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 photospheric 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
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. The $p$-value was calculated by using the one-tailed binomial test, null hypothesis frequency $= 0.5$.

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

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...
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 1b). 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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