

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 been suggested that their 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 stimuli⁸. 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^{6,9,9}. 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

in response to static visual stimuli, and the temporal constraints on the processing of visual information suggest that the oscillations do not form a basis for spatial binding, at least in the processing of static stimuli, which might be achieved in other ways¹¹.

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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
- 3 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., Schreier, 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 *TINS*¹, I would like to correct the statement made there (and elsewhere) that 'the 'superposition catastrophe' implicit in the Hebb² model has only recently been recognized and solved. 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*.

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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 Functions (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.

Before addressing these arguments we wish to emphasize that 'oscillations' and 'synchrony' need to be distinguished as being different variables that are not necessarily interdependent. Cells can synchronize their responses without engaging in regular oscillatory discharges and, conversely, responses may be oscillatory without being synchronized. Thus, the hypothesis that synchrony provides the code for feature binding^{2,3} cannot be validated or falsified by demonstrating the presence or absence of oscillatory firing patterns. Rather, what needs to be investigated is the correlation between the firing patterns of simultaneously recorded neurons and the dependence of synchronization probability on the feature constellation.

As we have pointed out, oscillations *per se* are unlikely to represent particular aspects of visual stimuli^{2,3}. Nevertheless, oscillatory response patterns are of interest because they reflect organized, temporally structured activity that is often associated with synchronous firing. In addition, oscillatory firing patterns offer certain advantages for establishing synchrony over larger distances^{2,3}.

However, there is an important methodological caveat concerning the detectability of oscillatory firing patterns which may, in part, be responsible for the fact that Tovée and Rolls did not observe oscillations in monkey IT (Ref. 1). Correlograms are usually computed over extended data epochs and often are even averaged over several trials to obtain sufficient numbers of entries. Because the stimulus-induced oscillations that have now been reported in a variety of substrates are never strictly periodic but instead contain a broad spectrum of frequencies²⁻⁴, autocorrelograms may fail to exhibit clear satellite peaks. This may be the case even if spike-triggered averages of local field potentials indicate that the cell's firing is locked to oscillations in these population signals⁵. Thus, the absence of multiple peaks and troughs in autocorrelograms does not exclude the possibility that the recorded

cell discharges in synchrony with others or that its response contains oscillatory episodes⁴. For these reasons, broad-banded oscillations may have escaped analysis by Tovée and Rolls. In fact, Nakamura *et al.*⁶ have obtained evidence that stimulation of IT neurons can indeed evoke oscillatory responses. These authors report oscillation frequencies in the α range, but about one-third of their recordings show frequencies in the γ range.

Contrary to Tovée and Rolls, we do not think that we have overestimated the incidence of oscillatory responses. First, we have always controlled by visual inspection the correspondence between the fitted Gabor functions⁷ and the raw correlograms, and the reader may assess the quality of the fits by examining the host of published correlograms. Second, our rating criteria were strict, allowing for a maximum of 5% false positive ratings, which is small compared to the observed fraction of 50–60% oscillatory responses^{4,7}. Third, in most cases averaged correlograms were classified, and thus we actually underestimate the incidence of oscillatory episodes, since the oscillation frequency shows considerable variability⁴. Fourth, other groups have confirmed the high proportion of oscillatory responses in cat visual cortex⁸. It needs to be emphasized, however, that most of our analyses have been performed on multiunit activity. Because adjacent cells in cat visual cortex tend to discharge in synchrony when they oscillate, multiunit recordings reduce the sampling problems and disclose oscillatory responses where single-cell analyses would have failed.

Finally, Tovée and Rolls argue that 'binding by synchronization' is incompatible with temporal constraints. Their argument rests on the assumption that strictly sequential processing is carried out in a serial hierarchy of cortical areas. They appear to assume that several cycles of synchronous discharges would be required at each processing level before cells at the respective next stage could

respond and in turn establish synchrony. We consider this a non-compelling assumption. First, it is conceivable that synchronous states emerge nearly simultaneously at different levels of processing. The short transmission times from primary visual cortex to IT (Ref. 9), the reciprocity of connections across levels and the parallel input from a variety of subcortical structures¹⁰ are compatible with nearly simultaneous, cooperative processing across different areas. Second, cross-correlation analysis with sliding temporal windows has revealed that synchrony can be established rapidly and does not require several cycles of preceding oscillatory activity¹¹. Third, there is no reason why the brain should not be able to draw reliable conclusions from the first burst of a synchronously discharging cell assembly if ambiguity is low. Integration over several cycles may be necessary only if binding ambiguities have to be resolved, if learning has to take place or if representations have to be maintained for some time.

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References

- 1 Tovée, M. J. and Rolls, E. T. (1992) *NeuroReport* 3, 369–372
- 2 Engel, A. K., König, P. and Schillen, T. B. (1992) *Curr. Biol.* 2, 332–334
- 3 Engel, A. K., König, P., Kreiter, A. K., Schillen, T. B. and Singer, W. (1992) *Trends Neurosci.* 15, 218–226
- 4 Kreiter, A. K. and Singer, W. (1992) *Eur. J. Neurosci.* 4, 369–375
- 5 Freeman, W. J. (1975) *Mass Action in the Nervous System*, Academic Press
- 6 Nakamura, K., Mikami, A. and Kubota, K. (1992) *NeuroReport* 3, 117–120
- 7 Engel, A. K., König, P., Gray, C. M. and Singer, W. (1990) *Eur. J. Neurosci.* 2, 588–606
- 8 Ghose, G. M. and Freeman, R. D. *J. Neurophysiol.* (in press)
- 9 Oram, M. W. and Perrett, D. I. (1992) *J. Neurophysiol.* 68, 70–84
- 10 Rodman, H., Gross, C. G. and Albright, T. D. (1989) *J. Neurosci.* 9, 2033–2050
- 11 Gray, C. M., Engel, A. K., König, P. and Singer, W. (1992) *Vis. Neurosci.* 8, 337–347