

## Seeing the whole picture

Recent experiments in the visual system suggest that the mechanism by which the brain combines the various qualities of an object into a whole image may involve the synchronous discharge of distinct neurons.

What could account for the unity of perception by the possessor of a brain in which the sensory representations of the various qualities of an object are arrayed over an enormous expanse of cortex? Recent work on the visual cortex from two European laboratories has disclosed a possible answer [1-3]. These papers reveal that sustained neuronal responses to visual stimuli are often periodic, at a frequency of 40-60 Hz, in phase with local fluctuations in the extracellular field potential. These oscillations in activity can be synchronous across long distances in cortex when neurons in distinct cortical sites are excited by visual stimulation with a single object. These observations raise the possibility that the synchrony of the discharge of neurons that respond to many features of a single object is the feature that unifies or binds together the different visual cortical representations of that object. Another object in the visual field may also produce sustained oscillatory activity in each of the same cortical areas, but these discharges, although they might occur in synchrony with one another, would not be in synchrony with those produced by the first object.

One insight from work in many laboratories over the past decade and a half is the tremendously distributed nature of sensory representation in the mammalian cortex. The situation has been investigated particularly extensively in the monkey visual system, where the current count of the number of distinct cortical visual areas is somewhere near 30, including separate areas apparently specialized for color, form, binocular disparity, and motion. This number seems only likely to increase as we learn more details, and is probably as high or higher in humans.

A consequence of this widely distributed sensory representation is the problem of associating the representations of the various qualities of a single object with the appropriate object, that is to say, with one another. Such an association seems to be necessary if the rest of the brain is to be able to deal with the object as a single entity. This problem becomes acute when distinguishing among several objects in the visual field, for example to determine that it is the nearer red ball that is moving to the left and the more distant green one moving to the right. Mere proximity on the cortical surface will not do the job, for if one has two objects in the visual field, the motion signals from the two objects (both in cortical area MT) will surely be in closer proximity to each other than either of them will be to the color and binocular disparity signals (in cortical area V4 and elsewhere) of either of the two single objects.

To solve this problem, one would expect that some feature of the brain activity would be common among the various brain representations of that object and different for the representations of different objects simultaneously in view. If there were some such common signal that could be interpreted by higher stages of the perceptual and motor systems, these recipient neural systems could then deal with the object, in all its sensory representational complexity, as a whole. It would not be surprising if there were some limit to the number of separate objects that one could deal with simultaneously in this way, and human psychophysical studies suggest such a limit to our own processing capacities [4,5], but there does seem to be a need for special brain machinery to unify object perception in even a limited way.

The sort of common signal that is easiest to imagine as suitable for making these transient associations between the qualities present in particular objects is one having to do with the discharge activity of neurons. Other sorts of signals seem likely to be too slow or too inflexible. Using synchrony in oscillatory neuronal discharge as the property that binds together the different sensory representations of a single object would allow downstream neurons in the perceptual and motor systems easily to decode which features belong to which object, if the downstream neurons were themselves to have independent oscillations in membrane potential or sensitivity with a similar period. Under these circumstances, even rather diffuse input connections from all the separate sensory representations would allow each of the downstream neurons to respond to only one of a number of different objects at a time. Different downstream neurons, whose intrinsic oscillations were at other phases, would respond to different objects.

Stimulus-specific oscillations in cortical activity have long been recognized in the olfactory bulb and elsewhere in the brain [6]. What is new in the recent experimental results is the extension of these findings to the visual system, where many details of sensory representations are known, and the finding that different coupled patterns of activity in response to different objects may coexist.

The actual findings to date provide only limited and correlative evidence that the visual cortical oscillations that have been observed play a part in perception. The main observation in support of this notion comes from experiments in which a single elongated stimulus that activates neurons at two distant sites produces synchronous oscillations at the two sites, but in which separate stimuli

that excite each of the sites equally do not give rise to synchronous oscillations [3]. More recent findings have clarified the cortical layers and cell types most likely to exhibit these oscillations [7] and have shown that the synchrony between oscillations in distant cortical sites can be attained within 1–2 cycles, sufficiently rapidly to be relevant to perception [8]. The distance over which the oscillation can be present has been extended as well, both among the most distant visual areas on one side of the brain and even between the two cerebral hemispheres [9]. Engel *et al.* [10] have recently shown that powerful synchronous oscillations between the two cerebral hemispheres are mediated by fibers that pass through the corpus callosum. This result suggests that even long-distance synchronization is mediated by reciprocal corticocortical connections rather than by some remote common input. Finally, the same cortical cells have been shown to participate in synchronous oscillations with different partners, depending on the stimulus configuration [9].

What is needed firmly to establish or to rule out a role for these oscillations in perception are both stronger correlative experiments and actual causal intervention. Minor alterations in stimulus properties can sometimes make great differences in the perception, and these differences have been exploited experimentally. Von der Heydt and Peterhans [11], for example, have shown that neurons in monkey cortical visual area V2 can respond to illusory contours. The perception of the illusory contours and the neurons' responses to them are eliminated by slight changes at the borders of the stimulus. If the cortical oscillations are responsible for perception, they too should be influenced by such small changes in visual stimuli. Ideally, one would like to use ambiguous stimuli that could be perceived in either of two different ways, together with chronic multiple-electrode recordings in alert animals trained to report which way they perceive the stimuli, to show that different patterns of cortical oscillations correlate trial by trial with different perceptions. Even stronger evidence would come from experiments in a similar alert animal in which electrical or pharmacological stimulation or suppression of oscillatory cortical activity could sensibly alter perception.

Although we are far from knowing the origin or significance of this rhythmic cortical activity, both of these issues are eminently open to experimentation. Results

in the next few years promise new insight into these important problems and their possible relationship to perceptual unity.

## References

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