The Integrative Action of the Visual System

Everything that the visual brain can know about the visual world is represented on about 2 million more-or-less discrete channels—the fibers of the optic nerves. Each one of these channels contains a limited amount of information about a very tiny part of the visual field, defined as the receptive field (RF) of a single retinal ganglion cell. While the fine grain of the representation is essential for high acuity vision, the discrete nature of the subunits poses a formidable problem for the rest of the visual system. How are the parts of the image that belong together integrated into coherent representations of *objects*, which are, after all, what matters in the world? In this lecture, we will consider an example of this problem as it pertains to visual *motion* processing and look at neural and behavioral correlates of the solution.

The Aperture Problem

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A more concrete way of thinking about the limited RFs of retinal ganglion cells is as “apertures,” depicted as circles in the illustration above. Importantly, these apertures create local motion signals that are frequently *ambiguous*. For example, if a vertical bar moves upwards and to the right, a neuron with a small RF positioned along the contour (C) can measure only the rightward component of motion. This measurement is ambiguous, because it is consistent with many possible directions of actual bar motion. Only neurons whose RFs are positioned over the bar’s terminators (T) can measure the direction of object motion accurately.

Neural Correlates

A particular region of the primate cortex, known as the "middle temporal area" or "MT," is particularly concerned with the analysis of visual motion. This has been shown in a number of ways, including the direct manipulation of a monkey's judgments concerning the direction of a moving stimulus by activating columns of neurons within MT. For our purposes, the most important basic feature of the response properties of MT neurons is that they are direction selective. That is, they fire much more vigorously to some directions of motion than to others.

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The cell shown in the illustration above, for example, responded well to stimuli moving downwards (270°, termed its "preferred" direction), but was silent to stimuli moving upwards (in fact, this neuron was suppressed below its spontaneous rate of firing by so-called "null" direction motion). Different MT neurons have different preferred directions, and neurons having similar preferred directions are clustered together into columns.

MT neurons receive the preponderance of their inputs from neurons in striate cortex (a.k.a. "V1" or "Area 17") but pool them over a considerable region. Thus an MT neuron whose RF *center* was located 10° degrees from the fovea might have a RF *diameter* of about 8°. The V1 RFs at a similar eccentricity would cover only a fraction of a degree, hence it requires on the order of hundreds of V1 neurons, whose RFs perfectly "tile" the visual field, to account for the larger

RFs found in MT. (The actual number of inputs is on the order of thousands, not hundreds.)

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This fact gives us the opportunity to ask whether, and, if so, how MT neurons might solve the aperture problem posed above. To do this, we measured the responses of MT neurons to bars that were oriented either perpendicular to their direction of motion (control) or *tilted* with respect to their direction of motion, as in figure 1 above. We found that the *earliest* directional signals in these neurons were heavily biased by the orientation of the bars. That is, they responded as if they saw predominantly the component of motion *perpendicular* to the contour. Thus the best stimulus for each condition is that for which this perpendicular component is moving down and left (indicated by the asterisks in the figure below). Another way of thinking about this early response is that the neuron's determination of direction is transiently "fooled" by the orientation of the bar.

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That this confusion is only transient is proven by the figure below, which shows the later responses from the same MT neuron. These later responses (> 150 ms) represent the true direction of stimulus motion regardless of its orientation. That is, the tuning curves for the three different relative orientations of bars collapse to a single, consistent representation.

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Thus these neurons are able to integrate terminator information and solve the aperture problem, but *it takes time*. We can watch the neurons in MT solve this problem by plotting over time the directional preferences of the neurons to tilted bars with respect to those of perpendicular bars. When we do this for bars of a particular length (in this case 3°) we see that a small population of MT neurons (about 60) converges to an orientation invariant representation of the direction of motion over the course of about 80 ms. If the bars are made longer or shorter, the convergence requires more or less time, as one might predict from the relative proportions of contour and terminator signal.

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Towards a Mechanism

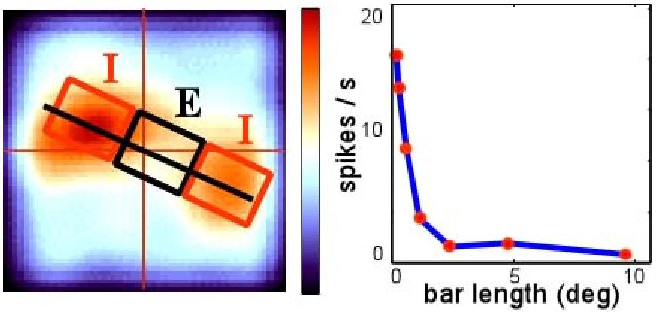
Given a robust neural correlate of the solution to the aperture problem, we can begin to ask questions about its mechanism. This is difficult in the CNS, since there are so many different connections, which translate into different routes by which information might be integrated. But we can start by categorizing them into those that are "feedforward" or "bottom-up" versus those that involve "feedback" from higher cortical visual areas (also called "top-down").

We already have two hints that the solution of the aperture problem may involve feedback. The first is that the process is relatively slow—certainly long enough for signals to have been processed by higher visual areas. A second hint comes from experiments in which the same kinds of MT neurons were recorded from monkeys that were *anesthetized*. It seems counter-intuitive, but MT neurons respond every bit as vigorously and are as directionally selective in anesthetized monkeys as they are in alert monkeys. This may be because MT is still relatively close to the retinal inputs (as few as six synapses from the photoreceptors). But as shown below, the MT neurons ability to solve the aperture problem is abolished by general anesthesia.

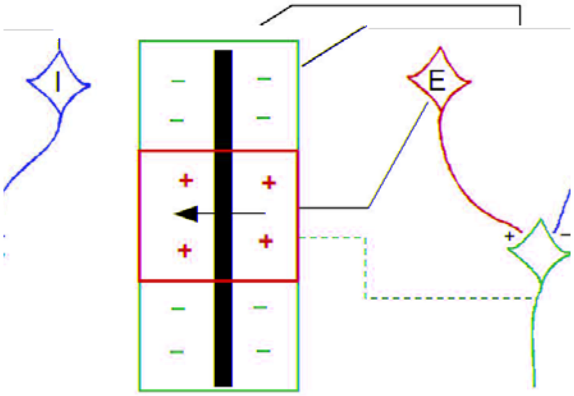
This is not compelling evidence for a role of feedback, but is enough to motivate us to undertake more difficult, but potentially more decisive, experiments. These will involve reversibly inactivating higher motion processing areas, such as MST and LIP, which are known to both receive inputs from MT and to project back to MT, and then asking what happens to the MT responses.

A Bottom-up Solution: End-stopping

One of the early discoveries of Hubel and Wiesel points to another possible way to solve the aperture problem. It's disarming in its simplicity and therefore rather counterintuitive: ignore contours and only pay attention to 2-dimensional discontinuities such as corner or line endings. The motion of such features is unambiguous.

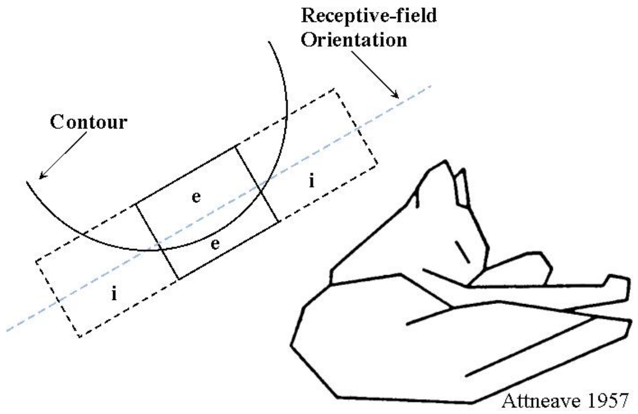


The receptive field of a visual neuron that does exactly this is shown in the figure above. The feature that allows the cell to ignore extended contours is called "end-stopping," and it is accomplished through a kind of lateral inhibition akin to that found in retinal ganglion cells and at many stages thereafter. This circuit, shown below, was first proposed by Hubel and Wiesel in 1965.



We were able to find a sizeable population of V1 neurons that were not only end-stopped, but direction selective as well. We further found that these neurons gave very reliable signals about the direction of motion of "terminators" (corners or ends of lines). Interestingly, some additional properties of end-stopping—such as the fact that it takes time to evolve and is greatly reduced for dim stimuli—explain certain peculiarities of motion perception. I will show you demonstrations of some of these in class.

It turns out that end-stopping is an extremely useful computation that probably subserves a number of important visual functions beyond solving the aperture problem for visual motion. It also appears to provide a partial solution to the problem of efficiently representing complex shapes and to the correspondence problem in stereopsis. Not bad for one small (but "essential") non-linearity! We believe it to be part of a general information processing strategy often referred to as "de-correlation" or "sparse coding."



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Conclusions

In this brief tour, we've seen an example of the nature of the problems that the cortex must solve. The example concerned visual motion processing, but it should be clear that the general nature of the problem applies across different visual modalities (such as shape and color), across different sensory modalities, and even into the realm of cognition. Thus we hope that by tackling this relatively humble example of integration in a system about which much is known (vision!), we will gain insights into the nature of the circuitry that underlies our mental life.

Further Readings . . .

. . . on the foundations of visual physiology:

Hubel, D. H. (1988) *Eye, Brain, and Vision*. New York, NY: Scientific American Library.

. . . on MT and motion integration:

Born, R. T. and D. C. Bradley (2005) Structure and function of visual area MT. *Annu. Rev. Neurosci.* **28**:157-89.

Pack, C. C., and R. T. Born (2001) Temporal dynamics of a neural solution to the aperture problem in visual area MT of macaque brain. *Nature* **409**:1040-2.

Pack, C. C., Livingstone, M. S., Duffy, K. R. and Born, R. T. (2003) End-stopping and the aperture problem: Two-dimensional motion signals in macaque V1. *Neuron*, **39**:671-680.

Pack, C. C., Gartland, A. J., and R. T. Born (2004) Integration of contour and terminator signals in visual area MT of alert macaque. *J. Neurosci.*, **24**:3268-3280.

. . . on cortical processing and perception:

Parker, A. J., and W. T. Newsome (1998) Sense and the single neuron: probing the physiology of perception. *Annu. Rev. Neurosci.* **21**:227-77.