news and views

that bursting in cortex is often the only way to get signals across synapses, with single action potentials often failing to evoke significant postsynaptic responses. Thus two key features of bursts—the silent preceding period of 100 ms or so, and the short interspike intervals during the burst—combine to ensure that bursts produce a maximum postsynaptic signal over both depressing and facilitating synapses, which is a neat trick. This suggests, then, that thalamic bursts should always evoke maximum EPSPs in cortex, whereas tonic firing would evoke relatively weaker responses.

As impressive and important as the results of Swadlow and Gusev are, there are two minor caveats that should be kept in mind. First, they limited their cortical sample to one of several cell types receiving direct thalamic input—the so-called fast-spike GABAergic interneurons—and

only further empirical data can tell us whether this result extends to other thalamic target cell types. However, Swadlow and Gusev point out that the thalamocortical synapses onto spiny stellate cells of layer 4, which are the other main cell type there to receive thalamic afferents, also display suppression and therefore should respond more vigorously to burst than tonic mode. A different argument with the same conclusion was offered above, namely that bursts should always be better at activating cortex regardless of synaptic properties. Second, their data were based on spontaneous activity, and it would be interesting to see how the system behaves when the thalamic relay cells are actively excited by sensory stimulation. There is no reason based on cellular properties why sensory stimulation should cause any fundamental differences in the properties described by Swadlow

and Gusev, but there is some evidence that sensory stimulation can cause more burst firing (reviewed in ref. 3). On balance, these caveats do not change the basic message: Swadlow and Gusev have provided powerful evidence that bursting in thalamic relay cells is important in getting information into cortex in normal, behaving animals.

1. Jahnsen, H. & Llinás, R. *J. Physiol. (Lond.)* **349**, 205–226 (1984).
2. Steriade, M. *Neuroscience* **101**, 243–276 (2000).
3. Sherman, S. M. *Trends Neurosci.* **24**, 122–126 (2001).
4. Sherman, S. M. & Guillery, R. W. *Exploring the Thalamus* (Academic, San Diego, 2001).
5. Swadlow, H. A. & Gusev, A. G. *Nat. Neurosci.* **4**, 402–408 (2001).
6. Castro-Alamancos, M. A. & Connors, B. W. *Prog. Neurobiol.* **51**, 581–606 (1997).
7. Lisman, J. E. *Trends Neurosci.* **20**, 38–43 (1997).

MT signals: better with time

David Bradley

A new study shows the evolution of a computation in cortical area MT. Neurons that calculate visual motion go from fast approximation to a slower, more accurate solution.

Because our visual system is so effective, we do not generally think about the computational challenges it must face. Vision is simple to us; we take it for granted. This is not unlike the way we used to think of our parents. We simply failed to appreciate the complexity of things they had to deal with.

So it is with the aperture problem, a computational 'subtlety' that must be handled before movement in the visual field can be accurately perceived. Any seeing animal that cannot solve the aperture problem is liable to find it difficult to survive, so critical is the ability to detect and analyze visual motion. Motion represents action, and for predators and prey alike, this places its importance above color, shape and perhaps any other kind of information in a visual scene. Thus, a recent study in *Nature*[1] that shows a neural solution to the aperture problem actually unfolding is especially exciting.

The aperture problem is easy to see,

harder to understand, and very difficult to solve. To see it, cut a hole in a piece of cardboard and put a piece of paper behind it so that the paper edge is visible in the aperture (the hole) and tilted (**Fig. 1a**). Now slide the paper directly to the right. The edge visible through the aperture does not appear to move right. Indeed, its movement appears to be perpendicular to its orientation. This is the aperture problem: edges seen through small apertures always seem to go in a direction perpendicular to their orientation.

To understand why this is a problem, consider that in primates, motion is first calculated by neurons in primary visual cortex (V1), whose receptive fields—which are just apertures—are tiny, usually less than the size of a dime seen at arm's length. If an object moves to the right, and a particular V1 neuron sees a vertically oriented edge, then it will correctly compute the object's direction. But many neurons, unfortunately, will get the wrong answer; they will respond as if the object were moving perpendicular to whatever orientation appears in their receptive field (**Fig. 4a**).

Any vector can be decomposed into

orthogonal components. Thus, the (red) vector representing the paper's rightward movement in Fig. 1a can be replaced with two vectors, orthogonal to each other, with one of the two new vectors parallel to the edge (**Fig. 1b**). Now imagine that the paper is actually moving parallel to that edge, sliding down and to the right. We would not see any movement, because there is no contrast along this edge, no texture. Therefore, returning to the situation where the paper is moving directly rightward, the component of motion parallel to the edge is invisible to us, so all we see is the component perpendicular to the edge.

This ambiguity disappears if there is a feature visible in the aperture—a line terminator, for example, or a T junction—because then the vector parallel to the edge becomes visible (because the feature creates contrast along that dimension). So the obvious solution would be to use larger apertures. But in doing this, the visual
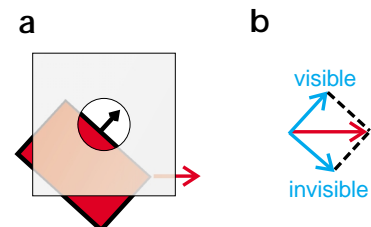

Fig. 1. The aperture problem. (**a**) Edges always appear to move perpendicularly to themselves when seen through an aperture. (**b**) The problem arises because the vector component parallel to the edge is invisible.

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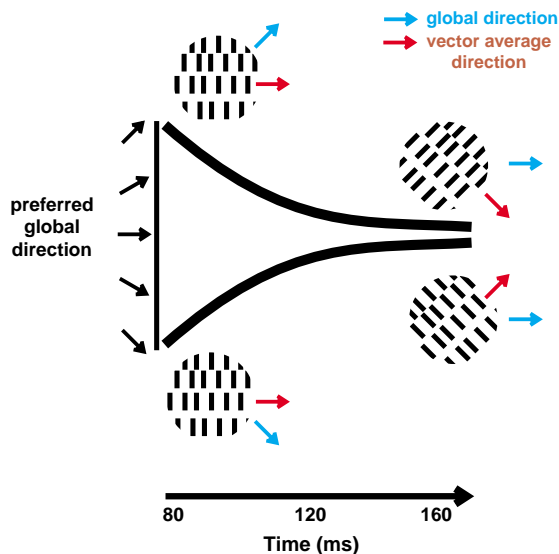*e-mail: dave@ccp.uchicago.edu*

Fig. 2. Schematic of the Pack and Born result. An MT neuron tuned for rightward motion is presumed to be responding to two different stimuli. The stimuli differ only in terms of the angle between the overall direction and the orientation of the line segments. At first, the neuron only senses the vector average, given mainly by the edge orthogonals (red arrow); thus, it prefers a different overall direction (blue arrows) for the two stimuli. Later, the neuron senses the true pattern direction and seems to ignore the edge orthogonals. A residual bias toward the vector average remains, however.

system would forego the ability to track motion at a fine scale. Alternatively, it is possible to compute the exact direction and speed of an object by combining several local motion samples, each ambiguous because of the aperture effect, but collectively specifying the object's velocity uniquely. The mathematical basis for this is essentially because two samples are needed to solve for two unknowns, the direction and speed of the object (Math Box). Note that the term velocity implies direction and speed, not just speed.

Even though it is theoretically possible to find an object's exact velocity, there has been controversy about whether or not humans actually do this. In some experiments, humans seem to only approximate object velocity by taking the vector average of local (aperture) velocity samples[2]. That is, the direction and speed they perceive correspond to the vector average, even when it differs from the real velocity of the object. But in other cases humans do better, accurately perceiving object velocity even when it differs substantially from the vector average[3]. These findings need not be contradictory, however, if we assume that the brain has more than one strategy. Given the diversity of images the visual system is likely to encounter, this seems like a good idea anyway.

Experiments by Pack and Born support this idea, showing that certain corti-

cal neurons are able to switch between two strategies in a very short time[1]. The authors trained rhesus monkeys to hold their eyes still while moving images were shown on a screen. The images were made of oriented line segments (**Fig. 2**), and they have the special property that their vector average direction can be very different from their global (overall) direction. This is because most local velocity samples that make up the vector average appear to point in the direction perpendicular to the lines (as in **Fig. 4a**), even though the overall stimulus may be moving in a different direction.

The authors simultaneously recorded the activity of area MT neurons, which derive input from V1 and have a central role in computing object direction[4,5]. Each of these neurons tends to prefer (respond preferentially to) a certain direction, which leads to an interesting question: which direction? Because each stimulus can have two different directions—the global direction and the vector average direction—the authors did not know beforehand how MT neurons would respond to the stimulus.

The answer was remarkable. At first, the neurons computed the vector average, which is determined mainly by the orientation of the lines. But then, after about 60 ms, the neurons switched to computing the global direction (**Fig. 2**). An MT

neuron, responding to two different stimuli (top versus bottom trace), seems to prefer a different overall direction for the two stimuli if one examines its behavior 80 ms after stimulus onset. What is consistent, however, is that the neuron responds best when the vector average of either stimulus points to the right. But at ~140 ms, the neuron responds roughly the same way to the two stimuli when their global directions are the same; in this case, their vector average directions do not seem to matter. This implies that initially, the neuron senses the vector average; then, presumably when new information arrives, this sense is refined to reflect the global direction.

That a vector average is computed before the more accurate global solution is intriguing. But is it really a meaningful event to the brain? Possibly the neural activity ephemerally associated with the stimulus's vector average is simply ignored while awaiting more reliable information (much as vote counts should be ignored until an election is complete). Earlier psychophysical studies showed, however, that the perceived direction of similar stimuli shifts, on a similar time scale, away from the vector average and toward the correct object direction[3,6]. Also, the Pack and Born monkeys themselves showed behavior that evolved in this way. The monkeys were trained to look at and follow a moving line segment, similar to the segments making up the stimuli discussed above; thus, the vector average of each segment was different from its actual velocity. Each time the monkeys tracked the target, their eyes were initially, briefly drawn toward the vector average; only after this did they track the target accurately. This is consistent with the idea that the monkeys perceived the vector average before the more accurate global velocity.
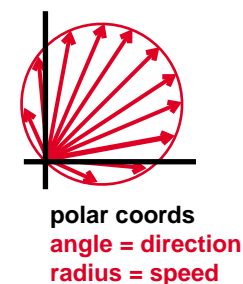

Fig. 3. Any velocity sample from a rigid moving object has to obey the the cosinusoidal relationship between speed and direction defined by that object's motion. This relationship is circular in polar space.
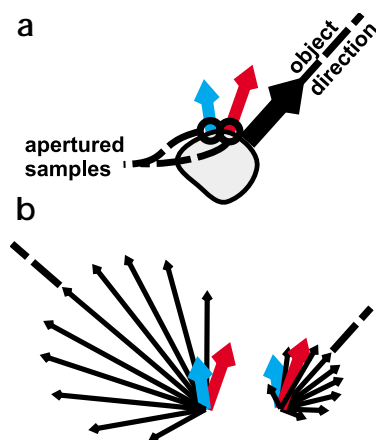
Fig. 4. The intersection of constraints principle. (**a**) Two local velocity samples being taken at the edge of a moving object. Neither of the sampled vectors points in the direction of the object. (**b**) How the object velocity (direction and speed) can be deduced. One simply finds the (unique) cosinusoidal distribution that is consistent with the two sampled vectors (right). The primate visual system may perform an analogous computation; we currently do not know.

MATH BOX

Assume a rigid, non-rotating object moving in a certain direction and at a certain speed. If one samples the velocity of an edge through any local aperture (**Fig. 2a**), the direction appears perpendicular to that edge, and the sample's magnitude (speed) is

*sample speed = object speed × **cos** (sample direction − object direction).*

Therefore, the more the sampled direction differs from the object direction, the smaller its apparent speed. The two unknowns in the equation are object direction and speed. With two vector samples, one generates two equations and can thus solve for these unknowns, at least in theory. In reality, more samples would be needed because of random measurement error.

The Pack and Born experiment clearly shows that MT neurons do something to overcome the aperture problem; in a way, that is, that goes beyond merely approximating the solution with a vector average. The importance of this finding will be to stimulate future theoretical and experimental work on the mechanisms by which this tricky computation is done. Luckily, the debate is well under way, and theorists in particular have laid mathematical foundations that let us now ask specific questions. According to one theory, the visual system exploits a mathematical principle known as the intersection of constraints (IOC), which states that for a rigid, non-rotating moving object, all local velocity samples have a cosinusoidal relationship between their direction and speed, and the phase angle and magnitude of this relationship are set by the object's direction and speed, respectively (Math Box). The relationship looks circular in polar coordinates (**Fig. 3**). The diameter of the circle is the object's speed, and the farthest point from the origin gives the object's direction. Any

local velocity sample that fits within this circular distribution is consistent with the linear motion of that object.

Now picture two local velocity samples from a rigid moving object (**Fig. 4a**, red and blue arrows) and consider the two cosine distributions in Fig. 2b, each representing a different object velocity. The two velocity samples are only compatible with the distribution on the right. Once the distribution is known, the object speed and direction are known, as explained above. Of course, because of noise, more than two samples are needed, but the principle is the same.

There is also a fundamentally different way to compute object direction. The aperture problem is based on the orientation of edges, which individually tend to be misleading. But when nearby edges have different orientations, this can create higher-order features that track more reliably with object direction[7]. Wilson and colleagues exploited this idea in their computational model[8], which combines one pathway for edge motion with another, slower pathway for higher-order features. That model, in addition to predicting a time course that would shift from the vector average toward the true object direction (as the feature pathway catches up), also predicted a persistent residual bias toward perception of the vector average direction. Pack and Born indeed found a similar bias (**Fig. 2**). Note that although these successful predictions lend credence to the two-pathway model, they do not necessarily argue against the IOC model discussed above, which until now simply has not yielded very specific predictions along these lines.

More studies are needed to hone in on the mechanisms that give MT neurons their special intelligence. It is important to distinguish between the IOC and feature-tracking mechanisms described above, or measure their relative contributions, as this will give hints about the basic kinds of computational strategy used in the brain. A key question, also, is how MT response properties depend on input connections, lateral connections (with other MT neurons) and feedback connections from higher cortical areas. Finally, we need to understand the extent to which MT response properties derive from the identity of their synaptic inputs, and to what extent they depend on the biophysical mechanisms that integrate and transform these inputs. Thus, the Pack and Born study answers an important question but leaves us with many new ones— and that is the exciting part.

1. Pack, C. C. & Born, R. T. *Nature* **409**, 1040–1042 (2001).

2. Rubin, N. & Hochstein, S. *Vision Res.* **33**, 1385–1396 (1993).

3. Yo, C. & Wilson, H. R. *Vision Res.* **32**, 135–147 (1992).

4. Dursteler, M. R., Wurtz, R. H. & Newsome, W. T. *J. Neurophysiol.* **57**, 1262–1287 (1987).

5. Newsome, W. T., Britten, K. H. & Movshon, J. A. *Nature* **341**, 52–54 (1989).

6. Lorenceau, J., Shiffrar, M., Wells, N. & Castet, E. *Vision Res.* **33**, 1207–1217 (1993).

7. Chubb, C. & Sperling, G. *J. Opt. Soc. Am. A* **5**, 1986–2007 (1988).

8. Wilson, H. R., Ferrera, V. P. & Yo, C. *Vis. Neurosci.* **9**, 79–97 (1992).

9. Heeger, D. J., Simoncelli, E. P. & Movshon, J. A. *Proc. Natl. Acad. Sci. USA* **93**, 623–627 (1996).