The spatial tuning of achromatic and chromatic vision in budgerigars

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Birds are assumed to use half of their cones (double cones) to detect fine spatial detail while their other half (single cones) is used for color vision. However, the spatial resolution of the color pathway in birds has never been studied. We determined the spatial contrast sensitivity to achromatic and isoluminant red–green and blue–green color gratings in budgerigars (Melopsittacus undulatus). Contrast sensitivity to achromatic gratings has band-pass characteristics while that for red–green and blue–green gratings has low-pass properties. Maximum sensitivity is lower to blue–green than to red–green gratings and the acuity for both color gratings is less than half (ca. 4.5 cycles/degree) of that for achromatic gratings (ca. 10 cycles/degree). This suggests that achromatic vision in birds, as in humans and bees, is tuned for detecting fine detail while chromatic vision is tuned for viewing larger fields. Moreover, budgerigars detected gratings having both achromatic and chromatic contrasts more reliably at high spatial frequencies than gratings with either of these contrasts, suggesting that the single and double cone pathways are incompletely separated. The study demonstrates the importance of the spatial dimension of color vision; fine patterns remain unresolved even if they present large color contrasts.

Keywords: pattern perception, spatial vision, color vision, spatial contrast sensitivity, bird, psychophysics


Introduction

In humans and honeybees, the spatial resolution of the color (chromatic) channel is lower than that of the luminance (achromatic) channel (Giurfa, Vorobyev, Brandt, Posner, & Menzel, 1997; Mullen, 1985). Bees, for instance, can detect flowers providing achromatic contrast to the background from a much larger distance than flowers only providing chromatic contrast (Giurfa et al., 1997). Likewise, there are indications that birds use achromatic cues to discriminate fine details (Osorio, Miklósi, & Gonda, 1999) and to distinguish between simple visual textures (Jones & Osorio, 2004).

Interestingly, birds are believed to have photoreceptors almost completely specialized for either achromatic or chromatic vision. Humans and bees use the majority of their receptors (95% of the cones in humans (Wyszecki & Stiles, 1982) and the L-receptors in all ommatidia in bees (Srinivasan & Lehrer, 1988)) for achromatic vision, providing high resolution. Quite differently, research so far suggests that birds use only about half of their cones—single cones of four different spectral sensitivities—for color vision (e.g., Goldsmith & Butler, 2003, 2005; Osorio et al., 1999; Vorobyev & Osorio, 1998; reviewed in Martin & Osorio, 2008). The color discrimination abilities in birds have been studied in depth (reviewed in Kelber, Vorobyev, & Osorio, 2003; Martin & Osorio, 2008) but little is known about the relation between the achromatic and chromatic channels, and nothing is known about the spatial resolution of the chromatic channel. This lack of knowledge limits our understanding of how birds perceive color patterns, such as those of plumages and eggs, which are believed to be vital signals of fitness and identity (Bennett & Théry, 2007; Kilner, 2006).

A robust measure of the spatial resolution of a visual channel is the spatial contrast sensitivity function (CSF; De Valois & De Valois, 1990). Not only does this function allow for an estimation of acuity, it also describes to what spatial frequencies the visual channel is most sensitive. However, while the spatial contrast sensitivity of the achromatic channel has been determined for a number of species (De Valois & De Valois, 1990; Ghim & Hodos, 2006; Uhlrich, Essock, & Lehmkühle, 1981), the corresponding sensitivity in the color channel is only known for humans (Mullen, 1985).
In this study, we present the results from three experiments with budgerigars (*Melopsittacus undulatus*). First, we determined the CSF function for achromatic gratings. Second, we determined the CSF for isoluminant chromatic gratings. This was possibly since budgerigars have photoreceptors with known spectral sensitivities (Bowmaker, Heath, Wilkie, & Hunt, 1997; Goldsmith & Butler, 2003, 2005; Lind & Kelber, 2009), which allowed us to precisely adjust the stimuli so that single cones could be tested separately from the double cones. This is the first description of a CSF for the color channel in any animal besides humans (Mullen, 1985).

It is known that in humans, the CSF is higher for red–green gratings than for blue–yellow gratings, possibly because blue-sensitive cones are relatively scarce within the human retina. Similarly, in budgerigars, the short-wavelength-sensitive (SWS) cones are less abundant (ca. 10–12% of total cone population) than medium-wavelength-sensitive (MWS) cones (ca. 19–21%) and long-wavelength-sensitive (LWS) cones (ca. 16–20%; Hart, 2001; Wilkie et al., 1998). For these reasons, we determined the CSFs for both red–green and blue–green gratings, both types isoluminant to double cones.

While these tests serve to investigate the spatial tuning in either the achromatic or the chromatic visual channels in budgerigars, most naturally occurring stimuli provide contrast to both (De Valois & De Valois, 1990). Therefore, we performed a third experiment, in which we examined the detection of gratings with a constant low achromatic contrast but with variable red–green chromatic contrast.

**Methods**

**Animals**

Four budgerigars were acquired from local breeders and fed with seed mixes supplemented with vitamins and fruit. On experimental days, all food was given in the experiments except for a small seed portion given after completed sessions. The animals were kept in accordance with the ethical guidelines stated by the Swedish Board of Agriculture that also approved the experiments (M18-07).

**Experimental cage**

The trial cage (length 1580 mm, width 860 mm, and height 670 mm) was made of matte gray metal net. A starting perch was placed in one short end, opposite a gray plastic board with two stimulus windows (Perspex board, 80 x 80 mm, 420 mm apart). A feeding box with a perch and a removable lid was placed below each window.

**Stimuli**

Stimuli were presented behind the windows on an LCD monitor (SX3031W-H, Eizo Europe AB, see Figure 1 for screen spectrum). A white opaque Perspex board divided the cage and separated the stimuli so that the distance from the point of decision to the stimuli could be determined (1268 mm). The cage was lit by four fluorescent tubes (Biolux L18W/865; Osram, flicker frequency > 500 Hz) giving a luminance of 10–11 cd/m² from the gray plastic board and 160–170 cd/m² from a white standard placed on the cage floor.

**Behavioral procedure**

The birds were trained to choose between negative low-frequency high-contrast square-wave grating stimuli (tilted 45°) and positive uniform stimuli until they reached 80% correct choices in two consecutive sets of 20 trials each. Before each session, the birds were kept in the trial cage for 10 min. The birds indicated a choice by flying to either side of the divider. A choice of the positive stimulus gave the bird access to seeds in the feeding box for 4 s while a choice of the negative stimulus turned the monitor black and the bird had to return to the starting perch to start a new trial. Stimulus pairs were presented in sets of 12–20 trials mixing easy choices (high contrast) with more difficult choices (low contrast) and 1 to 5 sets were presented in each session depending on the bird’s motivation. The sets were repeated until each bird completed 40 choices for each combination of contrast and spatial frequency. Order and side of presentation were varied pseudorandomly so that positive stimuli appeared no more
than three consecutive trials on the same side and an equal number of times on the left and right sides.

For the contrast sensitivity tests (Experiments 1 and 2), the birds were tested with gratings for which contrast but not spatial frequency was varied in order to establish the contrast threshold for that particular spatial frequency. This procedure was repeated at different spatial frequency levels to establish a spatial contrast sensitivity function. For the tests of detection of gratings with both achromatic and chromatic contrasts (Experiment 3), the birds were tested with gratings of different spatial frequencies at four different contrast levels.

Stimuli

Stimuli were produced in Matlab R2008a and presented on the screen with Microsoft PowerPoint v. 12.2.5. Radiance was measured with a spectroradiometer (RSP900-R; International Light), and luminance was measured with a radiometer (ILT1700 with detector SPM068-01, International Light). The monitor was recalibrated every 2 weeks. In the achromatic tests (Experiment 1), positive stimuli were uniform and either 20% brighter or 20% dimmer than the square-wave gratings to exclude luminance as a cue. For the color tests (Experiments 2 and 3), positive stimuli were gratings of a high frequency (23.4 cycles/degree) that made them appear uniform even for humans (human acuity for isoluminant color gratings is about 11–12 cycles/degree; Mullen, 1985) and matched to the negative gratings in brightness and color (see electronic Supplementary material for more details).

The sensitivity of budgerigar photoreceptors was modeled using a visual pigment template (Govardovskii, Fyhrquist, Reuter, Kuzmin, & Donner, 2000) and a model of oil droplet absorbance (Hart & Vorobyev, 2005) together with absorbance data of the visual pigments, the oil droplets (Bowmaker et al., 1997), and the ocular media (Figure 1, and see appendix in Lind and Kelber, 2009 for used values).

Quantum catches of cones and the Euclidean distance between loci within color space were calculated as described elsewhere (Balkenius & Kelber, 2004). Contrasts in individual receptor types were calculated as Michelson contrast based upon quantum catches (Srinivasan & Lehrer, 1988). Our criteria for isoluminance are (i) that the contrast for double cones is below the minimum contrast threshold of the achromatic contrast sensitivity test (0.098 at 1.42 cycles/degree; Figure 2) and (ii) that this is true even if the absorbance spectrum of the double cones is shifted 10 nm toward shorter or longer wavelengths. The second criterion is important since the principal member of double cones contains a pigmented oil droplet while the accessory member lacks an oil droplet but contains a low concentration of carotenoids in the position where the oil droplet is found in the principal member (Bowmaker et al., 1997). This causes a slight difference in spectral sensitivity between the two double cone members below 470 nm, which is important to consider when constructing the blue–green stimuli (the spectral output of the red–green stimuli contained negligible amounts of light below 500 nm, Figure 1). The difference between absorbance of both members of the double cones is smaller than the hypothetical shift of 10 nm that was taken into account; thus, the second criterion for isoluminance ensures that the chromatic gratings were isoluminant for both members of the double cone. In addition, this secures the isoluminance of the chromatic gratings in spite of the variation in spectral sensitivity of the double cone that is found in budgerigars (Bowmaker et al., 1997).

Average contrast for the double cones in all color gratings was 0.014, and maximally, the contrast reached 0.050 (for the calculations with a shifted absorbance spectrum, the average was 0.020 and the maximum was 0.09).

Data analysis

Logistic functions were fitted to the results from all birds in each test using bootstrapping (2000 simulations; Wichmann & Hill, 2001a, 2001b) with psignifit (http://www.bootstrap-software.org/psignifit/toolbox.php) in Matlab. From these functions, the threshold of detection (72.5% correct choices, binomial test, n = 40, p < 0.01) was interpolated. The double exponential function fitted to the CSF using achromatic gratings was acquired from Uhlrich et al. (1981), and both this function and the linear functions used to predict acuity to color gratings were fitted to the data using the program fit in Matlab. Similarity between psychometric data sets was tested using Monte Carlo simulations (100,000 simulations) with pfcomp (for download, see Internet address above) in Matlab. Analysis using a general linear model procedure with R gave the same results. For further detail, see electronic Supplementary material.

Results

Experiment 1: Contrast sensitivity to achromatic gratings

First, we tested the birds with achromatic gratings that provided equal contrast to all cone types. The resulting CSF for achromatic stimuli has band-pass characteristics (Figure 2) typical for luminance channels in other vertebrates (De Valois & De Valois, 1990; Uhlrich et al., 1981). Maximum sensitivity (10.2, inverse Michelson contrast) is
reached at 1.4 cycles/degree and the high-frequency cutoff (predicted detection limit) is located at 10 cycles/degree (Figure 2).

**Experiment 2: Contrast sensitivity to color gratings**

Next, we tested the birds with color gratings that provided contrast only for single cones while double cone contrast was kept below the minimum contrast threshold measured with achromatic gratings (Figure 2). The stimuli were red–green and blue–green gratings located along different axes within the color space of budgerigars (Figure 3). As a measure of color contrast, we use the Euclidean distance between the two colors in each grating within the color space of budgerigars (Figure 3, but see electronic *Supplementary material* for color distance in receptor noise-limited opponent color space).

When tested with high-contrast achromatic gratings in *Experiment 1*, the birds reached close to 100% correct choices, but when the birds were presented with red–green

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**Figure 2.** Spatial contrast sensitivity function for achromatic gratings. (a) Examples of psychometric data from contrast threshold tests at 1.2 and 7.2 cycles/degree (for all results, see electronic *Supplementary data*). Each open circle represents 40 choices from one bird. Filled circles are threshold values, which were interpolated from logistic functions that were fitted to the data (lines, see Methods section for details of fitting procedure). (b) Circles represent the inverse of the Michelson contrast thresholds and the dashed line is a double exponential function fitted to the data as suggested by Uhlrich et al. (1981). All error bars are 95% confidence intervals. Average stimulus luminance was 50 cd/m².

The average photon catch of single cones (sum of SWS, MWS, and LWS) and double cones was $1.19 \times 10^{13}$ and $1.41 \times 10^{13}$, respectively. The inserts are examples of the used stimuli.

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**Figure 3.** Color spaces with loci for the grating stimuli. (a) Loci for the color pairs (same symbols) of the red–green (red symbols) and the blue–green (blue symbols) gratings used in the spatial contrast sensitivity tests (*Experiment 2*). (b) Loci of the grating colors (A, B, C, D) used in the detection test (*Experiment 3*). In (a), loci of grating colors with very small separation distances have been excluded to enhance visualization. The neutral point is the filled gray circle denoted as N. The loci of spectral colors are not depicted but coincide with the triangular sides due to very small spectral overlaps between the spectral sensitivities of the receptors (Lind & Kelber, 2009). SWS, MWS, and LWS denote the short-wavelength-sensitive, medium-wavelength-sensitive, and long-wavelength-sensitive photoreceptors, respectively. The UVS dimension of the color space is ignored since stimuli did not contain light for the UVS cone.
color gratings in Experiment 2 directly after that, choice frequencies initially fell to a level around 50%. Between 168 and 288 training trials were needed for the birds to reach above 80% correct choices for a red–green grating with a high color contrast of 0.377 and a spatial frequency of 1.76 cycles/degree. In contrast to the CSF for achromatic gratings, the CSF for red–green gratings shows low-pass characteristics and reaches a maximum at the lowest tested spatial frequency (0.35 cycle/degree; Figure 4).

The tests with blue–green gratings could be performed after the tests with red–green gratings without any additional training. At all spatial frequencies, the spatial contrast sensitivity to blue–green gratings is lower than that to red–green gratings (Figure 4). This difference is more pronounced at lower frequencies since the CSF for blue–green gratings saturates at 1.17 cycles/degree, while no saturation could be detected in the CSF for red–green gratings within our test range. As a result, the cutoff values (predicted acuity) for blue–green and red–green gratings

![Figure 4](https://example.com/figure4.png)
gratings are similar (4.3 cycles/degree and 4.5 cycles/degree, respectively; Figure 5).

**Experiment 3: The detection of gratings with achromatic and color contrast**

In the final experiment, we examined the detection of four gratings with a constant low contrast for the double cones (0.12–0.14, Michelson contrast) but with different red–green contrasts for single cones (Figure 6). This experiment was conducted to examine if the results from detection tests using gratings with both achromatic and chromatic contrasts can be explained solely by the CSFs for the achromatic (double cone) and chromatic (single cone) channels (Experiments 1 and 2). If so, it would suggest a complete separation of spatial information transfer in the two channels.

First, we tested achromatic gratings, and just as expected from Experiment 1 (Figure 2), the detection of these gratings was very good (close to 100% correct choices) at medium spatial frequencies while decreasing both at lower and higher frequencies (series A in Figure 6).

Following this, we tested gratings that in addition to the achromatic contrast also provided red–green contrast (Table 1; series B–D in Figure 6) and found a gradual
improvement in the detection of the low-frequency gratings with increasing color contrast. This was true even when the increase in color contrast was paralleled by a small decrease in achromatic contrast for individual single cone types (Table 1; series B–C in Figure 6). To our surprise, grating detection improved with increasing single cone contrast also at high frequencies (series C–D in Figure 6).

### Discussion

#### The spatial tuning of achromatic and chromatic vision

The shape of the CSF in budgerigars (Figure 2) is similar to that of other bird species and vertebrates tested so far (De Valois & De Valois, 1990; Ghim & Hodos, 2006; Harmening, Nikolay, Orlowski, & Wagner, 2009; Uhlrich et al., 1981), showing clear characteristics of a band-pass mechanism adapted to encode medium and high spatial frequency content in stimuli. The maximum spatial contrast sensitivity of budgerigars is, as in all other bird species tested so far, very low, about two orders of magnitude lower than in humans (see, e.g., Ghim & Hodos, 2006; Harmening et al., 2009). The reasons for this are still unknown, although it has been suggested that birds trade absolute contrast sensitivity for other visual qualities, such as high spectral resolution (Ghim & Hodos, 2006).

The CSFs of the single cones have low-pass characteristics (Figure 4). Clearly, single cone mechanisms of budgerigars are tuned for detecting low spatial frequency content in stimuli. Furthermore, just as for humans (Mullen, 1985), contrast sensitivity depends on the grating colors used; the sensitivity to red–green gratings is higher compared to the sensitivity to blue–green gratings (Figure 4).

To further examine this, we analyzed the contrast provided to individual cone types at threshold levels. At maximum sensitivity (0.35 cycle/degree for red–green and 1.17 cycles/degree for blue–green gratings), the contrasts for MWS and LWS cones are similar while the contrast for SWS cones is much higher for blue–green than for red–green gratings (Table 2; see electronic Supplementary material for a complete table). This suggests that the CSF of single cones depends primarily on the MWS and LWS cones and less on the SWS cones.

It is uncertain but unlikely that optical factors, such as chromatic aberration (Hecht, 2002), limit SWS cone resolution considering the low spatial frequencies of the gratings used and the low density of SWS cones. Even more, the optical properties of the lenses (Lind, Kelber, & Kröger, 2008) and the oil droplets (Walls & Judd, 1933) might serve to reduce chromatic blur.

Even though contrast sensitivity is much lower to blue–green than to red–green gratings, the predicted acuity is

![ Table 1. Properties of stimulus gratings used in Experiment 3. Notes: Color contrast is measured in Euclidean distance between the grating colors within color space (see Methods section). Cone contrast is for individual cone types, measured as the Michelson contrast based on receptor quantum catches. Photon catch and luminance values are the averages for the two colors in each grating. ]

<table>
<thead>
<tr>
<th>Grating type</th>
<th>Red–green (0.35 cycle/degree)</th>
<th>Blue–green (1.17 cycles/degree)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Color contrast</td>
<td>0.109</td>
<td>0.311</td>
</tr>
<tr>
<td>Cone contrast</td>
<td>LWS 0.079</td>
<td>0.059</td>
</tr>
<tr>
<td>MWS 0.087</td>
<td>0.034</td>
<td></td>
</tr>
<tr>
<td>SWS 0.079</td>
<td>0.458</td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Contrast conditions at maximum contrast sensitivity for red–green and blue–green color gratings. Notes: Contrast values are as in Table 1.
not. A similar relationship between blue–yellow and red–
green gratings has been found in humans (Mullen, 1985).
An explanation for this could be that budgerigars have
similar sized retinal integration units for the mechanisms
encoding blue–green and red–green contrasts. In each
integration unit, there would be a higher representation of
MWS and LWS cones compared to SWS cones since the
latter type is relatively scarce within the retina (Hart,
2001; Wilkie et al., 1998). The consequence would be a
higher degree of pooling of MWS and LWS cones and
thereby higher sensitivity to low-contrast patterns, while
the acuity could be similar for both types of pattern due to
the same size, hence the same sampling frequency of
different types of integration units.

However, it is uncertain to what extent the blue–green
and the red–green gratings stimulate different or similar
chromatic channels. To gain further insights to this issue,
we need more information about the retinal mosaic, the
receptive fields of the bipolar and ganglion cells, and the
specific chromatic opponent mechanisms in birds, all of
which are poorly understood at present.

Simultaneous activation of the achromatic
and chromatic channels

In the third experiment, we found that the detection of
low-frequency gratings improved with increased color
contrast, even when this increase was paralleled by a
decrease in contrast to individual single cones (series B–C
in Figure 6, Table 1). This confirms the indication from
Experiment 2 that single cones mediate spatial information
at low spatial frequencies via chromatic pathways.
However, this improvement was not restricted to low
spatial frequencies. When a strong red–green color
contrast of 0.45 (series D in Figure 6, Table 1) was added
to the achromatic contrast, detection improved far above
the predicted acuity (4.5 cycles/degree, Figure 5) for red–
green gratings. Gratings with low achromatic contrast and
high chromatic contrast are thus detected over a broader
range of spatial frequencies than gratings with either of
these contrasts isolated.

The high color contrast in series D (Figure 6) mostly
resulted from a high contrast to the LWS cones (Table 1).
We therefore suggest that LWS cones contribute to
achromatic vision or double cones have a role in chromatic
mechanisms. Even though we cannot resolve this now, the
results imply that single cone and double cone pathways
might not be as fully isolated as previously assumed.

Conclusions

A common feature between the visual systems of bees,
birds, and humans is the use of color vision for detecting
contrast in larger fields compared to achromatic vision
that mediates detection of fine detail. Birds and humans
also share the property of having a higher spatial contrast
sensitivity to color gratings that predominantly activate
the green-sensitive and red-sensitive cones, even though
the acuity for different color gratings appears to be similar.
The agreement in the findings between humans and birds
suggests that these properties reflect general visual mechan-
isms in spatial vision of terrestrial vertebrates. Further-
more, our data suggest that the visual pathways of single
and double cones are not completely separated as previously
assumed, which may allow for a spatial acuity higher than
expected from double cone densities.

Color patterns are believed to be important cues for vital
bird behavior and our results show that spatial dimension of
color patterns needs to be considered in models of color
discrimination. From this perspective, it would be interest-
ing to reassess the signaling roles of color patterns, such
as plumage ornamentation that should be optimized for
fitness display but at the same time being inconspicuous
to predators (see, e.g., Marshall, 2000). Interestingly, fine
patterns in the plumages of birds such as budgerigars tend
to have high achromatic contrast, while color patches are
often large.

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