Of Cats And Men: Origins of Primate Color Vision Pathways

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Abstract

Most non primate mammals are known to possess dichromatic color vision based on short-wavelength-sensitive (S) and medium/long-wavelength-sensitive (ML) cone photoreceptors. However, the neural pathways carrying signals underlying the primitive "blue–yellow" axis of color vision are largely unexplored in these animals. We have recently characterized a population of color opponent blue-ON cells in electrophysiological single-cell recordings from the dorsal lateral geniculate nucleus (LGN) of anaesthetized cats. We found remarkable similarities to previous descriptions of primate blue-ON cells in terms of receptive field size and structure and the relative weight of functional inputs from the opponent cone classes. Moreover, cat blue-ON cells were found in the same layers as W-cells, which are thought to be homologous to the primate koniocellular system. The temporal frequency optimum of cat blue-ON cells was around 3 Hz, about one-third of that found in achromatic cells. Based on these data, we suggest that cat blue-ON cells are part of a "blue-yellow" color opponent system that is the evolutionary homologue of the blue-ON division of the koniocellular pathway in primates.

Keywords: color vision, neurophysiology, lateral geniculate nucleus.

Introduction

Trichromatic color vision found in most humans and many other primate species is based on the activity of three cone photoreceptor types with maximum sensitivity in the short (S or "blue"), medium (M or "green") and long (L or "red") wavelength bands of the visible spectrum. Trichromacy is, however, rather the exception than the rule among mammalian species (Jacobs, 1993; Nathans, 1999) because most mammals express S-cones and a single cone type in the medium-long (ML) wavelength band (Ahnelt & Kolb, 2000; Szél, Lukáts, Fekete, Szepessy, & Röhlich, 2000), and can make only dichromatic spectral discriminations (Jacobs, Fenwick, & Williams, 2001; Loop & Bruce, 1978; van Arsdel & Loop, 2004). The purpose of this paper is to review the results of our investigations on color-opponent blue-ON cells in cats and to compare their properties to achromatic neurons of the same species as well as to "blue-yellow" and "red-green" opponent neurons of trichromatic primates. Some of this research has been published before (Buzás et al., 2013).

Materials and Methods

Spike responses of achromatic and color opponent cells were recorded from the lateral geniculate nucleus of seven anaesthetized, paralyzed and artificially ventilated cats.

Stimuli were calibrated so as to modulate either both cone types together (achromatic stimuli) or S-cones or ML-cones alone (cone isolating stimuli). Cone-contrast of the stimuli was usually modulated sinusoidally and the first harmonic Fourier component of the instantaneous action potential rate was used as response measure.

On each recorded cell, a battery of tests was performed in order to measure contrast sensitivity, the relative weights of S- and ML-cone inputs, spatial and temporal frequency tuning and receptive field size.

Results

Over 200 recording sites were tested for the presence of S-cone driven responses. Blue-ON cells (n = 14) were identified on the basis of their contrast gain being higher to S-cone isolating than to achromatic stimuli. The rest of the neurons were more sensitive to achromatic stimulation and they were assigned to the group of achromatic cells (n= 31). Blue-ON cells were localized in the deep layers (C, C1, C2) of the LGN whereas achromatic cells were found throughout all layers.

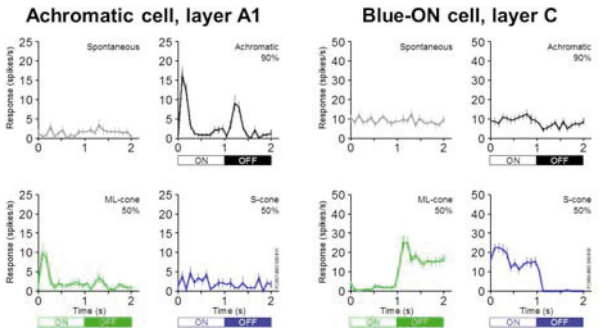

Figure 1: Peristimulus time histograms of spike responses of representative achromatic and blue-ON cells from the cat LGN. Stimuli were increments (ON) followed by decrements (OFF) of achromatic, ML- and S-cone isolating contrast as shown by the labels. Percent values indicate cone contrast.

In subsequent tests, blue-ON cells showed a number of functional properties distinguishing them as a separate population. Figure 1 illustrates responses of a typical achromatic cell and a blue-ON cell. In the achromatic cell, changes of achromatic contrast elicited transient ON and OFF responses. Modulating ML-cones in isolation evoked similar responses whereas the S-cone-isolating stimulus had no detectable effect on the spike rate. This suggests that the achromatic response was in fact due to stimulation of ML-cones alone. In the blue-ON cell, the achromatic stimulus

evoked only a feeble response. However, the same cell showed tonic OFF response to the ML-cone isolating stimulus and tonic ON response to the S-cone isolating stimulus. These are signatures of cone-opponent interactions.

We measured the relative weights of S- and ML-cone inputs for the recorded neurons using the "color circle" method described by Sun, Smithson, Zaidi, and Lee (2006). Achromatic cells showed only weak S-cone input (S-cone weight around 10%). Blue-ON cells however, received inputs from the two cone classes that were of equal magnitude but of opposite sign (S-cone weight around 50%). This balanced opponent interaction explains their low sensitivity to achromatic stimuli.

Spatial frequency tuning curves were obtained using cone isolating sine-wave gratings. A Gaussian receptive field model was fitted to the data in order to assess the size of each receptive field center. We found a significant correlation (r=0.75) between the radii of S- and ML-cone driven receptive field regions suggesting that the opponent receptive field regions are co-extensive. When compared to achromatic cells, the receptive field centers of blue-ON cells were about 2.7 times greater at any eccentricity.

The temporal properties of blue-ON cell responses gave further support to their specialization for signaling color. Firstly, the temporal frequency tuning curves of S- and ML-cone inputs were very similar to each other in all blue-ON cells suggesting that the chromatic signal is preserved at all stimulus frequencies to which the cells can respond. They were, nevertheless tuned to fairly low frequencies around 3 Hz for both S- and ML-cones, when compared to achromatic cells (around 10 Hz). Secondly, response latencies of blue-ON cells to visual stimulation were found to be similar for both cone types. Achromatic cells, however, had significantly lower latencies. These findings also support the idea that the S-cone system in cats is more sluggish than the luminance system.

Discussion

The properties of cat blue-ON cells highlight them as a functionally coherent population specialized for color vision. Our data also reveal remarkable similarities between blue-ON cells of cats and primates. These can be summarized as follows:

1. Prevalence of ON-type response to S-cone contrast (de Monasterio, 1979; Szmajda, Buzás, Fitzgibbon, & Martin, 2006; Tailby, Solomon, & Lennie, 2008) Blue-OFF cells may still exist in the cat LGN but they must be rare or very difficult to record from;
2. Nearly linear contrast dependence (Tailby, Solomon, et al., 2008; Tailby, Szmajda, Buzás, Lee, & Martin, 2008);
3. Spatially coextensive S- and ML-cone inputs (Crook et al., 2009; Wiesel & Hubel, 1966);
4. Relatively large receptive field size compared to cells carrying luminance signals (Solomon, Lee, White, Rüttiger, & Martin, 2005; Tailby, Szmajda, et al., 2008);
5. Anatomical localization in the "third visual channel" that is represented by W-cells in non-primates (Cleland, Levick, Morstyn, & Wagner, 1976) and by the koniocellular system in primates (White, Wilder, Goodchild, Sefton, & Martin, 1998).

The preference of the chromatic channel in cats for low temporal frequencies is also paralleled by the well-known temporal low-pass characteristic of human color vision (De Lange, 1958).

Taken together, our data support the idea that the two opponent channels of trichromatic color vision have different phylogenetic origins. A primordial color system (Mollon, 1989) representing the "blue-yellow" chromatic axis that is linked to the W- or koniocellular system appears to be present in all modern mammals suggesting their common ancestry. This system is dedicated to color vision. The "red-green" axis on the other hand, is linked to the parvocellular system in trichromatic primates, which also transmits signals of luminance based high acuity spatial vision. Indeed, parvocellular neurons in the retina and LGN include an entire spectrum ranging from purely "red-green" opponent neurons through mixed luminance and color sensitive cells to purely luminance sensitive ones (Buzás, Blessing, Szmajda, & Martin, 2006). This is consistent with the idea that "red-green" opponency emerged on the basis of a pre-existing achromatic circuit after the splitting of the ML-cone population into distinct M- and L-cone classes in the course of primate evolution (Jacobs, 2009).

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