The functional nature of neuronal oscillations

Singer and his colleagues have reported that oscillations of 30-70 Hz occur in cat and monkey visual cortex^{1,2} that can be synchronous across cortical columns³. They have suggested that these oscillations may form the substrate of a temporal binding code by becoming synchronized in different populations of cells that process different aspects of the same stimulus⁴. However, there are a number of points that should be considered. First, it has suggested that their been methods of statistical analysis may lead to an overestimation of the number of cells showing oscillatory activity⁵. The implication is that the number of cells exhibiting oscillations in the cat visual cortex is probably much lower than Singer and his colleagues suggest. In addition, reliable oscillations are even more difficult to demonstrate in the monkey visual cortex^{2,5,6}. Second, the frequency and amplitude of oscillations seem to decrease as the velocity of a stimulus decreases⁷. Indeed. we have found no evidence for oscillations in the monkey temporal visual cortex using static stimuli⁶. These findings suggest that oscillations are not involved in temporal binding in primates when information on static objects is processed. Third, temporal constraints may also minimize the usefulness of oscillations for the processing of visual stimuli. There may only be 10-20 ms of processing time at each visual cortical area for tasks such as object recognition 6,8,9 . Given that even a strongly stimulated visual cell fires at only about 100 Hz, there will be time for only one or two spikes from each active neuron to be used in information processing in each cortical area that is required for recognition^{6,10}. This suggests that oscillations that develop over tens of milliseconds and persist for hundreds of milliseconds in the visual system are unlikely to be crucial for object recognition. In conclusion, it can be argued that the low proportion of cells displaying the oscillation phenomenon, its absence in the monkey

Martin J. Tovée Edmund T. Rolls

Dept of Experimental Psychology, University of Oxford, South Parks Road, Oxford, UK OX1 3UD.

References

- 1 Gray, C. M. and Singer, W. (1987) Soc. Neurosci. Abstr. 13, 1449
- 2 Kreiter, A. K. and Singer, W. (1992) Eur. J. Neurosci. 4, 369-375
- Gray, C. M., König, P., Engel, A. K. and Singer, W. (1989) Nature 338, 334–337
- 4 Engel, A. K., König, P., Kreiter, A. K., Schillen, T. B. and Singer, W. (1992) *Trends Neurosci.* 15, 218–226
- 5 Young, M. P., Tanaka, K. and Yamane, S. (1992) J. Neurophysiol. 67, 1464–1474
- 6 Tovée, M. J. and Rolls, E. T. (1992) NeuroReport 3, 369-372
- 7 Gray, C. M., Engel, A. K. and König, P. (1990) Eur. J. Neurosci. 2, 607–619
- 8 Thorpe, S. J. and Imbert, M. (1989) in Connectionism in Perspective (Pfeifer, R., Schreter, Z. and Fogelman-Soulie, F., eds), pp. 63–92, Elsevier
- 9 Rolls, E. T. (1991) Curr. Opin. Neurobiol. 1, 274–278
- 10 Oram, M. W. and Perrett, D. I. (1992) J. Neurophysiol. 68, 70-84
- 11 Rolls, E. T. (1992) Phil. Trans. R. Soc. Lond. Ser. B 335, 11-21

I have read with interest the papers of Wolf Singer and his colleagues on their discoveries of synchronized oscillations in the cortex. While I greatly admire the technical expertise that has made possible such findings as those reported in the June issue of TINS¹, I would like to correct the statement made there (and elsewhere) that the 'superposition catastrophe' implicit in the Hebb² model has only recently been solved. recognized and This problem worried a number of us within a few years of the appearance of Hebb's monograph in 1949, and around 1970 I arrived at the same solution that von der Malsburg³ formulated some years later. In the paper4 in which I pointed out that synchronization of impulses was essential for segregating objects in a complex

field, I also recommended the postulate as a project for electrophysiologists:

Some of the hypotheses presented in this article, such as the idea that a figure generates synchronous firing in a number of cells, might be tested... it is to be hoped, therefore, that electrophysiologists might consider [the idea] to be worth following up experimentally...

The matter of priority is relatively unimportant (except perhaps for my ego), but the 1974 paper⁴ was also concerned with the role of the reciprocal (centrifugal) visual-system paths in attention, generalization and the integration of form, color, spatial location, etc. (the 'binding' problem), and present-day writers on these subjects seem to be unaware of the solutions I proposed. I think that some of these other speculations also merit experimental investigation, now that the techniques are available, and TINS must be a more effective place to make such a suggestion than the Psychological Review.

Peter M. Milner

Dept of Psychology, McGill University, 1205 Dr Penfield Ave, Montreal, Quebec, Canada H4A 3N1.

References

- 1 Engel, A. K., König, P., Kreiter, A. K., Schillen, T. B. and Singer, W. (1992) *Trends Neurosci.* 15, 218–226
- 2 Hebb, D. O. (1949) The Organization of Behavior, Wiley
- 3 von der Malsburg, C. (1981) The Correlation Theory of Brain Function (Internal Report 81–2), Max-Planck-Institute for Biophysical Chemistry
- 4 Milner, P. M. (1974) Psychol. Rev. 81, 521–535

Reply

Tovée and Rolls conclude that oscillations are unlikely to serve as a substrate for feature binding by synchronous firing of neurons because they found no evidence for oscillatory responses to static stimuli in monkey inferior temporal (IT) cortex¹. Moreover, they argue that we might have overestimated the incidence of oscillatory responses, and that the relevance of oscillations for cortical processing might be restricted by temporal constraints.