Predicting perception from population codes

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Treue and colleagues use electrophysiological recordings in monkeys and psychophysical experiments in humans to suggest that the shape of a population response in a motion sensitive region of the brain (area MT), rather than the peak of the response, determines motion perception.

When neuroscientists can consistently predict what people perceive by studying their neural activity, we will have achieved a remarkable level of understanding of brain function. A notable advance toward this goal is presented by Treue, Hol and Rauber[1] in this issue of *Nature Neuroscience*. These authors have used the response profiles of neurons in a motion-sensitive area of the monkey brain, area MT, to predict how humans will perceive moving stimuli.

The brain encodes many kinds of sensory stimuli using maps of neurons that are tuned to the properties of those stimuli. How does the neural activity in these maps subserve perception and sensory-guided action? Because neurons are broadly tuned, a single stimulus typically activates a large population of neurons—the so-called population response. Several different theories have been proposed for how population responses in turn mediate perception and action. The most obvious possibilities are that perceptual outcome is determined either by the peak of the population response or by its center of gravity (also known as the vector average of the response).

When only one stimulus is present, the peak and the center of gravity of the population response are the same. But what happens when two stimuli with different features occur at the same place and time? Both stimuli influence the population response, but are they perceived as independent? Do they both contribute to behavioral responses? How do the two stimuli interact? If the peak of the population response is the most important feature, then both stimuli would be perceived so long as the two stimuli are sufficiently different from one another that the population response contains a separate peak

for each. In contrast, if the center of gravity is important, then the location and number of peaks should not matter. Under the latter mechanism, subjects would perceive a single stimulus intermediate between the two actual stimuli, regardless of whether the population response has two separate peaks of activity.

Visual motion processing is one domain where these issues have been explored fairly extensively. Motion perception is thought to rely on the population responses in visual area MT, which is specialized for processing moving stimuli and contains a columnar organization for motion direction (for review, see ref. 2). Because of this topographical organization, microstimulation can be used to activate a population of neurons with similar motion preferences, thereby simulating the response to real motion. Microstimulation in concert with an actual moving visual stimulus is presumed to cause a population response in MT that corresponds to two different directions of visual motion— the actual direction of motion of the visual stimulus and the preferred direction of the cells being stimulated electrically.

What do monkeys see when this happens? Salzman and colleagues trained monkeys to indicate the perceived direction of motion, and found that they alternated between reporting the real motion direction and the stimulation-induced motion direction, as if perhaps they could see both and were simply picking one of the two on each individual trial[3]. However, we trained monkeys to track the motion using eye movements, and found that the animals responded as if they saw only the vector average of the two directions[4]. Both of these experiments likely involved a population response composed of two peaks of activity: the neurons whose preferred direction of motion matched the visual stimulus and the neurons at the tip of the microstimulating electrode. Perceptual judgments were correlated with the locations of these peaks, whereas eye movements were correlated with the vector average of activity in MT.

Microstimulation is artificial, of course. What happens when real stimuli moving in two directions are presented? When two patches of moving dots are superimposed on each other (a situation
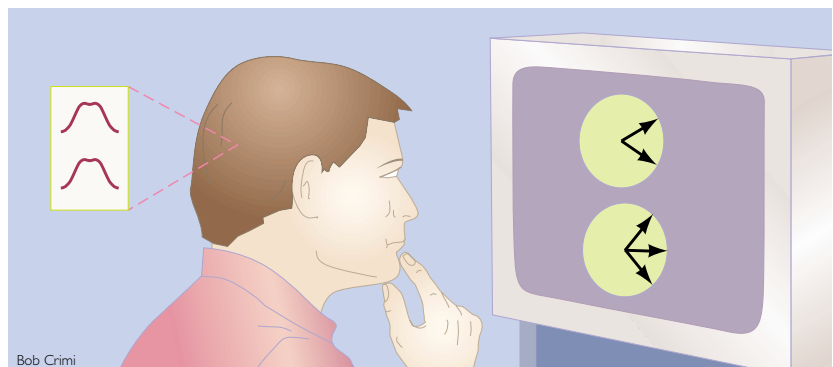
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Fig. 1. Electrophysiological recordings in visual area MT of rhesus monkeys by Treue and colleagues[1] suggest that the population response to a transparent motion stimulus with two components separated by ±40 degrees is probably the same as the population response to a transparent motion stimulus with three components (+50, 0, –50 degrees). Treue and colleagues predicted that human observers would therefore perceive the two stimuli as containing identical motion. This prediction was confirmed: human observers judged that both stimuli contained the same upward and rightward component, even though in one case this component had an angle of 40 degrees and in the other case it had an angle of 50 degrees.

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known as transparent motion), humans can perceive the two stimuli as distinct provided the directions of motion are separated by at least 10 degrees[5]. Clearly, the center of gravity could not subserve this percept—or else we would always perceive transparent motion as containing only one component of motion at a direction intermediate between the actual directions—but what about the peak(s) of the population response? Does the population response in MT contain separate peaks for each component of a transparent motion stimulus? Do these peaks merge together into one broad peak at the point where the two directions are too close to be resolved?

In an elegant series of experiments, Treue and colleagues[1] tested this hypothesis. Although the responses of MT neurons to both single and multiple stimuli have been well characterized (for review, see ref. 6), it is less clear how the population response varies as a function of the relative directions of the components of multiple stimuli. Treue and colleagues first studied the responses of monkey MT neurons to transparent motion stimuli. Their results show that because these neurons are broadly tuned for direction, the populations of neurons responding to each component of motion overlap quite extensively. For directions separated by less than about 90 degrees, only a single broad peak exists (although when the directions are farther apart, two separate peaks do appear). Importantly, this single peak occurs in monkey MT even when the directions are sufficiently different to be readily distinguishable to human observers (and presumably to the monkeys).

Thus, the relationship between neural activity and perception of the components of transparent motion does not seem to be based on the presence or absence of segregated peaks of activity, as would have been predicted by algorithms that identify peaks of activity (for example, winner-take-all). Rather, the transition from perception of two directions of transparent motion to perception of a single direction of motion must depend on some as-yet unidentified aspect of the shape of the population response in MT.

If the overall shape of the population response is critical to motion perception, then Treue and colleagues reasoned that stimuli that produce population responses having the same shape should produce the same percepts. Based on their recordings using two-component stimuli, Treue and colleagues designed three-component stimuli that should produce the same

population responses as certain two-component stimuli. For example, the population response to a transparent motion stimulus consisting of two components 80 degrees apart should be the same as the response to a motion stimulus with 3 components each 50 degrees apart (see Fig. 3 of ref. 1). If so, and if motion perception relies on this population of neurons, then the direction of motion of these two stimuli should be indistinguishable. They tested this hypothesis in human observers, and found it was indeed the case: these two very different motion stimuli appear perceptually to have the same components (**Fig. 1**).

A number of issues remain to be resolved. For example, do MT cells actually respond identically to the two- and three-component stimuli? Do the demands of the psychophysical task affect how MT represents motion information? Monkeys can certainly be trained to perform motion tasks like the one used by Treue and colleagues in humans, but there is reason to think that the task itself might influence population responses in MT. In particular, previous work by Treue and others has demonstrated that when an animal is attending to only one of two directions of motion, neurons in MT represent the attended direction much more strongly[7–9]. Thus, if MT neurons were studied while monkeys performed the psychophysical task used here in human observers, the presence and/or location of peaks in the population response might be different.

Perhaps the most intriguing aspect of this work is the notion that the shape of the population response in MT can be important for motion perception. There are well-defined algorithms for identifying peaks of activity (winner-take-all), or computing the center of gravity (for example, via vector averaging) to arrive at a perceptual judgment or behavioral response, and it is comparatively easy to imagine how neural circuits might perform these calculations (for example, see J.M. Groh, *Soc. Neurosci. Abstr.* **23**, 1560, 1997). Yet the findings of Treue and colleagues suggest that perception can be affected by details of the shape of the active population, details that are lost through either of these calculations. Therefore, we need to explore new algorithms for reading population codes.

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ChIPping away at potassium channel regulation

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Kv4 subunits form A-type potassium channels. To replicate native currents, these subunits require additional factors, now shown to be a family of calcium-binding proteins.

In a recent issue of *Nature*, Kenneth Rhodes and colleagues[1] present results that resolve long-standing questions

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concerning the molecular identity of A-type potassium channels. They describe the isolation and characterization of a family of calcium-binding proteins, the KChIPs (K+ channel interacting proteins; **Fig. 1**), that bind to the intracellular amino (N)-terminal domain of cloned Kv4 channels and endow them with many of the properties ascribed to native A-type potassium channels. Co-expression of the KChIPs and cloned