Spatial summation improves bird color vision in low light intensities

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ABSTRACT

Color guides many important behaviors in birds. Previously we have shown that the intensity threshold for color discrimination in the chicken depends on the color contrast between stimuli and their brightness. The birds could discriminate larger color contrasts and brighter colors in lower light intensities. We suggested that chickens use spatial summation of cone signals to maintain color vision in low light levels. Here we tested this hypothesis by determining the intensity thresholds of color discrimination using similar stimuli, patterns of grey tiles of varying intensity interspersed with color tiles, adjusted for this specific aim. Chickens could discriminate stimuli with a larger single color tile, or with a larger proportion of small color tiles, in lower light intensities. This is in agreement with the hypothesis that spatial summation improves color discrimination in low light levels. There was no difference in the intensity threshold for discrimination of stimuli with a single 6 × 6 mm color tile, stimuli with 30% colored tiles and stimuli in which color filled the whole pattern. This gives a first indication to the degree of spatial summation that can be performed. We compare this level of spatial summation to predictions from mathematical model calculations.

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1. Introduction

Color vision guides important behaviors of birds, such as finding food and choosing between mating partners (Bennett & Cuthill, 1994; Bennett, Cuthill, Partridge, & Lunau, 1997; Church, Bennett, Cuthill, & Partridge, 1998; Hunt, Cuthill, Bennett, Church, & Partridge, 2001; Maddocks, Church, & Cuthill, 2001). Bird color vision is mediated by four types of single cone photoreceptors sensitive to red light (long wavelengths, L), green light (medium wavelengths, M), blue light (short wavelengths, S) and violet or ultraviolet light (very short wavelengths, VS/UVS) (Hart, 2001; Osorio, Vorobyev, & Jones, 1999; Vorobyev, Osorio, Bennett, Marshall, & Cuthill, 1998). Bird cones are equipped with colored oil droplets that act as long pass filters and narrow cone spectral sensitivities. This is thought to improve color discrimination and color constancy (Barlow, 1982; Govardovskii, 1983; Vorobyev, 2003; Vorobyev et al., 1998) at the cost of the absolute sensitivity of color vision as the filtering will reduce absolute photon catch (Toomey et al., 2016; Vorobyev, 2003; Wilby et al., 2015).

We assume that color discrimination thresholds, including intensity thresholds, are set by noise (Lind & Kelber, 2009a; Vorobyev, Brandt, Peitsch, Laughlin, & Menzel, 2001; Vorobyev &

Osorio, 1998). Over a wide range of light intensities, Weber's law holds, so that sensitivity changes proportionally to light intensity (Lind, Chavez, & Kelber, 2013), and a constant Weber fraction (ω) describes the signal-to-noise ratio that sets discrimination thresholds (Brown, 1951; Lind et al., 2013; Olsson, Lind, & Kelber, 2015; Yebra, Garcia, Nieves, & Romero, 2001). At lower light intensities, the signal-to-noise ratio decreases as photon-shot noise and dark noise become more important (Osorio, Smith, Vorobyev, & Buchanan Smith, 2004).

Photon-shot noise is caused by the stochastic nature of photon arrival that follows Poisson statistics. For a photon sample size N, the uncertainty, or photon-shot noise, is $\sqrt{N}$, and the signal-to-noise ratio is $N/\sqrt{N}$, which is expressed as the de Vries-Rose law (De Vries, 1943; Rose, 1942, 1948). The absolute threshold of vision is set by dark noise, caused by spontaneous activation of the transduction cascade, indistinguishable from real photon absorption (Barlow, 1956; Rieke & Baylor, 1998, 2000). When the quantum catch of a photoreceptor is smaller than the standard deviation of the dark noise events, the light signal cannot be reliably detected.

In general, color vision is assumed to be restricted to higher light intensities than achromatic vision, because it requires comparison of the signals from two or more visual channels instead of summation, thus reducing the signal-to-noise ratio. Mathematical models predict that the higher the dimensionality of an

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animal's color vision the worse their color vision should be in low light (Vorobyev, 1997). Tetrachromatic birds, with light absorbing oil droplets, could therefore be at a disadvantage with regards to low light color vision compared to tri- and dichromatic mammals. Intensity thresholds for color discrimination have only been tested in four bird species, and all of them loose color vision at two to ten times higher light intensities than humans (Gomez et al., 2014; Kelber, Balkenius, & Warrant, 2002; Lind & Kelber, 2009b; Olsson et al., 2015).

It has been proposed that visual systems can use spatial and temporal summation, integrating the signals from several photoreceptors over time and space, to increase the photon sample (N) and reduce the effect of photon-shot noise (Barlow, 1958), at the cost of spatial and temporal resolution. This phenomenon is well documented in achromatic pathways e.g. (Donner, 1987; Stöckl, O'Carroll, & Warrant, 2016), but has only been suggested for chromatic vision (Kelber et al., 2002; Roth & Kelber, 2004).

In a previous experiment, we found that the intensity threshold for color discrimination in chickens depends on the chromatic contrast between the stimuli and on stimulus brightness (Olsson et al., 2015). We hypothesized that the chickens used spatial summation to maintain color discrimination in low light intensities. In this study we test this hypothesis, for the first time, by determining the intensity threshold for color discrimination in chickens, using stimuli which differ in the number and size of colored tiles.

2. Materials and methods

We determined the intensity threshold of color discrimination in chickens, by training them to a two-choice color discrimination task in successively lower light intensities. The stimuli were paper food containers, printed with color and grey tile patterns, similar to those that have been used with chickens before (Olsson, Wilby, & Kelber, 2016; Olsson et al., 2015; Osorio et al., 1999). We used four types of stimulus patterns, in which either 100% of the tiles, 10% of the tiles, one single large tile or one single small tile of the stimulus were colored, see Fig. 1 for examples. Stimuli that contained more or larger color tiles, should be discriminable at lower light intensities if spatial summation was important for color discrimination. We used a rewarded orange color (O+) and an unrewarded yellow color (Y−), and we repeated some tests with a rewarded green color (G+) and an unrewarded blue color (B−).

2.1. Animals

24 Lohman White chickens (Gimranäs AB, Herrljunga, Sweden) were obtained as eggs and hatched in a commercial incubator (Covatutto 24, Högberga AB, Matfors, Sweden) at the animal housing facility of Lund University. Both male and female chickens were used in the study. They were housed in 1×1 m boxes in groups of six to eight individuals. All experiments were carried out in accordance with the code of ethics of the World Medical Association (Declaration of Helsinki) and ethical approval was obtained from a local ethical committee (permit nr. M6-12, Swedish Board of Agriculture). Water was available *ad libitum* but during experimental days, access to food, commercial chick crumbs (Fågel Start, Svenska Foder AB, Staffanstorp), was restricted to training session and after the last training session of the day. On days with no training or testing, food was available *ad libitum*.

2.2. Experimental arena and illumination

The experiments were carried out in a wooden arena (0.7×0.4 m) painted matte grey and illuminated by fluorescent tubes (Biolux L18W/965, Osram, München, Germany). We measured the spectral radiance of the illumination (Fig. S1 in supplementary information) as reflected from a white standard placed on the floor of the experimental arena using a spectroradiometer (RSP900-R; International Light, Peabody, MA, USA). The intensity of the illumination was reduced with neutral density filters and a potentiometer, which controlled the light intensity of the fluorescent tubes. We measured the luminance of white paper placed on the floor of the experimental arena using a photometer (Hagner ERP-105 Luminance meter, with an SD17 detector. Hagner AB. Solna, Sweden). We used luminances of 350 cd m^{-2}, 15 cd m^{-2}, 1.5 cd m^{-2}, 0.6 cd m^{-2}, 0.3 cd m^{-2}, 0.1 cd m^{-2} and 0.05 cd m^{-2} (see Fig. S1 in supplementary information).

2.3. Stimuli

Color stimuli similar to those used in previous studies (Olsson et al., 2015, 2016; Osorio et al., 1999) were created in Adobe Illustrator CS5 (Adobe Systems Inc., San Jose, CA, USA) and printed on copy paper (Canon, Tokyo, Japan). A stimulus consisted of a printed pattern of tiles, forming a rectangle measuring 30 mm × 36 mm and folded into a cone-shaped food container. A given pattern contained only one of the colors (O+/Y−/G+/B−), besides grey tiles. We created four types of stimulus patterns. Two pattern types consisted of 270 tiles measuring 2 × 2 mm each, with 100% or 10% (Fig. 1A and C) colored tiles respectively. A third pattern type consisted of 120 tiles, each measuring 3 × 3 mm, with only 1 color tile (Fig. 1B), and the fourth pattern type consisted of 30 tiles, each measuring 6 × 6 mm, again with only one colored tile (Fig. 1B). In the patterns with multiple color tiles, a random amount of black ink, random K value in CMYK color coding, was added to adjust the intensity of each colored tile within a contrast range (the contrast between the highest and lowest intensity version of the color) of 0.15 for O+ and Y− and 0.08 for G+ and B−. In patterns with a single color tile, no black ink was added to the color tile. The remaining tiles in each pattern were assigned a random grey intensity, and the achromatic contrast, between the highest and lowest intensity grey tile was 0.3. The intensity range of colored tiles was within the intensity range of the grey tiles. The achromatic contrast between the stimulus pairs (O+ vs Y− and G+ vs B−) was lower than 0.1, the achromatic contrast threshold of chickens (Jones & Osorio, 2004).

2.4. Training and testing

We performed experiments with two pairs of stimulus colors, training some chickens to discriminate a positive (rewarded) orange (O+) from a negative (unrewarded) yellow (Y−) color, and others to discriminate a positive green (G+) from a negative blue (B−) color. The color difference between the colors were 2.6 and 3.3 just-noticeable-differences (JND) for the color pairs G+-B− and O+-Y− respectively. Each chicken had two training or testing sessions per day. Training started on the third day post-hatch. During the first day of training, groups of 4–6 chickens were placed in the experimental arena where they had access to two or three positive stimuli, orange (O+) or green (G+) food containers filled with food crumbs. The chickens learned to peck at the stimuli to spill out and eat the food. On the second day of training, the chickens were trained in pairs with only one positive stimulus, which was continuously refilled for ca. 5 min per session. On the third day, two chickens were initially placed behind a separating cardboard wall, and could access one positive stimulus filled with food after removal of the wall. This procedure was repeated on the fourth day, but with individual chickens, while a companion chicken was placed in an adjacent cage maintaining audio and visual contact to the experimental bird. On the fifth day of training, the negative stimuli, empty yellow (Y−) or blue (B−) food containers,