NEURONAL NETWORKS

Vibrations in the memory

Rodney J. Douglas and Kevan A. C. Martin

Of the many secrets that each of us carries in our brains, the one that we would all dearly love to know is how we remember things. How is it that *Music, when soft voices die,/ Vibrates in the memory*? How do we instantly pick out the individual face of a friend in a crowd, identify the aroma of freshly ground coffee, and carry out a conversation in a noisy café, all the while maintaining a coherent and stable view of the world? This complex process of segmentation and recognition may involve a temporal code based on the oscillatory activity of neural networks in the cerebral cortex. Whittington *et al.*, in a combined theoretical and experimental study of isolated networks described on page 612 of this issue[1], have been able to identify a network of inhibitory neurons as the likely source of these cortical oscillations.

Investigations of memory have concentrated on one part of the temporal lobe of the cerebral cortex known as the hippocampus. The link between hippocampus and memory was established through neurological patients who, through the misfortune of disease, stroke, surgery or accident, had impaired temporal lobe function. These patients appeared normal, except that they had no memory of events that had occurred a few minutes previously. Their tragic condition — temporal lobe amnesia — led to wide-ranging studies of the role of the hippocampus and related cortical structures in memory.

A central problem in memory is how information is represented by neurons[2]. One way in which memory could work is that neurons in the cerebral cortex could learn to 'recognize' the various things that make up our world. So individual neurons might learn to recognize the smell of coffee, the texture of a cup or the taste of cream, for example. But the number of such high-level 'feature detector' neurons scales unfavourably with the number of things to be encoded, and so most theories use combinations of neurons, each of which represents a simple feature, to code for different things. Each neuron then participates in the representations of many different things.

Population-based coding schemes dra-

VISUAL NEUROSCIENCE

Reflections on transparent motion

This striking image exemplifies the phenomenon of transparent motion, which has long been a puzzle. Objects in the visual world are constantly passing in front of one another, yet the brain has no difficulty in distinguishing them, in this case to perceive floating leaves drifting in one direction as the tiger moves in another. Extracting such information from the jumble that reaches the eyes is not trivial. But insights into how the task is accomplished come from a paper on page 609 of this issue, in which Bradley *et al.* describe the firing properties of neurons in a part of the monkey visual system known as the middle temporal (MT) cortical area.

MT is one of the 'higher' visual areas, in that the input it receives has already been sequentially processed by 'lower' brain regions, and in particular it seems to be concerned with the detection of motion. Neurons within MT are sensitive to the speed and direction of moving objects, and each neuron has a preferred direction of motion that stimulates its maximal response. Many are inhibited by motion in the opposite direction, and this inhibition is believed to help eliminate noise and ensure an accurate representation of the moving stimulus. But many also respond to stereoscopic disparity, which corresponds to the visual plane in which the stimulus occurs. The significance of this has been a mystery, because at first glance depth and movement appear to be unconnected. Yet it also seemed unlikely that a single brain area would be devoted to two unrelated tasks, and so the field has been in search of a unifying explanation.

Bradley *et al.* have now provided it. They recorded from neurons in area MT of rhesus monkeys trained to fixate on a display screen. Individual neurons were first stimulated by a pattern of dots moving in their preferred direction. Having confirmed the inhibitory effect of adding further dots moving in the opposite direction, the authors separated the two sets of dots into different visual planes (with coloured glasses similar to those used for viewing old 3D movies). They found that the inhibitory effect is strongest when both sets of dots lie in the same visual plane, and that it becomes weaker as the disparity increases. Similar results are obtained whether the two patterns overlap or are merely adjacent. The results suggest a simple explanation for how and why MT integrates direction and depth cues. Transparent motion normally arises when objects pass each other in different planes. By not having inhibition between movement in different planes, the brain can interpret the two movements as independent. If instead the two movements occur within the same plane, transparent motion is less likely, and the brain looks for other explanations (for instance, random noise).

Is this consistent with what we know from human psychophysics? In fact, for simple patterns such as two sets of dots moving past each other, subjects have no difficulty in perceiving two sets of coherent motion, even when both occur in the same plane. But for more complex stimuli, the task becomes more difficult, and the authors previously showed that stereoscopic disparity between the two directions can improve performance. They suggest that, in the real world, the visual system makes use of many clues to arrive at the correct interpretation, and they raise the possibility that MT may exploit not only depth, but also other features such as colour or texture to distinguish between the components of transparent motion. Faced with threats such as tigers hiding in the undergrowth, it is easy to believe that the primate visual system will have evolved to use all the help it can get.

Charles Jennings

matically increase the efficiency of information encoding. For example, if in a population of 1,000 ideal binary neurons, only one neuron discharges at any time, then that population can encode only 1,000 states, or about 10 bits of information. But if 5 per cent of the neurons are active at any time, the same population can encode as much as 282 bits (or 10^{85} states)[3]. Population coding, however, seems to require a mechanism by which all the neurons representing one thing are related or 'bound together'[4–6]. One theory is that neurons signal their relatedness by discharging nerve impulses in synchrony with each other at about 40 Hz. This is an attractive theory because 'brain waves' of various frequencies have been observed since the first electroencephalographic (EEG) measurements were made in humans in the 1920s, but the function of these brain waves has never been clear.

Quite simple feedback systems are prone to oscillation, so given their many recurrent connections it is not surprising that cortical circuits do the same. And it is exactly these recurrent circuits, which are similar to the attractor neural networks described by Hopfield[7] and others, that may provide a basis for associative recall. Unfortunately, classical associative memories remember and recall entire input scenes as single memories. Subcomponents of the scene (such as the face of our friend in the crowd) cannot be recalled independently. This restriction severely limits the ability of the associative networks to generalize, because commonly occurring components of complex scenes will not be recognized in new contexts[4,5].

So the theoretical and experimental challenge is to find a method that enables an associative memory to segment a scene into a number of components in a composite input and represent them separately and simultaneously. Theoreticians have now demonstrated that if associative networks are allowed to oscillate, then this problem can be partly solved. These oscillatory networks are able to express a few memory patterns simultaneously by representing each pattern by an oscillation of a different phase[5]. Thus, the discharge of neurons representing the components of any one pattern becomes temporally correlated, but anticorrelated with the discharge of neurons representing all other patterns.

A key link between collective oscillations and perception was made by Gray and Singer (see ref. 6) when they noticed that cortical neurons in the visual system responded to coherent visual stimuli by discharging synchronously at frequencies of around 40 Hz. Incoherent stimuli comprised of unrelated features did not elicit synchronous discharge. This suggests that the synchronization reflects a transient binding together of reverberating groups of neurons, each of which responds to a different feature of the same single perceptual object. Whittington *et al.*[1] have now been able to demonstrate that these 40 Hz oscillations can be evoked in thin slices of brain that were kept alive in a nutrient bath. The advantage of the brain slice is that neurons can be studied far more easily than in the whole brain. Whittington *et al.* were able to show pharmacologically that only a small subset of the known neurotransmitter receptors on hippocampal neurons were needed to generate the 40-Hz oscillatory activity of the network. The metabotropic subclass of the glutamate receptors, which are potent activators of the inhibitory neurons, were sufficient to provide tonic excitation, while the $\mathrm{GABA_A}$ subclass of inhibitory receptors provided sufficient inhibition to gate the excitation and generate the oscillation.

Theoretical studies of network oscillations have concentrated on the interaction of inhibitory neurons with excitatory neurons, and have often incorporated neurons with intrinsic oscillatory properties. The computer model of Whittington *et al.* is radically different. It consists of a network of inhibitory neurons, none of which is an intrinsic oscillator, driven only by tonic excitatory activation, yet it predicts their experimental results. In the context of hippocampal memory, their decision to explore the metabotropic glutamate receptor is delightfully perverse, because the NMDA receptor, another type of glutamate receptor, has long been the cynosure of theoreticians and experimentalists studying 'learning' synapses in the hippocampus.

Whittington and colleagues' complex experiments and simplifying theory have identified the synapses between the inhibitory neurons as being the critical components in determining both the occurrence of oscillatory activity and the frequency of the oscillations. The way is now open for direct studies of the details of the oscillatory mechanism, and its possible associative function, under the controlled conditions of the brain slice preparation. □

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DAEDALUS

Carbonated metal

MANY inventors have tried to make a foamed metal. None has really succeeded. No known detergent will whip molten metal up into frothy foam. Even in zero gravity, such a foam 'breaks' rapidly by the merging of its bubbles. Now Daedalus has a new approach.

He points out that ordinary chalk, calcium carbonate, has nearly the same density as aluminium. Accordingly, if chalk dust were suspended in molten aluminium, it would stay in suspension, or at least would separate out only slowly. But at the temperature of molten aluminium, calcium carbonate is beginning to decompose into lime and carbon dioxide. It has an appreciable vapour pressure. If the hydrostatic pressure falls below that value, each chalk particle will blow a bubble of carbon dioxide and turn into a grain of lime. Furthermore, the heat absorbed by the reaction will freeze a thin skin of solid aluminium around the bubble, stopping it from coalescing with others nearby. The result: foamed aluminium.

Pure aluminium and pure chalk are not quite perfectly matched for this process. DREADCO's chemists are stirring mixtures of various metal carbonates into a wide range of aluminium alloys, seeking the most compatible combination of density, melting point, vapour pressure, and heats of reaction and solidification. The final optimized process will melt the alloy under high pressure, stir in the carbonate powder, and allow the homogenized mixture to escape through a nozzle into normal atmospheric pressure. The alloy will foam, expand and solidify. If the nozzle is too narrow to permit full expansion, the foam will elongate instead, deforming its internal bubbles into long parallel ellipsoids or cylinders. Either way, a continuous column of foamed metal will emerge from the outlet.

Foamed metal will be a splendid new material. Like foamed polystyrene, its cellular structure will make it wonderfully light and rigid. Its lime inclusions will strengthen it further by impeding plastic flow (some turbine alloys are loaded with ceramic grains for this reason). Yet when forcibly bent it will tolerate drastic deformations. In all fields of engineering it will displace fully dense metal. Shipbuilders in particular should welcome a metal that floats. The grade with elongated bubbles will have the grain and character of hardwood, and may be best worked by carpenters — although the gritty lime will rapidly blunt their drills and saws. It will be easily and firmly joined by nails and wood-screws, but not by the traditional fish glue.

David Jones