Misperceptions of speed are accounted for by the responses of neurons in macaque cortical area MT

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A CENTRAL ASSUMPTION OF SYSTEMS NEUROSCIENCE is that the activity of neurons in sensory cortex is a core determinant of perception. This idea is particularly well established for the perception of visual motion. The primate visual system contains a cortical processing pathway from the primary visual cortex (V1) through the middle temporal (MT) and medial superior temporal areas to higher cortical areas in the parietal and frontal lobes specialized for the encoding of motion information (Gattass and Gross 1981; Maunsell and Van Essen 1983; Cheng et al. 1994). The specialization of this pathway is most apparent in the high proportion of neurons tuned to the direction and speed of moving stimuli present in their receptive fields (Dubner and Zeki 1971; Maunsell and Van Essen 1983; Snowden et al. 1992; Perrone and Thiele 2001; Priebel et al. 2003). In nonhuman primates, a link between the response of MT neurons and speed perception is supported by an impairment in speed discrimination performance after lesions of MT (Newsome and Pare 1988; Orban et al. 1995) and by the correlation between pursuit eye movements and the activity of speed-tuned MT neurons (Priebe et al. 2001). Similarly, MT\textsuperscript{+}, the presumed human homolog of area MT, is preferentially activated during speed discrimination tasks (Huk and Heeger 2000). More recent studies provide further evidence for the causality (i.e., a direct influence of speed perception on MT activity) of this link. Liu and Newsome (2005) showed that speed judgments of rhesus monkeys could be predicted by the trial-by-trial variation in responses of individual MT neurons. Additionally, by electrically stimulating small populations of MT neurons with similar speed preference, the authors were able to systematically bias performance toward the preferred speeds of the stimulated neurons in one of the two animals tested. McKeefy et al. (2008) observed that repetitive transcranial magnetic stimulation on V5/MT\textsuperscript{+} impaired speed perception, and, more specifically, it increased discrimination thresholds in humans. Altogether, these findings serve as evidence for a direct influence of the activity of MT neurons on speed perception. Although a number of studies investigated the mechanisms of speed tuning in MT and V1 (Perrone and Thiele 2001; Perrone et al. 2006), how MT activity is decoded into a speed percept is still not fully understood.

If the activity of MT neurons conveys a neural correlate of perceived speed, their activity could also account for the misperceptions of speed. In this study, we used a well-known speed illusion as a tool for addressing this question. Although human speed perception can be highly precise with discrimination thresholds as low as 6% for intermediate (4–32°/s) stimulus speeds (Orban et al. 1984; De Bruyn and Orban 1988; McKee et al. 1986), this perceptual precision is not veridical and independent from other factors. A number of biases have been reported in speed perception. One example is the so-called “field-size effect”, an increase in perceived speed with a decrease in stimulus size (Brown 1931; Snowden 1997; Ryan and Zanker 2001).

To test the hypothesis that the activity of neurons in area MT is the basis of perceived speed, we investigated the responses of MT neurons in awake, fixating rhesus monkeys moving stimuli of different aperture sizes. We observed changes in the responses and in the speed tuning of single neurons, consistent with the changes in perceived speed in human subjects, assuming a straightforward decoding mechanism to convert the MT population response into a percept. Together, our results suggest a neural correlate for the basic field-size effect and further strengthen the link between MT activity and perceived speed.

MATERIALS AND METHODS

Electrophysiological Methods

Three male rhesus macaque monkeys (\textit{Macaca mulatta}, 7–12 kg) were trained to perform a visual fixation task. After initial training, the
animals were implanted with a head post to prevent head movements during experimental sessions. Stainless-steel recording chambers of 20-mm diameter (Crist Instruments, Germantown, MD) were implanted on one hemisphere of each monkey (right hemisphere in Monkey Z and T and left hemisphere in Monkey D). All surgical procedures and experiments were approved by the district government of Lower Saxony, Germany. Head posts and recording chambers were implanted using standard surgical techniques under isoflurane anesthesia. Monkeys received fluid reward for correctly performing the visual task.

Apparatus. During training and recording sessions, monkeys were seated in a custom-made primate chair, in a dimly lit, separate experimental chamber, at a viewing distance of 57 cm to a Cathode-ray-tube computer monitor with a refresh rate of 75 Hz. The monitor covered a visual field of 30° vertical and 40° horizontal of visual angle at a resolution of 40 pixels degree.

Electrophysiological recordings. Extracellular action potentials of single units in the MT were recorded with single tungsten microelectrodes (4 Ω at 1 kHz; FHC, Bowdoinham, ME) controlled by a hydraulic micropositioner (David Kopf Instruments, Tujunga, CA). Neuronal signals were processed and recorded with a data acquisition system (Plexon, Dallas, TX). The electrode was inserted through the dura using a custom-made guide tube. Area MT was identified by its anatomical position, the typical patterns of activity and inactivity (layers of gray and white matter) along the electrode track, the high proportion of direction- and speed-selective units, and the ratio of receptive field size to eccentricity. Eye positions were sampled at 226 Hz with the use of an infrared video monitoring system (ET-49; Thomas Recording, Giessen, Germany).

Visual task. Figure 1 describes the task that the monkeys performed both for the initial investigation of direction and speed selectivity and for the following experiment. The animals initiated each trial by depressing a lever. They were trained to fixate a small square (0.15° × 0.15°) on the display throughout a variable trial duration of 4–6 s. A trial was considered as correctly completed if the animal kept its gaze within 1.25° of the fixation square and released the lever within 170–570 ms after a change in the luminance of the fixation point. Lever releases outside this time window or a break in fixation aborted the trials. Only correct trials were included in our analysis. The animals received fluid reward immediately following each correct trial. After aborted trials, a timeout of 300 ms delayed the initiation of the next trial.

Stimulus presentation. After isolating each unit, the classical receptive field (CRF) (i.e., the region of the visual field in which a stimulus directly evoked a response from the unit) was mapped with a mouse-controlled bar or random dot pattern (RDP) of variable size. To investigate the direction and speed selectivity of the units, RDPs moving coherently in 1 of 12 different directions (0, 30, 60, 90, 120, 150, 180, 210, 240, 270, 300, and 330°) and at 1 of 8 different speeds (0.5, 1, 2, 4, 8, 16, 32, and 64°/s) were presented in the receptive field within a stationary circular aperture. Each dot crossing the edge of the stimulus aperture was reassigned to a new random position on the opposite edge. In all electrophysiology experiments, the dot density of the RDPs was 10 dots/degree². The size of the dots was 0.01 degree². Background and dot luminance was 25 cd/m² and 86 cd/m², respectively.

In Experiment 1 (preferred speed experiment) and Experiment 2 (slope speed experiment), stimulus size and motion direction were adjusted to the preferences of each isolated neuron. In each trial, the RDP repeatedly alternated between one direction and its opposite. The speed of each motion phase of the stimulus within this sequence was randomly picked from the eight speeds listed above. Alternation of preferred and null directions and the randomization of speeds minimized effects of adaptation. The duration of each motion phase was 800 ms and with no blank interval between the successive phases. A trial contained up to seven successive phases depending on when the luminance change in the fixation point occurred. The time of the luminance change was determined pseudorandomly by choosing a frame within 4,000–6,000 ms of stimulus presentation.

For each neuron, three stimulus sizes were used. The largest stimulus nearly covered the CRF, whereas the diameter of the medium and small stimuli were one half and one quarter of the diameter of the largest stimulus. The diameter of the largest stimulus used for different units ranged from 8–18°. In some cases, receptive fields had a diameter of more than 18°. For these recordings, stimuli were centered on the most responsive part of the receptive field.

In Experiment 2, visual task (fixation) and the stimuli were identical to Experiment 1, with a difference in the use of stimulus speeds. Instead of moving at randomly chosen stimulus speeds (0.5–64.0°/s), all motion pulses in preferred or null direction were presented at a “slope speed” (see Eq. 2 in RESULTS). All other parameters for stimulus creation were the same as in Experiment 1. Because of the small number of different stimuli, it was possible to present more (at least 30, typically 40–50 trials) stimulus repetitions.

Data acquisition and analysis. Data acquisition and online analysis of neural activity was accomplished with custom software. Further data analyses and statistics were performed in MATLAB (MathWorks, Natick, MA).

For each stimulus condition we computed the average response rate of a neuron. In Experiment 1, this firing rate was determined on the basis of at least four repetitions (typically about eight) of identical stimulus presentations in different trials. The window for calculating firing rates was 720 ms long, starting from 80 ms after each motion phase onset, unless otherwise stated. The firing rates were then averaged across all presentations of each specific phase.

Speed-tuning curves (i.e., the response of a neuron as a function of stimulus speed x) were fit by a four-parameter logarithmic Gaussian:

\[ f(x) = B + A \times \exp \left( \frac{1}{2} \frac{(\log x_0 - \log x)^2}{\sigma^2} \right) \]

(1)

where B denotes the baseline firing rate, A is the maximal amplitude of the tuning curve above B, x₀ represents the preferred speed, i.e., the speed corresponding to the peak of the response profile, and σ (the tuning width) corresponds to the standard deviation of the log-Gaussian curve. Each tuning curve is based on at least seven data points collected over at least four interleaved presentations of the respective stimulus speed. Units not well fit by the log-Gaussian function were excluded from the analysis (see RESULTS). A speed
index was computed from each speed-tuning curve, by dividing the amplitude of the response (maximum firing rate – minimum firing rate) by the difference between maximum and spontaneous firing rate: 

\[ \text{amplitude} = \frac{R_{\text{max}} - R_{\text{spont}}}{R_{\text{max}} - R_{\text{base}}} \] 

(Liu and Newsome 2003). The spontaneous firing rate was the mean firing rate from at least four fixation-only trials without any RDPs presented on the display. Only units with speed-tuning indices above 0.4 were included. Additionally, in Experiment 1, units with preferred speeds beyond the measurement range (0.5–64.0°/s) were excluded.

**Psychophysical Methods**

Eleven naive human subjects and one author (P. Boyraz) participated in the psychophysical experiment. All subjects had normal or corrected-to-normal vision and signed an informed, written consent. Subjects were seated in a dimly lit chamber in front of a 22-inch Cathode-ray-tube display monitor with a resolution of 40 pixels/degree (1,200 × 1,600 pixels) and a refresh rate of 65 Hz at a viewing distance of 57 cm. Stimuli were created and displayed with the same custom software as the stimuli for the electrophysiological recordings.

During each trial, subjects were instructed to fixate a small (0.2 degree × 0.2 degree) dark square on the center of the display, and the head posture was stabilized with the help of a chin rest. In each trial, subjects had to choose the faster of two successively presented stimuli in a two-alternative, forced-choice paradigm. No feedback was provided as to whether the response was correct. The fixation point appeared before trial start and remained visible throughout the trial. One hundred and thirty milliseconds after the subject pressed the trial start key on a computer keyboard, the first RDP appeared. Both stimuli had a duration of 200 ms and were temporally separated by a blank period of 270 ms.

In an experimental session, reference stimuli moved at one of the reference speeds and had a diameter of 4 or 6°. Test stimuli had a diameter of 12°. A total of nine reference speeds (RS; 2, 4, 6, 8, 10, 12, 14, 16, or 18°/s) were used, and for each reference speed 25 test speeds were used (varying from 0.5 × RS to 2.5 × RS, in 0.1 × RS steps). In each trial, one reference speed and one test speed stimulus were compared. The presentation order and the location of the test and reference stimuli were randomized. All stimuli were centered at an eccentricity of 8°. Dot size was 0.015 degrees², and dot density was 10 dots/degree². Contrast between stimuli and background was maximal, with dark dots (0.08 cd/m²) on a bright background (68 cd/m²). In a given trial, both stimuli moved in full coherence either in the upward or downward direction.

A weighted up-down staircase was used to ensure that most of the speeds presented were in the perithreshold range of each subject. One ascending and one descending staircase (convergence points at 25% and 75%) were interleaved for each reference speed (Kaernbach 1991). The staircase procedure maximizes the number of trials within this region. The experiment was organized in three sessions. In each session, three adjacent reference speeds were used to prevent subjects from memorizing the reference speeds, as the use of a single reference speed might reduce the stimulus-size effect (Ryan and Zanker 2001). The order of the sessions was randomized across subjects. Each session consisted of 200 trials, and, for data presented here, all subjects completed a total of six sessions typically within 2–3 wk.

The proportion of trials in which the subjects reported the reference stimulus (i.e., the smaller stimulus) as faster was determined for each reference speed. The point of subjective equality (PSE, proportion of test speed to reference speed at 50%) and the speed discrimination threshold (proportion of test speed to reference speed at 84%) were measured for each reference speed and each stimulus size by fitting a logistic function to the psychometric data. Statistical analyses in the form of two-sided t-tests of mean PSE vs. the point of physical equality (PPE) were performed with MATLAB, and the P values in the results indicate the significance level from these analyses.

**Psychophysical measurements with Monkey Z.** After completing all electrophysiological recording sessions, Monkey Z was trained for the same two-alternative-forced-choice (2AFC) speed discrimination task as the human subjects. Initially, the animal was trained for a “same-size” paradigm, where standard and comparison stimuli were identical in every aspect but speed. The stimuli had 8° diameters and were presented at 8° eccentricity on the right and on the left of the fixation point. The monkey indicated the location of the faster moving stimulus (left or right of the fixation) by pulling a joystick lever toward that direction and was rewarded for correct responses. After his initial training for speed discrimination and after he reached an average hit rate of 75% and a speed discrimination threshold of about 40%, two sets of trials were randomly interleaved. In the first set, the diameter of the standard stimulus was decreased to 4° (“different-size” trials), whereas in the second set both stimuli were of the same size as in the training sessions (same-size trials). Different from the task design used for human subjects, only one standard speed was used (10°/s). This was done to ensure collecting sufficient number of trials for at least one psychometric function before the monkey lost his motivation. The rest of the task design was the same as in the task of the human subjects (randomized stimulus presentation order and position). Dots were bright on a dark background (see Stimulus presentation for the luminance, dot size, and density). The speeds of the test stimuli in the different-size set were 3, 5, 8, 13, 15, 18, 23, and 25°/s; in the same-size set, in addition to these, 9, 10, and 11°/s were also included. The reason for not presenting stimuli with the same or very similar speeds in the same-size condition was to avoid confusing the monkey with comparisons where the reward did not match his percept (see below). However, these were kept in the different-size condition to assess directly whether the probability of responses “smaller stimulus is faster” lay above 0.5 at PPE. In all trials, the monkey was rewarded only for correct responses (when the physical speed of the stimulus he had selected was faster). A minimum of 50 trials was collected for each speed comparison in both types of trials. No electrophysiological recordings were performed during or after the monkey was trained on the discrimination task.

**RESULTS**

**Psychophysics: Effects of Stimulus Size on Perceived Speed**

To quantify the field-size effect with the RDP stimuli that we used in the electrophysiological experiments, we measured the PSE for the speed of RDPs of different size. Figure 2A shows the results from this experiment with eight naive human subjects. Mean PSE for all tested conditions was above 1, indicating that the subjects overestimated the speed of the smaller RDP with respect to the speed of the larger RDP. When the test stimulus had a diameter twice as large as the reference stimulus (6 vs. 12 degrees, gray data points), on average, the reference stimulus was perceived to move 29% faster than the test stimulus of identical physical speed. For a larger difference in stimulus size (4 vs. 12° diameter, black data points), the mean PSE across all reference speeds was 44%. Both effects were highly significant across all reference speeds (P < 0.001). At the highest reference speed (18°/s) the mismatch was as high as 60%. This effect was consistent across all subjects. The minimum mean PSE across all reference speeds for a single subject was 18% for a 1:2 size ratio and 32% for a size ratio of 1:3. In all subjects, these effects persisted throughout the data collection, which typically took several weeks.

Our observations of an effect of size on perceived speed and the increase in the magnitude of the effect as a function of the
size difference between the test and reference stimuli match previous reports (Ryan and Zanker 2001). In addition to the main effect of field size, we also observed an increase in mean PSE with stimulus speed. That is, at 18°/s of reference speed the magnitude of the misperception (PSE) was significantly larger than the effect at 4°/s reference speed (P < 0.05). We based this comparison on 4°/s reference speed instead of 2°/s because the mean PSE values were less reliable at the low speed (see large error bars in Fig. 2A).

We also measured the speed bias in one monkey. After finalizing all recording sessions, one monkey (Monkey Z) was trained for a speed discrimination task similar to the task performed by human subjects. Note that this monkey contributed the largest number of neurons to the results from both experiments. Initially, both reference and test stimuli had the same diameter in each trial. After reaching a reliable speed-discrimination performance (see MATERIALS AND METHODS), we decreased the diameter of the reference stimulus to half of the test stimulus diameter in about half of the trials, while keeping all other parameters constant. Figure 2B shows the results from Monkey Z pooled from the first two days after introducing the size difference between the two stimuli. The two curves show the psychometric functions from the different-size trials (4 vs. 8° diameter, black data points) and the same-size trials (both 8° diameter, gray). Each data point is obtained from a minimum of 50 trials. Pooled from three sessions over two consecutive days, mean PSE was 1.08 for the same-size condition (ca. 400 trials) and 1.43 for the different-size condition (ca. 1,000 trials).

For both types of trials, the monkey was only rewarded for his correct responses (i.e., those matching a correct comparison of the physical speeds). Because the monkey did not receive reward for most of his biased responses, inevitably his bias diminished after several sessions in two days. The discrimination threshold for the different-size condition (1.04, threshold at 84%) was higher than for the same-size condition (0.64), which might be a result of the increased uncertainty caused by comparing stimuli of different sizes and unexpected changes in the reward. We did not observe any differences in discrimination thresholds of human subjects (data not shown), consistent with previous reports (McKee et al. 1986), but note that the human subjects, in contrast to the monkeys, did not receive any feedback. Overall, the data obtained from the monkey subject at and around the point of physical equality (see data points on Fig. 2B at speed ratio = 1.0) in the different size condition indicate a pronounced bias in perceived speed, in line with the observations from human subjects.

Electrophysiology: Effects of Stimulus Size on MT Responses

To investigate the effects of stimulus size on the speed-selective responses of MT cells, we performed two experiments in two independent samples of neurons. In Experiment 1, we tested the direct effects of stimulus size on the speed selectivity of single units by determining their speed-tuning curves. In Experiment 2, we followed a different approach and analyzed changes in the firing rate statistics for a single speed as a function of stimulus size. Finally, we modeled this hypothesis directly, by applying the behavior of our neuronal sample to a hypothetical population of neurons and observed that a simple population-average model could correctly predict the perceptual bias.

Data presented in this study are from a set of 100 recording sessions, 73 in Experiment 1 and 27 in Experiment 2, from a total of 95 recorded units (5 units were used in both experiments) in three monkeys. We excluded units with poor speed selectivity (if any of the three speed-tuning indices was below 0.4) and units with poor tuning fits (adjusted $R^2$ smaller than 0.4 for any of the three tuning curves). Units selected for the analyses all had speed tuning curves well fit by a log-Gaussian function (median of the adjusted $R^2$ for the largest stimulus: 0.92, mean $= 0.88 \pm 0.11$). For these units, the median speed-tuning index for a stimulus covering the receptive field was 0.96 (mean $= 0.96 \pm 0.20$, see MATERIALS AND METHODS for

![Fig. 2. Results from the psychophysical experiments with 8 human subjects and 1 monkey. A: gray and black data points and curves show the mean values of the point of subjective equality (PSE) for two measurements with a different size ratio between the test and the reference stimuli ($n = 8$). The smaller stimulus always moved at the reference speed. Except for the reference speed of 2°/s, all data points are above 1.0 (PPE: point of physical equality), and the difference between data points and 1.0 is highly significant (two-tailed $t$-test $P < 0.001$, i.e., subjects overestimated the speed of the smaller RDP with respect to the speed of the larger RDP in all conditions). Vertical lines show the standard error of the mean. B: psychometric functions obtained from the monkey. The gray line and data points are obtained from trials with two same-size stimuli, whereas the black line and data points are from trials with two differently sized stimuli. The reference speed was 10°/s. The arrows show the PSE (i.e., the speed ratio for which the monkey was equally likely to pick one or the other stimulus) for each curve. The error bars indicate the standard error. The center of the black curve is shifted away from the PPE and the majority of the black data points lie above the gray, indicating an increase in the apparent speed of the smaller stimulus. Note that for the same-size trials, we did not use test speeds close to the reference speed to avoid trials where the monkey’s response would frequently not match the reward contingency. In the interleaved different-size trials, however, stimuli with similar or same speed were presented, and the monkey often chose the smaller stimulus as the faster one.](http://jn.physiology.org/doi/fig/10.1152/jn.00005.2011)
the speed-tuning index). Discarding neurons with poorly fit tuning curves was necessary because our main analyses were based on parameters obtained from these fits. Units with preferred speeds beyond the measurement range (0.5–64.0°/s) were discarded from the analyses of Experiment 1, unless otherwise stated.

**Experiment 1: Shifts in Speed-Tuning Curves with RDP Aperture Size**

To determine the effects of stimulus size, we measured speed-tuning curves of 120 MT units for three stimulus sizes. Fifteen units were excluded because of preferred speeds out of the stimulus range (0.5–64.0°/s) and 32 units because of poor tuning curves (see selection criteria above), leaving 73 units (Monkey Z, 49 units; Monkey D, 11 units; and Monkey T, 13 units).

Figure 3 shows the speed-tuning curves of three sample units for three stimulus sizes (black, largest stimulus; dark grey, medium stimulus; light grey, smallest stimulus). These curves demonstrate a characteristic Gauss-shaped modulation of the response as a function of stimulus speed on a logarithmic scale. From the log-Gaussian fit, we recovered three parameters for each neuron: preferred speed, tuning width, and tuning amplitude (see Materials and Methods).

To test whether there is a systematic effect of stimulus size on preferred speed, we first normalized the preferred speeds by the preferred speed for the middle-size stimulus of each unit. Inset plots in Fig. 3 show normalized preferred speeds of the remaining 70 units was weaker for smaller stimuli consistent with the results of the previous analysis.

The results presented so far were based on the responses during the entire duration of the presentation of a motion phase (from 80–800 ms after motion phase onset). To investigate the time course of the modulation in preferred speeds, we reanalyzed our neuronal data on the basis of only the responses from the first 200 ms after phase onset (0–200 ms). For 3 out of 73 units, at least one of three speed-tuning curves were poorly fit; therefore, we discarded these from the data set. The mean modulation in preferred speeds of the remaining 70 units was 0.36 (median = 0.20, P < 0.0001), and the coefficients for the two-sided regression (γ = 0.927 ± 0.044, confidence interval: 0.88–0.96) were very similar to those from the analysis of the entire phase duration, suggesting that the modulation in preferred speeds existed to comparable extent in both early and late windows of the responses of the neurons.

Across the various analyses, our results clearly show that the preferred speed of MT neurons is positively correlated with stimulus size. We tested whether the effect of stimulus size on speed tuning varied between units with different speed preference. For example, do neurons with faster preferred speeds have larger size dependence? The data in Fig. 4C show that units with higher preferred speeds diverged from the diagonal.
more notably. Figure 5 depicts the relationship between preferred speed for the largest stimulus and the size-dependent modulation in preferred speed directly. The magnitude of the shift increased significantly with the preferred speed (Pearson correlation coefficient: 0.36, \( P = 0.002 \)). In fact, for neurons with preferred speeds slower than 10°/s, the modulation in preferred speeds was unbiased. For neurons preferring intermediate speeds, slopes showed a bias toward positive values, and, for neurons with the highest preferred speeds, slopes were exclusively positive. This result matches our observations in human subjects because the magnitude of the bias (PSE) increased as a function of reference speed (i.e., higher perceived speed for the smaller stimulus at higher speeds). This indicates that neuronal subpopulations with faster preferred speeds will contribute to a stronger bias at higher stimulus speeds.

To further understand the effect of stimulus size on speed-tuning curves of MT neurons, we examined whether size-dependent changes observed in preferred speed are accompanied by a change in tuning width and amplitude. Mean tuning width was 1.19 ± 0.56 (median = 1.02) in log units for the largest stimulus, and 1.26 ± 0.63 (median = 1.15) for the smallest stimulus. We did not observe any significant difference in tuning width in any of the three comparisons (repeated measures one-way ANOVA, \( P > 0.05 \)).

On the other hand, tuning amplitudes increased significantly with stimulus size (repeated measures one-way ANOVA, \( P < 0.0001 \)). Mean amplitude for the smallest stimulus was 33.0 ± 21.2 and for the largest stimulus 44.7 ± 25.6 spike/s. Figure 6 compares the amplitudes for a larger and for a smaller stimulus (each neuron contributes three comparisons to this figure). The majority of the data points lie above the diagonal, indicating that tuning amplitude increased with stimulus size. This obser-

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**Fig. 4.** Population results. **A:** histogram of modulation in preferred speed (PS) in all 73 neurons. The mean speed modulation is positive and significantly different from 0, indicating a positive correlation between preferred speed and stimulus size in the population. The black, dark gray, and light gray boxes in the histogram indicate the three monkeys. **B:** differences between normalized preferred speeds for large-medium and medium-small stimuli. All gray symbols indicate the neurons with a negative slope (negative size-dependent modulation) in preferred speed change, and black symbols indicate neurons with a positive slope (positive size-dependent modulation). **Insets:** schematic representation of the 4 possible alignments of 3 preferred speeds (symbols as in Fig. 3). A majority of the units with positive slopes (positive size dependency) were in the upper right quadrant, indicating that the significance of the data comes mainly from units with a clear increase in preferred speed with stimulus size. The units are sorted in three groups (see legend) according to their preferred speeds for the largest stimulus. Units with preferred speeds above 30°/s (circles) mostly had positive slopes (black circles) and fell in the upper right quadrant (i.e., preferred speed increases with stimulus size).

**C:** regression analysis of log-transformed preferred speeds for the largest and smallest stimulus. The majority of the data points lies below the diagonal, indicating that preferred speeds were slower for smaller stimuli. The equation for the linear regression was \( y = 0.921x - 0.007 \), CI, confidence interval.
The difference in response onset latency as the first bin after stimulus onset where the firing rate exceeded the mean spontaneous firing rate (mean response from fixation-only trials without stimulus presentation) by two standard deviations and continued to increase for the next two bins (Raiguel et al. 1999). The onset latency for three stimulus sizes was 29.42 ms (large), 30.60 ms (medium), and 30.45 ms (small). The difference between the latencies for the three sizes was not significant (repeated measures one-way ANOVA, $P = 0.93$).

We also computed the peak response latencies of each neuron for three stimulus sizes, as the bin with the highest response after motion phase onset. Although the peak response latencies showed a clear trend of increase with decreasing stimulus size (large, 165.23 ms; medium, 178.98 ms; small, 196.35 ms), this trend was statistically not significant (repeated measures one-way ANOVA, $P = 0.66$). The lack of significance was possibly due to many outliers from neurons that showed reduced responses for smaller stimuli and had noisy SDF curves. Peak response latencies obtained from the population SDFs averaged across the sample matched the values reported in earlier studies more accurately (large, 87 ms; medium, 86 ms; small, 93 ms). Another reason for the lack of significance might be that, whereas most neurons had higher responses for a larger stimulus, about 40% ($n = 29$) of neurons did not show an increase in response amplitude for the large stimulus, and the amplitudes were similar across the different stimulus sizes. The mean ratio of peak response latency (large/small) of these neurons was not different from 1 ($P = 0.13$). These results are in accordance with the response-magnitude latency dependence.

**Experiment 2: Changes in Firing Rate Statistics with RDP Aperture Size**

In Experiment 2, we used a receiver operating characteristic (ROC) analysis to investigate the influence of stimulus size on the firing-rate statistics of individual neurons at a single stimulus speed. We hypothesized that perceived speed is determined by pooling firing rates across the MT population. In other words, perceived speed is based on a readout mechanism that interprets a change in firing rate as a change in stimulus speed. We wanted to know whether a decrease in stimulus size results in a change in firing rate of single neurons that could also be obtained by an increase in stimulus speed.

ROC curves are widely used in signal detection theory (Green and Swets 1966) and medical diagnostics, as well as in choice-probability analyses where a correlation between neuronal activity and psychophysical data is sought (Britten et al. 1992; Liu and Newsome 2005). Here we use ROC curves to quantify the separation between distributions of firing rates evoked by different stimulus sizes. For this purpose, after mapping the receptive field and determining the preferred direction, we determined the speed-tuning curve with a stimulus approximately covering the excitatory region of the CRF, which also served as the largest stimulus in Experiment 2. We computed the two steepest segments ($x_S$) of the tuning curve (one on the ascending and the other on the descending arm) with the equation

$$x_S = x_0 \times \exp\left[\frac{-\log\sigma^2}{2}\right] \exp\left[\pm \log\sigma \sqrt{\log\sigma^2 + 4} \right]$$

The resulting two $x_S$ values correspond to the two speeds with the largest values for the roots of the second derivative of the fitted log-Gaussian. For clarity, we termed the speeds corresponding to these two high slope points of the tuning curve as the lower (for the ascending arm) and the higher (for the descending arm) slope speed. We used one of these two speeds as the constant stimulus speed of Experiment 2. The chosen

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**Fig. 6.** Comparison of tuning amplitude for different stimulus sizes. Tuning amplitude in the population of neurons ($n = 73$) for 3 pairwise comparisons of stimulus size (triangles: small vs. large, squares: small vs. middle, asterisks: middle vs. large stimulus). The solid symbols indicate the means in each subplot.
slope speed depended on the speed-tuning profile and the overall responsiveness of the unit. According to their preferred speed, we categorized units roughly as low pass (<10°/s), band pass (>10°/s and <30°/s), and high pass (>30°/s). In most cases, we used the ascending slope speed for high-pass and band-pass units and the descending slope speed for low-pass units. For each stimulus size, we computed a histogram of firing rates (bin size = 1 spike/s). We then summed the frequencies in each bin cumulatively and plotted the cumulative sums in pairs (i.e., largest stimulus vs. half diameter stimulus). The resulting curve corresponded to the ROC curve, and we computed the area under this curve (AUC) for further analysis.

There are at least two advantages to this approach. First, it enabled us to analyze neuronal responses independent from any assumptions made by the tuning-curve fitting procedures. Second, by concentrating on only a single point of the tuning curve, where the log-Gaussian fit was the steepest either on the ascending or on the descending arm, we were able to collect a large number of trials for each stimulus size. We picked the stimulus speed from the steepest region of the tuning curve. Here, a neuron is most sensitive to a change in speed because changes in speed result in the largest changes in firing rate (Seung and Sompolinsky 1993; Butts and Goldman 2006; see also Hol and Treue 2001).

Figure 7 illustrates our procedure in one sample unit. Figure 7A shows the speed-tuning curve of the unit, measured for the largest stimulus that was matched to the size of the receptive field. The black arrow indicates the preferred speed, and the gray arrow shows the speed at the point with the highest slope in the ascending portion of the tuning curve. Note that the appearance of the steepness in this plot changed because of the log-speed axis. After setting the speed constant at the ascending slope speed, we measured firing rates for three stimulus sizes in a larger number of trials (40–50). We compared all firing-rate distributions pairwise by computing the area under the ROC curve, their firing rate at the descending slope speed. For both types of slope speed, we categorized units roughly as low pass (<10°/s), band pass (>10°/s and <30°/s), and high pass (>30°/s). In most cases, we used the ascending slope speed for high-pass and band-pass units and the descending slope speed for low-pass units. For each stimulus size, we computed a histogram of firing rates (bin size = 1 spike/s). We then summed the frequencies in each bin cumulatively and plotted the cumulative sums in pairs (i.e., largest stimulus vs. half diameter stimulus). The resulting curve corresponded to the ROC curve, and we computed the area under this curve (AUC) for further analysis.

The results are summarized in Fig. 8 as a stacked histogram of all adjusted AUC values obtained from 27 units in two monkeys (Monkey Z and D). The histogram contains three adjusted AUC values of each unit for each pairwise comparison (e.g., AUC for “small vs. large”). The mean AUC of the sample was 0.60 (SE = 0.02, median = 0.62). This increase above 0.5 was highly significant (both monkeys together: $P < 0.01$, 2-tailed t-test, $n = 27$; Monkey Z: median = 0.60, $P = 0.01$, 21 units; Monkey D: median = 0.57, $P = 0.34$, 6 units; AUC values from 3 comparisons averaged for each unit). These results indicate that a reduction in stimulus size caused the following changes: for a smaller stimulus, units with fast or moderate preferred speeds (preferred speed >10°/s) increased their firing rate at their ascending slope speed, whereas units with low preferred speeds (preferred speed <10°/s) decreased their firing rate at their descending slope speed. For both types
of neurons, the change in firing rate was in the same direction as that caused by an increase in stimulus speed.

Our results from Experiments 1 and 2 are in agreement. Both sets of measurements indicate a shift in speed preference toward lower speeds with a decrease in stimulus size.

Application of a Population-Average Model to Neuronal Data

Theoretically, if the speed-tuning curve of a neuron is known, the speed of a moving stimulus can be estimated from the response of the neuron to the stimulus. However, because the speed tuning of MT neurons displays a bell-shaped curve, a stimulus moving at a speed on the flanks of the tuning curve will remain ambiguous to a linear decoder. To overcome this problem, the decoder must use the activity of a population of neurons (Georgopoulus et al. 1986).

We implemented a population model of speed coding to determine what perceptual effects can be accounted for by the shifts in tuning curves that we observed in Experiment 1. We made the following assumptions: 1) In area MT, stimulus speed is encoded by single neurons using a “labeled-line” code (also known as the identity code), where each neuron signals the presence of a specific speed (“label speed”, e.g., the preferred speed of the neuron for the largest stimulus). 2) The vote of each neuron for its label speed is weighted by the firing rate of the neuron. 3) Label speeds are evenly distributed across the population in a logarithmic speed space from 0.1 to 256.0°/s. 4) The size-dependent change in the preferred speed of MT neurons follows the regression line obtained in Experiment 1 (see Fig. 4C). The model equation for the population vector (center-of-mass) had the following equation

$$SL' = \frac{\sum (RL_i \times LS_i)}{\sum (RL_i)}$$

Here, $SL'$ is the perceived speed for a large stimulus, decoded from the population response as the sum of label speeds of single neurons ($LS_i$), weighted by the response of each neuron ($RL_i$), normalized by the summed activity of the population, $\sum (RL_i)$.

We computed the responses for large and small stimuli ($RL_i$ and $RS_i$) using a log-Gaussian function

$$RL_i = \exp\left\{-\frac{1}{2}\left[\frac{\log(PSL_i) - \log(x)}{\log(\sigma)}\right]^2\right\}$$

where $x$ denotes the input speed, $PSL_i$ shows the preferred speed for a large stimulus, and $\sigma$ refers to population variance. We set the $\sigma$ as the mean tuning width from our neuronal sample. To obtain responses to a small stimulus, we computed the preferred speeds for the small stimulus, using the preferred speeds for the large stimulus and the regression coefficients obtained in analysis shown in Fig. 4C. Results are shown in Fig. 9, B–C. The two curves in B show the response of the population for a large ($RL_i$, solid line) and for the smaller ($RS_i$, dashed line) stimulus for an input speed of 18°/s. The population tuning curve peaks at a higher label speed for the smaller stimulus because the distribution of weights is shifted toward neurons that prefer faster speeds.

The ratio between the two population activities can be considered as analogous to the PSE value in the human psychophysics experiments. This ratio is plotted in Fig. 9C as a function of the input speed. The open circles are obtained by using the same data set as in Figs. 4–6 ($n = 73$). The PSE was above 1 across the entire range of input speeds and increased with input speed. To assess the influence of high-pass neurons, we repeated the regression analysis (Fig. 4C) including units with preferred speeds higher than the experimental range (>64°/s), given that these neurons passed other criteria for data analysis (regression coefficient $r = 0.89$, confidence interval: 0.84–0.94). Typical preferred speed for these units for any size of the stimulus was below 120°/s with the tuning curve of one unit peaking at 258°/s for the largest stimulus (adjusted $r^2$ for this particular tuning curve fit was 0.997). The PSE estimated by the model from data including the high-pass neurons is shown with the square symbols. The estimated PSE was higher than that from our standard data set across all input speeds. The solid circles show the mean PSE from human subjects as in Fig. 2A for a comparison, and the asterisk indicates the PSE obtained from the monkey. When we tested only high-pass...
units (preferred speed >30°/s) and ignored the low- and band-pass ones, the model predicted an unrealistically high bias (not shown). When all neurons contributed to the population average, on the other hand, the prediction of the bias was more realistic, as seen in Fig. 9C (open circles and squares). This is in agreement with the assumption of the labeled line model that all neurons contribute equally to the speed estimate.

The model predictions presented so far were adequate to estimate the sign of the field-size effect on the basis of the changes in the speed tuning of our neuronal sample. However, there were two complications to consider. First, the model underestimated the bias to a certain extent, when neurons with preferred speeds above the measurement range were not included. Second, there was one potential conflict with the effects of luminance contrast, as reported in other studies. A decrease in the luminance contrast of RDPs causes a decrease in preferred speed of MT neurons (Pack et al. 2005; Krekelberg et al. 2006). This change in speed tuning parallels the change caused by a reduction in stimulus size in our study, indicating that the simple population-average model, such as the one we applied above, would predict an increase in perceived speed with a decrease in contrast, i.e., a mismatch between the two effects from a population code point of view.

To address the effects of both stimulus size and contrast, we considered the changes in the total population response. In our neuronal data, when stimulus size was reduced, we observed a small decrease in response amplitude at single neuron level, as expected from size-tuning mechanisms (see Experiment I). When stimulus contrast is reduced, response amplitude decreases as well, as expected from the contrast sensitivity function.

We tested the assumption that a decrease in stimulus size would not affect the total population response as much as a decrease in stimulus contrast. Significant effects of contrast on perceived speed emerge after large reductions of stimulus contrast (as low as 10–20%; Thompson 1982; Krekelberg et al. 2006). When the contrast of a stimulus is reduced, most neurons in the population reduce their peak responses, whereas, when stimulus size is decreased, the reduction in total population response may not be as strong. It has been shown that suppressive effects of the surround are more predominant at high contrast than at low contrast (Pack et al. 2005). At high contrast, when a stimulus becomes smaller, for some neurons the inhibitory surround effects are reduced, optimizing the stimulus size. Conversely, although a larger stimulus may evoke higher responses from some neurons, it may increase the suppressive effects of the surround. To implement this in the model, we replaced the population sum in the denominator of R, C equations (Eq. 3) by a constant ($\alpha$).

Hence the perceived speeds for a small stimulus (Eq. 5) and for a large stimulus (Eq. 6) are computed by the following equations

$$SS' = \frac{\sum (RS_i \times LS_i)}{\alpha}$$

$$SL' = \frac{\sum (RL_i \times LS_i)}{\alpha}$$

When we set $\alpha$ as the total population response to a large-size, high-contrast (i.e., “optimal”) stimulus, i.e., $\alpha = \Sigma(RL_i)$, this variant of the model provided a very close prediction to our psychophysical data with the size effect (Fig. 9C, triangles). When we set $\alpha$ as the total population response to the smaller stimulus, i.e., $\alpha = \Sigma(RS_i)$, the estimated PSEs across all reference speeds decreased by a 10% but still followed the trend from the human psychophysics. The rationale for using the total population activity as the normalizing factor ($\alpha$) is that this activity is available to the decoder in a discrimination task. Also, it is the relative speed of the stimulus being reported rather than the physical speed. Although one of the two stimuli in the task could evoke a higher population response, the interchangeability of the denominator suggests that any reference population activity that is not too far from the activity evoked by any of the two stimuli will successfully decode the perceived speed and predict the speed bias. However, we...
obtained the most accurate estimates of the input speeds when the normalization was done by the optimal activity (i.e., summed population response to the large stimulus).

Furthermore, we observed that, when responses \( R_1 \) were decreased (e.g., for a low-contrast stimulus), the trend of the model PSE estimates changed its sign, indicating that the perceived speed of the low-contrast stimulus was decreased compared with a high-contrast (i.e., optimal) stimulus. Reducing the model neuron responses by 30% decreased PSEs about 30% at 10%/s reference speed (model predictions not shown).

In summary, the population-average model predicts the psychophysical observation from our physiological data from MT. Furthermore, when the population activity is normalized by an internal representation of an optimal stimulus, differential changes in response amplitudes may account for the seemingly opposite effects of stimulus size and luminance contrast.

**DISCUSSION**

This study was designed to investigate whether the response properties of MT neurons to moving patterns account for the field-size effect in perceived speed. In the preferred speed experiment (Experiment 1), we determined speed-tuning curves for MT neurons for different stimulus sizes and observed that the preferred speeds of the neurons increased for larger stimulus sizes. In the slope-speed experiment (Experiment 2), we determined the effect of stimulus size on the responses of MT neurons to stimulus speeds along the sides of the speed-tuning curve of each neuron and found that a decrease in stimulus size modulated the firing rate analogous to an increase in stimulus speed. The results from the two experiments are in agreement and support the hypothesis that the changes in the population activity of speed-selective neurons in area MT are the basis for the decrease in perceived speed with increasing stimulus size.

Our results are well matched to the psychophysically observed field-size effect; implementing a simple population model of speed coding, we show that the shift in preferred speeds observed in Experiment 1 can account for the increase in perceived speed with decreasing stimulus size. Similarly in Experiment 2, the responses of MT neurons are modulated by a decrease in stimulus size in the same way as by an increase in perceived speed. Each neuron can be considered as voting for faster or for slower stimulus speed, depending on the relative positions of the stimulus speed and the preferred speed of the neuron (Krekelberg et al. 2006; Hietanen et al. 2008). A comparison of the activity of two cells or two subpopulations with different preferred speeds can provide an estimate for speed. This is also consistent with a two-channel model of speed (Thompson 1982), in which neurons are subdivided in fast and slow channels, instead of comprising a continuum of labels as in the model we implemented.

We observed that in humans the magnitude of the speed misperception increased with increasing reference speed (Fig. 2). Similarly, the shift in preferred speed with stimulus size was largest for neurons that preferred higher speeds (Fig. 4C and 5). This match between perception and neural responses further strengthens the link between the field-size effect and the activity of MT neurons and suggests that a readout from MT activity provides a good account for the changes in perceived speed.

### Effect of Stimulus Size in Monkey Z

We were able to reproduce the effect of field-size on perceived speed in one monkey, using a standard 2AFC speed discrimination task similar to our human psychophysics design. When the monkey was performing a speed discrimination task with one stimulus having half the diameter of the other, both moving at 10%/s, he reported the smaller stimulus to move about 40% faster than the larger stimulus. This effect was comparable to the bias in humans.

For long-term studies, it may not be advisable to reward the monkey veridically if the choices of the animal are biased. A specifically designed paradigm should be used, where the feedback (e.g., juice reward) does not contradict the animal’s percept, especially when the stimuli differ in a salient aspect, e.g., a large size difference. One suitable method might be a combination of two rewarding schemes: random rewarding for perithreshold trials (i.e., trials at PPE and with small speed differences) and veridical rewarding for trials with large speed difference, where the monkey’s judgments are mostly consistent with the reward. However, if the location of the animal’s PSE is not known before setting these boundaries, the monkey may quickly learn to guess for difficult perithreshold trials. Therefore, more sophisticated experimental designs may be needed for long-term experiments.

### Effect of Contrast on Speed Tuning and Considerations on the Predictions of the Population-Average Model

Another well-known factor that affects perceived speed is the luminance contrast of a moving pattern. Lowering the contrast induces a decrease in perceived speed (Thompson 1982; Blakemore and Snowden 1999; Hurlimann et al. 2002). According to a labeled-line model, such an effect would require that the preferred speeds of MT neurons shift toward higher speeds at low contrast, causing a shift in the population activity toward slower speeds, reducing perceived speed. However, electrophysiological studies with macaque monkeys showed that, for many neurons in MT, preferred speed decreases with a reduction of contrast (Pack et al. 2005; Krekelberg et al. 2006), and a similar observation has also been reported for area V1 (Livingstone and Conway 2007).

Several studies suggested that, when a bias term is used in the population-average model, neuronal data could account for the reduction in perceived speed (Priebe and Lisberger 2004; Pack et al. 2005). Without such manipulations, the contrast-dependent and the size-dependent changes in MT responses seem contradictory within the framework of a population-average code. In the population-average model we implemented, we observed that when the modeled population response was normalized to the population response to a reference stimulus, a reduction in response amplitudes caused a decrease in perceived speed for low-contrast stimuli. However, this prediction is mainly addressing the sign of the misperception, and we did not aim at a quantitative comparison for the effect of contrast. Further studies may be needed to resolve this issue.

In a labeled-line code, one of the most important determinants of the outcome is the distribution of labels (i.e., preferred, or label speeds). When applying such a model to neuronal data, the distribution of preferred speeds in the data can change the predictions of the model. Most studies with a limited size of
neurons reported a bell-shaped distribution for the preferred speeds in MT (Maunsell and Van Essen 1983; Cheng et al. 1994; Mikami et al. 1986). However, a sampling bias is often inevitable, and there is evidence that the distribution is highly uniform on a logarithmic scale on the basis of a study with a larger number of speed-selective MT neurons (Nover et al. 2005). This distribution scheme is in accordance with a labeled-line coding of speed. When we included units that preferred speeds faster than our measurement range (64°/s), the predicted bias increased strongly (Fig. 9C). This suggests that high-pass neurons may play a critical role in the magnitude of the perceptual bias.

Although our results do not rule out other types of models for speed, e.g., Bayesian models (Weiss et al. 2002), or two-channel ratio models (Thompson 1982; Thompson et al. 2006; Hammett et al. 2005), the labeled-line-population model appears to be more plausible for physiological data because such models have been shown to map behavioral outcomes on selective neuronal responses successfully (Churchland and Lisberger 2001; Churchland et al. 2007; Sundberg et al. 2006).

Possible Biological Explanations for the Change in Speed Preference

Is the field-size effect resulting from top-down mechanisms? Our neuronal results from the two experiments with a fixation task suggest that the misperception does not purely depend on the engagement of working memory or of attention. Instead, they support the hypothesis that already the encoding of speed is dependent on stimulus size. This encoding bias is then revealed perceptually when performing a speed-discrimination task.

It has been shown that, in MT, neurons with smaller CRFs tend to have slower preferred speeds (Mikami et al. 1986). Related to this, direction-selective neurons in V1, which provide the major input to MT, have much smaller receptive fields than MT neurons and tend to prefer slower speeds (Churchland et al. 2005). The preference for faster speeds in later cortical areas is possibly due to the spatial integration of visual information along the visual pathway (i.e., a larger number of presynaptic neurons with smaller receptive fields providing input to a postsynaptic neuron with larger receptive field). A candidate biological explanation for the size-dependent shifts in MT tuning curves may rely on the specifics of these convergence mechanisms. However, so far it was not clear whether neurons would show variable tuning preferences for differently sized stimuli within their receptive fields. This piece of information is important because it is the output of MT neurons that has been linked to the perception of speed (Newsome and Pare 1998; Orban et al. 1995; Huk and Heeger 2000; Priebe et al. 2001; Liu and Newsome 2005; McKeefry et al. 2008).

Another possible explanation of the shift in preferred speeds may lie in the type of the stimulus we have used. As the diameter of a RDP becomes smaller, the ratio between the net motion and flicker increases because the proportion of dots disappearing on the edge and reappearing on the other side within a period of time increases as well. We have previously shown an increase in perceived speed for stimuli with dots of shorter lifetime, i.e., the time a dot was undergoing translation before being replotted at a random location, or when flickering dots were added to the display (Treue et al. 1993). Therefore, increased flicker or additional stimulus components at high temporal frequencies may underlie the changes in speed preference of MT neurons.

The known effects of luminance contrast could not have interfered with our psychophysical and physiological results because in any given experiment the dot and the background color (hence the contrast) were fixed. A recent study revealed that luminance, i.e., amount of light emitted per unit area, also induced a bias in perceived speed; stimuli of high luminance appeared to move faster than those of low luminance (Vaziri-Pashkam and Cavanagh 2008). Due to the fixed dot and background colors, the luminance was constant within any experiment presented in this study.

We also considered possible effects of contrast polarity. To test whether the field-size effect exists in both contrast polarities, we performed a control experiment with four additional subjects. We kept all parameters identical to those described for our human psychophysics but reversed the luminance of dots vs. background (dots: 84 cd/m²; background: 23 cd/m²), closely matching the intensities used in the experiments with the monkeys. The mean PSE at a reference speed of 4°/s was 1.08 (P > 0.5) and at a reference speed of 18°/s 1.40 (P = 0.02), showing a trend of increase similar to the mean PSE obtained from the experiments with the original contrast polarity. All mean PSE values, except for those for the two slowest reference speeds (2–4°/s), were significant (P < 0.05). These results are in agreement with those from Ryan and Zanker (2001), who also used bright dots on dark background. This may suggest that the absolute intensity of light may not induce any bias on perceived speed when the light is identically distributed across the stimuli to be compared.

How does the encoding of speed depend on stimulus size? Although some or all factors listed above may play a role in the outcome of the field-size effect, the specific mechanisms behind receptive field properties that explain the dependence of speed tuning on stimulus size remain unclear.

In conclusion, our results demonstrate that stimulus size-dependent responses of MT neurons can account for biases in perceived speed and that a simple labeled-line code for motion speed is consistent with these perceptual effects of stimulus size. Although these experiments were not designed to reveal specific receptive field mechanisms for the field-size effect, our results strengthen the link between MT activity and perceived speed and suggest a general mechanism for how some perceptual biases can result from input-dependent, systematic variability in neuronal responses.

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DISCUSSIONS

No conflicts of interest, financial or otherwise, are declared by the authors.

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