Representing retinal image speed in visual cortex

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Speed preferences in MT neurons are found to be unaffected by changes in stimulus pattern, supporting the hypothesis that these neurons represent retinal image velocities.

When we move, or when objects in the world move, the visual images projected onto our retinae change accordingly. Over 50 years ago, the psychologist J.J. Gibson noted that important environmental information is embedded in local retinal image velocity (that is, both speed and direction), and thus began the investigation of the mechanisms by which such velocities might be estimated. Most physiological models of visual motion posit that neurons in area MT (a small extrastriate region of visual cortex) of the primate brain are velocity selective, responding most strongly to a visual stimulus moving in a preferred direction and with a preferred speed, and disregarding other stimulus attributes such as color and pattern. Many studies have confirmed the encoding of direction by these neurons. In this issue, Perrone and Thiele[1] present experimental data from neurons in area MT that confirm a prediction of these theories regarding the representation of speed.

Some neurons in the primary visual cortex (area V1) of primates are motion sensitive. Each of these neurons responds vigorously to a visual pattern with a preferred orientation moving in a preferred direction, but less so or not at all for patterns with the wrong orientation or in the opposite direction. These V1 neurons do not seem to provide the characteristics one expects in a velocity representation, however, because they

confound changes in stimulus pattern (such as orientation) with changes in stimulus velocity[2,3].

As an alternative, it has been proposed that MT neurons provide an unambiguous representation of velocity. These neurons receive their primary input from direction-selective cells in V1 (ref. 4). The vast majority of MT neurons, like their V1 afferents, are direction selective[5], but a substantial number of these neurons, unlike their V1 afferents, maintain their direction preference while largely ignoring changes in the stimulus pattern[3]. MT cells are also tuned for speed[5–7]. Until now, however, there was only unpublished evidence (W.T. Newsome, M.S. Gizzi and

J.A. Movshon, *Invest. Opthal. Vis. Sci. Suppl.* **24**, 106, 1983) for the invariance of MT speed preferences with respect to stimulus pattern.

Perrone and Thiele tested whether MT speed preferences are invariant to changes in stimulus pattern, by measuring responses to moving sinusoidal grating stimuli (adopting the experimental protocol of Newsome, Gizzi and Movshon, 1983). A moving sinusoidal grating may be characterized by its orientation, spatial frequency (in units of cycles per degree of visual angle) and temporal frequency (in units of Hertz or cycles per second). The grating speed is determined by its temporal frequency divided by its spatial frequency[8]. This relationship leads to a simple prediction regarding the responses of speed-tuned neurons to drifting gratings[9] (**Fig. 1**). A set of speed tuning curves for a hypothetical MT neuron (**Fig. 1a**) shows responses to gratings of different spatial frequencies. Changing the spatial frequency leads to a rescaling of the curve, but its shape and position are unaffected. That is, the neuron shows stable selectivity for stimulus speed, regardless of spatial frequency. Replotting the same data as a set of temporal frequency tuning curves (**Fig. 1b**) shows that the temporal frequency tuning is strongly affected by changes in spatial frequency.
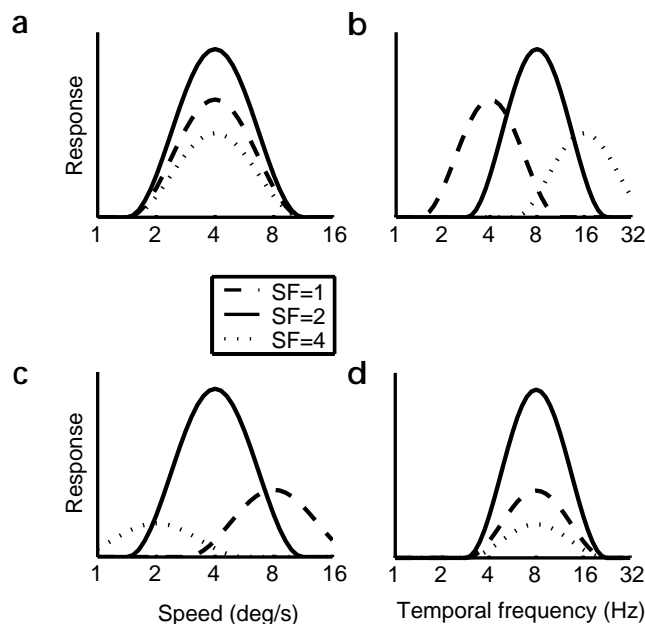
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Fig. 1. Speed tuning versus temporal-frequency tuning. (**a**) Speed tuning curves of a hypothetical MT neuron, measured with drifting sinusoidal gratings. (**b**) Temporal frequency tuning curves of the same MT neuron (replotted from **a**, using the relationship that grating speed is temporal frequency divided by spatial frequency). (**c**) Speed tuning curves of a hypothetical V1 neuron. (**d**) Temporal frequency tuning curves of the same V1 neuron.
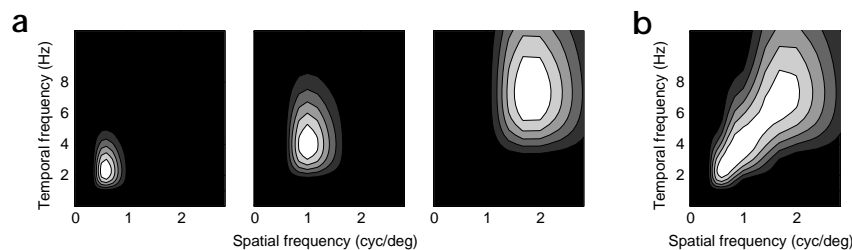
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Fig. 2. Construction of a speed-tuned MT neuron from V1 afferents[13]. (**a**) Spectral receptive fields for three hypothetical V1 neurons. (**b**) Spectral receptive field of a hypothetical speed-tuned MT neuron, constructed by summing the three V1 afferents (compare with Fig. 6 of Perrone and Thiele[1]).

This behavior may be contrasted with that of a typical V1 neuron that is tuned for temporal frequency[10,11], but not for speed (**Fig. 1c** and **d**).

Perrone and Thiele recorded MT responses to an array of spatial and temporal frequencies, and plotted the responses of each neuron as a surface like those in Fig. 2. The surface represents the full spatiotemporal frequency selectivity (dubbed the 'spectral receptive field' by the authors). They fit the resulting spectral receptive field of each neuron with an elliptical Gaussian function, and used the tilt of the best-fit Gaussian to classify the neuron as being selective for temporal frequency or for speed. The spectral receptive fields of V1 neurons are parallel to the spatial and temporal frequency axes[10,11] (**Fig. 2a**), but Perrone and Thiele report that for roughly 60% of their MT neurons, the spectral receptive fields were tilted along lines emanating from the origin (**Fig. 2b**). Thus, for these neurons, preferred speed was largely independent of spatial frequency. In addition, they demonstrated that the tilt of the best-fit Gaussian accurately predicted the preferred speed of each neuron, as measured directly with a moving bar.

Computational theories explain the emergence of velocity selectivity in MT neurons through a suitable combination of V1 afferents[2,3,6,9,12,13]. A simplified version of this construction is shown in Fig. 2, in which the spectral receptive field of a hypothetical MT neuron (**Fig. 2b**) was computed directly by summing those of three V1 neurons (**Fig. 2a**). The resulting MT neuron is tuned for a much broader range of spatial frequencies than its V1 afferents, and has a spectral receptive field that is tilted along a line emanating from the origin.

The experimental results of Perrone and Thiele provide a much-needed addition to the body of evidence supporting the hypothesis that MT neurons compute and represent local retinal image velocities. Although many previous authors had measured speed tuning in these neurons, those experiments did not rule out the possibility that the neurons were actually selective for temporal frequency (as are V1 neurons) instead of speed. The data reported by Perrone and Thiele, on the other hand, demonstrate that at least some MT neurons are selective for speed *per se*. A relatively minor criticism of their work is that the measured spectral receptive fields are not very well characterized by elliptical Gaussian functions. Instead of using Gaussian fits, the analysis could have been strengthened by using previously published non-parametric methods for evaluating whether the spectral receptive fields were parallel with the axes or tilted[14], and by relying more heavily on existing computational models of MT responses (cited above). It is unlikely that these alternate analyses would have changed the main conclusion that some MT neurons are speed-tuned, but it might, for example, have resulted in a larger proportion of neurons being classified as speed-tuned.

A more subtle but fundamental issue is that although a tilted spectral receptive field is sufficient to produce speed selectivity, it is not absolutely necessary. For example, if an MT neuron has a relatively narrow spatial frequency bandwidth, the tilt of its spectral receptive field would be difficult to measure. There is an alternative test that can provide more definitive evidence for velocity selectivity (E.P. Simoncelli, W.D. Bair, J.R. Cavanaugh & J.A. Movshon, *Invest. Opthalm. Vis. Sci. Suppl.* **37**, 1996)[15].

The construction of velocity selectivity in MT from V1 afferents (**Fig. 2**) is analogous to the construction of orientation selectivity in V1 from LGN afferents, as originally proposed by Hubel and Wiesel and elaborated by many subse-quent authors. Thus, even though the response properties of the neurons in these two cortical areas are very different, they seem to be based on a common canonical computation. The underlying cortical circuitry and biophysical mechanisms responsible for orientation selectivity in V1 are still hotly debated, but given the commonality of the computational principles that seem to apply in both V1 and MT, we may optimistically hope that the circuitry and biophysical mechanisms in these two (and perhaps other) cortical areas may also follow a canonical form.

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