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# Spatial Frequency and the Magno-Parvocellular Distinction–Some Remarks

**Bernt Christian Skottun**
Skottun Research, Oakland, California, USA

**John R. Skoyles**
Centre for Mathematics and Physics in the Life Sciences and Experimental Biology (CoMPLEX), University College London, London, United Kingdom; Centre for Philosophy of Natural and Social Science, London School of Economics, London

**ABSTRACT** Many researchers have attempted to use suprathreshold contrast stimuli of low or high spatial frequencies to selectively stimulate (or bias stimuli for) the magnocellular or parvocellular subcortical visual pathways. While this can be done at contrast threshold, the possibility of doing so at suprathreshold contrasts is less clear and is reviewed here. Research on monkeys indicates that (1) magno- and parvocellular neurons are similar when compared at the same visual field eccentricity. Also, (2) koniocellular neurons seem comparable to magno- and parvocellular cells with regard to spatial properties. In addition, (3) cortical neurons are highly selective for spatial frequencies making it possible that response differences associated with high and low spatial frequencies reflect cortical rather than subcortical factors. It is concluded, that the manipulations of spatial frequency in suprathreshold stimuli provides a poor means for separating the magnocellular and parvocellular systems.

**KEYWORDS** Suprathreshold; schizophrenia; dyslexia; contrast; magnocellular

## INTRODUCTION

The early part of the primate visual system contains three parallel streams. These are the magnocellular, the parvocellular and the koniocellular systems.[1–4] In order to determine the functional roles of these systems in normal and nonnormal subjects investigators have sought psychophysical or noninvasive electrophysiological techniques that (i) can isolate one of the systems or, alternatively, (ii) can make stimuli biased towards one of them. Particular efforts have been focused on developing ways to differentiate magnocellular responses from parvocellular ones. A number of stimulus parameters have been used in these efforts. Examples of these stimulus parameters are colour, contrast, movement, and temporal frequency. Also prominent among these stimulus parameters is spatial frequency. It has been proposed that by selecting certain spatial frequencies, or by selecting particular spatial frequencies in combination with other stimulus dimensions, it is possible to selectively activate the magno- or parvocellular systems or, at least, to use spatial frequency to bias the stimuli towards processing by one of them.

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*Address correspondence to* John Skoyles, Ph.D., Centre for Philosophy of Natural and Social Science Lakatos Building, London School of Economics, Houghton Street, London WC2A 2AE, UK. E-mail: j.r.skoyles@lse.ac.uk

The theoretical basis for these proposals is the finding that the neurons of the magnocellular system tend to respond preferentially to stimuli of lower spatial frequencies than do the neurons of the parvocellular system. In particular, there is evidence that the magno- and parvocellular systems may be isolated using spatial frequency at the contrast detection threshold. It has been established that contrast detection (i.e. contrast sensitivity) is determined by magnocellular system at spatial frequencies below about 1.5 c/deg and by the parvocellular system above this frequency.[5,6] However, researchers have also attempted to separate the two systems using spatial frequency with suprathreshold stimuli, i.e., with stimuli well above the contrast detection threshold. The question posed by the present report is if, or to what extent, can spatial frequency be relied upon to differentiate magno- and parvocellular responses at suprathreshold contrasts. (The effect of spatial frequency at contrast threshold is not the topic of the present remarks.).

Many of the instances in which the spatial frequency of suprathreshold stimuli have been used in attempts to isolate (or bias the stimuli for) one of the two subcortical streams have occurred in connection with investigations of dyslexia and schizophrenia. The reason for this is that claims have been made by some researchers that these conditions are associated with magnocellular deficits.[7,8]

For instance:

- Merritt and Balogh[9] used masking stimuli of 1.0 c/deg and 13.0 c/deg in order to "assess the relative contributions of the visual system's transient and sustained channels to the backward masking deficit characteristic of the schizophrenic spectrum" (p. 573). (Some investigators have used the terms "transient" and "sustained" to refer to the magno- and parvocellular systems. This terminology has its root in the psychophysical literature of the 1970s before the characteristics of the magno- and parvocellular systems had been explored. These terms have been largely replaced by "magnocellular" and "parvocellular" in more recent texts. However, the terms "transient" and "sustained" can sometimes still be encountered.)
- Lehmkuhle et al.,[10] used stimuli of 0.5 c/deg and 4.5 c/deg at 10% contrast in order to activate, respectively, the "transient" and "sustained" systems in children with reading disability.
- Green et al.[11] blurred the stimuli "to reduce reliance on sustained visual channels and hence increase reliance on the transient channels" (p. 946) when testing schizophrenic individuals. (Blurring a stimulus has the effect of reducing amplitudes predominantly at high spatial frequencies so as to shift the energy towards lower frequencies.)
- Demb et al.[12] used moving 0.4 c/deg gratings of 3%, 6%, 25%, 50% ,and 100% contrast in order to obtain fMRIs which reflect predominantly magnocellular inputs.
- Also in connection with schizophrenic patients, Slaghuis and Curran[13] carried out a masking experiment in which a 3.0 c/deg target was masked by either a 1.0 c/deg or a 11.0 c/deg stimulus (both masking stimuli had a contrast of 0.5, i.e., 50%). The two masking stimuli were supposed to activate magno- and parvocellular systems, respectively. With regard to the 1.0 c/deg stimulus Slaghuis and Curran[13] stated that this stimulus "primarily engages transient channels" (p. 47). In regard to 11.0 c/deg stimulus they wrote "... a 11.0 c/deg grating stimulus engages sustained channels only" (p. 47).
- Vaegan and Hollows[14] used 0.25 c/deg gratings of 5%, 10%, 20%, 30%, and 50% contrast to stimulate the magnocellular system of dyslexic readers (among other groups). To activate the parvocellular system these authors used 4.0 c/deg and 8.0 c/deg bars. These stimuli appear to have been of >75% contrast.
- Recently, Butler et al.,[8] used gratings of 1.0 c/deg and 5.0 c/deg of 80 % contrast in order to bias the stimuli towards, respectively, the magno- and parvocellular systems in order to elicit visually evoked potentials (VEPs) in schizophrenic individuals.

These examples show that many researchers in creating psychophysical and noninvasive electrophysiological tests have relied upon low and high spatial frequency stimuli of suprathreshold contrast (i) to selectively activate the magno- and parvocellular systems, or (ii) at least have assumed that the spatial frequency in such stimuli may be used to bias the stimuli for the magno- and parvocellular systems. This raises the question how far present research actually supports the use of spatial frequency with suprathreshold stimuli to experimentally separate or bias the stimuli for these two systems. The goal of this report is to examine this question.

## SINGLE CELL RECORDINGS

Most of our knowledge about the magnocellular and parvocellular systems derives from work upon

nonhuman primates such as macaque monkeys. Such nonhuman primates are generally assumed to provide an appropriate model for the human visual system with regard to the magno- and parvocellular pathways. Often this assumption is implicit, but in some cases it is explicitly stated.

For instance, Butler et al., (p. 418)[8] wrote: "Recent visual evoked potential work in humans with magnocellular and parvocellular preferential stimuli demonstrates that the spatial characteristics and contrast dependence of these pathways are similar to those found in monkeys. . . "

We will therefore examine the use of spatial frequency in experiments involving human subjects on the basis of the spatial frequency tuning characteristics of magno- and parvocellular neurons found in the "monkey." Relatively little is currently known about the koniocellular system. What is clear is that koniocellular neurons occupy the interlaminar spaces in the LGN, which are sometimes referred to as K-lamina. Also, the koniocellular system has been linked to the processing of color variations along the blue-yellow axis.[4]

Kaplan and Shapley[15] determined the spatial resolution of LGN cells in monkeys (spatial resolution in this study was "the spatial frequency at which the response disappears"). These authors divided the neurons into X- and Y-cells based on spatial linearity: X-cells are those cells which have a null-phase, and Y-cells are those neurons for which a null-phase cannot be established. The X/Y distinction had initially been applied to the cat.[16] Using this test, it was found that nearly all parvocellular neurons are X-cells, but that the magnocellular system contains both X- and Y-cells, though the majority of them are X-cells. (Magnocellular Y-cells make up about 15% of the magnocellular neurons according to Blakemore and Vital-Durand,[17] or 1/3 of the magnocellular neurons according to Kaplan and Shapley[15]).

For cells with receptive fields between 3 deg and 10 deg eccentricity Kaplan and Shapley[15] found the average spatial resolution of the parvocellular neurons to be 8.0 c/deg (N = 59). By comparison, the average spatial resolution for the magnocellular X-cells was 5.7 c/deg (N = 20), and 2.2 deg (N = 7) for the magnocellular Y-cells.

Like Kaplan and Shapley,[15] Blakemore and Vital-Durand[18] divided the cells into X- and Y-cells. They found mean resolution limits for parvocellular neurons, magnocellular X-cells and magnocellular Y-cells to be 20.1 c/deg, 18.8 c/deg and 12.3 c/deg, respectively. The difference between parvocellular neurons and magnocellular X-cells, however, was not statistically significant. The finding of substantially higher resolution values than those of Kaplan and Shapley[15] most likely arises from the fact that the resolution for all cell classes increases with decreasing eccentricity. Unlike the sample of Kaplan and Shapley,[15] that of Blakemore and Vital-Durand[18] contained cells subserving central vision.

In the Figure, we have re-plotted, from Figure 6 of Blakemore and Vital-Durand,[18] data showing Log spatial resolution as a function of eccentricity. Open squares show the data for parvocellular neurons, and filled squares represent the data for magnocellular X-cells. The data for magnocellular Y-cells are represented by stars. The solid and dashed lines are the regression lines for the parvocellular neurons and magnocellular X-cells, respectively. As can be seen, the data are fitted well by straight lines. Furthermore, the line describing the parvocellular neurons is very similar to the one fitted to the magnocellular X-cells. This indicates that once eccentricity is taken into account, there is little difference between magnocellular X-cells and parvocellular neurons with regard to their spatial resolution. (Also, the Figure shows that the few magnocellular Y-cells, represented by stars in the figure, are distributed in a manner roughly consistent with that of the two other cell types.)

The lack of difference between magno- and parvocellular neurons with regard to spatial resolution could have been the result of optical factors. If the optics were degraded (e.g., the refraction was incorrect or the optical media had become cloudy) in the physiological experiments this could have reduced the spatial resolution and caused the resolution in the two cell types to appear similar. There are reasons for believing that this does not apply to the study of Blakemore and Vital-Durand.[18] These authors[18] measured visual resolution for human observers and plotted this along with the spatial resolution for the cells (see their Figure 7). If the optics had been degraded in the physiological experiments this would have shown itself in reduced resolution in the cells relative to the behavioral acuity. Blakemore and Vital-Durand[18] did not find this. Furthermore, degraded optics would have affected predominantly resolution for neurons serving central vision because this is where resolution is the highest. In the data of Blakemore and Vital-Durand[18] we see no evidence that neuronal resolution is reduced relative to the behavioral data specifically in central vision. On the contrary, if

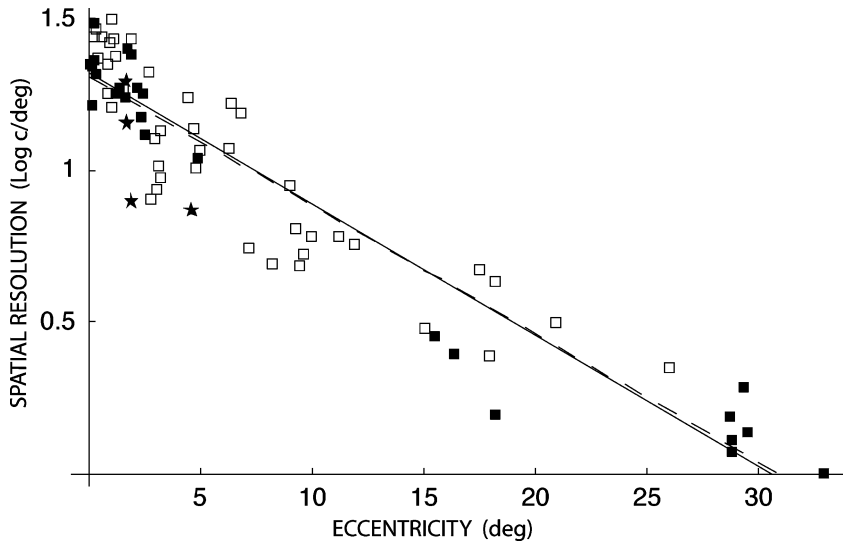


**FIGURE** **Spatial resolution as a function of eccentricity replotted from Figure 6A of Blakemore and Vital-Durand.[18] Open squares represent parvocellular neurons and filled squares represent magnocellular X-cells. The stars represent magnocellular Y-cells. The data are for cells with receptive fields in the nasal retina of the contralateral eye. Solid line is the regression line for parvocellular neurons and the dashed line is the regression line for magnocellular X-cells (the lines are also re-plotted from Blakemore and Vital-Durand[18]). Note that the distributions of magno and parvocellular neurons are very similar, and that the two regression lines are nearly superimposed.**

anything relative to behavioral acuity the neuronal acuity appears to be somewhat higher in central vision in comparison to near peripheral vision.

Spear et al.[19] found the optimal contrast sensitivity for magno- and parvocellular neurons to be at 0.73 c/deg (SD = 1.60) and 0.99 c/deg (SD = 2.15), respectively (see their Table 4). The diameters of the centre mechanisms were found to be 0.115 deg (SD = 0.054) and 0.091 deg (SD = 0.049), respectively, and the surround diameters were, respectively, 1.23 deg (SD = 0.62) and 0.58 deg (SD = 0.43). The spatial frequency resolution for the magno- and parvocellular cells were 6.07 c/deg (SD = 2.21) and 7.53 c/deg (SD = 3.28), respectively. However, with regard to all these measures, there was considerable overlap between the magno- and parvocellular neurons (as indicated by the standard deviations).

Levitt et al.[20] fitted spatial frequency vs. response data with differences of Gaussians, i.e., one Gaussian for the centre mechanism and one for the surround and determined the "characteristic frequency" for the center mechanisms (see Levitt et al.[20] p. 2115, for details). The receptive fields of retinal ganglion cells and LGN cells are conventionally modeled as the difference of two Gaussians–one wide function for the surround and a narrower one for the centre mechanism. A Gaussian function in the space domain has, in the frequency domain, a Gaussian amplitude spectrum centred at zero spatial frequency. And, narrower spatial Gaussians give wider Gaussian amplitude spectra. Therefore, a smaller spatial Gaussian will have larger amplitudes at higher spatial frequencies than a broader spatial Gaussian. Thus, the high spatial frequency characteristics, including spatial resolution, of retinal ganglion cells and LGN cells are determined predominantly by the centre mechanism.

The "characteristic frequency" which is a measure of the Gaussian of the center mechanism in the frequency domain provides a reasonable measure of the spatial resolution for a given cell. For the whole sample of Levitt et al.,[20] the average characteristic frequencies were 2.82 c/deg (SD = 1.68) and 4.57 c/deg (SD = 2.73) for the magno- and the parvocellular neurons (see Table 3 of Levitt et al.,[20]). When the sample is restricted to include only neurons with receptive fields within the central 5 degrees, the values for the magnocellular neurons increased to 3.55 c/deg (SD = 1.94), while, in contrast, the values for the parvocellular neurons remained unchanged (although the SD increased to 2.75), because very few parvocellular neurons were eliminated by restricting the sample to the central 5 degrees. This again indicates that much of the spatial frequency difference between magno- and parvocellular neurons depends on eccentricity and that when this factor is taken into account the difference between them is relatively modest.

Because the different studies have employed different measures of spatial characteristics it is difficult to make direct quantitative comparisons between them. However, what is important is that within each study the same measures are applied to magno- and parvocellular neurons. Based on these comparisons one finds that the differences between magno- and parvocellular neurons are modest with regard to spatial characteristics. This, however, should not be taken to mean that there are no differences between magno- and parvocellular neurons with regard to spatial properties,[19,20] but only that the spatial properties of magno- and parvocellular neurons are relatively similar. This general conclusion is also consistent with the work of Hicks et al.,[21] Marrocco et al.,[22] and Lee.[23] The difference between the two cell classes appears to be particularly small when comparison is made between neurons subserving the same eccentricity. (Also, Crook et al.,[24] measured spatial resolution of phasic, spectrally non-opponent retinal ganglion cells and tonic, spectrally opponent ganglion cells and found them to be similar when eccentricity was taken into account.)

## DISCUSSION

The above overview shows that the differences in spatial resolution and spatial frequency tuning between magno- and parvocellular neurons are modest, particularly so when one takes account of eccentricity. That is to say, the above considerations indicate that it may be very difficult to use spatial frequency in suprathreshold stimuli to differentiate magno- and parvocellular responses by applying stimulation at a given eccentricity. For instance, Butler et al.[8] used centrally fixated stimuli subtending 6.1 × 4.6 degrees. Based on the regression lines in the Figure, we find that magnocellular neurons have average spatial resolution of between 15.0 c/deg and 20.2 c/deg at eccentricities between 3.05 deg (= 6.1 deg/2; assuming central fixation) and 0 deg. The range of resolution for parvocellular neurons over the same range of eccentricities is from 15.4 to 20.9 c/deg. Given that these ranges are close to being identical, it would seem that any biasing toward the parvocellular system that may have been achieved by using a 5.0 c/deg stimulus, as was used by Butler et al.,[8] would have been very small.

There is, nevertheless, a tendency in all the reviewed studies for the average spatial tuning of magnocellular neurons to be shifted somewhat towards lower frequencies relative to parvocellular neurons. This may suggest that it could potentially be possible to use spatial frequency to bias a high contrast stimulus for either the magno- and parvocellular system. However, it is not clear to what extent the difference in spatial tuning reflects sampling differences with regard to eccentricity. The fact that optimal spatial frequency and spatial resolution fall off with eccentricity (Figure) means that one can obtain apparent differences in average spatial tuning measures between magno- and parvocellular neurons if eccentricity is not controlled for.

For instance, in the sample of Levitt et al.,[20] 82 out of 84 parvocellular neurons had their receptive fields within the central 5 degrees, whereas only 33 out of the 75 magnocellular neurons had their receptive field within 5 degrees. (These values are for the neurons for which characteristic spatial frequency was determined. Levitt et al.,[20] Table 3.) On the basis of the relationship depicted in the Figure, one would therefore expect the magnocellular neurons to have lower spatial resolution than the parvocellular neurons. However, this would reflect a difference in distribution with regard to eccentricity and not a genuine difference in spatial tuning. In order to make the claim that parvocellular neurons are tuned to higher spatial frequencies than are magnocellular neurons, it is not sufficient to cite average values without considering the eccentricities at which the receptive fields are located.

Given the distributions of spatial resolution values in the Figure it, moreover, appears that the two cell types are particularly similar when it comes to their spatial characteristics at high spatial frequencies. On this basis it would seem that claims such as those of Slaghuis and Curran (p. 47)[13] that "a 11.0 c/deg grating stimulus engages sustained channels only" are unlikely to be correct. Thus, the use of high spatial frequency suprathreshold stimuli to bias the stimuli for the parvocellular system appears problematic.

The prospects of using low spatial frequencies to bias the stimuli for the magnocellular system may perhaps be a potentially better option. There are two possible reasons for this: (i) Not only do magnocellular neurons on average have somewhat lower optimal frequencies than parvocellular neurons, but (ii) they also appear to have somewhat less pronounced low-frequency attenuation than parvocellular neurons.[15]

However, it is not clear that using low frequency to bias the stimuli for the magnocellular system represents much more than a theoretical possibility as far

as suprathreshold stimuli are concerned. For instance, it is established that parvocellular system responds to very low spatial frequency stimuli. Using a masking paradigm Legge,[5] for example, found that the parvocellular system (at the time referred to as the "sustained system") responded to 0.375 c/deg stimuli at a contrast as low as 1.65% (these values were taken from Figure 6 of Legge[5]). This means that a pure magnocellular response can be obtained at a low spatial frequencies but only when using very low contrasts (i.e., below 1.65% in the case of a 0.375 c/deg stimulus).

To be able to obtain a purely magnocellular response using combinations of high contrast and low spatial frequencies thus seems questionable. To what extent one may be able to obtain a "predominantly magnocellular response" at low spatial frequencies with high contrast stimuli is also unclear. For example, in order to bias the stimuli for the magnocellular system, Butler et al.,[8] used 1.0 c/deg stimuli of 80% contrast. Given that 1.0 c/deg is slightly below the crossover point between magno- and parvocellular detection (i.e., slightly below 1.5 c/deg) it is possible that the magnocellular system might have been somewhat more activated by this spatial frequency. However, the high contrast in this case may have favoured the parvocellular cells given that these increase their response approximately linearly with contrast whereas magnocellular responses tend to saturate at low or medium contrast levels. Thus, a 1.0 c/deg stimulus of 80% contrast, one would expect, would be a potent stimulus for the parvocellular system.

Magno- and parvocellular neurons are not the only ones to consider since the subcortical pathway also contains the koniocellular system. As compared to magno- and parvocellular neurons relatively little is known about the spatial characteristics of koniocellular neurons. However, in one study Sceniak et al.,[25] recorded from geniculocortical afferents within the visual cortex, and classified afferents as respectively magnocellular, parvocellular or koniocellular according to their cone inputs.

With regard to spatial characteristics Sceniak et al., (p. 3478)[25] wrote: "There was a trend toward the konio inputs showing smaller spatial extent of summation (median = 0.41 deg) compared with either magno (median = 0.50 deg) or parvo (median = 0.53 deg) inputs." The differences between the types of afferents were, however, not statistically significant. Thus, it may be that not only are magno- and parvocellular neurons similar with regard to spatial characteristics, but that all three subcortical cell types are similar in this regard. (The somewhat smaller spatial scale of the koniocellular cells suggests that these neurons may in particular make it more difficult to isolate parvocellular activation at high spatial frequencies. It should also be kept in mind that the potential of future data about koniocellular cells can only complicate, not simplify the task of differentiating the magno- and parvocellular responses.)

Magno- and parvocellular neurons have relatively modest low frequency attenuation. Thus, high contrast low frequency stimuli would be expected to activate both these types of cell to some degree. Cortical neurons, on the other hand have more pronounced low frequency attenuation. Also, different cortical neurons are selectively tuned for different ranges of spatial frequencies.[26] Therefore, going from high to low spatial frequencies would be expected to cause larger shifts in the populations of stimulated cortical cells than in the populations of subcortical neurons. For these reasons, responses associated with low and high spatial frequencies cannot simply be equated with, respectively, magno- and parvocellular neurons.

As stated in the *Introduction*, the present analysis is based largely on the assumption that the monkey provides an appropriate model for the human visual system with regard to the magno- and parvocellular pathways. This may not necessarily be the case. Dacey and Petersen[27] measured the size of the dendritic arbors of human midget and parasol ganglion cells in anatomical preparations. (Midget and parasol cells provide the input to, respectively, the LGN parvo- and magnocellular neurons.) Dacey and Petersen[27] found that the human dendritic arbors of parasol cells were larger than those in the Macaque monkey but that the arbors of the midget cells were of similar size. This might suggest that the spatial frequency difference between magno- and parvocellular neurons is larger in the human than in the monkey.

The size of dendritic fields would at most be an indirect measure of spatial tuning since it is highly problematic to infer functional properties from cell morphology. Dacey and Petersen (p. 9669)[27] themselves point this out with regards to the observations of Crook et al.,[24]: "... the resolving power of individual midget cells studied electrophysiologically is, somewhat paradoxically, no better than that of parasol cells at the same eccentricity...."

The fact that the dendritic fields of parasol cells are substantially larger than those of midget cells yet they have the same spatial resolution indicates that

spatial resolution is not a direct result of dendritic field size. Lee (p. 637)[23] made a similar point: "[c]enter size should... be determined by the cone sampling aperture rather than the dendritic three size" and Kilavik et al. (p. 992)[28] noted with regard to the owl monkey that "there is an increase in RF centre size with increasing eccentricity, and there is a limited correlation between these centre sizes and retinal ganglion cell dendritic tree sizes." Therefore, it appears difficult to deduce spatial tuning properties from the size of dendritic arbors.

Also, comparisons between the effects of magno- and parvocellular lesions on monkey contrast sensitivity, for example,[29,30] to studies of human contrast sensitivity in which magno- and parvocellular contributions can be differentiated (such as e.g., in the study of Legge[5]) suggest at least an approximate correspondence between human and monkey data.

Furthermore, Blakemore and Vital-Durand[18] (see their Fig. 7) measured human spatial resolution using psychophysical methods as a function of eccentricity. They found that these values matched closely the spatial resolution for the monkey cells. Although this does not preclude the possibility that there may be interspecies differences with regard to magnocellular tuning relative to parvocellular tuning, it shows that two key aspects of the visual system linked to them—the overall spatial resolution as well as the effect of eccentricity—are similar between humans and nonhuman primates. These considerations do not mean that there are no differences between human and monkey cells (in fact, it would be surprising if there were none), but rather that, at the present time, there is no direct evidence to indicate the existence of any difference sufficiently large to invalidate the monkey as a model for the human visual system with regard to the magno- and parvocellular streams. Clearly, the possibility of human-monkey differences is not something that can be relied upon in a ways so as to make it possible to use spatial frequency to differentiate magnocellular responses from parvocellular ones in tests of human performance.

In the *Introduction* it was pointed out that a number of investigators have used spatial frequency in combination with other stimulus dimensions in attempts to isolate magno- or parvocellular responses or to bias the stimuli for one of the two systems. The two most relevant stimulus dimensions in this connection are temporal frequency and contrast. In the case of temporal frequency the problem is that magno- and parvocellular neurons are very similar with regard to temporal tuning. For instance, Hawken, Shapley, and Grosof[31] found no difference in temporal tuning between magno- and parvocellular neurons. Levitt et al.[20] found small differences between average measures. Therefore, it appears difficult to rely upon temporal frequency to differentiate magno- and parvocellular neurons.[32]

In the case of contrast, the problem is that human psychophysics[5,33] and lesion studies in monkeys[3,29,30,34–36] have indicated that contrast sensitivity under many conditions are mediated by the parvocellular system. The magnocellular system mediates detection only when the stimuli have low spatial frequencies and/or high temporal frequencies.[6] This means therefore that it may be possible to use contrast to obtain pure magno- and parvocellular responses.

However, it seems that this possibility is limited to contrasts very close to the detection threshold. Very low contrast stimuli, moreover, tend to give weak responses which limit their usefulness as a potential research variable, for example, in the recordings of visually evoked potentials. Due to the fact that magnocellular responses, at low contrast, increase more rapidly with contrast than parvocellular responses it may be possible, to obtain a predominantly magnocellular response at contrasts in a range somewhat above the threshold region. However, this possibility is limited to conditions under which the magnocellular system has the lower threshold. With regard to spatial frequency this would mean spatial frequencies below about 1.5 c/deg.[6] Because of the shallower increase in response with contrast at low contrast in parvocellular neurons, the possibility of obtaining a predominantly parvocellular response under the conditions where the parvocellular cells have the lower contrast threshold, however, is more limited.

In conclusion, although magno- and parvocellular systems can be differentiated using spatial frequency at contrast detection threshold, the present review of research indicates that it is difficult to use spatial frequency to differentiate the two systems using high contrast stimuli. Also, the review shows that the degree to which spatial frequency makes it possible to bias the stimuli for either of the two systems is fundamentally unclear.

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