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Discussion

A few words on differentiating magno- and parvocellular contributions to vision on the basis of temporal frequency

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ABSTRACT

A number of authors have proposed that changes in temporal frequency within the range of 0–30 Hz may be used to differentiate contributions from the magno- and parvocellular systems. The present analyses estimate the percentage of active magnocellular cells as a function of frequency based on published cut-off values for magno- and parvocellular cells. These analyses indicate that varying the temporal frequency over the range of 0–30 Hz has little effect upon the percentage of active magnocellular cells. The analyses were also carried out for a series of hypothetical cut-off frequencies and standard deviations of these frequencies for magnocellular cells. The results of these simulations indicate that even large alterations in these values do not alter the above conclusion to a noteworthy extent.

1. Introduction

A number of authors have used, or advocated the use of, variations in temporal frequency to differentiate contributions from the magno- and parvocellular systems to visual tasks (Liu et al., 2006; Denison and Silver, 2012; Violante et al., 2012; Denison et al., 2014; Stein, 2014; Thompson et al., 2015; Kristensen et al., 2016).[1] The temporal frequency variations used in such attempts have typically been within the range of 0 Hz to 30 Hz. For instance, Denison and Silver (2012) used frequencies of 0, 6, 9, 15, 22.5, and 30 Hz, and most recently Kristensen et al. (2016) made use of stimuli modulating at 5, 10, 15, and 30 Hz in order, in their words, to "... capitalize on the fact that magnocellular and parvocellular pathways have distinct temporal frequency preferences." The underlying assumption being, it would seem, that changing the temporal frequency over the range of 0–30 Hz, or over some part of this range, would alter the relative contributions of magno- and parvocellular cells.

Early reports (Derrington and Lennie, 1984; Livingstone and Hubel, 1988) tended to emphasize the difference between the magno- and parvocellular systems in regard to temporal resolution. For instance, Derrington and Lennie (1984) wrote in their abstract: "Parvocellular units were most sensitive to stimuli modulated at temporal frequencies close to 10 Hz; magnocellular units to stimuli modulated at frequencies nearer 20 Hz." (However, in the body of the paper they modified this to: "Magnocellular units were most sensitive when temporal frequency was between 10 and 20 Hz ..." Derrington & Lennie, 1984; p. 234).

On the other hand, more recent quantitive studies have found relatively modest differences between the two cell types in regard to temporal frequency tuning. Spear et al. (1994) found the optimal temporal frequencies of magno- and parvocellular cells to be 5.77 Hz and 5.55 Hz, Hawken et al. (1996) found no difference in temporal frequency tuning, and Levitt et al. (2001) found optimal temporal frequencies of 7.94 Hz ($\sigma = 4.80$ Hz) and 6.76 Hz ($\sigma = 3.24$ Hz) for magno- and parvocellular cells, respectively. These observations suggest that the difference between magno- and parvocellular cells is small and that it may be difficult to separate the contributions from the two systems based on differences in optimal temporal frequency (Skottun and Skoyles, 2008).

However, rather than focusing on the optimal temporal frequencies it seems that a clearer separation of magno- and parvocellular cells may be obtained at temporal frequencies well above the optimal frequencies (Skottun and Skoyles, 2008). This prompts the question of how large changes in temporal frequency would be required in order to obtain a meaningful change in the relative contributions from the two systems.

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[1] Some investigators have made use of differences in temporal frequency in combinations with differences in spatial frequency in suprathreshold stimuli in attempts to differentiate inputs from the magno- and parvocellular systems (e.g., Liu et al., 2006; Violante et al., 2012). Given that there are small differences between magno- and parvocellular cells with regard to spatial tuning when eccentricity has been taken into account (Skottun, 2015) it is difficult to see that adding spatial factors will improve separation dramatically when using suprathreshold stimuli.

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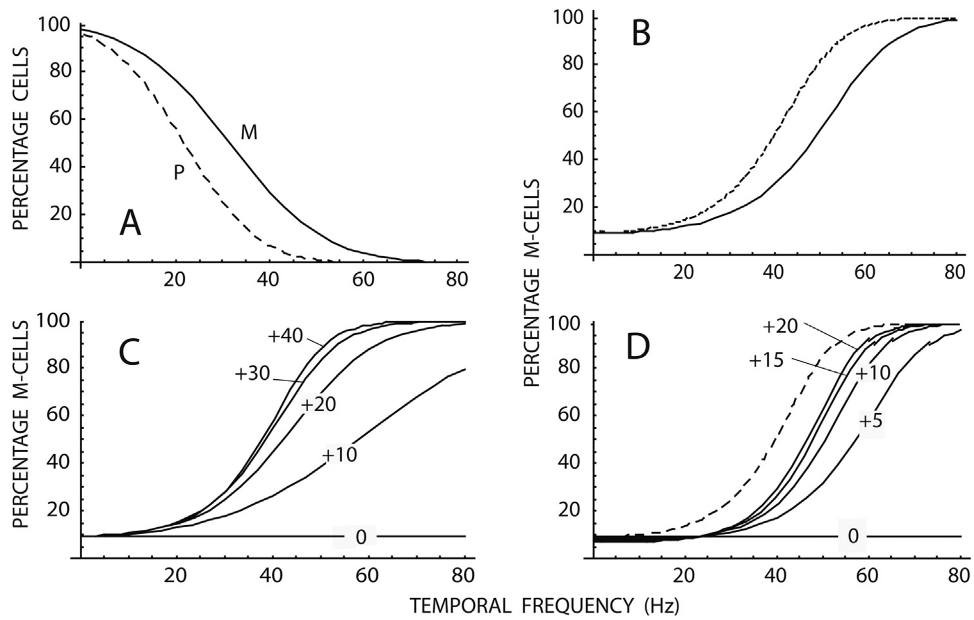

Fig. 1. (A) The percentage of magno- (solid line) and parvocellular cells (dashed line) that are active as a function of temporal frequency. (B) The percentage of active magnocellular cells out of the total of active magno- and parvocellular cells as a function of temporal frequency. Estimates based on the cut-off values and standard deviations of Levitt et al. (2001) are indicated with solid line. The dotted line gives the percentage of magnocellular cells based on the characteristic frequencies reported by Movshon et al. (2005). (C) Estimated percentage of active magnocellular cells for 5 different hypothetical cut-off frequencies for the magnocellular cell: 21.88 Hz + 0 Hz, 21.88 Hz + 10 Hz, 21.88 Hz + 20 Hz, 21.88 Hz + 30 Hz, and 21.88 Hz + 40 Hz. The cut-off frequency of the parvocellular cells was held constant at 21.88 Hz. In order to illustrate the effects of only altering the cut-off frequency the standard deviation of the magnocellular cells was held constant and equal to that of the parvocellular cells (i.e., 12.30 Hz). (D) Estimated percentage of active magnocellular cells for 5 different hypothetical standard deviations of the cut-off frequencies for the magnocellular cell: 12.30 Hz + 0 Hz, 12.30 Hz + 5 Hz, 12.30 Hz + 10 Hz, 12.30 Hz + 15 Hz, and 12.30 Hz + 20 Hz. The cut-off frequency was held constant at 21.88 Hz and was the same for both types of cells in order to illustrate the effects of only changing the standard deviation. The dashed line indicates the case where the magnocellular cut-off frequency is 21.88 Hz + 40 Hz and the standard deviation is 12.30 Hz + 20 Hz.

2. Percentage of active magnocellular cells as a function of temporal frequency

Levitt et al. (2001, their Table 3) determined the mean cut-off values and the standard deviations of these values for magno ($N = 59$) and parvocellular cells ($N = 70$) in the Macaque. The average cut-off values were found to be 31.62 Hz and 21.88 Hz for magno- and parvocellular cells, respectively, with corresponding standard deviations of 15.85 Hz and 12.30 Hz. By assuming the distributions of cut-off values to be Gaussian it is possible to estimate the percentage of active cells as functions of temporal frequency. (The reason for selecting a Gaussian distribution is that this distribution is a continuous distribution which is defined in terms of its mean and standard deviation. Also, this distribution ought to be familiar to most readers.) The calculations were carried out in *Mathematica* (*Wolfram Research Inc*) making use of the Error Function i.e., the *Erf* function in that programming system.[2] The percentage of active magno- and parvocellular cells as functions of temporal frequency are shown in Fig. 1A with solid and dashed lines, respectively.

Based on these estimates the percentage of active magnocellular cells out of the total number of both magno- and parvocellular cells that are active was estimated. In this connection it is necessary to take account of the fact that there are about 10 times as many parvocellular cells as magnocellular neurons (Ahmad and Spear, 1993; Peters et al., 1994). The percentage of active magnocellular cells out of all the active magno- and parvocellular cells is given by $100\,N_m/(N_m + 10\,N_p)$, where N_m and N_p denote the number of active magno- and parvocellular cells, respectively. This percentage as a function of temporal frequency is indicated with solid line in Fig. 1B.

As can be seen, the percentage of active magnocellular cells is quite low for low temporal frequencies. Over the range of temporal frequencies of 0 to 30 Hz the percentage of magnocellular cells increases from 9.2% to 17.5%. This means that the change in active magnocellular cells over this range of frequencies is less than 8.5%. It seems, therefore, doubtful that a meaningful shift in the contribution from the parvocellular system to the magnocellular system can be obtained over this range of frequencies. It is first at a frequency of 49.1 Hz that the number of active magnocellular cells exceeds the number of active parvocellular neurons. A temporal frequency of 49.1 Hz is quite high, however, and brings one into a range of temporal frequencies where cortical filtering becomes a factor (Skottun, 2013).

Movshon et al. (2005) determined the temporal characteristic frequency for magno- and parvocellular neurons in the Macaque. The characteristic frequency was determined in a way different from that used by Levitt et al. (2001) to calculate the temporal cut-off frequency: Levitt et al. (2001) determined the half maximum response at the high temporal frequency slope whereas the characteristic frequency reported by Movshon et al. (2005) was a parameter used in fitting curves to the data. However, both values were explicitly presented as measures of temporal resolution. The median temporal characteristic frequencies (for adult monkeys) were 22.0 Hz and 49.7 Hz for parvo- and magnocellular cells, respectively. While the value for the parvocellular cells is negligibly different from that reported by Levitt et al. (2001) (i.e., 22.0 Hz versus 21.88 Hz) the median characteristic frequency for magnocellular cells determined by Movshon et al. (2005) is considerably higher than the mean cut-off frequency reported by Levitt et al. (2001) (i.e., 49.7 Hz vs. 31.62 Hz). Movshon et al. (2005) did not provide standard deviations for their values. By using the standard

[2] The percentage of active cells was calculated as: $100\,(1.0 - (\mathrm{Erf}[((\omega - \omega_m)/(\sigma\sqrt{2}))] + 1.0)/2)$, where ω denotes temporal frequency, ω_m gives the mean cut-off frequency and σ denotes the standard deviation.