

Is grandmother an oscillation?

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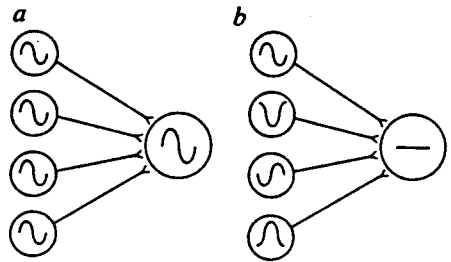
THE realization that visual information is processed through successive stages in many separate areas of the cortex has led to a dilemma. How are the distributed representations of the visual features that have to do with a single object in the world put together so that they can create a perception or influence action? That is, when a green furry tennis ball and an ebony billiard ball are seen in the same part of the visual field, how can the colour, motion and texture properties of each ball be associated, so that the black colour and smooth texture of the billiard ball is not ascribed to the tennis ball? Three new papers¹⁻³ from two laboratories, one on page 334 of this issue², provide a clue.

Several proposals have been put forward to solve this problem. A now-classic notion is that significant combinations of features are hierarchically extracted and combined in specific cortical areas specialized for the recognition of certain classes of objects^{4,5} or, at the extreme, in the receptive fields of single neurons⁶. In some higher cortical areas, there could be, for example, 'grandmother' neurons responding selectively to the precise combinations of visual features that are associated with one's grandmother. Either such cells would not be able to signal the location of stimuli very accurately or there would have to be a separate grandmother cell for each region of the visual field. It is also not clear how the many different features that might be associated with one's grandmother could be combined in any very selective way without a 'combinatorial explosion' in the numbers of cells required⁷. This would lead to the sort of problem Little Red Riding Hood had when her grandmother cells failed to discriminate the wolf's grey fur, sharp white teeth and heavy breathing from her grandmother's normal benign appearance.

These shortcomings have led to an alternative notion — that the representations in the brain of various visual properties of objects in the world are combined only transiently, rather than in fixed receptive fields, in some way that makes the conjoint output of different property-specific detectors available to the mechanisms for perception or action. Some years ago, Crick⁸ suggested a mechanism by which the neurons of thalamic reticular nucleus below the cortex could unify the perceptual qualities represented in different cortical areas. He proposed that a neural 'searchlight' would simultaneously illuminate all the neurons that are activated by the same object in the world.

The recent work from Gray, Singer and colleagues, reported in this issue² and else-

where¹, and from Eckhorn and colleagues³, raises a related possibility: that neurons in the visual cortex activated by the same object in the world tend to discharge rhythmically and in unison. Such a one-note neural harmony could, in principle at least, provide the neurons at higher cortical levels with stronger inputs so that they associate the activities of lower-order neurons with one another (see figure). If the discharges of the texture-, colour-, depth- and movement-sensitive neurons



Four lower-order neurons providing input to one higher-order neuron. *a*, Neuronal activity in the lower-order neurons is shown oscillating in phase. The resulting postsynaptic potentials sum in the target cell, producing a large oscillation in its membrane potential. At the peak of this oscillation, the membrane potential of the higher-order neuron would exceed the discharge threshold, and the cell would fire rhythmic, high-frequency bursts of spikes. *b*, The activities in the lower-order neurons do not oscillate in phase, so the higher-order neuron receives a more nearly constant input. The resulting steady membrane potential in the higher-order neuron either would be below the threshold for spike discharge or would, in any case, not allow it to discharge at the high frequencies characteristic of neuronal responses to sensory stimuli.

concerned with the tennis ball were to oscillate in phase with one another and out of phase with the billiard ball responses, this might enable perceptual mechanisms to assign the furry texture, green colour and blinding speed to the one object and the smooth texture, ebony colour and moderate speed to the other. I have made a simple estimate that, with reasonable assumptions about the duration of postsynaptic potentials, such a mechanism would enable higher-order cells to distinguish inputs from one set of neurons from those of 10 or more sets of neurons, if each set responds to different objects in the world at different phases or frequencies. If, instead of summing, synaptic inputs can interact multiplicatively⁹, cortical cells could detect phase-locked activity with even more sensitivity.

This new evidence provides only the first hints that the visual cortex uses such mechanisms. Gray and Singer¹ find that visual stimulation can cause many neurons in visual cortex to discharge their action

potentials rhythmically at about 40–50 Hz in very lightly anaesthetized (and, as reported in an abstract elsewhere, awake) animals. This rhythmicity is accompanied by an oscillation in the extracellular field potential and seems to originate in the cortex, as it was not evident in recordings from the main input to the visual cortex from the thalamus. Eckhorn and colleagues' find that oscillatory field potentials evoked by some visual stimuli are in phase even between the two primary visual cortical areas (17 and 18) in the cat and that the field potentials in one area are in phase with the action potential discharges in the other. In their paper in this issue¹, Gray *et al.* report that oscillations in the discharge are commonly in phase for neurons with overlapping receptive fields, irrespective of their selectivity for a particular stimulus orientation². But when the authors record at sites more than 2 mm apart, where receptive fields no longer overlap, they find that oscillations are rarely in phase except for neurons with the same orientation specificity.

The most surprising observation comes from two cases in which pairs of recording sites were located half a visual cortex (7 mm) apart. Receptive fields of the neurons at the two sites had a common orientation specificity and were aligned so that they could be stimulated by a single long bar of light (see Fig. 3b of ref. 2 on page 336). Neuronal discharges at the two sites were well correlated only when the cells were stimulated with a single long bar. When they were simultaneously activated by two shorter bars that did not bridge the gap between the two receptive fields, the correlation disappeared. In that sense, the correlated discharge can be considered as depending on the global property of the stimulus — whether it is a single or two different objects.

Numerous questions are raised by these tantalizing observations. Where does the rhythm come from? Many workers have dismissed findings of rhythmic discharge in the central nervous system as artefactual, as rhythmicity can be induced by certain anaesthetics or by damage. Further work demonstrating that such phenomena are definitely present in awake animals will be needed to satisfy these critics. Even if not an artefact, the oscillations may be epiphenomena:

observations of rhythmicity and its correlation with particular stimuli do not allow the conclusion that the nervous system makes use of such information. This point will be difficult to address except by demonstrating that many global aspects of visual stimuli are accompanied by correlated rhythmic discharges. In particular, it would be intriguing to know whether a single bar or edge produces such correlated activity when and only when it appears as a single object; a physical discontinuity that does not degrade the perception of the bar as a single object, as when the bar is partially occluded³, should not destroy the correlated oscillations. It will be even more intriguing to see whether neurons in the different cortical areas specialized for colour, depth, motion and so on exhibit correlated, rhythmic discharges when

they respond to the same stimulus in the real world.

Observations of this type could provide compelling evidence that perceptual mechanisms of the brain do engage in the analysis of brain rhythms. The suggestion that coherent oscillations in activity identify the members of subsets of a large neuronal population may, however, still be an important one, even if these subsets are not closely tied to perception. Exploring the rhythms of the brain, revered by the pioneers of electroencephalography but now mostly dismissed as irrelevant to neural information processing, may even come back into fashion. □

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