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

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Abstract

In humans, the perceived speed of random dot patterns (RDP) moving within small apertures is faster than that of RDPs moving within larger apertures at the same physical speed. To investigate the neural basis of this illusion, we recorded the responses of direction and speed-selective neurons in the middle temporal area (MT) of macaque monkeys to stimuli varying in size and speed. Our results show that the preferred speed of MT neurons is slower for smaller stimuli. This effect was larger for neurons preferring faster speeds, matching our psychophysical observation in human subjects that the magnitude of the misperception is larger at higher stimulus speeds. Our physiological data indicate that across a population of speed-tuned neurons in MT, decreasing the size of a stimulus would shift the activity profile to neurons tuned for higher speeds. Modeling a labeled-line read-out of this shifted profile we show an increased apparent speed, in line with the psychophysical observations. This link strengthens the evidence for a causal role of area MT in speed perception. The systematic shift in tuning curves of single neurons with stimulus size might reflect a general mechanism for feature-mismatch illusions in visual perception.

INTRODUCTION

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 (MST) 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; Priebe et al., 2003). In non-human 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\(^+\), the presumed human homologue 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 dependence 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 perception towards 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+ 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 2006; Priebe et al., 2003, 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\(^{\circ}/\text{s}\)) stimulus speeds
(Orban, 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 to 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 (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 in 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 CRT 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 pix/deg.

**Electrophysiological Recordings.** Extracellular action potentials of single-units in the middle temporal area (MT) were recorded with single tungsten microelectrodes (4MΩ at 1 kHz, FHC, Bowdoinham, ME) controlled by a hydraulic micropositioner (David Kopf Inst., Tujunga, CA). Neuronal signals were processed and recorded with a data acquisition system (Plexon Inc., 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 using 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° x 0.15°) on the display throughout a variable trial duration of 4 to 6 seconds. 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 (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 one of 12 different directions (0, 30, 60, … 330°) and at one of 8 different speeds (0.5, 1, 2, 4, 8, 16, 32, 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/deg². The size of the dots was 0.01deg². 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 7 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 4000 – 6000 ms of stimulus presentation.

For each neuron, three stimulus sizes were used. The largest stimulus nearly covered the classical receptive field, whereas the diameter of the medium and small stimuli were 1/2 and 1/4 of the largest stimulus’ diameter. The diameter of the largest stimuli used for different units ranged from 8° to 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˚/s), all motion pulses in preferred or null direction were presented at a ‘slope speed’ (see Formula 2 in Results section). 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 a neuron’s average response rate. In Experiment 1, this firing rate was determined based on 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. a neuron’s response as a function of stimulus speed $x$) were fit by a four parameter logarithmic Gaussian:

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

where $B$ denotes the baseline firing rate, $A$ is the maximal amplitude of the tuning curve above $B$, $x_0$ represents the preferred speed, i.e. the speed corresponding to the peak of the response profile, and $\sigma$ (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, dividing the amplitude of the response (maximum firing rate – minimum firing rate) by the difference between maximum and spontaneous firing rate: \( R_{\text{max}} - R_{\text{min}} / R_{\text{max}} - R_{\text{base}} \) (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°/s) were excluded.

**Psychophysical methods**

Eleven naive human subjects (with normal or corrected-to-normal vision) and one author (PB) participated in the psychophysical experiment. Subjects were seated in a dimly lit chamber in front of a 22-inch CRT display monitor (LaCie Ltd.) with a resolution of 40 pix/deg (1200 x 1600 pixels) and a refresh rate of 85 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 deg x 0.2 deg) 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. 130 ms 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 9 reference speeds (‘RS’, 2,4,6,8,10,12,14,16,18°/s) and for each reference speed 25 test speeds were used (varying from 0.5 x RS to 2.5 x RS, in 0.1 x 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 deg² and dot density was 10 dots/deg². Contrast between stimuli and background was maximal, with dark dots were dark (0.08 cd/m²) on a bright background was bright (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 insure that most of the speeds presented were in the peri-threshold 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 the peri-threshold range and thus provides a more accurate measurement 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 weeks.

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 form of two sided t-tests of mean PSE vs. the PPE (point of physical equality) were performed with MATLAB and the p-values in the corresponding results section indicate the significance level from these analyses.

*Psychophysical measurements with Monkey Z.* After completing all electrophysiological recoding sessions, Monkey Z was trained for the same 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˚ diameter 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 reaching 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 section on electrophysiological recordings for the luminance, dot size and density). The speeds of the test stimuli in the different-size set were 3,5,8,13,15,18,23,25˚/s; and in the same-size set, in addition to these, 9,10 and 11˚/s were also included. The reason for not presenting stimuli with 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: The effects of stimulus size on perceived speed

To quantify the field-size effect with the RDP stimuli we used in the electrophysiological experiments, we measured the point of subjective equality (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 deg, 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 °, 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 & 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 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, since 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 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 °ø, black) and the “same-size” trials (both 8 °ø, gray). Each data point is obtained from a minimum of 50 trials. Pooled from 3 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. 1000 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). Since 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: The 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 ± 0.11). For these units, the median speed tuning index for a stimulus covering the receptive field was 0.96 (mean = 0.96 ± 0.20, see Methods for the speed tuning index). Discarding neurons with poorly fit tuning curves was necessary, since our main analyses were based on parameters obtained from these fits. Units with preferred speeds beyond the measurement range (0.5-64°/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. 15 units were excluded due to preferred speeds out of the stimulus range (0.5°- 64°/s) and 32 units because of poor tuning curves (see selection criteria above), leaving 73 units (monkey Z: 49 units, monkey D: 11 units, 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 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 sample units as a function of stimulus diameter relative to the receptive field diameter. We fitted a straight line through the
preferred speeds and used the slope of the line as an indicator of the sign and magnitude of the change in the speed preference. The slopes of the fits for the three example neurons (0.37, 0.87 and 0.32 from left to right in Fig. 3A) are positive and indicate an increase in preferred speed with increasing stimulus size.

The slope was positive for the majority of the units (54 of 73 units, 74% of the population) indicating an increase in preferred speed with increasing stimulus size. Fig. 4A shows the distribution of the size-dependent modulation in preferred speeds across our sample of cells. The mean slope of 0.26 was significantly larger than zero (SEM = 0.06, median = 0.23, p < 0.001, t-test) and was similar in each of the three monkeys (for Monkey Z: median = 0.21, mean = 0.23, p = 0.013 and Monkey T: median = 0.26, mean = 0.33, p = 0.016). Given the small number of neurons (n = 11), the effect did not reach significance for Monkey D (mean = 0.33, median = 0.36, p = 0.056).

To examine how the size dependency is distributed across our neuronal sample, we compared the difference between normalized preferred speeds for largest and medium stimulus to the difference between normalized preferred speeds for medium and smallest stimulus for each neuron. Figure 4B shows this distribution. The largest number of neurons is located in the upper right quadrant, indicating that most neurons increased their preferred speed with stimulus size in a continuous manner. Furthermore, the majority of these cells were those that preferred speeds higher than 30˚/s (we arbitrarily classify these units as “high-pass”, and units preferring speeds slower than 10˚/s as “low-pass”) for the largest stimulus (black circle symbols).

To analyze the stimulus size dependent modulation in preferred speeds, we also fitted regression lines to pairs of preferred speeds (largest vs. smallest, largest vs. medium, medium vs. smallest stimulus). Since the two preferred speeds in each regression are both dependent...
variables, we performed a two-sided regression. As the modulation in preferred speeds for cells preferring higher speeds was larger, we log-transformed the non-normalized preferred speeds.

Figure 4C shows the results of this analysis. The formula for the obtained regression was $y = 0.92 * x - 0.007$ (confidence intervals: 0.88-0.96). The majority of the data points were below the diagonal, indicating that preferred speeds were slower 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 based only on the responses from the first 200 ms after phase onset (0 - 200 ms). For three 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 ($y = 0.927 * x - 0.044$, confidence intervals: 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 neurons’ responses.

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 Figure 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, since 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 sp/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 observation is relevant in the context of surround inhibition.
At a given stimulus speed, a neuron’s response should be at maximum for stimuli roughly
covering the excitatory area, i.e. the classical receptive field (CRF), but might be lower for
stimuli larger or smaller than the CRF, since many MT neurons have an inhibitory surround and
are tuned for stimulus size (Allman et al., 1985; Raiguel et al., 1995; Xiao et al., 1995 and
1997). Data points representing the comparison between the amplitudes for the largest and
smallest stimuli (Fig. 6, triangle symbols) are above the diagonal (filled triangle shows the
mean, asterisks and squares indicate middle vs. large and small vs. middle stimuli,
respectively). Responses to the larger stimuli were higher for most neurons, indicating that
stimulus size was appropriately matched to the receptive field size and inhibitory surrounds did
not influence our data.

We also assessed the relationship between stimulus size and response latency. In
general, latencies are longer for non-optimal stimuli that elicit lower responses than more
effective stimuli that elicit higher responses (Raiguel et al, 1999; Maunsell et al., 1999). Since
most MT neurons display size tuning, stimuli that match the size of the excitatory receptive field
should be more optimal than smaller stimuli. To investigate possible changes in latencies, we
first computed the spike density functions (SDF) of all neurons for the three sizes of stimuli. For
each neuron, we averaged spikes across multiple presentations of a motion phase in 1 ms bins
within the entire duration of the stimulus motion phase (0-800 ms). The motion phase was in
the preferred direction and at the raw preferred speed (i.e. one of eight stimulus speeds to
which the neuron showed its highest raw firing rate). We smoothed the SDFs with a Gaussian
window of 10 ms standard deviation and normalized each SDF to its maximum for the largest
stimulus. We calculated the 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 continues 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 while 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 read-out 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 classical receptive field, 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:

$$x_s = x_0 \times \exp\left(\frac{-\log \sigma^2}{2}\right) \exp\left(\pm \frac{\log \sigma \sqrt{\log \sigma^2 + 4}}{2}\right) \quad (2)$$

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 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 ($< 10^\circ$/s), band-pass ($>10^\circ$/s and $< 30^\circ$/s), high-pass ($>30^\circ$/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. ½ 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. Firstly, it enabled us to analyze neuronal responses independent from any assumptions made by the tuning curve fitting procedures. Secondly, 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, since 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. Fig. 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 grey arrow shows the speed at the highest slope on the ascending arm of the tuning curve. Note that the appearance of the steepness in this plot changed due to 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. Fig. 7B shows an example comparison of firing rate distributions for largest vs. smallest stimulus of the same neuron. The AUC is a measure of discriminability of the responses to a larger stimulus and a smaller stimulus and has a value between 0 and 1. For two distributions that are completely separated, the AUC value is either 1 or 0. As the degree of overlap between the two distributions increases, the AUC approaches 0.5. For the sample neuron, the AUC for large vs. small comparison was 0.87 (Figure 7C), indicating that
the firing rates for the small stimulus were higher than those for the large stimulus.

The speed tuning profiles of the single units influenced our choice for the slope speed. For example, for some units, only one slope speed fell within the range of the experimental speeds. Therefore, the results from the ascending slope were predominantly from units that preferred higher speeds and the descending slope speed was chosen mostly for units that preferred lower speeds (Figure 8D).

We hypothesized that if MT neurons are responding to a decrease in stimulus size in the same way as they respond to an increase in stimulus speed, at the chosen slope speed, the firing rate should decrease on the descending arm and increase on the ascending arm of a tuning curve. Consequently, the divergence of distributions will have opposite signs for the two different slopes. Therefore, we inverted the sign of the AUC values of “descending” units to make the separation between response distributions of these units and the “ascending” units comparable. We called the resulting AUC values adjusted AUC.

The results are summarized in Figure 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 (SEM=0.02, median=0.62). This increase above 0.5 was highly significant (both monkeys together: p<0.01, two-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 three 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 Experiment 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 a neuron’s speed tuning curve is known, the speed of a moving stimulus can be estimated from the response of the neuron to the stimulus. However, since 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 (Georgopoulos 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 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 neuron’s preferred speed for the largest stimulus). (2) Each neuron’s vote for its label speed is weighted by the neuron’s firing rate. (3) Label speeds are evenly distributed across the population in a logarithmic speed space from 0.1 to 256 °/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 formula:
Here, $SL'$ is the perceived speed for a large stimulus, decoded from the population response as the sum of single neurons' label speeds ($LS_i$), weighted by each neuron's response ($RL_i$), 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:

$$RL_i = \exp \left( -\frac{1}{2} \left( \frac{\log (PSL_i) - \log(x)}{\log \sigma} \right)^2 \right)$$  \hspace{1cm} (4)$$

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 Figure 4C. Results are shown in Figure 9B-C. The two curves in B show the response of the population for a larger ($RL_i$, 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, since 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 Figure 9C as a
function of the input speed. The open circles are obtained by using the same data set as in Figures 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 intervals: 0.84-0.94). Typical preferred speed for these units for any size of the stimulus was below 120 °/s with one unit's tuning curve peaking at 258 °/s for the largest stimulus (adjusted r² 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 filled 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 Figure 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 based on 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 random dot patterns causes a decrease in preferred speed of MT neurons (Pack et al., 2005; Krekelberg et al.,
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 Exp.1). 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. 2006b). 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 the model (Equation 3) by a constant (α).

Hence the perceived speeds for a small stimulus (Eq. 5) and for a large stimulus (Eq. 6) are computed by the following formulas:
When we set \( \alpha \) as the total population response to a large-size, high-contrast (i.e. “optimal”) stimulus, i.e. \( \alpha = \sum (RL_i) \), this variant of the model provided a very close prediction to our psychophysical data with the size effect (Figure 9C, triangle symbols). When we set \( \alpha \) as the total population response to the smaller stimulus, i.e. \( \alpha = \sum (RS_i) \), 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 \( R_i \) 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 to a high-contrast (i.e. optimal) stimulus. Reducing the model neurons 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.

--- Fig. 9 ---

**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 neurons’ preferred speeds 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 each neuron’s speed tuning curve 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, MT neurons’ responses 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 neuron’s preferred speed (Krekelberg et al.,
2006b; 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 (Figure 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 read-out 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 peri-threshold 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 peri-threshold trials. Therefore, more sophisticated
experimental designs may be needed for long-term experiments.

The 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 towards 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., 2006b) 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 and Born, 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). But a
sampling bias is often inevitable and there is evidence that the distribution is highly uniform on
a logarithmic scale based on 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, since 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 classical receptive fields 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, since 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 random dot pattern becomes smaller, the ratio between the net motion and flicker increases, since 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 life-time, 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, since 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, 2009). 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 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.

REFERENCES


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Figure Captions

**Figure 1** Fixation task and stimulus presentation. Each trial was initiated when the monkey foveated the fixation point and depressed a lever. A series of 100% coherently moving RDPs were presented moving in preferred and null direction at random speeds (0.5-64˚/s), centered in the receptive field of the neuron. The monkey was trained to maintain fixation for a variable duration of time (4 to 6 seconds) until a subtle luminance change in the fixation point.

**Figure 2** Results from the psychophysical experiments with eight human subjects and one monkey. A: The 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, see legends). 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.

**Figure 3** A-C: Speed tuning curves of three example neurons. The three curves in each plot show the modulation in response to three stimulus sizes (black: stimulus diameter (ø) corresponds to receptive field (RF) ø, dark gray: stimulus ø is 1/2 of RF ø, light gray: stimulus ø is 1/4 of RF ø. Inset plots show the preferred speeds (fitted log-Gaussian means) as a function of the ratio between the stimulus and the receptive field ø.

**Figure 4** Population results. A: Histogram of modulation in preferred speed in all 73 neurons. The mean speed modulation is positive and significantly different from zero, 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: The 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). The inset figures are schematic representation of the four possible alignments of three preferred speeds (symbols as in figure 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 = 0.921 * x - 0.007.

Figure 5  Relationship between modulation in preferred speeds and preferred speed for
the largest stimulus. Each dot represents one neuron. The shift in preferred speeds
indicates a significant positive correlation with the preferred speed of the neuron for the
largest stimulus, suggesting that the size dependence of preferred speeds was larger for
high-pass neurons.

Figure 6  Comparison of tuning amplitude for different stimulus sizes. Tuning amplitude in
the population of neurons (n=73) for three pairwise comparisons of stimulus size (triangles:
small vs. large, squares: small vs. middle, asterisks: middle vs. large stimulus). The filled
triangles indicate the means in each subplot.

Figure 7. ROC analysis in a sample neuron. A: Speed tuning curve of the neuron (data
points and the solid line) measured with a stimulus covering the receptive field (16 deg ø).
The grey arrow indicates the speed at the point with the highest slope in the ascending
portion of the tuning curve. The black arrow marks the preferred speed of the neuron. B:
Firing rate histograms of the same neuron for the largest (16 deg ø) and smallest (4 deg ø)
stimulus (black and gray respectively). C: ROC curve computed from the two distributions in
B. The area under the ROC curve (AUC) for this neuron is larger than 0.5, indicating that the
two distributions in B are separate and the firing rates for a smaller stimulus are higher than
for a larger stimulus.

Figure 8  Population results from Experiment 2. A total of 27 single units were recorded for
this experiment. Due to the pairwise comparison of the ROC curves from three stimulus
sizes, each unit contributed three AUC values to the respective histograms. A: The adjusted
AUC values for units where a stimulus speed from both ascending and descending slopes
was used. B and C: Results from these two types of recordings separately. The mean
adjusted AUC value for the population was significantly above 0.5 regardless of whether the
stimulus speed was chosen from the ascending or descending portion of the tuning curve.
D: Distribution of preferred speeds in the neuronal sample. Black and grey histograms show
the use of ascending and descending slopes, respectively.

Figure 9 Application of the population average model. A: Schematic of the population
vector average model. The population consists of homogeneously distributed speed
channels. The peaks of the tuning curves correspond to the label speeds of different
channels. To compute an estimate for the input speed, the label of each channel is weighted
by its activity and then the sum is normalized by the total population activity. B: Population
activity obtained from predicted activity of single neurons (see Eq. 3) for the largest (solid
line) and smallest stimuli (dashed line). For an input speed of 18, which corresponds to the
highest reference speed used in the psychophysical measurements, estimate speed for the
largest stimulus was 18 and for the smallest stimulus 23.3, resulting in a 29% increase in the
perceived speed. C: Predicted ratio between population activities for largest and smallest
stimulus sizes (i.e. ratio between weighted average of population activities indicated with the
two curves in 9C, across a range of input (i.e. reference) speeds. The solid circles show the
psychophysical data as in Figure 2 (4 deg vs. 12 deg stimulus diameter). The asterisk
indicates the PSE obtained from the monkey (4 deg vs. 8 deg stimulus diameter). The open
circles are model estimates for PSE based on the responses of the neuronal population with
preferred speeds not exceeding 64 °/s (n=73); the open squares indicate the estimates
based on the response of a population that included neurons with preferred speeds
exceeding 64 °/s (n=81). The triangle symbols show the model PSE prediction when the
total population activity in the denominator was replaced by a constant.
Figure 1
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Figure 2
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Figure 3
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Figure 4
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Figure 5
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Figure 6
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Figure 7
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A
Firing rate (sp/s)

Speed (°/s)

pref. sp. = 94.4 °/s
slope sp. = 3.8 °/s

B
Frequency

Firing rate (sp/s)

C
Large stimulus

Small stimulus

AUC = 0.87
Figure 8
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Figure 9
Boyraz & Treue