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On Identifying Magnocellular and Parvocellular Responses on the Basis of Contrast-Response Functions

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It has been proposed that magnocellular and parvocellular sensitivity in schizophrenic individuals can be assessed using steady-state visually evoked potentials (VEPs) to either low-contrast stimuli or stimuli whose contrast is modulated around a high contrast "pedestal" (Green MF, Butler PD, Chen Y, et al. *Schizophr Bull*. 2009;35:163–181). This suggestion faces 2 difficulties: (1) To use low-contrast stimuli to activate the magnocellular system is inconsistent with lesion studies that have shown that under many conditions, the parvocellular system responds to the lowest contrasts and (2) To rely on contrast-response relationships to identify magnocellular and parvocellular responses is difficult because other neurons exist in the visual system that have contrast-response relationships similar to those of magnocellular and parvocellular cells.

Key words: VEP/steady state VEP/ssVEP/koniocellular/schizophrenia/vision/contrast/contrast-response/magnocellular

Introduction

Schizophrenia, it has been proposed, is associated with a deficiency in the magnocellular part of the visual system.[1] A difficulty with this suggested link is that contrast sensitivity has generally provided little support for magnocellular deficits in those with schizophrenia.[2] Also backward masking, which by some has been proposed as a test of magnocellular activity, has provided little support for magnocellular deficits.[3] Several other methods, eg, vernier acuity, stereopsis, and red stimuli, have been proposed for testing or as indicators of magnocellular sensitivity. However, these methods have problems associated with them.[4–6] Recently, Green et al[7] have argued for the use of steady-state visually evoked potentials (ssVEPs) to magnocellular- and parvocellular-biased stimuli to investigate the sensitivity of magnocellular and parvocellular systems in schizophrenic subjects. We here comment on the main assumptions behind this proposal.

Anatomy of the Early Visual System

The magnocellular and parvocellular systems are 2 parallel streams that, along with the koniocellular system,[8] make up the sensory input to the primary visual cortex.[9] The magnocellular and parvocellular systems originate in different types of retinal ganglion cells, occupy separate layers in the lateral geniculate nucleus, and terminate in separate input layers in the primary visual cortex (V1). Inside V1, however, a considerable amount of intermixing of the inputs takes place.

From V1 onwards, 2 cortical pathways have been identified: the dorsal and ventral streams. Initially, it was thought that these represented the continuations of, respectively, the magnocellular and parvocellular systems.[10] It has, however, become evident that the situation is more complicated. For instance, lesion studies have demonstrated that Area V4 of the ventral stream receives significant magnocellular input,[11] and anatomical studies have revealed that middle temporal area (Area MT) of the dorsal stream receives substantial parvocellular[12] as well as koniocellular input.[13] Thus, it is problematic to use tests of dorsal and ventral function to assess magnocellular and parvocellular responsivity (eg, see Skottun and Skoyles[14]).

Contrast-Response Functions

The technique proposed by Green et al[7] is based on the method of Zemon and Gordon.[15] In this method, stimuli are either presented at low contrast, in order to "bias" them for the magnocellular system, or are "modulated

around a high static contrast (pedestal)''[7(p166)] so as to be ''biased'' for the parvocellular system by avoiding ''the low-contrast regions where magnitudes of M-pathway [i.e. magnocellular-pathway] responses rise steeply with increase in contrast.''[7(p166)] According to Green et al, ''[t]his task is based on the differential response to contrast of the M and P pathways [i.e. magno and parvocellular pathways] . . . The M pathway shows a steeply rising increase in response to increases in low contrast and then nearly saturates at about 16–32% contrast . . . The P pathway does not respond until about 10% contrast or greater and has a linear increase in response throughout the entire contrast range . . . The slope of the linear portion of the contrast-response curve is referred to as contrast gain, and it is about ten times greater for the M than P pathway.''[7(p166)]

With regard to the notion that the magnocellular system responds to lower contrast than the parvocellular system, there are reasons to be cautious. Although single-cell recordings have indicated that the magnocellular neurons have the lower contrast thresholds,[16] behavioral studies, in which lesions have been placed in either the magnocellular or the parvocellular layers of the lateral geniculate nucleus, have found that the largest losses in contrast sensitivity occur following parvocellular lesions.[9,17–21] This means that the parvocellular system has the lower contrast threshold in these cases. It is mainly when the stimuli are of low spatial frequencies (below about 1.5 cycles/degree)[22] and high temporal frequencies that the magnocellular system has the lower contrast threshold. Contrast sensitivity studies in humans are also consistent with these observations.[23–25]

These findings mean that the parvocellular system mediates detection of the lowest contrast under many, if not most, conditions. (The fact that the magnocellular system mediates detection under some conditions and the parvocellular system mediates detection under other conditions is what allows contrast sensitivity to differentiate magnocellular from parvocellular deficits and from general reductions in sensitivity.) Given the discrepancy between single-unit recordings and behavioral tests, it is problematic to assess magnocellular sensitivity based on the assumption that the magnocellular system has the lower contrast thresholds. This is particularly so when the spatial frequency spectra of the stimuli are not well defined. In the case of ssVEP, the proposed stimuli are ''isolated check stimuli'' (see figure 2 in Green et al[7]), which, it would seem, are poorly suited in this context because they have energy at a number of different spatial frequencies (see figure 1 in Skottun and Skoyles[26]).

With regard to the shapes of the contrast-response functions, there is little doubt that magnocellular neurons have steeper functions than parvocellular cells at low contrast and that their functions show more pronounced saturation. However, what is not clear is that magnocellular and parvocellular responses can be identified on this basis. The main reason for this is that the shapes of the contrast-response functions of the magnocellular and parvocellular neurons are not unique to these cell types. For instance, neurons in cortical area V1 have contrast-response functions similar to parvocellular neurons.[27] Area V1, of course, receives both magnocellular and parvocellular inputs. Also, in the owl monkey (*Aotus azarae*)[28] and the marmoset (*Callithrix jacchus*),[29] the koniocellular neurons have pronounced response saturation, perhaps even more pronounced than magnocellular neurons (see figure 12 in Kilavik et al[28]). Further, neurons in the Area MT show high contrast gain and saturation similar to that of magnocellular cells.[27] Thus, steep or shallow response functions and high or low degrees of saturation are not features that are unique to, respectively, the magnocellular and parvocellular neurons.

The above considerations do not only apply to ssVEPs but are also relevant for other attempts at assessing magnocellular sensitivity based on contrast-response relationships. Recently, it has been suggested that the ability to recognize emotional expressions in faces is the result of magnocellular activity because the effect of contrast on this task is similar to that on magnocellular responses.[30] In this connection, it should also be pointed out that there are other perceptual functions that have a similar relationship to contrast. For instance, orientation discrimination thresholds decrease (ie, the sensitivity increases) rapidly with contrast just above detection threshold and then levels off and remains relatively constant over the rest of the contrast range.[31] Yet, to attribute this to the magnocellular system would face the problem that neurons in this system have little selectivity for orientation, at least compared with the selectivity for orientation found in cortical neurons. Also, the ability to discriminate orientations is reduced in amblyopia.[32] Amblyopia is not linked to the magnocellular system. If anything, it appears to be related to the parvocellular system.[33,34] These observations, therefore, suggest (1) that perceptual performance may be related to contrast in a way that resembles the contrast-response function of magnocellular cells without this having to reflect magnocellular activity and (2) that a deficiency unrelated to the magnocellular system can cause reduced performance on perceptual tasks that have a contrast relationship like that of magnocellular cells.

In connection with ssVEPs, it should be noted that magnocellular neurons in macaque and marmoset are more susceptible to adaptation than are parvocellular cells.[35,36] The effect of adaptation is well described by an increase in the half saturation constant (c_{50}).[35] That is to say, adaptation makes the contrast-response functions of magnocellular neurons become more like those of parvocellular cells. A repeating stimulus, such as the ones used in ssVEP, is likely to cause adaptation. This means, therefore, that ssVEP has the potential to reduce the difference between magnocellular and parvocellular

neurons. This would work against the aim of this method, which is to separate magnocellular and parvocellular responses.

Testing Magnocellular Sensitivity

As for testing magnocellular sensitivity, it appears that the simplest, most direct, and best-established test is contrast sensitivity. As mentioned above, lesions studies in monkeys,[9,17–21] as well as human psychophysics,[23–25] indicate that sensitivity to stimuli of low spatial frequency and high temporal frequency reflects activity in the magnocellular system, whereas detection of stimuli of medium and high spatial frequencies is mediated by the parvocellular system (see Skottun[22] for a brief review). Thus, by noting patterns of contrast sensitivity abnormalities, one can infer the state of the magnocellular system. This, however, means that several spatial frequencies need to be tested and that it is not sufficient to simply test one condition. This method, it would seem, also makes it possible to differentiate subcortical magnocellular deficits from cortical abnormalities because we know of no cortical abnormality that results in contrast sensitivity reductions limited to low spatial frequency stimuli.

Another test, which seems promising, is one proposed by Pokorny and Smith.[37] This method is based on the assumed abilities of single magnocellular and parvocellular neurons to signal differences in contrast. Because these abilities are inferred from the contrast-response functions of the 2 cells types, it may potentially face some of the problems associated with the ssVEP method as explained above. Also, the theory behind this method is based on responses from individual neurons. It is not known if, or to what extent, contrast discrimination can be accounted for in terms of individual magnocellular and parvocellular cells. For instance, the fact that there is a far larger number of parvocellular neurons than magnocellular cells may have a bearing on contrast discrimination. Also, it is not known to what extent this method can isolate subcortical factors from cortical ones. Finally, this method has, to our knowledge, not been established through lesion studies in monkeys.

A third method is the use of isoluminant color stimuli. This has been tested in monkeys: Schiller et al[38] recorded the responses from magnocellular neurons to luminance and isoluminant color stimuli. It was found that magnocellular neurons respond much weaker to the isoluminant stimuli. The problem, however, is that so do parvocellular cells under many conditions.[39] For instance, parvocellular cells shift their spatial frequency response function toward lower spatial frequencies when tested with isoluminant color stimuli (see, eg, figure 7.8 in De Valois and De Valois[40]). This means, therefore, that in the case of high spatial frequency stimuli also, parvocellular neurons may respond more weakly to isoluminance than to luminance. Consistent with this Merigan and Maunsell[9(p391)] have pointed out that "the P pathway is not fully functional with isoluminance stimuli." In addition, chromatic aberration may cause high spatial frequency isoluminant color stimuli (eg, stimuli with sharp color edges) to create luminance artifacts. With such stimuli, an achromatizing lens ought to be used.[41] Therefore, to rely on isoluminant color to differentiate magnocellular and parvocellular responses requires some caution.

Conclusions

The present considerations should not be taken to mean that VEP is not a valuable tool for exploring the brain's responses to visual stimuli in schizophrenia. Rather, the point of the present remarks is that to identify magnocellular and parvocellular contributions to ssVEP on the basis of contrast-response relationships as proposed by Green et al[7] presents 2 problems: (1) Under many conditions, the parvocellular system responds to lower contrast stimuli than does the magnocellular system. Thus, to rely on low-contrast stimuli to obtain a predominantly magnocellular response in psychophysical tests is likely to be unreliable. (2) Although the shapes of the contrast-response functions of magnocellular and parvocellular neurons are different, there exist other neurons that have functions similar to those of these 2 cell types. Thus, in order to attribute a given response to the magnocellular or parvocellular systems, one has to be able to exclude the possibility that the responses do not actually originate with neurons of these other types.

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