Striving for coherence

Wolf Singer

To explain how the brain interprets the world, Descartes postulated that we have a single centre — the pineal gland — where all sensory signals converge and are evaluated jointly, where decisions are reached and future actions planned. But progress in neurobiology has forced us to adopt a different view — that nowhere do we have a single centre to evaluate or coordinate computations. So how are the results of many parallel computations bound together to permit coherent perception and action?

On pages 430 and 434 of this issue, Rodriguez et al.1 and Miltner et al.2 address this question by investigating the temporal coherence of electroencephalographic (EEG) signals recorded from people performing cognitive tasks.

To represent perceptual objects or motor programmes in systems that do not converge, the idea is that a particular content is represented by jointly activating an assembly of cells, rather than by the response of an individual, highly specialized neuron. The advantage is that an almost unlimited number of different assemblies — each representing different contents — can be generated, because subsets of cells drawn from the large (but limited) pool of functionally specialized neurons in the cerebral cortex can be dynamically regrouped. However, this mechanism must allow the neurons that participate in a particular assembly to be identified unambiguously. The responses of all the neurons in a particular assembly must then be labelled, to ensure that they are processed jointly at subsequent stages.

Based on theoretical considerations1 and data from multi-electrode recordings in the visual cortex3, it has been proposed that responses are bound together and labelled by synchronized firing of the individual neurons with a millisecond precision. The assumption is that such synchronized activity sums more effectively than nonsynchronized activity in the target cells at subsequent processing stages. If so, synchronization could increase the effect that a selected group of neurons has on other populations with great temporal specificity. Jointly raising the effect of a subset of responses is equivalent to functional binding because it favours further joint processing of the selected responses.

The EEG studies by Rodriguez et al.1 and Miltner et al.2 were designed to test the predictions derived from this hypothesis. Signals from the EEG reflect, with high temporal resolution, the activity of many neurons in the cortical area beneath the electrodes. This prevents precise localization of neuronal responses, but facilitates the detection of synchronous activity. The responses of distributed neurons summate effectively — and then give rise to measurable fluctuations of the EEG signal — only if they are well synchronized. Typically, EEG fluctuations are periodic and cover a broad frequency range (from less than 2 to greater than 60 Hz), indicating that neurons in the cerebral cortex can oscillate synchronously in various frequency bands.

The new studies1,2 concentrate on the so-called gamma frequency range, which is centered around 40 Hz. The authors selected this frequency because precise synchronization of neuronal responses is often associated with oscillations in the 40-Hz range. But it is not trivial to detect these oscillations. Synchronized firing is usually short-lived (100–300 ms) and, except for an initial component, the oscillations are not phase-locked to the stimulus because they are self-generated. This prevents averaging and requires a method that allows brief bursts of synchronous activity to be detected in single trials. New analytical tools have made it possible to confirm that these transient gamma-oscillations exist in the human brain, and...
to establish close relations between them and cognitive processes 2.

Rodriguez et al. and Miltner et al. now show that local oscillatory responses can synchronize across different cortical areas — the time course and topological distribution of synchronization showed a high degree of task-related specificity. These results from humans closely resemble those obtained by intracortical recording from cats 3. Rodriguez et al. 4 asked people to inspect pictures that could, on occasion, be recognized as a face (Fig. 1). They found that scrutinizing the pictures was associated with increased gamma activity over cortical regions known to be involved in visual processing. But precise phase-locking of these oscillations across cortical areas occurred only when the subjects identified a face. This state of heightened synchrony was transient. It dissolved shortly before the subjects responded by pressing a key, giving way to a second episode of phase-locked gamma activity associated with the motor response, which had a different topological distribution. The authors suggest that such dynamic changes in the phase relations between spatially distributed oscillating groups of neurons could reflect the transient formation of assemblies that are bound by synchrony and represent first perception of the stimulus and then the motor programme.

Miltner et al. 5 tested the hypothesis that if people learn the association between a visual and a tactile stimulus, they should form a neuronal assembly comprising cells responsive to the visual and the tactile stimuli, respectively. The authors observed a marked increase of gamma activity after the visual stimulus was presented. Notably, they also found a selective increase of gamma coherence between the visual cortex and the cortical area representing the hand that had received the tactile stimulus. This coherence must have developed as a consequence of conditioning, because it disappeared when the learnt association was lost (that is, after a sequence of visual stimuli not connected to a tactile stimulus were presented). Moreover, such coherence was not seen for signals from the area representing the non-conditioned hand. Finally, the increased coherence was confined to a narrow band around 40 Hz, supporting the idea that synchronization of oscillations in this frequency range is involved in cognitive processes.

The new results provide further evidence that synchronization might allow the selective association of distributed neurons. However, neither these nor previous studies have demonstrated this in the vertebrate brain, because we cannot yet disrupt synchronization in the relevant frequency band without affecting other response variables. But a functional role for synchronization has been demonstrated in the insect olfactory system 6. There is also indirect evidence from psychophysical studies, which suggests that the brain binds responses together and interprets them as related if they are made synchronously by the neurons that evoke them 7,8. If the brain interprets responses as related when they are made synchronously by internal mechanisms (as was the case in the people studied by Rodriguez et al. 3 and Miltner et al. 5), gamma oscillations could well be the mechanism that binds neurons into functionally coherent assemblies.

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Mathematics

Counting up to four

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Place marbles in a straight line. You can arrange them so that they are not evenly spaced. But can you arrange them so that no subset of k marbles, including non-neighbours, for k \( \geq 3 \), is evenly spaced (Fig. 1, overleaf)? Again, the answer is yes: if d is the distance between the first two marbles, just put the third one at distance 2d from the second one, the fourth at distance 2^2d from the third, and so on, the nth being then at a distance 2^{n-1}d from the (n – 1)th. But then the distance between the marbles grows extremely fast, and they are spaced more and more widely apart: the density of the alignment (that is, the proportion of occupied sites between the first and the last one) tends to zero as the number of marbles increases. What happens if we impose non-zero density? The answer is that for any integer k and non-zero density \( \delta \) there will be