time. A tuning curve for Vernier offset could also be obtained by flashing the targets on the receptive field. It seems premature to claim that such results in cortical cells demonstrate a specific sensitivity for relative position when a simpler explanation based on sensitivity for absolute position is possible.

In the case of cat retinal ganglion cells, experiments have revealed thresholds as low as 1 arc min for simple positional sensitivity and models based on linear summation account for these results[4-6]. For monkey cortical cells our own measurements and theoretical predictions[2] showed positional thresholds as low as 10–20 arc s. With the addition of a temporal component[5], these models also predict the kind of results obtained by Swindale and Cynader in cortical cells.

Indeed, all the current results for cortical cells in hyperacuity tasks are readily predicted from similar linear models of receptive field organization. There is good evidence that linear models can be applied to the spatial summation properties of cortical simple cells and to the linearly-summating subunits of complex cells[7-9]. If a specific nonlinear mechanism for extracting relative position were to be demonstrated in cortical cells this would be highly significant, but present evidence indicates that cortical cells have thresholds in the hyperacuity range by virtue of essentially the same type of mechanism that is present in retinal ganglion cells. This similarity is reinforced by the recognition that the firing of a striate cortical cell is ambiguous in much the same way that the firing of a retinal ganglion cell is ambiguous. Changes of contrast, position, spatial frequency, orientation and direction of drift are all effective in altering the firing rate of cortical neurons.

For these reasons, it is also mistaken to conclude that the existence of cortical neurons with positional sensitivity in the hyperacuity range is an argument against the existence of a fine-grain spatial reconstruction[10]. Strictly speaking, current neurophysiological data do not address this question directly. Psychophysics has pointed to the importance of interpolation over a spatially-sampled luminance profile and to the necessity of constructing an exact signal for spatial location, but it is an open question whether this is accomplished by the construction of a fine-grain spatial map or by other means.

The most interesting feature of comparing the hyperacuity performance of retinal and cortical neurons is that the cortical transformation of information preserves very well the accuracy of the positional signals supplied by the retina, even though cortical cells acquire new forms of selectivity, such as orientation and binocularity. The existence of single neurons at several levels in the visual system with thresholds close to those of a psychophysical observer strikingly demonstrates the precision of organization of the early visual pathways and the high quality of the 'components' used for visual computation.

A. J. PARKER
M. J. HAWKEN
University Laboratory of Physiology, Parks Road, Oxford OX1 3PT, UK

1. Swindale, N. V. & Cynader, M. S. *Nature* **319**, 591–593 (1986).
2. Parker, A. J. & Hawken, M. J. *J. opt. Soc. Am.* **A2**, 1101–1114 (1985).
3. Martin, G. R. *Nature* **319**, 540 (1986).
4. Scobey, R. P. & Horowitz, J. M. *Vision Res.* **12**, 2133–2143 (1972).
5. Enroth-Cugell, C., Robson, J. G., Schweitzer-Tong, D. E. & Watson, A. B. *J. Physiol., Lond.* **341**, 279–307 (1983).
6. Shapley, R. & Victor, J. *Science* **231**, 999–1002 (1986).
7. Movshon, J. A., Tolhurst, D. J. & Thompson, I. D. *J. Physiol., Lond.* **283**, 53–77; 78–99 (1978).
8. Schumer, R. A. & Movshon, J. A. *Vision Res.* **24**, 565–571 (1984).
9. Spitzer, H. & Hochstein, S. *J. Neurophysiol.* **53**, 1244–1265; 1266–1286 (1985).
10. Barlow, H. B. (1979) *Nature* **279**, 180–190; Crick, F. H., Marr, D. & Poggio, T. in *The Cerebral Cortex* (eds Schmitt, F. O. & Worden, F. G.) 505–533 (MIT Press, Cambridge, Massachusetts, 1980).

SWINDALE AND CYNADER REPLY—It is obvious that the information required to make hyperacuity judgements must be present in the signals from the retina. As such judgements can be made for spots of light that stimulate only small numbers of retinal ganglion cells[1], it is not surprising that absolute positional sensitivity in retinal neurons can be as good as the sensitivity to Vernier offset demonstrated behaviourly. The fact that calculated retinal positional sensitivities[2,3] may be even higher than those needed to account for behavioural hyperacuity implies, as Martin suggested[4], that the limiting factors in hyperacuity are cortical and not retinal in origin. Thus it makes sense to study hyperacuity in the cortex and not, as Parker and Hawken would have us do, in the retina.

Although retinal signals contain the information about absolute position required for hyperacuity judgements, such judgements involve comparisons of the positions of features that are further apart than the sizes of ganglion cell receptive fields[5]. Furthermore, changes in the retinal position of the stimulus (caused for example by eye movements) during or between successive presentations, do not degrade acuity[5]. For both these reasons it is unlikely that a signal from the type of retinal detector hypothesised by Parker and Hawken will, on its own, be much use as a basis for a hyperacuity discrimination.

The claim that our results are "readily predicted" from linear models of receptive field organization is not supported. We know of no theoretical predictions of the acuity of retinal or cortical neurons for moving Vernier stimuli. Our preliminary modelling indicates that linear summation within a simple cell's receptive field would produce tuning curves flatter than those observed, and the same is almost certain to be true for retinal cells. There is however experimental evidence for non-linearities of integration along the receptive field axis of simple cells[6-8] which could increase the Vernier sensitivity of an otherwise linear cell.

It is true that the firing rate of a cortical cell is an ambiguous signal but it is certainly less ambiguous than the firing of a retinal cell, by virtue of the cortical cell's feature selectivity. In any case, these ambiguities may not pose as serious a problem for relating cortical neuronal responses to psychophysics as one might suppose. In psychophysical experiments, potentially confounding variables such as the brightness, contrast, length and velocity of the bars in a Vernier target are normally kept constant, and it is possible that random variations in these parameters would indeed degrade performance. If such variations were present it might still be possible to disambiguate a response by combining signals from cells (for example, by subtracting the signals from cells with the same contrast sensitivity, but different Vernier sensitivities).

There are other reasons besides our experimental results (or our interpretation of them) for supposing that a fine-grain representation of receptive field position is not a necessary prerequisite for explaining hyperacuity. One is that the receptive field sizes of the cells involved in such a representation will be no smaller than those of the more coarsely spaced fields of the cells that form the input. Their positional sensitivities will be no greater than that of their inputs, and it is not clear how this extra stage would help the subsequent extraction of information about relative position. The other evidence is the lack of a neuronal substrate for a fine grain representation in the cat: there is no evidence for a layer of closely packed cells with small non-oriented receptive fields as there is in the monkey. Nevertheless, cats have hyperacuity.

N. V. SWINDALE
M. S. CYNADER
Department of Psychology, Dalhousie University, Halifax, B3H 4J1, Canada

1. Sullivan, G. D., Oatley, K. & Sutherland, N. S. *Percept. Psychophys.* **12**, 438–444 (1972).
2. Shapley, R. & Victor, J. *Science* **231**, 999–1002 (1986).
3. Geisler, W. S. *J. opt. Soc. Am. A* **1**, 775–782 (1984).
4. Martin, G. R. *Nature* **319**, 540 (1986).
5. Westheimer, G. *Prog. sensory Physiol.* **1**, 1–30 (1981).
6. Burr, D., Morrone, C. & Maffei, L. *Expl Brain Res.* **43**, 455–458 (1981).
7. Hammond, P. & MacKay, D. M. *J. Physiol., Lond.* **337**, 69–87 (1983).
8. Richter, J. & Ullman, S. *Biol. Cybern.* **53**, 195–202 (1986).

Matters Arising

Future contributions to Matters Arising should instead be sent to Scientific Correspondence and need not be sent to the authors of the original article in advance. Priority will be given to letters of less than 500 words and five references.