Information processing

Neural populations revealed

Terrence J. Sejnowski

How are actions represented in the brain? Microstimulation of a discrete point in the deeper layers of the monkey superior colliculus produces a very fast saccade of the eyes with a particular direction and amplitude that depends only on the location of the microelectrode[1,2]. The latency is short (20–30 ms) and the response is machine-like. This is reminiscent of an invertebrate 'command' neuron whose firing can cause a complex coordinated behaviour to occur (see page 278 of ref. 3). The pattern of activity in the superior colliculus preceding a saccade is, however, quite widespread[4] and it has been generally assumed that the summation of the responses in the active population determines the eye movement. This hypothesis predicts that the neurons with peak activity in the motor map code the location to which the eyes move. Lee, Rohrer and Sparks, in their elegant experiment published on page 357 of this issue[5], provide conclusive proof to the contrary, that the information coding for eye movement in the superior colliculus is represented by the distributed firing pattern of all the neurons that are activated. Such distributed representations of sensory information and motor commands may be quite common in the brain.
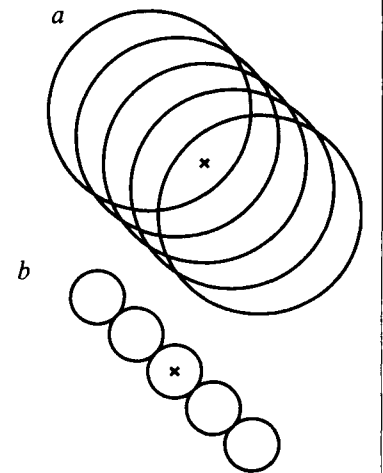
A region in the deeper layers of the superior colliculus about 2 mm in diameter containing about 100,000 neurons is activated just before a typical saccade. Imagine that each of these neurons has attached to it an arrow representing the direction and magnitude of the eye movement that occurs when the stimulating electrode is centred on that neuron. Imagine further that the 100,000 vectors attached to these neurons are added vectorially, each arrow weighted by the activity level of its neuron. The resultant vector accurately predicts how the eyes will move. Lee *et al.* show[5] that when a subset of these neurons is deactivated by lidocaine, and can no longer contribute to the vector average, the eye movement will miss the target precisely as predicted by the resultant vector. This suggests a very large population of neurons contributes to the coding of a simple eye movement.

The use of such a large population to represent a single vector might seem wasteful. It can be shown, however, that a large population of neurons with broadly tuned response properties can code information more efficiently than a 'command' neuron representation in which only a single neuron is active for each eye movement[6,7] (see figure). Moreover, accuracy is not lost in a distributed representation, as long as only one eye movement is being represented at any given time. Thus, far from being a 'sloppy' way to organize information, coarse population coding is efficient, accurate and relatively insensitive to noise in the responses of single neurons.

Will this lesson learned in the oculomotor system generalize to other action systems, such as the control of the limbs,

which have more inertia and more degrees of freedom than eyes? Single neurons in the motor cortex of monkeys respond during reaching with broad tuning for direction of movement[8]. When the same vector-averaging procedure used in the superior colliculus is performed on a large population of cortical neurons, the direction of the population vector is congruent with the direction of movement of the hand. But the critical inactivation experiment has yet to be performed in motor cortex, partly because the organization of hand movements in the cortex is not as regular as the motor map of eye movements in the superior colliculus.

Distributed representations pose several problems for organizing complex systems like brains. How are decisions to be made when the relevant information is spread out over such a large population? How are so many neurons coordinated when precise timing is of the essence, as in playing a piano? How can new actions be learned without interfering with other actions produced by the same population of neurons? Experimental answers to most of these questions are not yet available. One source of intuition into the

properties of distributed representations that is available comes from network models composed of simple neuron-like processing elements. The design of distributed network models of the sensory–motor interface is just beginning[9], but it is already clear that the issue of learning is central in developing and maintaining precise registration between sensory and motor representations (refs 10–12; D. Rumelhart, personal communication).

Network models of distributed sensory transformations are also being actively pursued, including models for the spatial transformation between retinal and head coordinates in parietal cortex[13] and the representation of three-dimensional shape in visual cortex[14]. Many counterintuitive properties of distributed representations can now be demonstrated with computer simulations. Some of the mysteries of population codes may be revealed by a combined effort to both model and measure distributed sensory and motor representations in the brain. □

Comparison of coarse and fine strategies for coding eye movements in the superior colliculus. Each point in the two-dimensional motor map in the intermediate layers of the superior colliculus represents a vector coding a particular magnitude and direction for an eye movement. Each circle encloses those neurons which contribute to a single eye movement, called the motor point image. The cross represents the centre of activation for a particular saccade. *a*, When the coding is coarse, many neurons contribute to a single eye movement and the same neurons contribute to many different eye movements (overlapping circles). *b*, For fine coding of an eye movement fewer cells are active and different eye movements are coded by different subpopulations (non-overlapping circles). The experimental evidence favours coarse coding in the superior colliculus[4]. Although more neurons are active in the coarse array, the movement is represented with greater accuracy than in a fine array with the same number of neurons. In general, the number of neurons required to code position to the same accuracy in a two-dimensional array decreases as $1/d$, where d is the size of the coding region[6]. A problem with coarse coding arises when two positions must be represented at the same time. The vector addition model predicts an eye movement which is halfway between the two positions.

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Terrence J. Sejnowski is a professor of Biophysics, Biology, Electrical and Computer Engineering, and Computer Science at the Johns Hopkins University, Baltimore, Maryland 21218, USA.