Moving the mental maps

The brain's maps of the outside world must be shifted when the point of view changes. Recent experiments on cortical neurons imply that this is done by modulating a distributed population code for position.

"Map me no maps, sir, my head is a map, a map of the whole world" [1]. We all share Fielding's sense that mind is spatial: we talk of exploring some new avenue of thought, of failing to follow the thread, of not knowing where to turn, of making an imaginative leap. Indeed, the history of neurophysiology began with the charting of motor cortex [2], encouraging the pseudo-science of phrenology to parcel out the human faculties over the cortical surface; and the ease with which we can now create bewitching technicolour maps of the activity of conscious human brains has tended to revive a similarly simple-minded, concept-free approach to brain science. But there is one aspect of cerebral mapping where recent work has, on the contrary, posed a remarkably puzzling conceptual problem: given that they are embodied in neurons whose positions are necessarily fixed, how is it possible for mental maps to be moved?

The answer lies in a particular form of spatial representation called population coding. Most maps take good care that one point on the map corresponds to one point — or at least, a discrete area — in the outside world. Such an arrangement is found in the visual pathways from the retinal fovea, and provides maximum visual acuity; but elsewhere in the brain it is rare. Instead, we tend to find convergence and divergence, blur and overlap: individual units in the periphery project diffusely to many central neurons, which in turn receive information from wide-ranging receptive fields. As a result, discrete stimuli are represented not as isolated pin-pricks of activity in single cells, but rather as a smudge, a bell-shaped mound of activity (Fig. 1) in lots of cells at once. Rather as in a hologram, each point on the map contains a little information about every point in the outside world.

Ultimately, of course, it has to be like this, for the whole point of having a brain at all is to bring together information from diverse sources in order to decide on a response — what Sherrington called the brain's "integrative action." It is true that neural blur implies a loss of acuity — the ability to discriminate between fine patterns of stimulation — but it is only in very particular

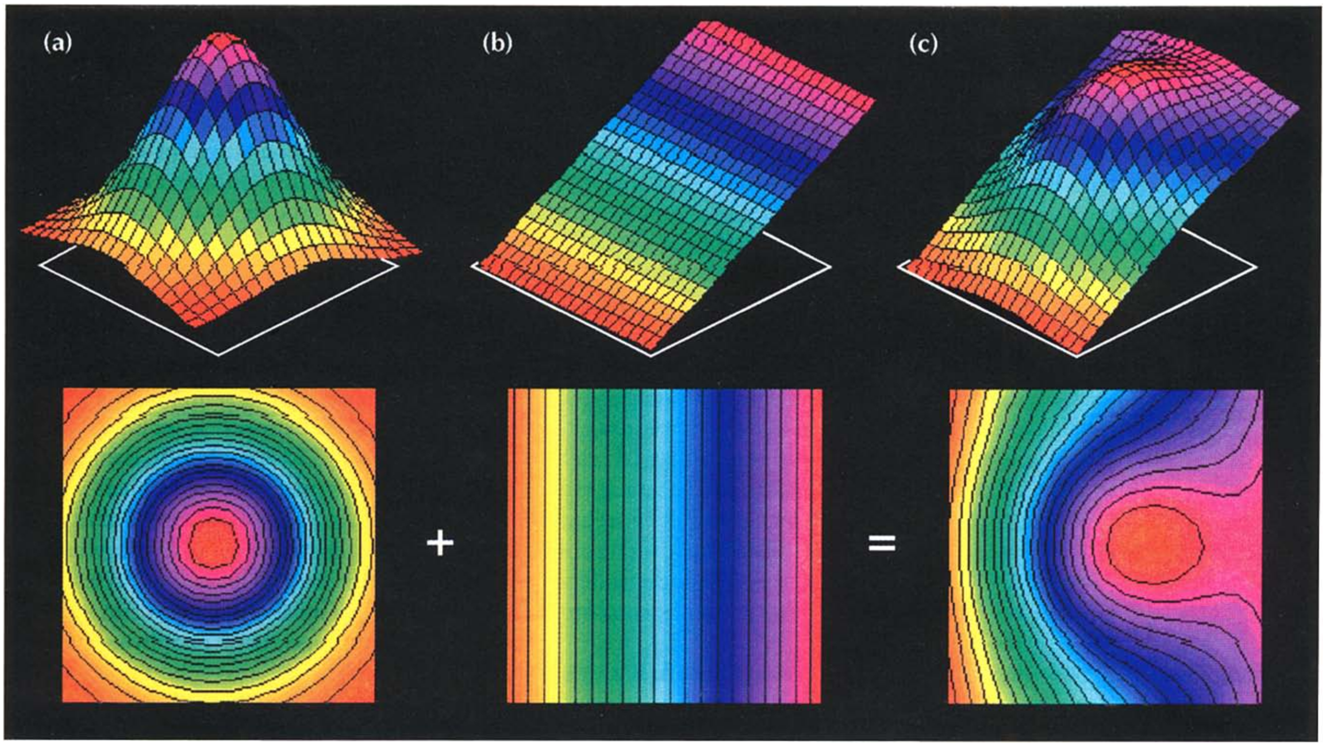

Fig. 1. With population coding, a single stimulus may result in a distributed hump of neuronal activity **(a)**, the peak of which represents the stimulus location. Adding a uniform gradient **(b)** to the field of neurons displaces the position of the peak **(c)**, and thus moves the apparent stimulus location.

cases, like the fovea, that acuity has much value. More often it is not the resolution of stimuli that we require, but their localization: a logically distinct function [3], and a matter simply of where the crest of the hump is. One can demonstrate this easily for the skin with a pair of dividers: one can always find a pair of locations such that the subject can tell at which of the two a single point is applied yet, paradoxically, cannot distinguish between both points being stimulated and only one.

In fact, the redundancy introduced by population coding brings several positive advantages. Pathways become less vulnerable to local damage, and central neurons can be more flexible in what they respond to. Within hours of amputation of a limb, or even immobilization in plaster, the body map in the somatosensory cortex starts rearranging itself to eliminate the useless area, by changing the relative strengths of the inputs the neurons receive from different sources; similar changes can be brought about simply by repeated novel stimulation [4,5]. These are relatively slow adaptational changes, but maps can also be shifted in a matter of milliseconds. One of the beauties of population coding is that all we need do to move the map is to apply an additional gradient across the whole map. This moves the crest, and therefore shifts the apparent location of the object (Fig. 1b,c).

Why would we want to move our maps? Simply because we ourselves move and change our viewpoint. The brain's job is to compute responses from stimuli, but unfortunately the bits of our bodies that detect stimuli do not have a fixed spatial relationship to the bits that do the responding. When we move our head or eyes to the right, we have to allow for this change of viewpoint when calculating what to do to reach out to touch a visual object that is now on the left but previously was straight ahead. A particularly clear-cut example of having to take change of viewpoint into account occurs in the control of saccades, the eye-movements that are made in order to look at a novel visual stimulus. These movements are exceptionally fast, and can be completed in as little as 20 or 30 milliseconds. During a saccade, the eye muscles are driven primarily by a burst of high-frequency firing that makes the muscles contract at a nearly constant velocity, and the duration of the burst determines where the eye ends up. One might think that the burst was simply turned off the moment the visual system discovers that the eye has reached the intended target, but it is easy to show that the delay in the loop from visual stimulus to brain and back to the muscles is far too long for direct feedback of this kind to be possible [6].

In fact, it appears that the saccade is controlled not by direct but by internal feedback, using a moving map. Knowing the commands being sent to the eye muscles, the oculomotor system can work out from this 'efference copy' and from past experience where the eye must be at every instant during the saccade. When it appears to have reached the target, the pulse is turned off and — if all is well — the eye does indeed come to rest on the target. Although the details are not entirely clear, it seems that this piece of virtual reality is played out, at least in part, in the superior colliculus, at the top of the brainstem [7]. Deeper layers of the colliculus embody a motor map of the visual world, of rather low acuity and enormous overlap [8], so that a single saccadic target generates a broad heap of activity similar in general terms to what is shown in Figure 1a. This map is basically retinotopic: that is, it represents objects according to where their images lie on the retina, with the fovea at the centre. When a novel target appears in the periphery, and the eye starts to make a saccade to look at it, the corresponding hump of activity appears to move across the colliculus in response to the efference copy until it reaches the centre, where it activates a set of inhibitory neurons that cut off the burst of activity in the motor neurons and bring the eye to a stop (Fig. 2).

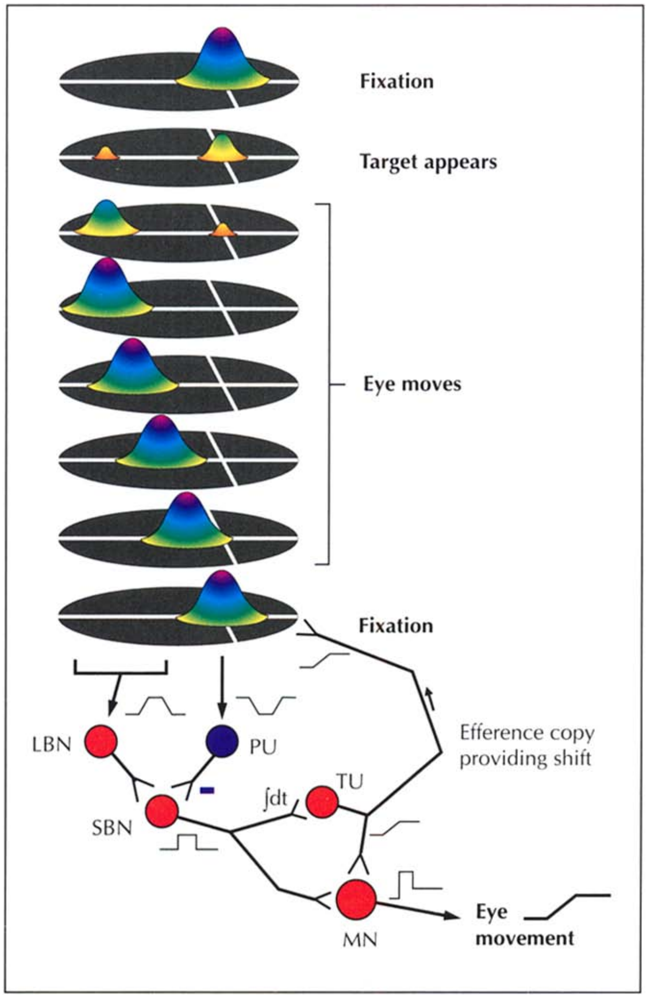

Fig. 2. Efference copy of the commands sent to eye muscles during a saccade may be used to shift a collicular map of target position relative to the eye. The collicular map is illustrated by the series of snapshots on the left; when, in this virtual arena, the target reaches the fovea, the command to the eye muscles is turned off by an inhibitory interneuron. LBN, long-lead burst neuron; SBN, short-lead burst neuron; PU, inhibitory pause unit; TU, tonic unit (whose activity reflects the position of the eye at any moment); MN, motor neuron. The small traces next to neurons indicate the approximate time courses of their activities; TU is driven by SBN indirectly via an integrator (∫dt). After Guitton [7].

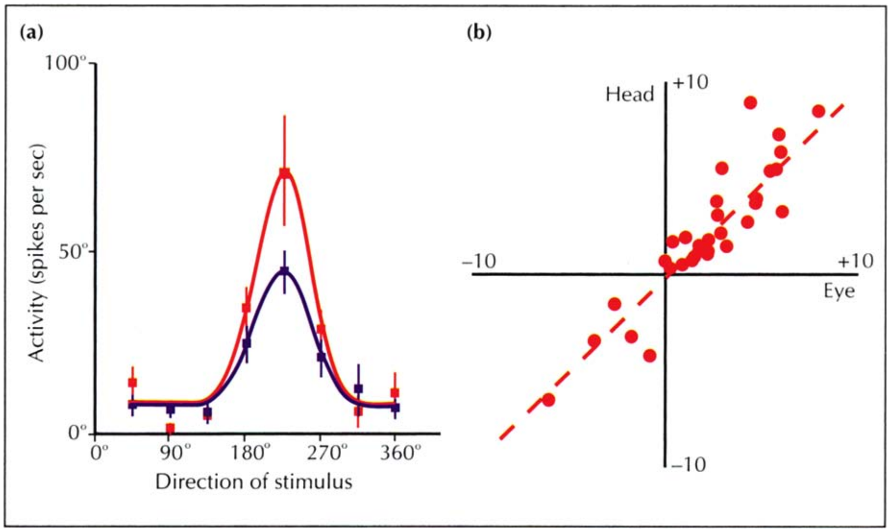

Fig. 3. Evidence for population coding in monkey parietal cortex. **(a)** Response of a typical neuron to targets presented in different directions, for two different head positions, 32° apart (red and blue). The neuron is broadly tuned to stimulus direction: on moving the head, its preferred direction does not change, but the overall activity is modulated by head position. **(b)** Saccade-related activity was measured in response to initial eye or head position, and for many cells it was essentially linearly related to both. This graph plots, for 31 separate cells, the slope of the corresponding regression lines for head and eye sensitivity, showing that on average they respond in the same way to both, in other words to total gaze deviation. Modified from Brotchie *et al.* [10].

Another brain region where the shifting of population-coded maps seems to occur is the posterior parietal cortex [9]. Peter Brotchie and his colleagues [10] have recently recorded from saccade-related neurons in this area, in alert monkeys trained to move their heads to align with pre-determined targets and to make saccades to look at visual stimuli. Now, the relation between head and body is very similar to that between eye and head — to work out where a visual target is in space (with the body fixed), we need to know the direction of the line of sight in space. This is technically known as gaze, and is defined as the sum of the deviation of the eye in the head and the deviation of the head itself with respect to the body. Clearly, gaze is something the brain must calculate if it is to respond correctly to targets under conditions in which the head is free to move as well as the eyes.

Brotchie *et al.* [10] have shown, first, that for a given head position many of these neurons do indeed have all the characteristics of population coding, responding not to a single target but to a broad sweep of the visual field (Fig. 3a). Then, by comparing the responses of the same cell to the same target (same, that is, in visual terms) with the head or eye at different deviations, they find modulation of the cells' responses, not shifting the peak sideways, but rather changing the scale of their activity. By looking at combinations of eye and head movement, they have also been able to show that the degree of modulation is, for most cells, essentially driven by gaze angle, thus taking into account the position of the eyes as well as the head (Fig. 3b). In other words, all the ingredients are present for generating the kind of shifting map shown diagrammatically in Figure 1, though the authors emphasize that there are many other cells in the region responding to a varying degree of visual, eye-position and head-position signals, forming something very like an adaptive neural network.

Once we have such an arena within which these dramas can be enacted in real time, we may of course also use it to rehearse before the event, to see whether the denouement is going to be to our liking, whether the play has a happy ending. It is clear that we can, for instance, do trial explorations in our heads. Sitting here at home feeling hungry, I can deduce that were I to take a left turn here, a right turn there, open the door and walk in I would find myself in my kitchen, which is where the glucostatic mechanisms of my hypothalamus and limbic system tell me that I want to be. Undoubtedly our brains embody such larger-scale maps of our environment — very likely in the hippocampus [11] — and they seem to be ultra-mobile, shifting not just in response to turns of the head and eye, but to gross translation of the body over an arbitrary extent. How do they do *that*?

References

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