

Dissociation of Neuronal and Psychophysical Responses to Local and Global Motion

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Summary

Most neurons in cortical area MT (V5) are strongly direction selective [1–4], and their activity is closely associated with the perception of visual motion [reviewed in 5]. These neurons have large receptive fields built by combining inputs with smaller receptive fields that respond to local motion [6]. Humans integrate motion over large areas and can perceive what has been referred to as global motion. The large size and direction selectivity of MT receptive fields suggests that MT neurons may represent global motion. We have explored this possibility by measuring responses to a stimulus in which the directions of simultaneously presented local and global motion are independently controlled. Surprisingly, MT responses depended only on the local motion and were unaffected by the global motion. Yet, under similar conditions, human observers perceive global motion and are impaired in discriminating local motion. Although local motion perception might depend on MT signals, global motion perception depends on mechanisms qualitatively different from those in MT. Motion perception therefore does not depend on a single cortical area but reflects the action and interaction of multiple brain systems.

Results

Our stimuli were made from multiple local motion pulses. Each pulse was a small, brief, spatially and temporally band-limited target, containing motion in one of two directions (Figure 1A and Movie S1, available online). The motion of these targets is encoded by local or short-range motion sensors, like those in the primary visual cortex [7]. We created global motion by chaining these pulses together, suitably separated in space and time, to create long-range apparent motion [8]. Our experiments compared perceptual and physiological responses to motion conditions in which the short-range (local) and long-range (global) elements of the stimuli moved in the same or in opposite directions [9–12]. In our physiological experiments, we characterized the receptive fields of isolated MT neurons

using conventional methods. We then chose stimulus parameters so that the spatiotemporal frequency content of the pulses was in a favorable range for the neuron and their spacing placed five or more pulses within the classical excitatory receptive field.

Isolated single motion pulses presented in the center of the receptive field generally evoked brisk, directionally selective responses (Figure 1B, top two rows). We presented stimuli containing these local and global motions in both the preferred and null directions so that all four combinations of local and global motion were shown. For two typical neurons (Figure 1B, bottom four rows), all stimuli containing local motion in a neuron's preferred direction evoked similar responses, regardless of the direction of global motion. All stimuli containing local motion in the neuron's null direction were ineffective, regardless of the direction of global motion. To ask whether MT responses were determined by the local directional content of the stimulus, we compared responses having the same local motion but opposing global motions (Figure 1C). The direction of global motion had no systematic influence on the strong responses typically evoked by preferred local motion (Figure 1C, open symbols) or on the typical weak or suppressed responses to null local motion (Figure 1C, filled symbols).

We computed directional indices (DIs) separately for the local motions (averaged across all global motion conditions; Figure 2, marginal distribution on the abscissa) and the global motions (averaged across all local motion conditions; Figure 2, marginal distribution on the ordinate). The distribution of local DI centers near 0.9, reflecting the prevalence of directional selectivity for local motion. The distribution of global DI centers near 0, reflecting the general lack of selectivity for global motion. Comparing the local DI and global DI for 85 neurons reveals no particular relationship ($r = 0.02$, $p = 0.86$) (Figure 2, scatter plot). To capture the combined local and global selectivity of each neuron, we subtracted the global DI from the local DI to compute a quantity we call "local dominance." This value would be 1.0 for a neuron perfectly selective for local motion and indifferent to global motion, and -1.0 for a neuron with the opposite selectivities. Nearly all local dominance values were positive, suggesting that the responses of the MT neurons we studied were determined almost entirely by the local motion and were insensitive to the global motion (Figure 2, oblique marginal distribution). The values for the neurons whose data are shown in Figure 1B are highlighted in red; their difference values were 0.89 and 0.59, respectively.

The distribution of local dominance centers below 1.0, which might suggest a consistent, if weak, global motion preference. Examination of the scatter diagram in Figure 2 reveals, however, that this value is attributable to neurons that were not completely selective for local motion. This can also be seen by inspecting the responses of the two example neurons in Figure 1B to isolated local pulses (top two histograms): the neuron on the left was strongly selective for these pulses, whereas the one on the right was markedly less so. This difference is reflected in the responses to the compound stimuli shown in the other histograms in Figure 1B.

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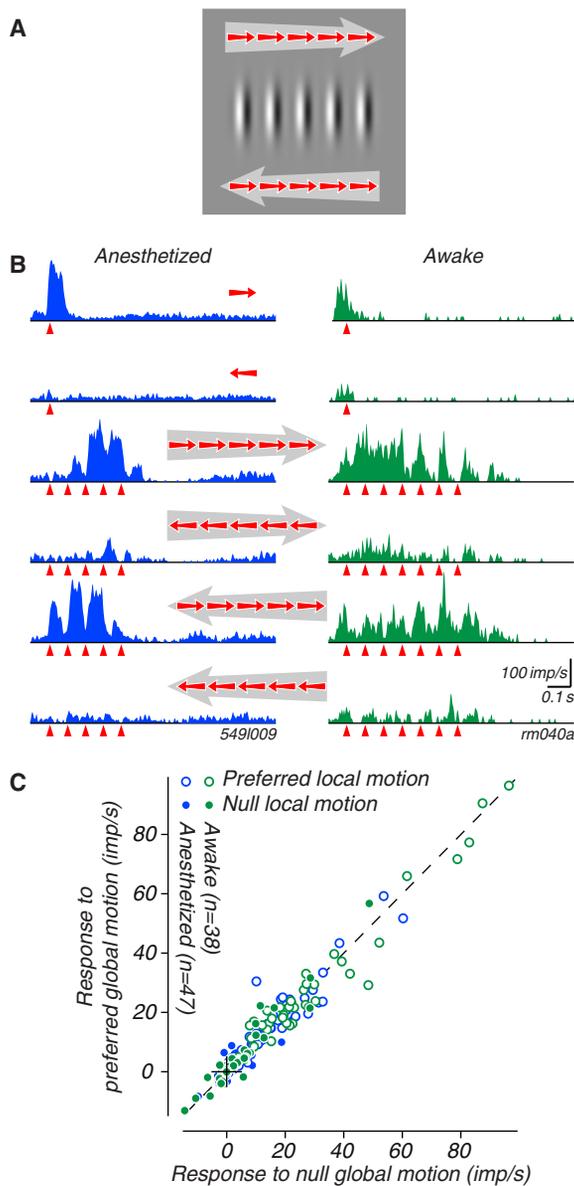


Figure 1. The Responses of MT Neurons to Local and Global Motion

(A) An illustration of our local-global motion stimulus. In this example, five pulses of local motion, each drifting to the right, are presented in sequence from left to right or right to left; the large arrows indicate the direction of global motion, the small arrows indicate the direction of local motion. In our physiology experiments, these directions were arranged to correspond to the preferred and null directions for each neuron under study and represent two of the four possible directional combinations of local and global motion.

(B) Response histograms for two MT neurons, one recorded in an anesthetized macaque at New York University (left, in blue) and the other in an awake macaque at Stanford (right, in green). The rows contain data from different stimulus conditions: the top two rows show responses to single local motion pulses presented in the center of the receptive field, and the bottom four rows show responses to the combinations of local and global motions indicated by the small red and large gray arrows. The red triangles indicate the timing of each local pulse (five for the neuron on the left, seven for the neuron on the right).

(C) A comparison of the responses of 85 MT neurons (47 from anesthetized macaques [blue symbols] and 38 from awake macaques [green symbols]) to stimuli containing preferred local motion (open) and null local motion (filled) when the global motions were in the null and preferred directions.

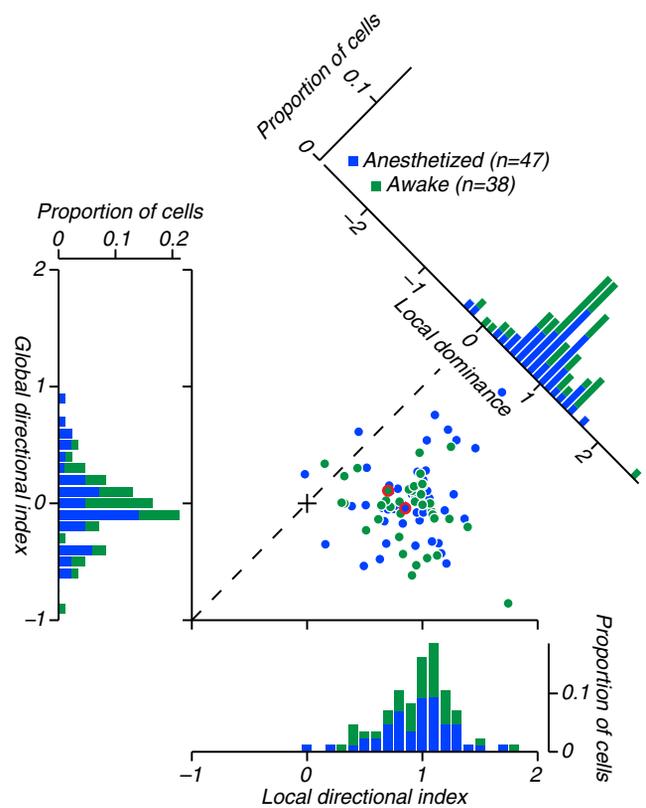


Figure 2. A Comparison of Directional Selectivity for Local and Global Components of Motion

Local DI values are plotted against global DI values for 85 MT neurons. Data from anesthetized monkeys is in blue; data from awake monkeys is in green. The marginal distributions on the ordinate and abscissa capture the directional selectivity for the global and local motions, respectively. The mean and standard error of local DI was 0.90 ± 0.05 for anesthetized recordings and 0.88 ± 0.05 for awake recordings. For global DI, the values were 0.04 ± 0.05 for anesthetized recordings and -0.05 ± 0.05 for awake recordings. The oblique marginal distribution is of the difference between local and global DI, which we term local dominance. The mean and standard error of local dominance was (0.85 ± 0.06) for anesthetized recordings and (0.92 ± 0.08) for awake recordings. The values for the neurons whose data are shown in Figure 1B are highlighted in red; their local dominance values were 0.89 and 0.59, respectively.

The data in Figures 1 and 2 were taken under conditions in which the speeds of local and global motion matched, but we explored a wide range of global motion speeds in many neurons and observed the same pattern of results (Figure 3A). We also measured responses to a variant stimulus in which the local motion pulses were replaced with static flashed targets that had the same spatial structure but lacked motion and were flashed on with the same time course as the local motion. The responses to these “global-motion-only” stimuli lacked direction selectivity both for this example (Figure 3B) and on average, demonstrating that global motion did not influence the response even when local motion signals were absent.

We made recordings from neurons with a wide range of receptive field locations (centered between 2 and 28 deg from the fovea), sizes (6–30 deg), preferred spatial frequencies (0.1–1.7 c/deg), and drift rates (0.7–5.7 Hz). The locations and sizes of receptive fields are shown schematically in Figure 4A. The receptive fields of neurons recorded from both anesthetized animals (in green) and awake animals (in blue) covered

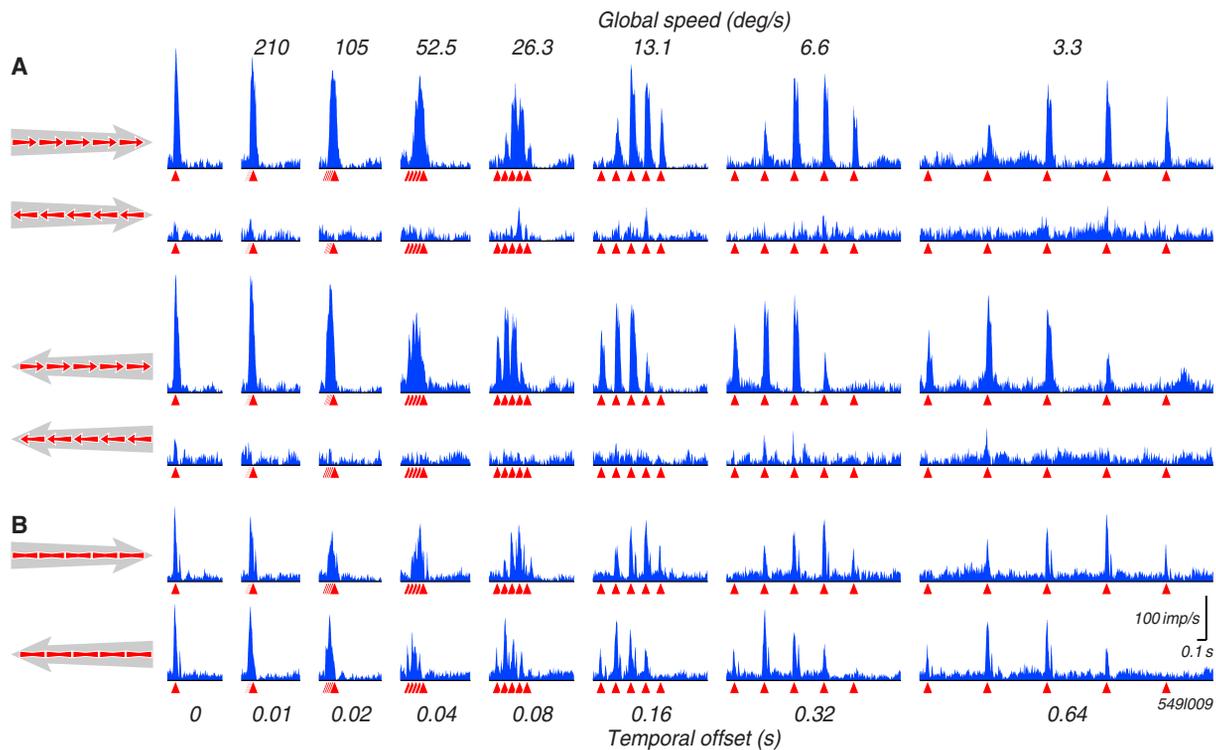


Figure 3. The Responses of an MT Neuron to Local and Global Motion across a Range of Global Speeds, and in the Absence of Local Motion

(A) Response histograms for the MT neuron, shown in the left column of Figure 1B, over a range of global speeds. The rows show responses to combinations of local and global motions whose directions are indicated by the small red and large gray arrows (the preferred direction is marked as rightward). The columns show responses to different global speeds, which decrease from left to right. The leftmost column shows the condition when all local motion pulses (which moved at 26.8 deg/s) are presented simultaneously (an “infinite” global speed, or none). The red triangles indicate the offset of each local pulse. (B) Response histograms for the same MT neuron but for stimuli that did not contain local motion.

the contralateral field within 10 deg of the horizontal meridian from the center of gaze out to at least 20 deg. The distributions of preferred spatial frequency and drift rate for neurons recorded from anesthetized animals are shown in Figures 4B and C. We did not make the same tuning measurements in the awake animals, but we believe that the distributions were similar on the basis of responses measured during the search for the most effective Cauchy order and speed for the pulses. We examined the correlations between all of the properties captured in these plots and the local directional index, global directional index and local dominance. None were significant.

These results show that the responses of MT neurons were determined entirely by the local motion content of our stimulus and uninfluenced by its global motion. This was true for stimuli of a wide range of global speeds and for recordings from both awake and anesthetized animals, though it should be noted that our stimulus design required that the pulses be separated by distances greater than those that usually elicit robust directional responses with conventional apparent motion stimuli in MT neurons [4, 13]. Under these conditions, MT neurons do not integrate motion information across their receptive fields, but behave instead as though they simply pool local motion signals wherever they originate within the receptive field [14].

What makes these physiological observations particularly interesting is that under identical viewing conditions, our perceptual experience is dominated by global motion, as can be seen in Movies S1, S2, S3, and S4. When the pulses are presented in isolation, local motion is easy to see (Movie S1), but when the same pulses are imbedded in a global motion

sequence, they appear to move in the global direction regardless of their true local direction (Movie S2). When the local motion is opposite to the global motion, the stimulus sometimes appears “jumpy,” as if the motion were in discrete steps and not continuous, but the overall direction perceived was that of the global motion. This dissociation between our percept—dominated by global motion—and the neuronal responses in MT—dominated by local motion—stands in sharp contradistinction to the common view that the activity of neurons in MT is closely associated with our experience of motion [15]. We therefore decided to make psychophysical measurements to explore this dissociation between expected and actual perceptual experience.

Observers viewed global motion sequences of five elements arranged in a horizontal row 4 deg below the fixation point and judged the local motion of the central pulse. Initially the stimuli were identical to those used in physiological experiments (Movie S2); there was local motion in all five pulses. We then realized that observers might “peek” at the local motion signals in pulses other than the one in the center. Though none of our data indicated that any of our observers did this, we decided to remove this potential cue by replacing the flanking elements with pulses of the same spatial structure and duration but without local motion. This change makes little difference to the percept of global motion (Movie S4). We chose the location, spatial and temporal frequencies for the local pulses, and the speeds of global motion so that they fell within the range that was optimal for the neurons in our recordings; the values we chose are indicated in red on each

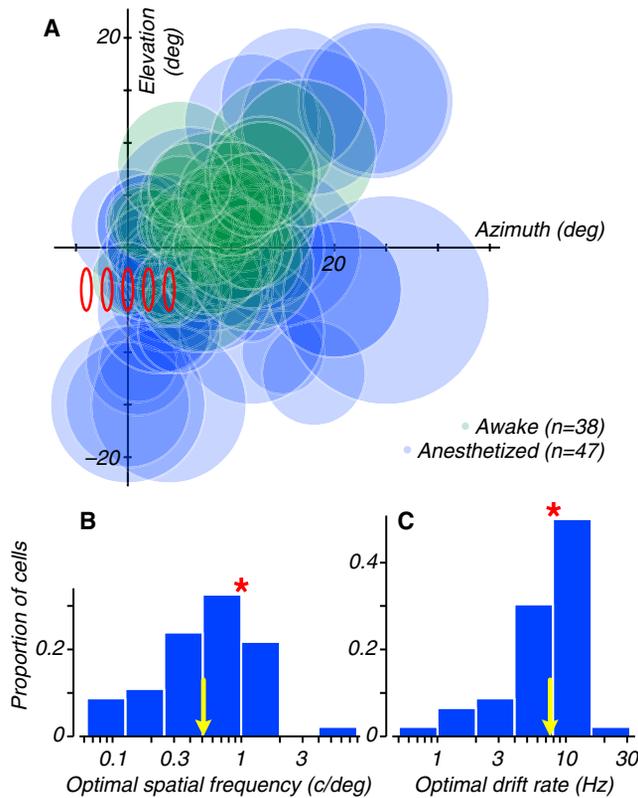


Figure 4. Receptive Field Locations, Sizes, and Spatiotemporal Frequency Preferences for Neurons in MT

(A) Semitransparent circles schematically show the positions and sizes of the receptive fields of the MT neurons recorded from anesthetized macaques (in blue) and from awake macaques (in green). The red ellipses indicate the positions of the five local motion pulses in our psychophysical experiments.

(B and C) The distributions of optimal spatial frequency and drift rate for neurons recorded in anesthetized macaques. Yellow arrows indicate geometric means. The red asterisks indicate the values of each parameter used in psychophysical experiments.

part of Figure 4. The observers reported the direction of the local motion of the central patch (the only pulse with local motion); no feedback was given. We adjusted the durations of the local motion pulses for each observer to span a range over which individual performance ranged from near chance to near perfection and measured the slope and intercept of the resulting psychometric functions to estimate motion thresholds and discrimination bias.

When the flanking and central patches were presented simultaneously, there was no global motion and subjects judged the motion of the central patch with reasonable accuracy and without bias (Figure 5A, thick lines). As in the physiological experiments, we created global motion by staggering the onset times of the pulses. Global motion influenced our observers' judgments of local motion in two ways: it reduced their sensitivity to local motion and often also biased observers so that they reported local motion in the direction of the global motion. Both effects can be seen in the example psychometric functions in Figure 5A. The sensitivity loss reduces the slope of the function, and the bias shifts the intercept with chance (the point of subjective equality). The average results for seven subjects show both the threshold elevation and the bias evident from the individual functions and further

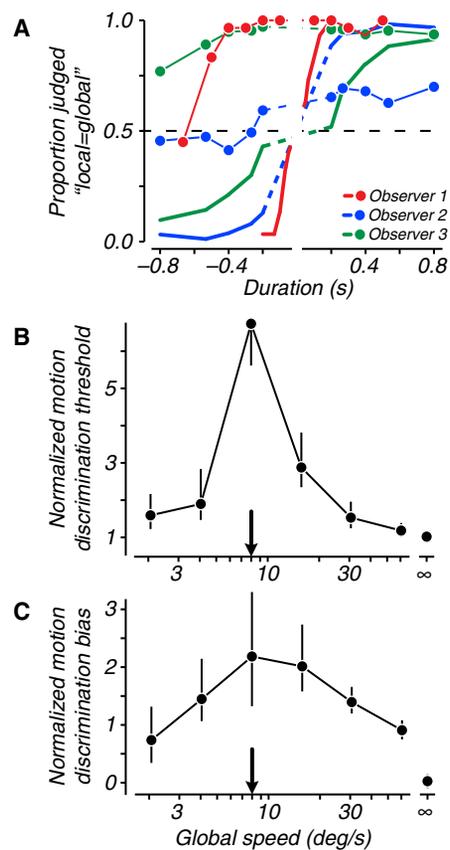


Figure 5. The Influence of Global Motion on Judgments of Local Motion

(A) Psychometric functions for three observers judging the direction of local motion of a single pulse presented below fixation and flanked by four other pulses. The ordinate plots the proportion of trials on which the local motion was judged to be in the same direction as the global motion defined by the sequence of pulse presentations. The abscissa plots the duration of the local motion pulse, and negative "durations" are assigned to pulses whose local motion was opposed to the global motion sequence. Thick lines show data collected in the absence of global motion (when all pulses were presented simultaneously). The slope of the psychometric function measures sensitivity to motion direction and the intercepts are near 0, revealing that the observers had little bias to report one motion over the other. The data points connected by thin lines represent judgments when the global motion was at a speed matched to the local motion in each patch. For one observer (data in red) the effect of the global motion was to shift the psychometric function to the left, reflecting a change in the local motion that was equally often judged to be in the same or opposite direction as the global motion (the point of subjective equality). For a second observer (data in blue), the effect of the global motion was to shallow the psychometric function, reflecting a reduction in sensitivity to variations in the strength of the local motion signal. For the third observer (data in green), both effects were evident.

(B and C) The effects of global motion on the slope of the psychometric functions (B, sensitivity) and on the shift in the point of subjective equality (C, bias) for seven observers. The points with infinite abscissa values correspond to the condition in which all local pulses were presented simultaneously. The data are normalized for each observer by the standard deviation of the Gaussian whose integral describes the psychometric function measuring their discrimination performance in the absence of global motion. Note that for some conditions, one or the other measure could not be extracted (e.g., the subject whose data are in blue in Figure 5A did not have a measurable threshold in the global motion condition). The means shown are taken for the valid measurements at each speed, and the error bars represent the standard errors.

show that these effects were most pronounced when the speed of global motion matched the speed of local motion (Figures 5B and C).

Discussion

There is a striking contrast between our physiological results—showing that MT neurons signal only local motion—and our psychophysical results—showing that observers' perceptual reports of local motion can be dominated by the global motion within which they are imbedded. This seems inconsistent with the view that our experience of directed motion derives directly and simply from the activity of directionally selective neurons in MT. How might this discrepancy be explained?

One speculation is that the signals supporting our percept of global motion might arise in a separate neural circuit containing neurons selective for the direction of global motion and that our perceptual experience reflects the outcome of a competition between mechanisms sensitive to local and global motion. We found only local motion sensitivity in MT, and there is evidence that motion representation is also locally dominated in cortical area MST, MT's main downstream target [16]. But there are many other areas in the visual cortex, and in principle any of them might represent the global motion signal. Evidence that two competing systems are involved comes from the suppression and capture of local motion percepts by global motion (Figure 5). We have demonstrated informally that parametric manipulations which weaken the percept of global motion (such as increasing the spacing between pulses), or which strengthen the percept of local motion (such as increasing the duration of each pulse), profoundly affect perceived motion. These variations in the percept are not correlated with a variation in the directionality of MT neurons.

An especially potent manipulation is to present the stimulus in the peripheral visual field, which uncovers a vivid experience of local motion that cannot be seen when the same stimulus is viewed centrally (readers can experience this while viewing [Movie S2](#) by directing their gaze to a position about five times the width of the movie frame to one side). This suggests that neural circuits devoted to information from the peripheral retina may be relatively more sensitive to local motion than those devoted to central retina [10, 11]. The relative decline in the strength of global motion signals with peripheral viewing might occur because these signals are processed by areas more devoted to the representation of the central retina, many of which belong to the "ventral stream" of visual information processing that is usually not thought to have a role in motion processing, but which may signal long-range apparent motion [17, 18].

Another possibility is that perceptual experience is based on signals from early topographically organized areas, including MT, but is decoded using a more complex strategy than simply reading motion signals from populations of directionally tuned neurons [13, 19]. For salient objects in sparse fields, like the elements of our stimulus, a perception of motion arises when a correspondence is established between a feature at two times. Long-range apparent motion can occur under circumstances that do not offer any consistent local direction signal, as when an object appears, disappears, and then reappears a substantial distance away [8]. Any visual area that encodes the location of features with sufficient spatial and temporal fidelity could inform such an operation, and MT is one such area, though by no means the only one. All that is required is to track an identifiable feature as it is displaced. Our results indicate that single MT neurons do not track features to support the perception of long-range apparent motion, but

the population activity of these neurons could be a viable source of information for downstream computations. The competition between local and global motion percepts could then result from a conflict between the local signals within MT (implying motion in one direction) and the long-range motion of features in a population map (implying motion in the other).

There is no ready way to distinguish these explanations, but in either case it is clear that to understand the perception of local and global motion, we will need more complex accounts of the relationship between neuronal activity and perception than the ones we now use.

Experimental Procedures

Neuronal Recordings

Stimuli

Stimuli consisted of sequentially presented local motion pulses, each containing an elongated, brief, spatially and temporally band-limited drifting grating. The spatial frequency content of these pulses was chosen to match the response preference of the neuron and band-limited by ensuring that at least one cycle of the dominant spatial frequency was contained within the contrast envelope. The contrast of each local pulse ramped up and down following either a raised cosine or a Cauchy function. The duration of the local pulses was 80 ms for the awake recordings and was set to be long enough to elicit a directional response for the anesthetized recordings, usually about 70 ms. Five to seven pulses were shown at a spacing of roughly 2 deg (range 0.7 deg–2.9 deg), chosen to place all the pulses within the neuron's receptive field. The temporal offsets between pulses were set so that the global speed matched, as closely as possible, the preferred local speed, which we estimated in preliminary experiments. We presented randomly interleaved stimuli with the four possible combinations of preferred and null local and global motion for at least five repetitions of every stimulus condition. Stimuli were generated by laboratory computers and shown on gamma-corrected CRT monitors with a spatial resolution of 1024 × 731 pixels and a frame rate of 100 Hz for the anesthetized recordings and 800 × 600 pixels and a frame rate of 60 Hz for the awake recordings.

Recording

We recorded extracellular activity from direction-selective MT neurons in six anesthetized and two awake adult macaque monkeys by using conventional methods previously described [20, 21]. We present data from both preparations because the anesthetized recordings allowed us systematically to explore a wide range of parameters and to more accurately tailor the stimulus to each cell's stimulus preference, whereas the awake recordings were free of any potential influence of anesthesia. For the anesthetized recordings, we maintained anesthesia with an intravenous infusion of sufentanil citrate in lactated dextrose saline (4–30 $\mu\text{g}/\text{kg}/\text{h}$ in 4–10 $\text{ml}/\text{kg}/\text{h}$). We infused vecuronium bromide to prevent eye movements (0.1 $\mu\text{g}/\text{kg}/\text{h}$). To record from MT, we passed microelectrodes through a small durotomy centered roughly 16 mm lateral to the midline and 3 mm posterior to the lip of the lunate sulcus at an angle of 20 deg from horizontal in a ventroanterior direction. All procedures for these recordings were performed in compliance with the National Institutes of Health's *Guide for the Care and Use of Laboratory Animals* and were approved by the New York University animal welfare committee.

For the awake recordings, a head holding device, eye coil, and recording cylinder were implanted under general anesthesia. The recording cylinder was placed over the primary visual cortex and MT was accessed via a posterior approach through a stainless steel guide tube that extended 4–5 mm caudal to the superior temporal sulcus. All procedures for these recordings were performed in compliance with the National Institutes of Health's *Guide for the Care and Use of Laboratory Animals* and were approved by the Stanford University administrative panel on laboratory animal care. During recording sessions, the animals were rewarded periodically for maintaining gaze within 2 deg of a fixation target.

The first step in our anesthetized recordings for each neuron was to measure the optimal direction, spatial and temporal frequency, and size with drifting sine-wave gratings. We used the results to choose parameter values for subsequent local-global experiments. We included almost all well-isolated and responsive neurons, although we excluded a few cells responsive only to very low spatial frequencies for which we could not create a multielement effective stimulus. We followed a similar but less

formal sequence for the awake recordings, in which we mapped a cell's receptive field and checked its directional selectivity with smoothly drifting bars.

Data Analysis

We computed neuronal responses over an epoch beginning 25 ms after the start of the first motion pulse in each sequence and ending 45 ms after the end of the last and then subtracted the baseline response.

To quantify the directionality at the two spatial scales, we computed standard directional indices as the ratio of the null response to the preferred response subtracted from one; this ratio gives local DI and global DI. To quantify the dominance of the directionality for the local motion relative to the global motion, we subtracted global DI from local DI. We excluded three neurons that had atypical responses owing to a failure to continuously isolate them for the duration of the presentation stimulus or incorrect parameterization of the stimulus.

Psychophysics

Procedures for our psychophysical experiments were approved by the New York University committee on activities involving human subjects. Seven observers, having given informed consent but naive to the particular purpose of the experiment, viewed a display consisting of a horizontally arranged global motion sequence containing five elements presented in a horizontal row 4 deg below the fixation point (Movie S4); the pulses were spaced 2 deg apart (Figure 4A). For the data reported here, the dominant spatial frequency of the pulses was 1 c/deg and the local drift rate was 8 Hz, giving a local speed of 8 deg/s (Figure 4A–C, red asterisks). The position and speed of the stimuli were chosen to loosely match those used in the physiology. The speed of global motion was determined by the temporal interval between pulses and ranged from 0 (simultaneous presentation of all five patches, an “infinite” global speed) to 800 ms (a global speed of 2.5 deg/s). The central element contained local motion to the left or right, whereas the four flanking elements contained pulses of the same spatial and temporal structure and duration, each containing equal mixtures of local motion in the two directions. The observers' task was to report the direction of the local motion of the central patch; after an initial training period, they were not given feedback about the accuracy of their choices.

We controlled the visibility of the local motion by varying the duration of each pulse; the range of durations used depended on individual observers' sensitivity to the motion. On a given trial, the local motion could be either rightward or leftward, and we varied pulse duration by using the method of constant stimuli. We randomly mixed trials containing leftward and rightward local and global motion.

The resulting data were compiled into psychometric functions (Figure 5A), which were fit to cumulative Gaussians with a maximum likelihood technique. From each fit we extracted a slope, the inverse of which was taken as the discrimination threshold, and an intercept, which was the point of subjective equality, i.e., the local motion duration that resulted in an equal number of reports of leftward and rightward motion.

Supplemental Information

Supplemental Information includes four movies and can be found with this article online at doi:10.1016/j.cub.2011.10.049.

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