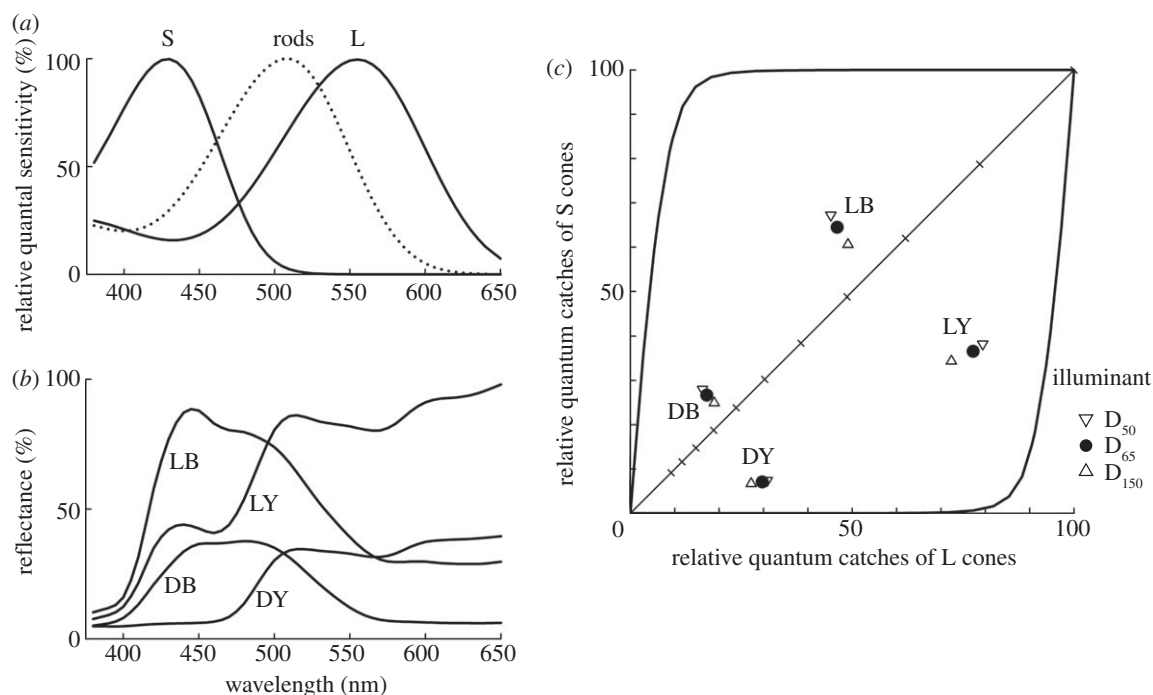
Figure 1. Spectral characteristics of the photoreceptors of the dog eye and the stimuli used in the experiments. (a) Normalized spectral sensitivity functions of the dog's short-wavelength (S) and long-wavelength (L) cones and rods calculated using the visual pigment templates of Govardovskii et al. [15]. (b) Spectral reflectances of the LB, LY, DB and DY papers measured with Color I 7 Benchtop Spectrophotometer (X-rite Inc., USA). (c) Locations of the four stimuli in the dog's two-dimensional colour space, calculated for three different daylight illuminants [16]. The colours are represented as points in the two-dimensional colour space where the relative quantum catches of L- and S-sensitive cones of a dog are placed along the coordinate axes. The solid closed curve encloses colours of any reflective (non-self-luminous) surfaces under daylight illumination [5]. Colours of achromatic surfaces lie on the diagonal of the figure. Tick marks on the diagonal are away from each other on the distance of just-noticeable difference in brightness for Weber fraction of 0.27, as it was previously demonstrated for the dog [17].

be more informative for dogs than achromatic cues when discriminating and recognizing visual objects.

Unlike previous studies, we intentionally used visual stimuli that could be discriminated by the dogs according to both their brightness and chromaticity. The animals' preference for either of those cues was ascertained in the tests that followed the training. This approach to investigating the ranking of features was first proposed with regard to visual perception in passerine birds [12,13]. A similar method was used more recently for examining the preference between two different behavioural strategies of spatial orientation in fish [14]. According to this approach, animals are first trained to discriminate between a pair of visual stimuli that differ in two features at the same time. In the tests, the combination of the features in the stimuli is reversed, so that each of the testing stimuli has only one of the two characteristics that were initially combined in the positive training stimulus. Thus, according to the test results, it is easy to find out which of the features of the stimuli was used during the training and which, thereby, is more informative for the animals.

Using this paradigm, we initially trained the dogs to discriminate between two coloured stimuli that differed both in brightness and chromaticity (e.g. dark yellow, DY versus light blue, LB), rewarding correct choices with food. After that, the dogs had to make a spontaneous choice without reward between the test stimuli in which one of the features was reversed (e.g. light yellow, LY versus dark blue, DB) to ascertain which of the features was used by the dogs during the training. If the trained dogs consistently chose the test stimuli of the same colour as the positive training stimulus, despite the difference in brightness, we could conclude that colour was a more informative cue for the dogs than brightness.

2. Material and methods

Two shades of yellow (LY and DY) and blue (LB and DB) papers, spectral properties of which are given in figure 1, were used as visual stimuli in the experiments. The reflectance spectra of the four types of papers were chosen so that each 'dark' stimulus (DY and DB) reflected less light compared with either of the 'light' (LY and LB) stimuli throughout almost the entire visible (to the dog's eye) spectrum (figure 1b). Thus, it was possible for the dogs to distinguish the dark stimuli from the light stimuli solely according to their brightness difference, no matter which cone type, or which combination of the two, determined the dog luminous efficiency function. Location of the stimuli in the dog's colour space is given in figure 1c.

Eight previously untrained dogs (Canis familiaris) took part in the experiments. All the dogs were outbred animals, so the possibility of bias due to breed was minimal [18]. All the animals were experimentally naive. The experiments were performed outdoors under natural ambient daylight conditions. The illumination spectra were not controlled in the experiments. However, even though the season, time and location where the experiments were performed varied, the correlated colour temperatures of the daylight illuminant were certainly within the range of 5000–15 000 K. The locations of the colours of the stimuli (figure 1c) calculated for three different types of illuminants clearly demonstrate the low degree of illuminant metamerism for the stimuli, as the shifts in the colour space due to metamerism are negligible relative to the distances between the colours of the stimuli.

In every experimental session, a fresh set of paper stimuli was used for each of the dogs. The animals were divided into three groups, each of which was trained and tested with stimuli of different combinations of chromaticity and brightness.

The experimental set-up provided animals with a simultaneous two-choice situation. Visual stimuli were made from

Table 1. Discrimination scores for test sessions. The stimuli columns specify the pair of coloured stimuli presented in different trials, '(+)' identifying the positive training stimulus, while '(−)' identifies the negative one. The scores represent the number of trials in which the dogs chose corresponding stimuli. *p*-value was calculated by using the one-tailed binomial test, null hypothesis frequency = 0.5.

dog	sex	training trials		test trials		
		stimuli	scores	stimuli	scores	*p*-value
La	F	DY(+) : LB(−)	88 : 2	LY : DB	10 : 0	0.001
Ji	F	DY(+) : LB(−)	172 : 8	LY : DB	16 : 4	0.006
De	M	DB(+) : LY(−)	89 : 1	LB : DY	10 : 0	0.001
Di	F	DB(+) : LY(−)	87 : 3	LB : DY	10 : 0	0.001
Co	F	DB(+) : LY(−)	80 : 10	LB : DY	7 : 3	0.172
Ti	M	DB(+) : LY(−)	84 : 6	LB : DY	9 : 1	0.011
Uk	F	LB(+) : DY(−)	86 : 4	DB : LY	10 : 0	0.001
Zi	F	LB(+) : DY(−)	86 : 4	DB : LY	9 : 1	0.011

coloured paper squares of 15 × 15 cm printed using a HP Color LaserJet 2600n printer. The stimuli were placed in front of two equal feedboxes at 75 cm from each other. The feedboxes were covered with lids that, when unlocked, could be removed easily by the dogs with their paw or snout. In both training and test trials, each of the feedboxes contained a piece of raw meat. In the training trials, the positive stimulus indicated the unlocked feedbox, whereas the second feedbox remained locked, though both feedboxes appeared identical. In the test trials, both feedboxes were locked. Between the trials, the dogs were kept behind a screen at a distance of about 7 m from the point from which they approached the experimental set-up at the beginning of each trial. Only water was provided to them between the trials. After the set-up was prepared for a new trial, the experimenter would take the dog to the point 5 m from the set-up, from which it would face the stimuli for the first time in the trial. The dogs approached the set-up without interference from the experimenter. The experiment would end after the dog had made its choice and got/not got the reward.

Each daily training session consisted of 10 trials. The position of the visual stimuli during each session was changed according to Gellermann [19] to prevent any positional bias. After the dogs were trained to discriminate training stimuli (the dogs were considered as trained after they had chosen the positive stimulus in more than 8 trials out of 10 in at least two consecutive training sessions), we proceeded to the test sessions: one trial with the test stimuli was embedded in the sequence of 10 trials. During the remaining nine trials of the test session, the training continued. In the test sessions, the side and the sequence position of the test stimuli were varied from one consecutive session to another in order to prevent any situational adaptation in the dogs during the test trials. All the dogs except one were tested in 10 consecutive sessions. Thereafter, the total dataset for each dog represents the number of times either of the test or training stimuli was chosen in 10 test and 90 training trials, respectively. For one dog (Ji), the number of the test sessions was doubled.

3. Results

The results for all the dogs are given in table 1. As can be seen from the results, all the dogs preferred to choose the test stimuli according to the chromaticity, not the brightness, with half of the dogs making their choice exclusively by colour in all 10 tests. For two dogs (Ji and Co), the test results were less consistent. In the case of Ji, an additional 10 test

sessions provided statistically significant preference for colour. For Co, no additional tests were performed. Co also performed poorly during training trials of the test sessions, showing the worst score among the group. The extent to which the animals were motivated to accomplish the experimental task, their agitation, their ability to concentrate on the task, the way they responded to the absence of the food reward in the test trials—all these individual traits caused a certain distortion in the general pattern of the score results. Yet, despite the individual differences, the general pattern remained obvious for all the dogs.

4. Discussion

According to the results, the dogs could certainly use chromaticity when they discriminated the stimuli. But the key question is whether they did so because colour is a more reliable cue (i.e. dogs preferred to use colour despite significant difference in brightness) or because the difference in brightness between the light and the dark stimuli during the training was too small for dogs to use it. The way the colours of the stimuli are distributed in the colour space (figure 1c) makes the latter suggestion unlikely. Though the data on the dog visual system are too scarce for making any suggestions about the metrics of the colour space, it is known that dogs discriminate brightness differences of spatially separated achromatic visual stimuli according to Weber's Law, with a Weber fraction of approximately 0.22–0.27 [17]. In our experiments, we designed the stimuli so that the difference in both pairs (LB versus DY and LY versus DB) considerably exceeded this value and could be used by the dogs when making the choice. Table 2 clearly demonstrates that in either pair of stimuli the difference in brightness was significantly larger than the minimum perceptible value both in the long- and in the short-wavelength part of the spectrum. Hence the dogs were able to discriminate the stimuli according to their relative brightness, no matter which of the two cone types was predominantly involved in the process. In addition, all the dogs were divided into groups that were trained and tested on different pairs of stimuli—still none of them used brightness in these experiments (table 1).

It is known that a number of animal species with good colour vision (from hawkmoths to fish and birds) are difficult

Table 2. Brightness ratio of the stimuli in the light/dark pairs as seen by L- and S-sensitive cones of the dog. The brightness value of each stimulus was computed by integrating the product of its reflectance spectrum, the cone spectral sensitivity (figure 1) and the illuminant spectrum. Standard D65 daylight was assumed as illumination light [16].

pair of the stimuli	light/dark ratio for the L-cones	light/dark ratio for the S-cones
LB versus DY	1.57	9.40
LY versus DB	4.49	1.37

to train to recognize visual objects according to their brightness [20–22]. Also, distinctive brightness difference does not prevent these animals from learning to recognize objects according to colour. The results of our study show that, besides trichromatic and tetrachromatic animals, this category also includes dogs—the species that possesses only two types of cones. It should be noted that the preference for chromatic over achromatic cues in dichromats should differ based on the specific behavioural and visual context, as well as depend on the relative chromatic and achromatic contrast. In our experiments, we used stimuli that differed significantly in their relative reflectance spectra (figure 1*b*). With colours that differ less, dogs may have different priorities. Particularly, it has been demonstrated by Pretterer *et al.* [17] that dogs can discriminate achromatic stimuli, which do not differ in chromaticity at all, if they are of sufficient achromatic contrast . However, the approach used in our work allowed us to show that, given a significant chromatic contrast, dogs might prefer colour over relatively significant achromatic contrast: in the experiments, the dogs did not use obvious achromatic cues when discriminating the coloured papers—even when the difference in brightness was several times higher than the just-noticeable difference. The preference for chromatic cues has also been demonstrated previously for dogs and some other dichromatic mammals in another experimental paradigm (namely, in studies on determination of the increment-threshold spectral sensitivity functions) [3,23,24]. Our results, together with the results of the above-mentioned studies, suggest that colour can be a fundamental characteristic of visual objects and visual scenes as perceived by dogs that may enable the discrimination and recognition processes even in those vertebrates that possess the minimal required set of cone photoreceptors, as is the case for most mammals.

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