

Representation of Movement

N S C Price and R T Born, Harvard Medical School, Boston, MA, USA

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Introduction

Motion sensitivity is a fundamental aspect of vision for most animals. While the most obvious use for representing motion is to determine if an object is moving, analysis of motion serves a number of other roles. Assessing movements in the environment is critical to track, avoid, or intercept objects that may be food, friends, or foes. Motion analysis can be used for trajectory prediction, including determining if a moving object can be intercepted and the time to contact with the object. It also enables the resolution of ambiguities in two-dimensional relationships between objects. For example, depth information can be recovered through motion parallax, while motion segmentation can be used for camouflage breaking as occurs when a hidden animal only becomes distinct from its surroundings when it moves.

Motion can also be self-generated by eye, head, or body movements. Analyzing self-motion helps calibrate proprioception and locomotion and can be used to stabilize the retinal image to prevent motion-induced blur. The significance of analyzing motion is highlighted by the large proportion of motion-sensitive neurons in all animals that have been studied to date and the finding that while many of these species are insensitive to other visual modalities, such as disparity or color, no species lack motion sensitivity.

The focus here is on the neural representation of visual motion in primates, drawing briefly on results from models and psychophysics. The assessment addresses how the representation of movement changes along a hierarchy of brain regions that all contain motion-sensitive neurons and how this neural encoding ultimately affects perception and behavior.

Fundamentals of Motion Detection

In order to detect motion in a given direction a scene must be sampled at a minimum of two points in space at two different times. For example, the motion sensor in [Figure 1\(a\)](#) is sensitive to motion to the right if the time taken to traverse the distance Δd between the two input channels matches the temporal delay Δt . In addition, there must be a nonlinear interaction between the inputs from the two channels to ensure that the time-averaged output of the detector is direction selective. Early studies of the retina suggested

that inhibition of responses to motion in the opposite direction to the preferred (the 'antipreferred,' or null, direction) is critical for generating physiological direction selectivity. This inhibition could either act linearly as subtraction or, more likely, nonlinearly as a shunting inhibition to suppress responses to motion in the antipreferred direction.

An early model incorporating the three basic requirements was Reichardt's cross-correlator, which was inspired by studies of the optomotor response of beetles ([Figure 1\(b\)](#)). The Reichardt detector is best stimulated by spatial wavelengths four times the separation of the input channels, since this leads to a 90° phase difference between the intensity variations at the two inputs (spatial quadrature). Further, for wavelengths less than twice the input channel separation the detector can suffer from spatial aliasing, as predicted by Shannon's sampling theorem. An important variant, the spatiotemporal energy model, incorporates simple linear spatial and temporal prefilters that reduce aliasing and help constrain the range of stimuli to which the detector responds ([Figure 1\(c\)](#)). This model highlights the idea that motion-sensitive neurons are filters tuned along a set of stimulus dimensions such as spatial and temporal frequency, rather than simply feature detectors, as suggested by the model in [Figure 1\(a\)](#).

With only two input channels, it is obvious that an 'apparent motion' stimulus, in which the stimulus appears at one location, and then the next, without physically moving between the two locations, could stimulate the detectors described in the preceding paragraphs as effectively as true, continuous motion. Similarly, motion sensors like the Reichardt detector can also falsely detect motion in random luminance flicker. These observations raise the obvious problem of determining whether the two input channels have been sequentially activated by one moving object or by two different objects – the so-called correspondence problem. A special form of this problem exists even for single objects that contain extended contours – as is the rule in natural scenes – due to the limited size of the sampling regions. The true direction of a moving edge viewed through a circular aperture cannot be resolved, a dilemma known as the 'aperture problem.' For example, in [Figure 2\(a\)](#), the edge could be moving slowly to the right, or more rapidly along a diagonal up and right, or down and right. Related to this is the issue of determining whether two adjacent local motion cues belong to one or two objects ([Figure 2\(b\)](#)). This problem is resolved if the vertex of an object is visible through an aperture, since it provides an unambiguous two-dimensional (2D) motion

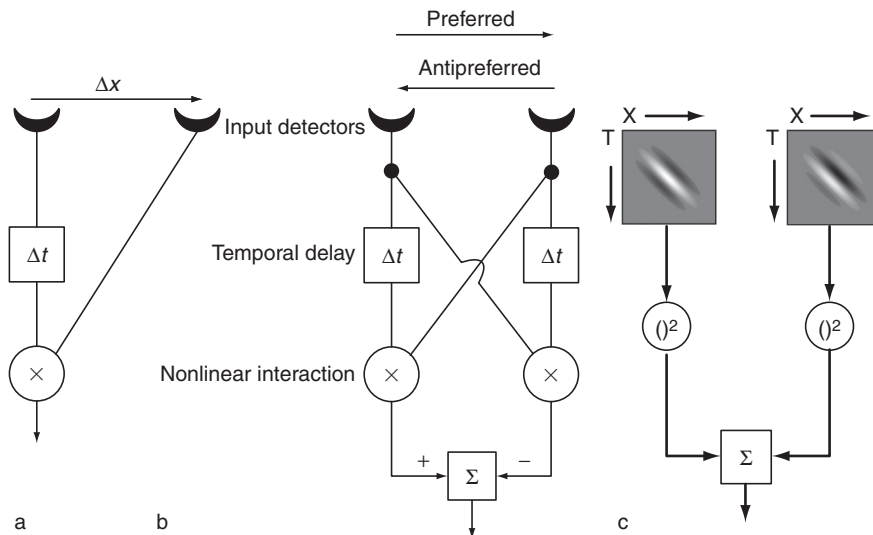


Figure 1 Models of motion detection. (a) An elementary motion detector that prefers motion to the right incorporates spatial separation of input channels (Δx), a temporal delay (Δt) in the left channel, and a nonlinear interaction between the input channels (in this case, multiplication, ' \times '). (b) In the Reichardt cross-correlator, the outputs of two elementary motion detectors preferring motion in opposite directions are subtracted. (c) The spatiotemporal energy model calculates motion energy by combining the squared outputs of two oriented space and time (X, T) filters that are in quadrature. The slant in the contour plots of the space–time filters indicates that they prefer motion to the right.

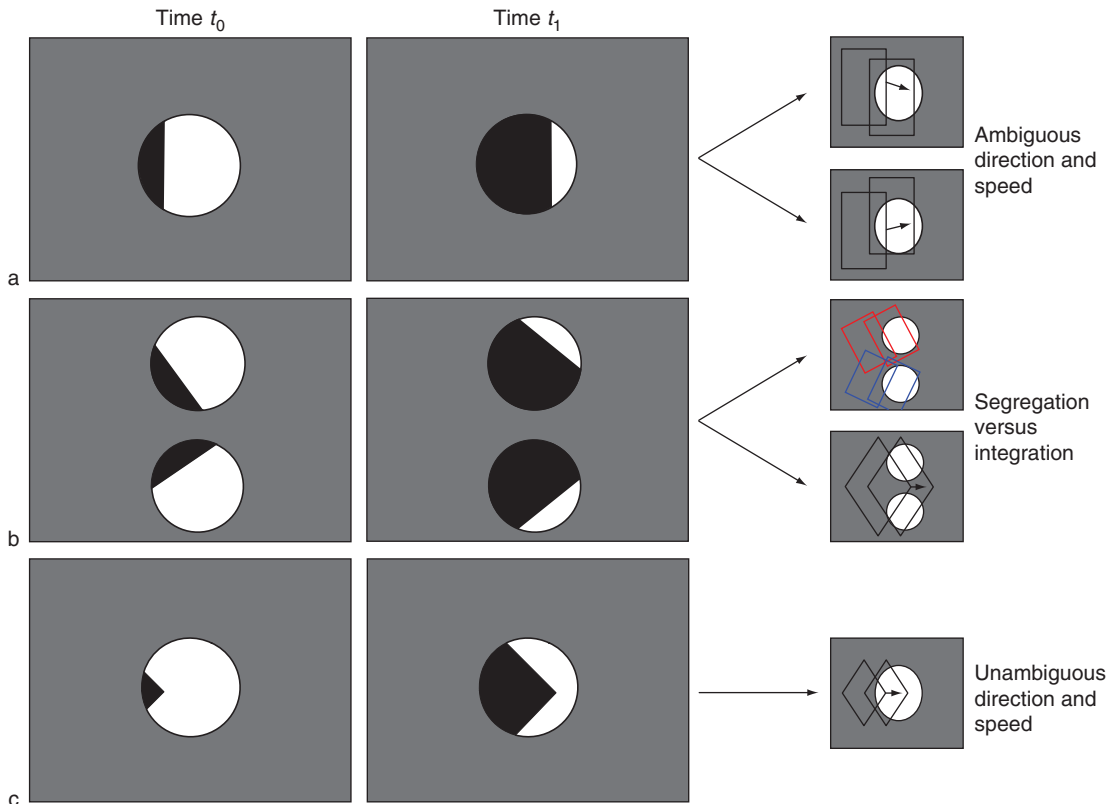


Figure 2 The aperture problem and motion segregation and integration. Each row shows the view through one or two apertures at two points in time and on the right, the possible object motions that could account for these views. (a) The direction and speed of a single moving edge are ambiguous, thus creating the aperture problem. (b) The motion of two edges viewed through two apertures can be segregated, meaning that they are treated as independent objects with ambiguous direction and speed, or integrated, resulting in an unambiguous percept. (c) An object vertex provides two-dimensional information and thus an unambiguous percept of speed and direction.

cue (Figure 2(c)). Thus segmentation (determining which local motion cues belong together and which do not) and integration (combining the cues that do belong together) are important, interdependent processes for determining what global movements are actually happening in the environment.

One reason for pooling the responses of local motion detectors is to create robust responses in the face of low signal-to-noise ratios. In this context, noise could arise from local motion detectors signaling directions contrary to the true global motion direction due to flicker or spatial aliasing. Alternatively, the strength or certainty of a motion signal may be weak because of low luminances or contrasts. Two primary methods exist for decreasing noise sensitivity: first, signals from many detectors can be averaged over a large spatial region or over an extended period of time; second, a detector can incorporate motion opponency, whereby preferred and antipreferred direction motions respectively excite and suppress the detector's response. Motion opponency is explicit in the Reichardt detector (Figure 2(c)) and serves to reduce the response to stationary flicker or simultaneous motion in the preferred and antipreferred directions.

Introducing noise to stimuli has been a powerful method for probing the neural basis of motion perception. Changing stimulus strength, or dot coherence (the proportion of dots that move in a single direction versus those that move in random directions), affects both the perception and neural response to motion. Thus variable coherence dot stimuli have allowed investigators to measure the relationship between a neuron's activity and the perception of motion. The results of such studies have provided the most compelling links between neural activity and perceptual decisions to date.

Psychophysics

A student of physics can explain that motion is represented by a velocity vector, consisting of a speed and a direction. Since speed represents the change in position over time, it is conceivable that the visual system is not explicitly sensitive to motion, *per se*, but generates motion sensitivity by judging changes in position over time. However, there is ample evidence demonstrating that position and motion are independently represented. The most compelling demonstration of this independence is the motion aftereffect (MAE; also known as the 'waterfall illusion'): after observing a moving pattern, a stationary pattern appears to move in the opposite direction. This produces a strong sense of motion without the perception that the pattern changes position over time. Akinetopsia (visual motion blindness) also demonstrates the

segregation of motion and position processing. In this condition, which can be caused by damage to the parieto-occipital cortex, moving objects do not appear to move smoothly and continuously but rather suddenly jump to a new location. Further, the condition is only associated with deficits in motion processing, without changes in acuity or localization abilities.

A number of fundamental psychophysical observations are critical for understanding the physiological work that will be described in subsequent sections. First, humans and primates are exquisitely sensitive at distinguishing the direction and, to a somewhat lesser degree, the speed of spatially or temporally adjacent motion stimuli. Intriguingly, the perceived speed of an object is dependent on many factors, including the contrast, size, and spatial frequency content of the stimulus, but also on how long the object has been viewed. The influence of viewing duration is also highlighted by the MAE, in which the percept of a stimulus depends on what had been viewed previously.

Psychophysical studies have shown that we can be 'fooled' by apparent motion. Thus a succession of short displacements is perceived as smooth motion, provided these displacements are less than 15–20 arc min. Watching television provides a clear demonstration of this: while objects appear to move smoothly across the screen, they are constrained spatially and temporally by the screen's pixels and refresh rate. In addition to short-range apparent motion, 'phi,' or long-range apparent motion, has been described, in which two flashes of light separated by much more than 20 arc min are interpreted as a single moving flash provided they have a suitable temporal separation. In addition, the long-range process can be distinguished from the short-range process by its sensitivity to shape and color, its failure to reverse directions for inverting contrast sequences (reverse phi), and its ability to integrate sequences across the two eyes (interocular transfer). These differences indicate the existence of multiple mechanisms in the visual system for detecting and analyzing motion.

The role of vision in guiding locomotion is evident fromvection – the visually induced illusion of self-motion. This may be experienced when looking through the window of a stationary vehicle at another nearby stationary vehicle. If the other vehicle moves forward, one can experience a vivid sensation of moving backward. This arises because motion of the entire visual scene is generally attributable to eye, head, or body movements and is typically interpreted as such. This suggests that there are specialized mechanisms for detecting and interpreting optic flow fields characteristic of those generated during self-motion. These same mechanisms are also important for controlling

eye movements that serve to keep the image stable on the retina during self-motion. In the absence of such mechanisms, image quality would be severely degraded due to motion blur.

Anatomy

The basic anatomical organization of the visual system has been described as a processing hierarchy with extensive feed-forward and feedback connections between discrete areas (Figure 3). Motion processing is strongly associated with the dorsal stream, and is relatively segregated from the ventral form pathway as early as the retina and lateral geniculate nucleus (LGN). In primates, motion information is primarily carried by the so-called magnocellular stream, beginning with parasol retinal ganglion cells in the retina,

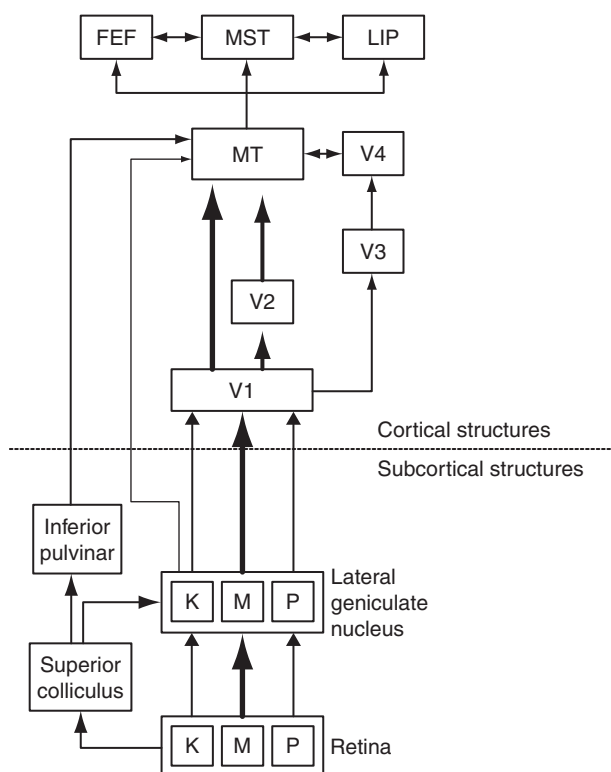


Figure 3 Major motion processing structures along the dorsal stream. Retinal information comprising koniocellular (K), magnocellular (M), and parvocellular (P) processing channels originates in subsets of retinal ganglion cells and is passed to the superior colliculus and lateral geniculate nucleus. The primary stream for motion information is via the M cells in the retina and lateral geniculate nucleus through V1, then directly to the middle temporal area (MT). An indirect cortical stream also exists via V2, and much weaker inputs to MT exist via the superior colliculus and inferior pulvinar and directly from the K cells in the lateral geniculate nucleus. Information is also shared between MT and V4, and also reaches higher-order areas such as the frontal eye field (FEF), middle superior temporal area (MST), and lateral intraparietal area (LIP).

which project to the more ventral, magnocellular layers of the LGN and subsequently to layers 4C α and 6 of primary visual cortex (V1 but also known as 'striate cortex' or area 17). Subsequently, information reaches the middle temporal area (MT) predominantly through direct projections from layers 4B and 6 in V1, but also via indirect inputs from the thick stripes of V2 as well as V3. MT can be considered a motion-processing gateway in the cortex: it is the earliest of the visual areas in the hierarchy to contain predominantly motion-sensitive neurons, and the majority of these neurons are highly direction selective.

MT passes information to a number of additional cortical areas, including the dorsal and lateral compartments of the middle superior temporal area (MST), where neurons are sensitive to wide-field optic flow generated by body movements (MSTd) and pursuit eye movements (MSTl). Both MT and MST project to a range of higher-order cortical areas such as area 7a, the lateral intraparietal area (LIP), and frontal eye fields (FEFs) to guide decision making and eye movements; and to subcortical structures such as the accessory optic system, pontine nuclei, superior colliculus, and pulvinar to guide eye movements such as pursuit and optokinetic nystagmus. Although all the cortical and subcortical regions are highly interconnected, we will focus mainly on the properties of neurons in the feed-forward cortical hierarchy of the early dorsal stream, from the retina to MST. This provides a useful method for describing how the representation of movement changes from the retinal input channels sampling the visual world to neural codes more closely associated with perception.

Direction Selectivity

As early as the retina, neurons are found that prefer motion in one direction over another. Retinas in the turtle and rabbit have been studied more extensively than have those of other species, with up to one-third of all retinal ganglion cells (RGCs) in the turtle estimated to be direction selective, with similar proportions of directionally biased amacrine and bipolar cells. However, despite their presence in most vertebrate species, the role and prevalence of direction-tuned retinal cells in the primate are not clear, probably because of the large expansion of the midget (parvocellular) system in primates compared to other species. Furthermore, it appears that virtually all direction-selective RGCs in the primate retina project to brain stem structures, such as the nuclei of the accessory optic system, where they are involved in reflexes for gaze stabilization.

Both the proportion of direction-tuned neurons and the strength of their direction tuning (how much they prefer motion in the preferred direction over other directions) increase in areas along the dorsal stream. The direction selectivity underlying primate motion perception first arises in V1, where 20–30% of all cells are directionally biased. These cells are mainly confined to output layers 4B and 6, tend to respond to a narrow range of orientations, and have high contrast sensitivity and relatively small receptive fields. In V2, only ~15% of neurons are highly direction selective; however, such cells are prominent in layers 3B and 4 of the thick stripes, which receive significant projections from layer 4B in V1 and which subsequently project to MT.

In area MT, nearly all neurons are highly selective for the direction of motion. In addition, many neurons also show inhibition by motion in the null direction, a property which may give rise to the MAE. Another important feature of MT is that direction-selective neurons are organized into a map, with neurons that are tuned to the same direction of motion grouped together in columns, and adjacent columns representing different directions of motion. At subsequent processing stages, such as MST, essentially all cells are motion sensitive, but many prefer more complex types of motion rather than simple translation. In MSTd, approximately half of the cells are sensitive to translation, but many are sensitive to rotation in the fronto-parallel plane, rotation in depth, or expansion or contraction. These optic flow patterns are consistent with those produced by locomotion and, indeed, many MSTd neurons receive extraretinal inputs associated with locomotion. In contrast, neurons in MSTl are sensitive to motion produced by objects moving against a background. This requires a center-surround receptive field organization (see the section titled, ‘Spatial aspects of receptive fields’).

Temporal Frequency and Speed Tuning

Early quantitative studies of the visual system treated neurons as filters tuned along multiple stimulus dimensions, such as direction or speed. The full spatiotemporal frequency tuning of neurons can be tested using sine wave grating stimuli with a range of spatial frequencies (SFs) and moved with a range of temporal frequencies (TFs). Grating speed is then given by $v = \text{TF}/\text{SF}$. A spatiotemporal frequency (STF) tuning plot can be generated from the responses to individual gratings (Figure 4). Simple cells in V1 are predominantly temporal frequency tuned, meaning that contours in their STF plots are oriented such that the TF giving the largest response is constant regardless of the grating's spatial frequency

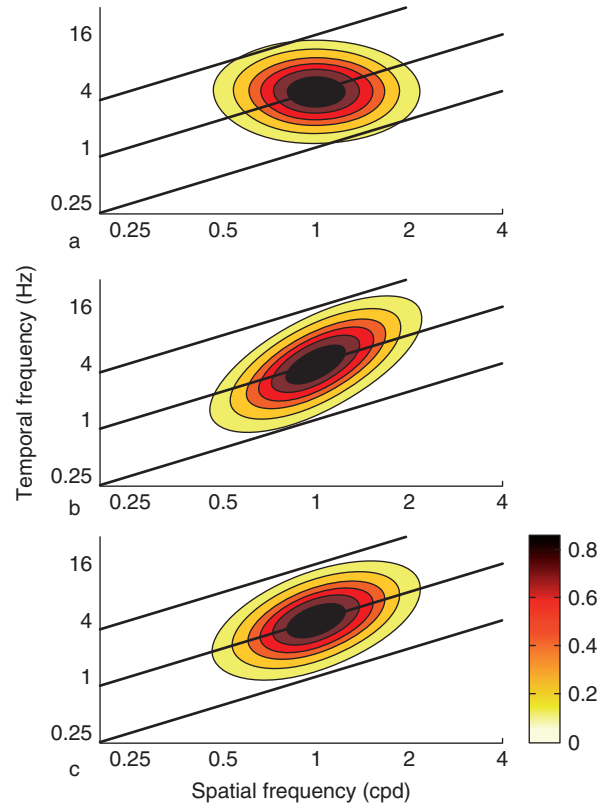


Figure 4 Spatiotemporal frequency (STF) tuning. STF plots are generated by plotting a neuron's mean spiking rate in response to moving gratings with a range of spatial and temporal frequencies. Temporal frequency (TF) tuning (a) implies that contours in the STF align along a single TF, regardless of the grating spatial frequency (SF). Speed tuning (c) implies that the STF contours align with an iso-speed line, such that the ratio of preferred TF to preferred SF is a constant. (b) STF plots can also show oriented STF contours that are indicative of neither TF nor speed tuning.

(Figure 4(a)). While one-fourth of V1 complex cells and MT cells also show temporal frequency tuning, a similar proportion show form-invariant speed tuning, meaning that contours in their STF plots are oriented along an iso-speed line (Figure 4(c)). The remaining half of V1 complex and MT cells show oriented STF plots that are not aligned with a constant TF or constant speed (Figure 4(b)). The major difference between complex cells and MT neurons is that MT neurons show nonlinear interactions when tested with stimuli containing multiple spatial frequencies. Thus speed-tuning bandwidths calculated using textured stimuli are smaller for MT neurons than for V1 complex cells, and these bandwidths are narrower than would be predicted based on linear predictions from the responses to single spatial frequencies.

Temporal frequency tuning and speed tuning confer different advantages. TF tuning allows a detector to reliably judge the motion of a given object, regardless of the viewing distance. Speed tuning allows a

detector to reliably judge the motion of an object, regardless of its form. Perceptually, speed judgments are strongly dependent on the nature of the stimulus, with stimuli having low SF perceived as moving faster than those with high SF. This effect is consistent with the observation of neurons with slanted STF plots that do not show true speed tuning.

Spatial Aspects of Receptive Fields

A neuron's motion sensitivity is dependent on the spatial structure of its receptive field – its size, shape, and subdomains. In V1, V2, and MT, receptive fields have a bias toward the central 5° of the visual field and tile the entire contralateral hemisphere; however, they do not extend more than 10–15° ipsilateral of the vertical meridian. In V1, foveal receptive field sizes are extremely small (<1° diameter) but increase with eccentricity. At a given eccentricity, receptive fields are approximately two to four times larger in V2 than in V1, and larger still in MT. This changes in MST, where the tiling of receptive fields (RFs) extends 20–40° into the ipsilateral field, and foveal RFs are 10–15° in diameter. Further, the relationship between eccentricity and RF size is much weaker in MST than in V1–MT.

Receptive field size limits the separation of a motion detector's inputs, thus affecting the neuron's spatial frequency tuning bandwidth and the maximum resolvable step size that can be detected as motion. However, this maximum step size does not systematically change along the cortical hierarchy. Thus, despite MT receptive fields being ~10 times larger than those in V1 at a given eccentricity, neurons in the two areas are sensitive to a similar range of step sizes, and these step sizes match those that have been determined psychophysically. This suggests that MT does not calculate direction selectivity *de novo*, but elaborates on the motion analysis performed by output neurons from V1. Perceptually, long-range apparent motion can be perceived for displacements larger than those that stimulate V1 and MT neurons. Although not explored physiologically, this may be achieved through the attentive tracking of stimulus features that change position over time. However, the perception of long-range apparent motion suggests that motion processing may occur independently of V1 and MT at higher cortical levels than those studied so far.

From the level of the retina to MST, neurons display 'extraclassical' receptive fields or modulatory surrounds. For example, MT neurons respond well to motion in their preferred direction presented only in a small region at the center of their receptive fields. If the stimulus is enlarged to cover a suppressive

surround, the neuron ceases to respond to the motion. This type of center-surround opponency for motion is likely to contribute to the extraction of local motion contrast that is created when objects move against a textured background or during pursuit eye movements, which produce a stationary object on the fovea surrounded by background motion in the direction opposite the eye movement. Center-surround receptive fields can also help assign border ownership and may contribute to motion segmentation, by determining if local motion cues belong to the same or different objects.

The opposite problem, motion integration, requires combining multiple local motion signals to determine the true direction of a larger object. The aperture problem described previously (see the section titled 'Psychophysics') provides a good demonstration of this: only by assuming that two different local motions belong to the same object can the information be combined to decode the correct direction of the object (Figure 2(b)). It is currently unclear by what mechanisms the visual system solves this problem. Some models propose that the visual system first extracts only the local one-dimensional (1D) motion perpendicular to the orientation of moving edges. Subsequently, this local motion information is nonlinearly combined using an 'intersection of constraints' calculation. Indeed, there is psychophysical and physiological evidence for the existence of orientation-selective filtering at early stages of motion processing followed by pattern-sensitive neurons in MT that can signal motion directions that are not orthogonal to an object's orientation. Many of these results have come from studies employing plaid stimuli, which contain two overlapping gratings with different orientations. Under some circumstances, the stimulus appears to move coherently, so that the perceived direction of motion is not orthogonal to the orientation information present in the pattern.

However, recent studies have also suggested that an alternative strategy may be employed, in which intrinsically 2D visual features, such as line endings or vertices, are first identified through nonlinearities, such as end-stopping, as found in some V1 cells. Motion information about these features is then selectively combined to calculate object motion. It is quite likely that multiple strategies are available to the visual system, with different ones predominating depending on viewing conditions. This is consistent with the concept of the visual system as a 'bag of tricks,' in which multiple mechanisms have evolved to take advantage of different environmental cues.

In MT and MST, spatial subdomains or asymmetries are evident in receptive fields, possibly as a result of combining inputs from spatially separated

V1 neurons with different preferred speeds, directions, or disparities. In addition to the preference of MST neurons for complex motion such as rotation and expansion, asymmetries within MT receptive fields appear to create neurons tuned for spatial gradients in speed or disparity. Such receptive field substructure may contribute to the perception of 3D surfaces or motion in depth.

Temporal Aspects of Motion Processing

When presented with an unchanging motion stimulus, the responses of most neurons change over time. The most commonly described changes are attributable to neural adaptation, in which the neuron's firing rate declines approximately exponentially over time. Adaptation was originally attributed to a kind of 'neural fatigue,' such as might be produced by depletion of neurotransmitter, but this cannot be the sole mechanism since adaptation is observed even when stimuli are presented briefly or when they do not elicit large responses. Further, adaptation rates and levels are highly stimulus dependent, being influenced by contrast, spatial frequency, temporal frequency, speed, and direction. Interestingly, adaptation does not simply change the amplitude of a neuron's response to a specific stimulus, but it can temporarily change a neuron's tuning. For example, after prolonged exposure to a grating, the tuning curves of V1 neurons shift away from the adapting grating's TF, SF, and direction. Conversely, attractive shifts have been observed in MT neurons, in which the preferred direction of many neurons shifts toward the direction of the adapting motion.

Neural adaptation is a very general mechanism present in multiple levels of the visual system as well as in other sensory systems. For example, photoreceptors are faced with light intensity variations spanning over 10 orders of magnitude, but the information that a neuron employing a rate code can transmit is limited by its maximum spiking rate. By adapting to the mean luminance in a scene, photoreceptors can increase the range of stimuli to which they can respond and also signal only changes in light intensity, which are of greater behavioral relevance than is the absolute light intensity (Figure 5). Similarly, a motion-sensitive neuron can adapt to the mean speed of a stimulus, reducing redundancy in the information encoded by its spikes. Perceptually, this dynamic range optimization is evident in studies of speed perception. During prolonged viewing of motion, the perceived speed of the stimulus declines approximately exponentially with viewing duration. This is accompanied by an enhanced ability to detect changes in speed, indicative of the functional role of adaptation in increasing motion sensitivity. An interesting by-product of adaptation, in combination

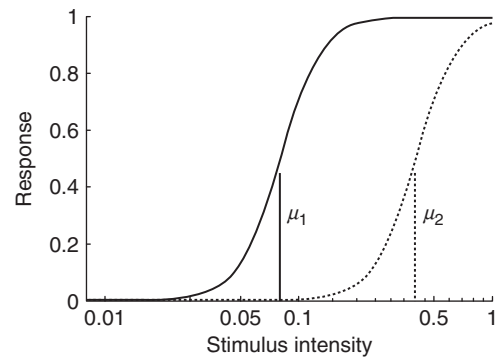


Figure 5 The functional role of adaptation. The sigmoid curves represent the normalized stimulus–response relationship for a hypothetical neuron. In a given adaptation state (e.g., with mean stimulus intensity μ_1) the neuron's spiking rate cannot cover the full range of stimulus intensities. If the mean stimulus intensity shifts to μ_2 , then the neuron dynamically shifts its tuning curve so that it can better represent changes in stimulus parameters.

with the directional opponency described above, is that prolonged viewing of a constant direction of motion can produce illusory motion of stationary patterns, as in the MAE.

Changes over time in neural responses to a constant stimulus can also reflect ongoing processing rather than adaptation. A striking example of this is that over ~ 60 ms, the responses of MT neurons change from reflecting the component of motion perpendicular to the orientation of a moving line segment to reflecting its true direction of motion. Similarly, when presented with plaid stimuli, consisting of two superimposed gratings, the responses of pattern motion-sensitive neurons evolve from initially being component motion sensitive. This demonstrates the dynamic coding of visual stimuli and provides further evidence that motion information may be processed collaboratively between a range of visual areas.

Higher-Order Aspects of Motion Representation

In addition to the more basic neural representation of movement that encodes the direction, speed, and location of motion within a scene, the visual system performs an array of higher-order motion computations. Areas along the dorsal stream progressively incorporate a greater proportion of extraretinal information into their coding of the retinal signal. This takes two main forms: copies of motor commands and attentional signals. So-called efference copy of eye movements and body movements can be used to help distinguish self-motion from object motion, and it can also be used to prepare the visual system for sudden changes in the visual inputs, such as those accompanying saccades. In such situations the motor

signal may allow neurons to transiently shift their spatial receptive fields or to suppress processing of the rapid self-generated motion. Attentional modulation of neural signals typically results in increased responsiveness to stimuli in the region of visual space to which attention is directed, or to distant objects that share features of the attended object, such as its direction of motion. Attention can also change receptive field shapes and response timings. While the precise mechanisms underlying these phenomena are unclear, many of the effects can be attributed to simple changes in response gain. Since areas further along the dorsal stream have larger receptive fields, the effect of attention acting in lower cortical areas could be to provide the higher-order areas with a representation of the visual world that is relatively dominated by the attended stimuli.

Another higher order aspect of motion representation is the integration of information between the form and motion pathways. The three-dimensional structure of objects can be extracted from motion and parallax cues generated by either object motion or movements of the observer. For example, during locomotion, objects at different distances generate distinct patterns of optic flow, leading to discontinuities in the local motion field. This allows the visual system to segment local motion vectors at the discontinuity and integrate local motion vectors on either side of the discontinuity. The perception of biological motion, in which observers recognize a moving animal or human form using only sparse information about the positions of the joints over time, may represent the highest form of the integration of local motion cues. However, it is also possible that moving animal forms are recognized predominantly from multiple template-matching operations of the static form across time, and that motion *per se*, as discussed previously (see the section titled 'Psychophysics'), is irrelevant.

Conclusion

Over four decades of physiological investigation of motion processing and over a century of quantitative psychophysical studies have given us great insight into the representation of motion at the single-neuron level and at the perceptual level. However, it is still not clear how the responses of a population of neurons are combined to generate perception, or which brain areas are associated with the perception of specific stimuli. The most basic link between a brain region and perception is that the activity in the area is correlated with the strength of the percept. In addition, microstimulation studies and lesion studies help link anatomical regions with behavior and perception. A wealth of studies has led to the strong association of

MT with the perception of stimulus speed, direction, and depth, and the association of area MST with heading detection and object tracking. However, it is still not clear which neurons in these areas contribute to perception, how different neurons may be recruited for different tasks, and how their responses are combined. Determining how motion is represented at the population level for guiding perception and behavior remains one of the great technical and analytical challenges for future studies of vision.

See also: Canal–Otolith Interactions; Motor Psychophysics; Neural Coding of Spatial Representations; Spatial Orientation: Our Whole-Body Motion and Orientation Sense; Spatial Transformations for Eye–Hand Coordination; Spatial Cognition; Spatial Cognitive Maps.

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