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Review

On the use of spatial frequency to isolate contributions from the magnocellular and parvocellular systems and the dorsal and ventral cortical streams

Bernt C. Skottun

Ullevaalsalleen 4C, 0852 Oslo, Norway

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ABSTRACT

Many authors have claimed that suprathreshold achromatic stimuli of low and high spatial frequency can be used to separate responses from different entities in the visual system. Most prominently, it has been proposed that such stimuli can differentiate responses from the magnocellular and parvocellular systems. As is reviewed here, investigators who have examined stimulus specificity of neurons in these systems have found little difference between magno- and parvocellular cells. It has also been proposed that spatial frequency can be used to selectively activate the "magnocellular-dorsal stream". The present review indicates that cells in Area MT of the dorsal stream do prefer very low spatial frequencies. However, the review also shows that cells in Area V4 of the ventral stream respond, not only to relatively high spatial frequencies, but also to low frequency stimuli. Thus, low spatial frequencies cannot be relied upon to selectively activate the dorsal stream.

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E-mail address: berntchrskottun@gmail.com

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1. Introduction

A number of authors have stated, or implied, that magno- and parvocellular neurons respond to, respectively, low and high spatial frequencies in achromatic stimuli, or that they have, respectively, low and high spatial resolution (Livingstone and Hubel, 1987, 1988; Merritt and Balogh, 1989; Butler et al., 2001, 2003, 2007, 2009; Bar, 2003; Stein, 2003; Pourtois et al., 2005; Boden and Giaschi, 2007, 2009; Carretie et al., 2007; Nieuwenhuis et al., 2008; Laycock et al., 2009; Bocanegra and Zeelenberg, 2009; Kiss et al., 2010; Borst, 2013; Nicol et al., 2013; Pallett and Dobkins, 2013; Abrams and Weidler, 2014; Breitmeyer, 2014; Caplette et al., 2014; Chan et al., 2014; Corradi-Dell'Acqua et al., 2014: Denison et al., 2014; Flevaris et al., 2014; Goodhew et al., 2014; Javitt, 2015; Kim et al., 2015; Miskovic et al., 2015). (In earlier work the terms "transient system" and "sustained system" were used. These are currently held to correspond to the magno- and parvocellular systems.) As a consequence it has been proposed that spatial frequency may be used to separate contributions from the magno- and parvocellular systems in vision experiments (Slaghuis and Curran, 1999; Butler et al., 2001, 2003, 2007; Keri et al., 2004; Martinez et al., 2012, 2013; Rassovsky et al., 2013; Denison et al., 2014; Javitt, 2015). Some authors have sought to link low spatial frequency stimuli to the dorsal stream (Martinez et al., 2013; Goswami, 2015; Javitt, 2015) or to the "magnocellular-dorsal stream" (Laycock et al., 2009; Gori et al., 2014a,b; Gori and Facoetti, 2015; Zhao et al., 2014). Claims of these kinds have been made in connection with reading or dyslexia (Stein and Talcott, 1999; Stein, 2003; Boden and Giaschi, 2007, 2009; Quercia et al., 2013: Gori et al., 2014a,b; Zhao et al., 2014; Gori and Facoetti, 2015), schizophrenia (Slaghuis and Curran, 1999; Butler et al., 2003, 2007, 2009; Martinez et al., 2008, 2012, 2013; Kiss et al., 2010; Bedwell et al., 2013; Calderone et al., 2013; Laprevote et al., 2013; Rassovsky et al., 2014; Javitt, 2015; Kim et al., 2015) and perception of emotion in images of faces (Vuilleumier et al., 2003; Holmes et al., 2005; De Cesarei and Codispoti, 2013). The claims have to a large extent been made without references to empirical data. The present review examines if, and to what extent, magno- and parvocellular systems can be distinguished based on spatial frequency and also to what extent the dorsal stream differs from the ventral stream in terms of responses to spatial frequencies.

2. The subcortical magno- and parvocellular systems and the dorsal and ventral cortical streams

The magno- and parvocellular systems are two streams in the visual system of primates which stretch from the ganglion cells in the retina, through the Lateral Geniculate Nucleus (LGN), to the input layers of the primary visual cortex, i.e. Area V1 (Merigan and Maunsell, 1993). Although the distinction is primarily anatomical there are also functional differences. Most notably, magnocellular neurons tend to respond to higher temporal frequencies than do parvocellular cells although the difference is smaller than commonly acknowledged (Skottun and Skoyles, 2008a) and parvocellular cells show some specialization for processing of color stimuli. In addition to the magno- and parvocellular systems there is also the koniocellular system. Since questions about high and low spatial frequencies have focused almost exclusively on the magno- and parvocellular systems this system will not be discussed here.

From the primary visual cortex (Area V1) it is possible to discern two cortical streams: the dorsal and the ventral streams (Maunsell and Newsome, 1987). The former is centered upon Area MT, also known as Area V5, which is thought to play a dominant role in perception of movement, and the latter is centered upon Area V4 which is held to be important for color vision. Some authors have sought to portray the dorsal and ventral streams as continuations of, respectively the magnocellular and parvocellular systems. Thus, one may encounter expressions such as "magnocellular-dorsal stream" and the "parvocellular-ventral stream" (e.g., Gori et al., 2014a,b). However, there are good reasons for not lumping the subcortical systems and the cortical streams together. For one, the dorsal stream receives "robust" input from the parvocellular system (Nassi et al., 2006) and the ventral stream receives about equally strong input from the two subcortical systems (Ferrera et al., 1994). Also, lesions placed in the cortical stream have different effects from those placed in the subcortical systems (Merigan and Maunsell, 1993). In the particular case of dyslexia the results relating to visual deficiencies become less conflicting once the subcortical systems are held separate from the cortical streams (Skottun, 2015).

3. Spatial frequency in the magno- and parvocellular systems

Kaplan and Shapley (1982) determined spatial resolution in magno- and parvocellular cells in the LGN of Macaque monkeys. In addition to classifying the cells as magno- or parvocellular they were also divided into X- and Y-cells. The X- and Y-cell classification was initially introduced to classify retinal ganglion cells in the cat (Enroth-Cugell and Robson, 1966). X-cells are cells which have a spatial phase at which counter-phase flickering gratings give no response. Y-cells, on the other hand, have no such null phase. These categories can be applied to cells in the monkey. In these animals it has been found that practically all parvocellular cells are X-cells. So are most of the magnocellular neurons. Only a minority of magnocellular cells are Y-cells (Kaplan and Shapley, 1982; Blakemore and Vital-Durand, 1986).

The distributions of cells with regard to spatial resolution from Kaplan and Shapley (1982) have been re-plotted in Fig. 1. The average resolution values were: parvocellular X-cells: 8.0 c/deg ($N = 59$); magnocellular X-cells: 5.7 c/deg ($N = 20$), and magnocellular Y-cells: 2.2 c/deg ($N = 7$). The latter value reflects linear responses. When determinations were based on non-linear responses the average for magnocellular Y-cells rose to 4.9 c/deg. Based on these values and the distributions in Fig. 1 it might seem that parvocellular cells have somewhat higher spatial resolution than magnocellular neurons. However, the cells had receptive fields with eccentricities ranging from 3 to 10 degrees. Since spatial resolution declines with eccentricity and since magnocellular cells tend to have receptive fields at larger eccentricities it may be that the difference reflects a difference in eccentricity. This is, in fact, how Levitt et al. (2001) interpreted these findings.

Derrington and Lennie (1984) found that the receptive fields of magnocellular neurons of the Macaque were larger than those of parvocellular neurons at any given eccentricity. However, based on the data presented in Fig. 6 of their paper it appears that the difference is small and that there is considerable overlap. Also, the effect was mainly confined to ipsilateral retinae. Derrington and Lennie (1984) fitted regression lines to their data. In the case of contralateral retinae (their Fig. 6A and C) the line crossed the 0 degree eccentricity at 0.03 degrees for the parvocellular cells and a little below 0.04 degrees for magnocellular cells. For 30 degrees eccentricity the values for the lines were 0.127 and 0.153 degrees for parvo- and magnocellular cells, respectively. In the case of ipsilateral retinae (Fig. 6B and D of Derrington and Lennie, 1984) the values for 0 degree eccentricity were 0.034 and 0.055 degrees for parvo- and magnocellular cells, respectively. For 30 degrees eccentricity the values for both cell types were 0.26 degrees.

The findings of Derrington and Lennie (1984) are somewhat at odds the results of Blakemore and Vital-Durand (1986) who, instead of measuring receptive field size, determined spatial