Frequency-Doubling Technology and Parasol Cells

Swanson et al. have reported an excellent study of the responses of macaque retinal ganglion cells (RGCs) to Goldmann size III stimuli and contrast-modulated grating stimuli. They estimated the contrast gain of the initial rising phase of the contrast response function of the cells. From the physiology shown, the extracelluar recorded RGCs are parasol and midget RGCs and are referred to in terms of their lateral geniculate nucleus (LGN) targets as M- and P-cells, respectively. The ratios of the gains for the two RGC types indicated that size III stimuli have higher relative gain for M-cells than the grating stimuli. Given that the gratings are described as displaying the frequency-doubling (FD) illusion, this may be taken to mean that the stimuli of the FDT perimeter do not preferentially stimulate a pathway that is useful for glaucoma diagnosis.

The original idea of FD stimuli was that they might stimulate nonlinear Y-cells. Such cells had been reported from extracellular recordings of the M-layers of the primate LGN and so were dubbed M cells. No anatomic substrate was known. The concept was that if humans were like all other mammals, Y-like cells should be larger and less densely overlapping than their X-like (parasol cell) partners. Cell losses could be more easily detected if the lower densities meant few of these Y-cells saw each point in visual space. Recently, anatomic substrates for primate Y-cells have been reported: the smooth monostriatified cells. These cells match the proposed requirements for cell density but otherwise receive the same inputs as the smaller, denser parasol cells and are anatomically similar to cat α-cells, the original Y-cells. Thus, whether parasol cells prefer size III stimuli to gratings may say nothing about FDT perimetry. Parasol cells projecting to the superior colliculus have also been reported to have Y-like responses. Swanson et al. do not cite these recent papers on parasol Y-cells.

Another caveat is that the grating stimuli used would probably not display the FD illusion. A recent examination of the probability of humans reporting FD at 8 parts of the visual field indicates that subjects would have only a 50% chance of reporting an FD percept for the grating stimuli used. That study also indicated two possible independent sources of the FD illusion at every point in the visual field. So perhaps FD has multiple causes, some of which are useful for visual field assessment. By contrast, small size II stimuli may promote test–retest variability.

Ted Maddess

ARC Centre of Excellence in Vision Science, Centre for Visual Sciences, Research School of Biology, Australian National University, Canberra, Australia.
E-mail: ted.maddess@anu.edu.au
Supported by Australian Research Council (ARC) Grant CEO 561903.
Disclosure: T. Maddess, P

References


Author Response: Frequency-Doubling Technology and Parasol Cells

The authors thank Dr. Maddess for his letter. As previously, he suggests that nonlinear Y-like retinal ganglion cells are responsible for the frequency-doubling (FD) illusion, an argument that we challenged in White et al. on three grounds: (1) No evidence was obvious at that time of a separate nonlinear Y-like MC cell class in primate retina ganglion cells; (2) even if there were such nonlinear ganglion cells, the responses of linear MC cells to FD stimuli are robust, and there is no reason they should be ignored; (3) no spatially modulated signals (which might underlie the FD illusion) could be expected from the nonlinear responses of such ganglion cells; their response is nonlinear in time but not in space. We suggested that the FD illusion is due to a psychophysical loss of phase sensitivity at a central site. Dr. Maddess only addresses item (1), the existence of nonlinear cells, referring to new anatomic and physiological studies that demonstrate the presence of a rare Y-like class of primate retinal ganglion cells. However, items (2) and (3) still refute his suggestion: The linear MC cells respond robustly to the FD stimuli, and the FD illusion cannot be explained by nonlinear responses of Y-like ganglion cells.

The purpose of our recent study was to compare MC and PC cell responses to stimuli used in conventional perimetry and FD perimetry. We did not make assumptions as to whether FD perimetry is related to the FD illusion, or whether M cells mediate the FD illusion. FD perimetry is a flicker-detection task, and there is very good evidence that the “regular” MC pathway mediates sensitivity to luminance flicker. We chose our FD stimulus parameters on the basis of stimuli used in clinical FD perimetry, which measures flicker sensitivity and not the FD illusion. In a prior clinical study we used the 12-Hz, 0.5-cyc/deg stimulus for FD perimetry and generated predictions that we tested with the present study, using a 13-Hz, 0.5-cyc/deg stimulus; 13 Hz was the closest approximation we could make to 12 Hz with this monitor, and any effect caused by such a small change in temporal frequency should be insignificant.

At the end of his letter, Dr. Maddess suggested that conventional size III stimuli may “promote” test–retest variability. We