

PERCEPTION OF VISUAL MOTION SPEED IN HUMAN AND MONKEY

PhD Thesis

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Herewith I declare that I have written my thesis with the title "Perception of visual motion speed in human and monkey" independently and with no other sources and aids than quoted.

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1 General Introduction

For humans, perception of the world depends largely on visual perception. Vision is undoubtedly the most influential and powerful source for knowledge among the five senses, capable of carrying an enormous amount of information of different qualities in short time. Perception of colors, brightness, shape, size, depth and motion provides us the information to move through the world, to grab objects, to define scenes, to recognize friends and to discriminate between apples and oranges without examining or tasting all fruits in the market.

The popular understanding of vision is that eyes and brain act as a camera combined with a computer, capturing a picture of the world and analyzing its components. Although this assumption is probably not thoroughly misguided, today we know that vision is a much more active and creative process than a mere photographic documentation. In particular, we must consider the astonishingly diverse amount of errors, which are the so-called *visual illusions*, that the human visual system makes. The active process of vision is enormously influenced by our prior knowledge and experiences, our current arousal state and not surprisingly by various physical properties of the observed scene, where these serve as the basis for illusions.

In this thesis, we will focus on two illusions, or *misperceptions*, of visual motion. Perception of motion is a crucial part of vision. Motion helps us set apart objects from their background and detect these objects. Observing an object in motion provides information about its relative position, depth, size and destination. The shape of the object can be constructed with the help of its motion (i.e. structure from motion). Motion also helps us recognize our friends from the way they walk (i.e. biological motion). Also, the perception of one's own motion (i.e. locomotion) is deduced from the relative motion of the outer space. For instance, if an expansional flow of the surrounding scene will give the observer the perception of moving forward.

Motion conveys great amount of visual information, but it is not perceived without errors. For example, under certain circumstances, when some of the critical parameters are varied, the speed of a moving object can be easily under- or over-

estimated. This thesis consists of a set of experiments investigating such biases of perceived speed.

An everyday example of speed misperception occurs when observing an airplane landing. In spite of its landing speed of about 240 km/h, it appears to move much slower than the cars on the highway with speeds as much as half of the plane's speed. It has been reported that smaller stimuli appear to move faster than larger stimuli, when both move at the same physical speed [41]. A similar but more hazardous everyday example may come about in traffic and at railroad crossings. Many drivers do not know that the larger the size of a vehicle, the slower its perceived speed. It has been reported that the majority of accidents taking place at railroad crossings occur due to the underestimated speed of an approaching train with a size larger than other vehicles [34].

Another dangerous speed illusion occurs in traffic, when fog comes in and visibility is reduced. In fog, contrast is reduced and this causes an underestimation of the speeds of moving objects [46, 45]. Drivers perceive the speed of other vehicles lower than it is, and, as the speed of the passing scene is underestimated, the drivers underestimate their own speed and tend to accelerate.

Although there has been a significant amount of information gathered about how visual speed is processed in the brain, the neural basis for speed misperceptions are unknown. The explanation of these phenomena will be in the activity of cortical areas that are involved in speed perception. A small extra-striate area, located in the superior temporal sulcus, area MT, comes to mind first, since the activity of this area is reported to link directly to speed perception [25].

In the first chapter of this thesis, we investigated and reproduced two speed misperceptions, which depend on stimulus contrast and stimulus size. Asking naive human subjects to judge the speed of two stimuli, we either varied the contrast (experiment 1) or the size (experiment 2) of one of the two stimuli. We observed variable effects of contrast and a highly salient and consistent effect of stimulus size on speed perception.

In the second chapter, recording from speed selective neurons in the visual area MT of awake macaque monkeys, we sought for a change in neuronal activity correlated to a change in stimulus size. In two independent experiments, we used

different approaches to investigate changes in neurons' responses. In Experiment I, we were interested in the changes of speed preferences of neurons. Varying the stimulus size, we measured the responses of neurons to a range of speeds (i.e. speed tuning curves). Our results indicated that neurons preferred slower speeds for smaller stimuli, indicating that tuning curves shifted toward slower speeds. In experiment II, we were interested in the actual activity (firing rate) of neurons at a constant speed, for different sizes of identical stimuli. The results of these experiments are in accordance with the results of the first chapter (experiment 2) and they support a current computational model of speed coding (i.e. vector average model of perceived speed).

2 Psychophysics of Speed Misperceptions Related to Luminance Contrast and Stimulus Size

2.1 Experiment 1: Truthful speed perception for complex patterns of different contrast

2.1.1 Abstract

The speed of a moving object is underestimated when its luminance contrast is low. We investigated the effect of contrast on perceived speed by performing four experiments. In experiment 1.1, we compared the effect of contrast with random dot patterns and sine wave gratings, in order to test the presence of the effect for different types of stimuli. We observed an effect of contrast with gratings but not with random dot patterns. Our findings with sine waves were similar to those reported in literature, and the effect of low contrast reversed at higher speeds causing an overestimation in perceived speed (experiment 1.2). In experiment 1.3, we replicated a recent study showing the effect of contrast with random dot patterns and observed a small effect. The discrepancy between the results of experiment 1.1 and 1.3 lead us to the assumption that the effect of contrast may depend on stimulus parameters, which varied between the two experiments. Consequently, we tested dot density and contrast polarity of random dot patterns and observed an increase in perceived speed with decreased dot density (exp 1.4). In conclusion, we report that the effect of contrast is not invariant for stimulus type and features and it may also vastly depend on the spatial composition of the stimulus.

2.1.2 Introduction

Motion, i.e. the direction and the speed of objects, is one of the essential information sources about our environment for the primate visual system. Speed is one of the two essential components of motion, which provides information about the depth and size of the moving object to the observer. To move through the world, we need such information frequently.

The perception of motion speed in humans has been investigated in detail throughout the last decades. It is known that human subjects are highly accurate in speed discrimination. Discrimination of different motion speeds is possible for a broad range of speeds (0.25-256°/s, [30]) and at moderate speeds (4-32°/s) a 6% difference in speed suffices for making the speeds of two moving objects discriminable [30].

Despite the fact that human speed discrimination is powerful, the perceived speed of a moving object is not necessarily always veridical and coinciding with its physical speed. A number of psychophysical studies reported the dependency of perceived speed on different stimulus features that cause an under- or overestimation of motion speed. Luminance contrast is one of these features. Thompson [46] showed the effect of contrast on perceived speed using sine wave gratings. He asked subjects to vary the speed of a grating to match the speed of the test grating. The largest effect he reported was approximately a 30% decrease in perceived speed when the test contrast and test speed were the lowest in comparison to the reference stimulus.

A number of studies replicated the change in perceived speed using sine wave gratings [4, 18]. Some studies focused on discrimination performances but did not find any effect of contrast on speed discrimination thresholds [28], whereas other studies reported increased thresholds as a result of low contrast at low speeds [20].

Sine wave gratings are the most commonly used stimuli to test the contrast dependence of perceived speed. A moving sine wave is a sinusoidal luminance variation across space and time and the speed of a moving sine wave is defined as the ratio of its temporal frequency (cycles/second) to its spatial frequency (cycles/deg). This basic relationship provides the opportunity to investigate the separability of spatial and temporal frequencies in speed coding. Each sine wave grating has

one spatial and one temporal frequency, which represents a single point in Fourier space. Random dot patterns, on the other hand, are broad-band stimuli (contain a broader spectrum of spatial and temporal frequencies). In fact, a single spot is one of the most complex patterns in Fourier space and random dot patterns are arrays of randomly positioned spots. This broad spectrum of spatio-temporal frequencies is a characteristic of natural scenes as well. Through Fourier analysis, every stimulus can be decomposed into numerous sine wave components.

The question, whether speed is coded solely as an independent variable or depends on the computation of spatial and temporal frequency channels, was addressed both in psychophysical [28, 44] and electrophysiological studies [33, 36], although it remains open. There are also indications from psychophysical experiments that the human visual system might use two separate mechanisms, one speed tuned and one spatio-temporally separable mechanism to code for motion speed [49, 39].

Because of the above described differences, several authors attempted to measure speed perception with multiple types of stimuli. For example, Blakemore et al. [4] used a number of different stimuli to test whether the effect depends on stimulus type and whether it would also apply for more complex stimuli. They reported the effect of contrast with sine waves and tested it also with Julesz patterns, which were created by setting each pixel randomly above or below the mean luminance level. They found an approximately 10 to 20% decrease in perceived speed for the lower contrast conditions with Julesz patterns. Nevertheless, authors discuss that 'these patterns produced a considerable intersubject variability in the effects of contrast upon perceived speed'. This might be due to the small number of subjects (3), where two of them were the authors.

In our experiments we investigated whether contrast would have the same effect on the perceived speed of broad-band stimuli and spatio-temporally limited sine wave gratings. Experiment 1.1 investigated the perception of speed as a function of contrast, type of stimulus and reference speed. It demonstrated that low contrast caused an underestimation of speed, the effect depended on stimulus type and on stimulus speed. Experiment 1.2 showed that if low contrast stimuli move at higher speeds, then their speed is not underestimated but overestimated. Experiment 1.3

adopted the design of another study and showed a small effect of contrast with RDPs. Finally, experiment 1.4 tested the stimulus parameters, which were differed between the above mentioned study and our experiment 1.1. We conclude that the magnitude of this effect of contrast is not universal and depends highly on the spatial content of the stimulus.

2.1.3 Methods

Subjects

A total of seventeen subjects with normal or corrected to normal vision participated in these experiments. Six subjects participated in experiment 1.1, another group of six subjects took part in experiment 1.2, and another five subjects were participants of experiments 1.3 and 1.4. All subjects were naïve to the purpose of the study and gave their informed consent. Subjects were paid for taking part in the experiments.

Experimental Setup

Subjects sat in a dimly lit experimental chamber to perform the experiments in front of a 22 inch CRT display monitor (Lacie, Electron22Blue IV, non-interlaced) with a resolution of 1200×1600 pixels and a refresh rate of 85 Hz, providing a frame duration of 11.7 ms. Head-posture and viewing distance were stabilized with the help of a chin-rest. The monitor was calibrated to obtain a linear grayscale. Subjects were viewing the monitor from a distance of 57 cm, therefore 1° of visual angle contained 40 pixels.

Procedure

For all psychophysical experiments of this study, the same procedure and speed discrimination task were used. For each trial, subjects were instructed to fixate a small ($0.2 \text{ deg} \times 0.2 \text{ deg}$) dark square on the center of the display and had to choose the faster of the two successively presented stimuli in a two alternative forced-choice (2AFC) paradigm. The fixation point appeared before the trial start and remained visible throughout the trial. After the subject pressed the trial start key, the first stimulus appeared with a 170 ms delay. Stimulus duration was 200 ms. Following a blank period (ISI) of 270 ms, the second stimulus was presented for 200 ms. The timing of stimuli was different in experiment 1.3. In this experiment, stimuli were presented simultaneously for 500 ms. An experimental session consisted of 200 trials and subjects typically completed 3-4 sessions per day. Within an experiment, sessions were run in random order and each subject ran all sessions of a given experiment.

A weighted up-down staircase procedure was used to increase the proportion of trials within 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 [21].

Stimuli

Both random dot patterns (RDP) and sine wave gratings (SW) were created and presented with a custom written software, which was also used for data collection. Stimulus and presentation parameters are summarized in table 1. In each trial of experiment 1, one of the two stimuli had a lower contrast and moved at always the same reference speed, where the other had a contrast and its speed varied from trial to trial (test speed).

In Experiment 1.1, reference speeds were 2, 4, 6, 8,10, 12, 14, 16, 18°/s. Experiment 1.2 had only one reference speed, which was set to 20°/s. In experiment 1.3 and 1.4 reference speeds were 4, 6, 8,10, 12, 14 °/s. For all reference speeds (RS), test speeds varied from $0.5 \times RS$ to $2.5 \times RS$ in $0.1 \times RS$ steps. In a given experimental session, the low and high stimulus contrasts were fixed and three reference speeds were interleaved. Only in experiment 1.3, three low contrasts were intermixed.

In experiment 1.1 and 1.2, each session contained either only random dot patterns or only sine wave gratings. In all remaining experiments, stimuli were only RDPs. The contrasts of the RDPs were calculated from the standard deviation of the mean luminance as a metric for contrast, since this measure considers the density of the dots and is therefore better suited for RDPs, [29].

In **experiment 1.1 and 1.2**, all stimuli had a diameter of 5° of visual angle and were presented at an eccentricity of 8°. RDPs consisted of dark dots on a gray background (34 cd/m²), moving 100% coherently in the vertical downward or upward direction (dot-size: 0.015 deg², dot-density: 10 dots/deg²). Sine wave gratings had a constant spatial frequency of 1.25 cycles/deg. Four different contrasts were used for the RDPs (8, 15, 30 and 50%) and for the gratings (5,10,30 and 50%, Michelson contrast). Preliminary tests showed that RDPs with 5% contrast were hardly visible for the subjects, whereas motion of 5% sine wave gratings

was still easily perceived. In both cases, the 50% contrast was used for the test stimulus. In each session, one of the low contrasts was used for only the reference stimulus. Contrasts were not interleaved and each session compared one low contrast to the highest contrast.

In **experiment 1.3**, stimulus parameters were matched to the parameters of a recent study [22]. The luminance of the background was set to 7.25 cd/m^2 , where the luminance of the high-contrast stimulus dots was 35.65 cd/m^2 and the luminance of the low contrast stimulus dots was 8.43 cd/m^2 providing a Michelson contrast of about 10% and a standard deviation of the mean luminance of 4%. Both stimulus diameter and stimulus eccentricity were 10° . Density of the dots was 1.2 dots/deg^2 , resulting in 100 dots within each stimulus aperture. All remaining parameters were kept the same as in experiment 1.1.

In **experiment 1.4**, in addition to stimulus contrast, the effects of dot density and luminance polarity on perceived speed were tested. Stimuli were 10° in diameter and were presented at an eccentricity of 8° .

In this experiment, either bright dots (68.50 cd/m^2) were presented on a darker surface (29.11 cd/m^2) or a dark dots (0.1 cd/m^2) were presented on a lighter (40.29 cd/m^2) surface. For both variations the contrast was the same (27%; standard deviation of the mean luminance), only the polarity of the contrast was reversed.

exp. no	stimulus duration (ms)	ISI (ms)	contrasts %	reference speeds ($^{\circ}$ /s)	eccentricity ($^{\circ}$)	stimulus diameter ($^{\circ}$)	dot density (dots/ deg^2)	stimulus type
1.1	200	270	5,10,30,50	2,4,6,8,10,12,14,16,18	8	5	10	SW
1.1	200	270	8,15,30,50	2,4,6,8,10,12,14,16,18	8	5	10	RDP
1.2	200	270	8,15,30	20	8	5	10	RDP
1.2	200	270	5,10,30	20	8	5	10	SW
1.3	500	0	4	4,6,8,10,12,14	10	10	1.2	RDP
1.4	200	270	27	4,6,8,10,12,14	8	5	10	RDP bright dots
1.4	200	270	27	4,6,8,10,12,14	8	5	10	RDP dark dots
1.4	200	270	27	4,6,8,10,12,14	8	5	2	RDP bright dots
1.4	200	270	27	4,6,8,10,12,14	8	5	2	RDP dark dots

Table 2.1: Table of stimulus and experimental parameters for experiments 1.1 to 1.4. The percentages in contrast column are the standard deviation of the mean luminance for random dot patterns and the Michelson contrast for sine wave gratings.

Data Collection and Analysis

Figure 2.1 illustrates an example of the psychometric data from one subject for a reference speed of $14^\circ/\text{s}$. The proportion of trials in which the subject reported the low-contrast reference stimulus as faster than the test stimulus was computed as a function of the ratio between test and reference speed. The point of subjective equality (PSE) and the speed discrimination threshold were determined for each reference speed and each stimulus contrast by fitting a logistic function to the psychometric data. The logistic function was fit by minimizing the maximum likelihood using the simplex algorithm method. Practically, the speed discrimination threshold corresponds to the difference along the x-axis between the center of the fitted curve (y-axis value 0.5) and the speed ratio where the y value was 0.34 larger or smaller than 0.5. In other words, the PSE refers to the location of the center of the fitted curve, which represents the speed ratio where the subject perceives both stimuli as moving at the same speed. The point of subjective equality (PSE) refers to the ratio between the speeds of reference and test stimuli, when they are perceived to have the same speed by the observer. A PSE value larger than 1 in our design indicates that the speed of the test stimulus (high contrast) had to be higher than the speed of the reference stimulus in order to be perceived as moving at the same speed. If PSE equals 1, the perceived speed of the two stimuli is equal when they have the same physical speed. As in all experiments of this chapter, the test stimulus had the higher contrast. A PSE below 1 indicates that the lower contrast stimulus is perceived as moving slower than the higher contrast stimulus.

To test whether the group means of the PSE values were significantly different from 1 (the point of physical equality) a two-sided t-test was used. Also, to test the effects of reference speed, stimulus type and contrast on PSE, a three-way repeated measures ANOVA was used. Data analysis was carried out with MATLAB (MathWorks, Natick, MA), and R environment statistics.

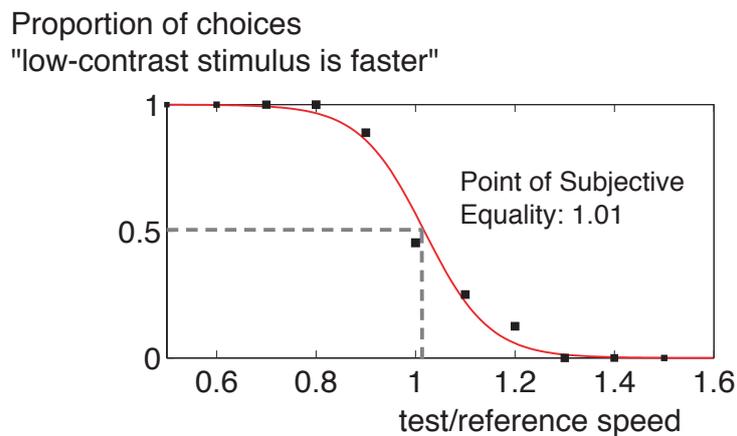


Figure 2.1: A sample psychometric curve of one speed discrimination session. Black data points are the raw psychometric function of the subject. Red curve is the logistic function fitted to the raw data. Here, the subject compared a reference stimulus moving at $14^\circ/\text{s}$ speed to various test speeds. The speed ratio between the two stimuli is given on the x-axis. The y-axis denotes the subject's proportion of choices for the lower contrast stimulus as the faster stimulus. The point of subjective equality (PSE) of this subject in this session was 1.01, which is the speed ratio corresponding to chance (50% on the Y axis). In this example, PSE is almost equal to the point of physical equality. The subject had a speed discrimination threshold of 0.1 for $14^\circ/\text{s}$ reference speed, which means an approximately 10% change in speed was reliably discriminable by the subject.

2.1.4 Results

The results are subdivided into four parts covering the four independent experiments with different sets of subjects. First, we attempt to replicate the well-known effect of contrast on speed perception with sine wave gratings and with random dot patterns (exp. 1.1). Then, we briefly inspect the reversal of this effect at higher speeds (exp. 1.2). Next, we replicate a study proving the effect of contrast with random dot patterns (exp. 1.3), with different parameters and experimental layout. Finally, we test two critical RDP parameters and how they affect the influence of contrast on the perceived speed of random dot patterns (exp. 1.4).

Experiment 1.1: The effect of contrast on perceived speed: sine wave gratings vs. random dot patterns

The results of experiment 1.1 are shown in figure 2.2(a-c). The data points in each subplot show the trend of the mean point of subjective equality values as a function of reference speed and type of stimulus.

In figure 2.2(a-c), each subplot presents the PSEs for a different level of reference stimulus contrast. Filled circles are from the experimental sessions with dot patterns and open circles are from the sessions with gratings. In figure 2.2a, the speed difference is the highest between the low (8% for the RDPs and 5% for the gratings) and high contrast (50%) stimuli. As one goes from plot (a) to plot (c) plot, the contrast difference between the two stimuli decreases. In figure 2.2a none of the PSE values for random dot patterns are different from 1 (two-sided t-test, $p > 0.05$).

In the experiment with sine wave gratings (SW), we observed a significant decrease in PSE values when subjects compared a 5% contrast grating to a 50% contrast grating (two-sided t-test, $p < 0.01$, figure 2.2a) for reference speed $4-8^\circ/s$. Similarly, when the subjects compared a 10% contrast grating to the standard grating, the effect was significant for reference speeds $6-8^\circ/s$ ($p < 0.05$). These results indicate that low-contrast gratings were perceived to move slower than high-contrast gratings. When subjects compared a 30% contrast stimulus to a 50% contrast stimulus, we observed no significant change in PSEs, although the trend of the data suggests a monotonic decrease for the lower speeds (Figure 1c,

open circles). In contrast to the gratings, we observed no change in PSE values for the RDPs in any of the contrast conditions ($p > 0.05$).

In additional analyses, a three-way repeated measures ANOVA (with three factors being stimulus type: 2 levels, reference speed: 6 levels and contrast: 3 levels) revealed significant effects of stimulus type and reference speed on PSE ($p < 0.05$) and a very significant interaction between the both ($p < 0.01$). This analysis did not show any significant effect of contrast on perceived speed, which presumably is a result of the fact, that we did not have a control condition (i.e. 50% vs 50% contrast comparison).

To summarize, in experiment 1.1, we observed the effect of contrast with sine wave gratings but not with random dot patterns. Furthermore, this effect seemed to be modulated by speed, meaning that, the underestimation of low-contrast stimulus' speed occurred only at speeds lower than $10^\circ/\text{s}$. Thompson [46, 47] has reported not only an underestimation of speed at lower speeds, but also an overestimation at higher speeds, that is, the effect of contrast reversed at moderate speeds depending on the spatial and temporal frequency of the gratings. Although the bias in perceived speed disappeared, we did not see any increase in perceived speed at higher speeds. That is, at higher speeds PSE values approached 1, but did not cross over. To test this mismatch, we performed experiment 1.2, where the reference speed was much higher ($20^\circ/\text{s}$) than reference speeds used in experiment 1.1.

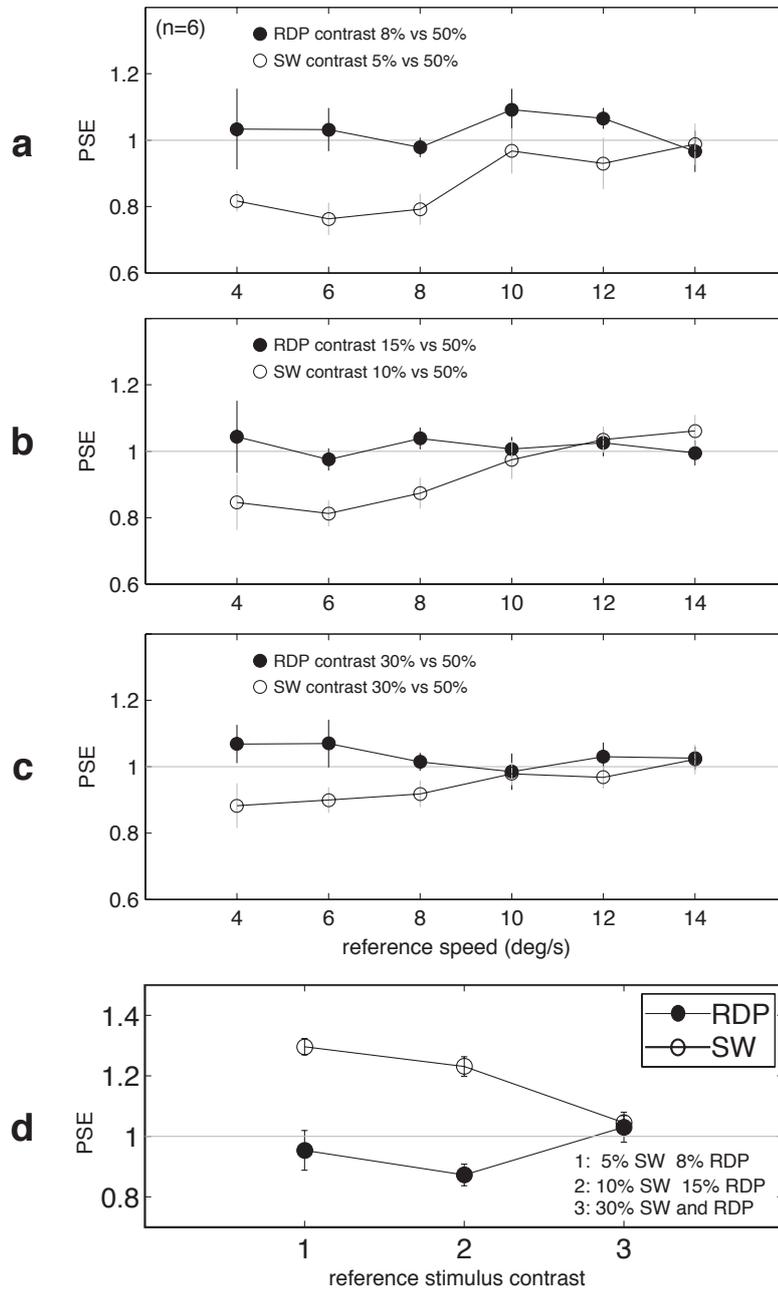


Figure 2.2: Results of experiment 1.1 in (a-c) and 1.2 in (d), that tested the effect of contrast on perceived speed with random dot patterns (filled circles) and sine wave gratings (open circles). Vertical bars represent the standard error of the mean (n=6).

Experiment 1.2: Reversal of the contrast effect at high speeds

Thompson [46] has reported the reduction in perceived speed at lower temporal frequencies along with an increase of perceived speed at higher temporal frequencies. In experiment 1.1, we tested a range of reference speeds from $4^\circ/\text{s}$ to $14^\circ/\text{s}$. Although the mean PSE declined at lower speeds, we did not observe any increase at higher speeds and perceived speed seemed to be stable and close to veridical when the subjects were asked to compare higher speeds ($10\text{-}14^\circ/\text{s}$). To examine this mismatch between our results and the literature, we measured the effect at a much higher speed ($20^\circ/\text{s}$) with a different group of six subjects. The three levels of low contrast were interleaved for both RDPs and gratings. Thus, in this study one constant reference speed was to be compared to its test speeds and the reference stimulus could be at one of the three low contrasts.

Figure 2.2d shows the results of this measurement. For the 5% and 10% contrasts, mean PSE values for sine wave gratings are significantly above 1 (two-sided ttest, $p < 0.05$, open circles), whereas the mean PSE values for dot patterns (filled circles) are not different from 1 (two sided ttest, $p > 0.01$). The increase in perceived speed with sine wave gratings, therefore, matches the findings of Thompson [46] along with the decrease at lower speeds reported in the experiment 1.1 and indicates that speed can be under- or overestimated at low contrast depending on the reference speed itself.

Experiment 1.3: Effect of contrast on speed perception with RDPs

Our results from experiments 1.1 and 1.2 (figure 2.2) showed no effect of contrast on perceived speed of RDPs, suggesting that the contrast effect is not present or at least not visible for broad-band stimuli such as RDPs. Interestingly, Krekelberg et al. [23] showed that both in human and monkey, perceived speed of random dot patterns are reduced at low contrast, to a comparable extent to the reduction in perceived speed with sine wave gratings. Their effect was about 40% speed underestimation, when subjects were comparing a 5% contrast stimulus to a 70% contrast stimulus. The discrepancy between this finding and our results of our experiments 1.1 and 1.2 may be due to the use of very different experimental parameters of the RDPs. We used a stimulus duration of 200 ms, while Krekelberg et al used a longer duration of 500 ms. Our RDPs consisted of dark dots on a lighter background, whereas Krekelberg et al. used light dots on a darker background. Density of dots was higher for our stimuli being 10 dots/deg². Another important difference was that we presented the stimuli successively, whereas, stimuli were presented simultaneously in the Krekelberg study. Therefore, we conducted an experiment with parameters matching the settings of Krekelberg et al..

Figure 2.3 shows the results of this experiment. The curve indicates the PSE values for 6 reference speeds. For all reference speeds, all PSE values were around 0.9 and significantly below 1 (two-sided t-test for all PSE values; $p < 0.001$), meaning that subjects perceived the speed of the low-contrast stimulus as 10% slower than the high contrast stimulus. The size of the effect was not as large as reported by Thompson or Krekelberg, still, our result was globally consistent with their findings. However, we did not observe any modulation of the effect depending on reference speed, meaning that the speed of the low contrast RDPs were not overestimated when they were moving at higher speeds. We observed a high variability of the effect among the subjects, which is also the reason for the large error bars in the plot.

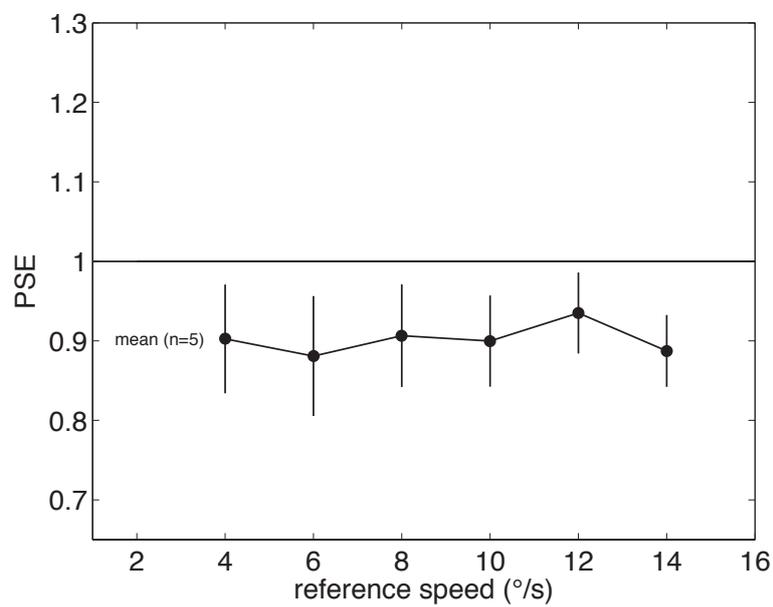


Figure 2.3: Results of experiment 1.3. Perceived speed of RDPs were low for low contrast when subjects were comparing random dot patterns in a design replicating Krekelberg et al.'s parameters. The curve shows the mean PSE values from all five subjects for all six reference speeds. All PSE values are significantly below 1. Vertical bars indicate the standard error of the mean.

Experiment 1.4: The influence of contrast polarity and dot density on perceived speed of low-contrast RDPs

Our results from experiment 1.1 and experiment 1.3 presented a discrepancy: in the former experiment we observed no change in perceived speed and in the latter there was a significant decrease, albeit small. We suspected that this variation in the effect may be a result of RDP parameters which were different between the two designs. One parameter was the polarity of contrast, that is, in experiment 1.1 we used dark dots on a lighter background, while in experiment 1.3 we used bright dots on a darker background. Another difference was the dot density. The density of dots was much higher in experiment 1.1 being 10 dots/deg² and in experiment 1.3 being 1.2 deg². To test the effect of contrast polarity and dot density directly, we prepared a new set of experiments. Dot density was set to either 2 dots/deg² or to 10 dots/deg², with either light dots on dark background or dark dots on light background. the same subjects participated as in experiment 1.3.

The results of this experiment are presented in figure 2.4 on page 28. Dots connected with solid lines denote the results with higher density RDPs and dots connected with dashed lines show the conditions with low dot density. Black lines mark the sessions with dark dots on a lighter background, while gray lines represent the sessions with bright dots on a darker background. Red data points mark the PSE values significantly different than 1 (two-sided ttest, $p < 0.05$).

We observed a significant effect of contrast only in one stimulus configuration. PSE was increased and significantly higher than 1 for dark dots with low density moving on a lighter background (black and dashed line, two-sided t-test, $p < 0.01$), when tested across all speeds. The mean increase in PSE was 8.8%. In the remaining conditions, PSEs were not different from veridical. In other words, a decrease in contrast did not lead to a wrong estimation of speed, regardless of the density of dots or the polarity of contrast. Instead, in the sessions with sparse dark dots on a lighter surface (dashed black line) perceived speed of the low contrast stimulus was globally above 1 for all reference speeds. The only significant decrease of perceived speed is observed in the condition with bright dense dots on a darker background at a reference speed of 6°/s.

In general, PSE increased significantly, both for dark and light dots, when dot

density decreased. On the other hand, the polarity of the contrast did not show any detectable effect.

The main result of this experiment was that for a low contrast RDP, a decrease in dot density increased the subjective equality point to a value larger than 1, i.e. the speed of these stimuli was perceived higher than the speed of stimuli with higher dot density.

Although the experimental session with bright and sparse dots (dashed gray line) resembles the stimuli in experiment 1.3 and although the same five subjects participated in both experiment, we did not see an effect in experiment 1.4. The main differences between the two experiments do not lie in the composition of the stimuli, but in their presentation. In experiment 1.3 stimuli lasted much longer and reference and test stimuli were displayed simultaneously. These results lead us to the assumption that not only the composition but also the presentation of the stimuli interacts with the effects of contrast on perceived speed.

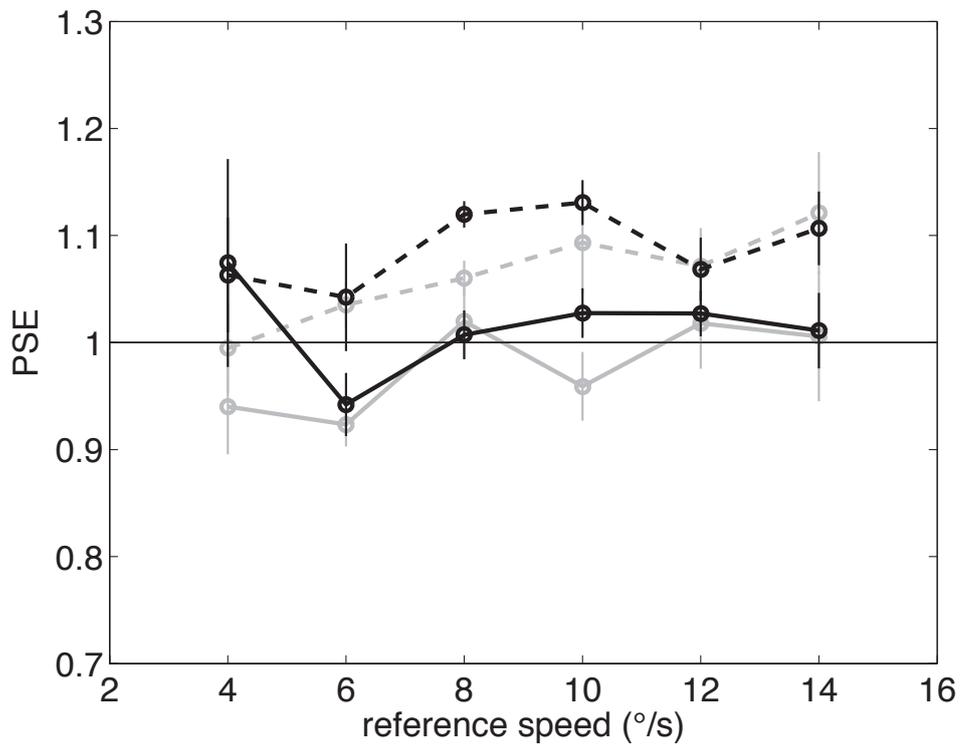


Figure 2.4: Results of experiment 1.4 testing effect of dot density and contrast polarity. Black or gray circles and lines indicate the sessions with dots darker or lighter than the background, respectively. Solid lines denote the sessions with higher dot density and dashed lines show the sessions with scarcer dot patterns. Error bars denote the standard error of the mean (n=5).

2.1.5 Discussion

In this set of experiments, we aimed to gain information about the effect of contrast on perceived speed. We began with addressing the question whether the effect depends on the type of stimulus. According to our results from experiment 1.1, at low contrast, subjects underestimated the speed of sine wave gratings but perceived the speed of RDPs veridically.

Our results with sine wave gratings matched the findings in the literature [46, 47]. Thompson has tested the effect of contrast on perceived speed with sine waves and has reported a 20-30% lower perceived speed for low contrast stimuli at the contrast levels he has used (0.045-0.25%). He reported an additional finding, namely that low-contrast stimuli were perceived as faster than high contrast stimuli, meaning that the effect reversed at high speeds [47]. The point where the PSE curve crosses over 1, which Thompson reported to occur at 8 cycles/s [46], corresponds approximately to $10^\circ/\text{s}$ in our experiments. Although we did not observe PSEs larger than 1 at higher speeds in experiment 1.1, the PSE for the higher speed ($20^\circ/\text{s}$) was larger than 1 and statistically significant. Given the constant spatial frequency of our sine wave gratings ($1.25 \text{ cycles}/^\circ$) the selected $20^\circ/\text{s}$ reference speed of experiment 1.2 corresponds to a temporal frequency of 25 cycles/s, which is much higher than the temporal frequencies used by Thompson [46].

In contrast to our findings in experiment 1.1, Krekelberg et al. recently showed an effect of contrast with RDPs [23], however, these authors used a different experimental design and RDP stimulus parameters. Therefore, in experiment 1.3, we aimed to replicate the experimental and stimulus conditions used by Krekelberg et al. After matching all controllable parameters of the experiment to theirs, (simultaneous presentation, longer stimulus duration, dark dots on brighter background, luminance, dot size, dot density, stimulus eccentricity and diameter) we observed a PSE of 0.9. This effect was far less than they reported ($\sim 40\%$). In addition to its moderate size, the effect we observed varied considerably from subject to subject.

The appearance of the effect in experiment 1.3 may be caused by one or several of the adjusted stimulus parameters, such as the very low contrast that is used (4%) along with a stimulus duration of 500 ms. In our other experiments with low contrast, we used a stimulus duration of 200 ms and we were unable to use such

a low contrast, random dot patterns were merely visible and the discrimination of motion speed was impracticable.

In experiment 1.4, we investigated two of the above mentioned differences in stimulus parameters closer. We raised the question whether the polarity of contrast might play a role in the effects of contrast on perceived speed and we also varied the density of dots as these were markedly different between the two experiments. We observed no effect of contrast for both polarities. Furthermore, in experiment 1.4, the speed of RDPs with less dense dots was significantly overestimated. Therefore, low dot density could not be the critical variable, which caused an underestimation of speed in experiment 1.3.

A decrease in the density of dots in an RDP stimulus is equivalent to an increase in its spatial frequencies. Inferred from previously reported results of Thompson (figure 2.5 on page 31), at a constant speed, as the spatial frequencies increase, the speed is overestimated at low contrast, and as the spatial frequencies decrease, stimulus speed is underestimated. RDPs are broad-band stimuli that contain both low and high spatial frequencies, and under certain stimulus configurations, the activation of both spatial frequency channels may cause a neutralization of the counter-effects. Contrast seems to have highly variant effects on the perceived speed of RDPs, where multiple spatial frequencies play a direct role. Therefore, we conclude that the effect of luminance contrast on perceived speed is interacting with the spatial frequency composition of the stimuli and the contrast effects with RDPs and other broad-band stimuli, including natural scenes, are definitely more complex than with sine wave gratings.

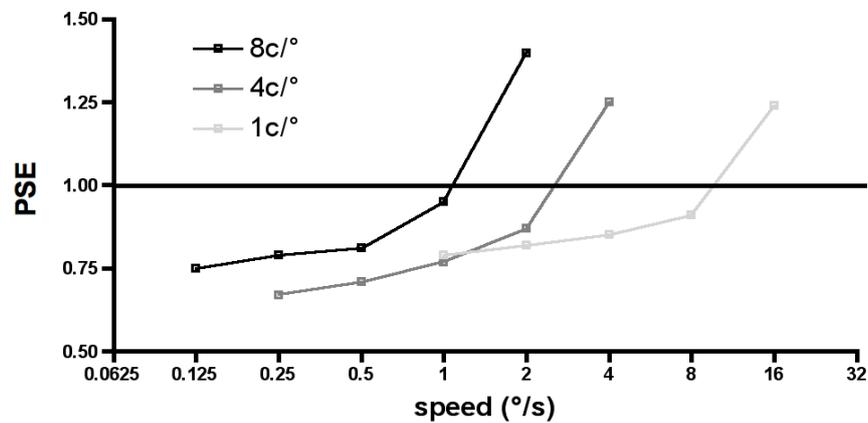


Figure 2.5: The influence of spatial frequency on perceived speed. Data re-plotted from Thompson [46], which are shown in their figure 2. At a given speed, at low spatial frequency (light gray), the speed of low-contrast stimulus was perceived slower than of high contrast stimulus. At high frequency, the speed of low-contrast stimulus was perceived faster than of high contrast stimulus.

2.2 Experiment 2: Quantification of the Field Size Effect on Perceived Speed in Humans

2.2.1 Abstract

At a constant speed, random dot patterns of smaller diameter are perceived to move faster than identical patterns with larger diameters. In a two-alternative forced choice paradigm, we investigated this stimulus size dependent misperception with eight subjects using RDPs of different sizes. A decrease in stimulus diameter lead to an increase in the perceived speed of the dot patterns. This result confirmed the findings in literature. In addition to this, we observed that the magnitude of the effect varied as a function of speed. The neuronal basis for this misperception is unknown, and it is clear that understanding the basis of such misperceptions could provide important information how motion speed is coded in the visual system. Our results from this experiment served as a basis for our electrophysiology experiments with awake monkeys presented in chapter 2.

2.2.2 Introduction

It has been shown that smaller random dot pattern stimuli (RDP) appear to move faster than larger RDPs, even if both patterns are otherwise identical and move at the same speed [41].

This misperception was first reported by Brown [7]. Brown showed that if one halves the linear dimensions of the motion field of a moving stimulus, one could double the perceived motion speed. He called this effect the principle of velocity transposition, today it is more commonly known as the basic field-size effect.

The neuronal basis of this misperception is yet unknown. Our primary aim is to search for an explanation of the misperception in neural responses, which we present in the second chapter of this thesis. To do this, we first aimed to find out the extent of the illusion with human subjects using RDPs, which we used in the electrophysiological recordings with monkeys.

Note that we used the terms aperture/field size and the stimulus size inter-

changeably.

2.2.3 Methods

Subjects

Eight subjects with normal or corrected-to-normal vision participated in experiment 2. All subjects were naïve to the purpose of the study and they performed the experiments after a brief training session. Subjects were paid for participating in the experiments and they gave their written informed consent prior to their participation.

Experimental Setup

Subjects sat in a dimly lit experimental chamber to perform the experiments in front of a 22 inch CRT display monitor (LaCie Ltd.) with a resolution of 40 pix/deg (1200×1600 pixels) and a refresh rate of 85 Hz. During each trial, subjects were instructed to fixate a small ($0.2 \text{ deg} \times 0.2 \text{ deg}$) dark square on the center of the display and the head-posture was stabilized with the help of a chin-rest. The viewing distance to the monitor was 57 cm.

Stimuli

Stimuli were created and displayed with an in-house C-based software, which was also used for online data analysis. All stimuli were circular RDPs. In an experimental session, the reference stimulus had either 4, 4.6 or 6° diameter. Test stimuli had a diameter of 12° . All stimuli were displayed at an eccentricity of 8° . Dot size was 0.015 deg^2 and dot density was 10 dots/deg^2 . Each dot had a random initial position and moved within the stimulus boundary until it disappeared. Dots reappeared at the opposite side of where they disappeared and continued moving as long as the stimulus lasted. Contrast between stimuli and background was maximum, where the dots were black (0.08 cd/m^2) and the background light (68.50 cd/m^2).

Procedure

In each trial, subjects had to choose the faster of two successively presented stimuli in a two alternative forced-choice paradigm. The fixation point appeared before trial start and remained during the trial. After the subject pressed the trial start key on a computer keyboard, the first stimulus appeared with a 130 ms delay. Both stimuli had a duration of 200 ms and there was a blank period of 270 ms between the first and the second stimulus. In a given trial, the smaller stimulus was moving at a reference speed (RS), while the other stimulus was moving at a test speed varying in each trial. A total of 9 reference speeds (2,4,6,8,10,12,14,16,18°/s) and for each reference speed 25 test speeds were used. Test speeds varied from $0.5 \times RS$ to $2.5 \times RS$ in $0.1 \times RS$ steps. A weighted up-down staircase procedure was used to increase the number of trials within 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 [21]. Stimuli were presented in sessions of 200 trials. There were a total of nine sessions. In each experimental session, we used three adjacent reference speeds (e.g. 2,4,6°/s) to prevent memorizing of one reference speed by the subjects, which might lead to disappearance of the effects as discussed in the literature [41]. Subjects were not asked to complete more than 3 or 4 sessions in a day to avoid fatigue effects and the order of the nine sessions were randomized across subjects.

Data Collection and Analysis

Proportion of choices “reference stimulus is faster” was collected for each reference speed. The stimulus moving at the reference speed was always the smaller stimulus. Figure 2.1 shown in the methods section of experiment 1 (page 19), illustrates an example of the psychometric data. The points of subjective equality (PSE) and the speed discrimination thresholds were measured for each reference speed and each stimulus size by fitting a logistic function to the psychometric data. The discrimination threshold corresponded to the difference between the center of the fit (50%) and the 84% performance point.

Statistical analyses in form of two-sided t-tests of mean PSE vs. the PPE (1.0)

were performed with MATLAB (MathWorks, Natick, MA).

2.2.4 Results

Figure 2.6 on page 36 summarizes the results. Data points connected with lines shaded in different grays show the PSE values averaged across the eight subjects. The black dots show the results with the largest size difference between reference and test stimuli (which is 1:3), whereas the light gray dots show the results with the smallest size difference (1:2). The results indicate that the stimulus size had a dramatic and consistent effect on perceived speed. The difference between PSE and 1 was highly significant for all reference stimulus sizes, except for the reference speed of $2^\circ/\text{s}$. The mean increase in PSE for a 1:3 size ratio was 44%, and for a size ratio of 1:2 it was 29%. Both effects were highly significant (two-sided t-test, $p < 0.001$). For a reference speed of $2^\circ/\text{s}$, the effect was the most variable (large error bars).

In addition to the increase in perceived speed with the decrease in stimulus size, we observed a monotonous rise in mean PSE as the speed of the reference stimulus increased, regardless of the size ratio between the two stimuli (upward trend of all three lines in figure 2.6).

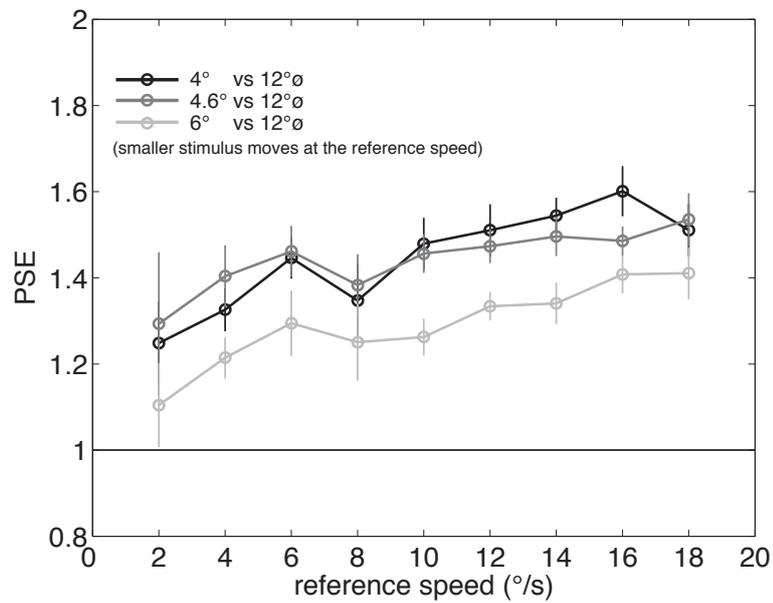


Figure 2.6: Mean PSE values in experiment 2 testing the effect of stimulus size on perceived speed. Except for the reference speed of $2^\circ/\text{s}$, all data points are above 1.0 and the difference between data points and 1.0 is highly significant (two-tailed t-test $p < 0.001$). As the reference speed increased, the magnitude of the effect increased as well. PSE for $18^\circ/\text{s}$ was significantly higher than PSE for $2^\circ/\text{s}$, for the 4 and 6° reference stimulus sizes (two-sided t-test, $p < 0.05$). Vertical lines show standard error of the mean ($n=8$).

2.2.5 Discussion

In this study, our primary intention was to reproduce and quantify a misperception of speed, which is based on the size of RDPs. The effect of size was known for a single moving object, as Brown reported already in year 1931: as the linear dimensions of the motion field is halved, the perceived speed of the object was doubled [7].

Ryan and Zanker [41] used RDPs in a two-alternative-forced choice paradigm and for a size ratio of 1:2 they observed an increase in perceived speed of about 25%. Our results were similar to those of Ryan and Zanker, however, we also tested the effect as a function of stimulus speed and observed a modulation of the effect. As the speed of the stimulus increased, the magnitude of the effect monotonously increased for the range of speeds we used ($2-18^\circ/s$) and the trend was similar for all stimulus sizes.

The increase in the magnitude of the effect depending on stimulus speed might be based on the summing up of effects of several stimulus parameters, which also might affect speed perception. This effects can be explained with a link to the results of the first experiment. As the stimulus size decreases, lower spatial frequencies of a stimulus will diminish and higher spatial frequencies will predominate. As seen in figure 2.5, at higher spatial frequencies stimulus speed is overestimated (black line) and at lower spatial frequencies it is underestimated (gray lines).

Also, the increase in the size of the effect as a function of speed might be again due to the fact that at higher spatial frequencies (smaller stimulus size) the slope and increasing trend of the PSE is steeper than at lower spatial frequencies (figure 2.5). therefore as the speed increases, the effect of spatial frequencies will be larger.

All in all, these results are in accordance with the literature and with the results of our first experiment, suggesting that the spatial composition of a stimulus has an important influence on its perceived speed.

3 Electrophysiology of Speed Processing in Area MT of Macaque Monkeys

3.1 Abstract

When viewed behind smaller apertures, random dot pattern stimuli appear to move faster than identical stimuli moving behind larger apertures. This influence of motion field size on perceived speed was reproduced and quantified with human subjects in the first chapter of this thesis. Here, we recorded from speed selective neurons of area MT of two awake macaque monkeys to investigate differences in neural responses for different sizes of stimuli. For this purpose, we conducted two independent electrophysiological experiments. In experiment I, we measured speed tuning curves of MT neurons using identical stimuli that matched the preferences of the unit but varied in size. We observed that speed tuning curves of MT neurons shifted toward slower speeds as the size of the stimuli decreased. In experiment II, we used an ROC analysis to obtain statistics of firing rates for differently sized stimuli. After measuring the speed tuning curves of each neuron with a stimulus covering the receptive field, we determined the speed at the steepest part of the tuning curve and presented the unit stimuli moving at this speed, since stimulus dependent variations in firing rate would be the largest. We observed that neurons responded to a decrease in stimulus size in the same way as if they were responding to an increase in stimulus speed. The findings of both experiments are in accordance with each other and with the psychophysical findings of chapter 1 (exp. II). Our results of speed tuned neurons account for a vector averaged computation of perceived speed in area MT.

3.2 Introduction

In the previous chapter, we have discussed how a decrease in motion field size increases perceived speed in human subjects. This chapter outlines our electrophysiological experiments with macaque monkeys, in search for neuronal correlates of the misperception. In the following, we will first briefly focus on the relevant response properties of the visual cortical area (area MT) we recorded from, which is reported to be directly involved in speed perception in primates. Then, we will summarize some of the frequently mentioned models of speed tuning, and finally, we will describe two independent experiments seeking the neuronal basis of the field-size dependent speed misperception.

3.2.1 Receptive field properties of area MT

Over the past three decades, pronounced amount of evidence has been collected, that a relatively small cortical area in the parietal cortex is directly associated with the perception of visual motion in primates. This area is called the medial temporal area, often referred to as area MT and also known as V5. It is a part of the extra-striate cortex, located in the posterior bank of the superior temporal sulcus [11, 1].

The most distinguishing characteristic of this area is a high proportion of directionally selective cells [11, 26], which are spatially organized in columns according to their selectivity. In addition to direction selectivity, the majority of MT neurons display clear tuning for motion speed [27], and more than 50% of these neurons are tuned for binocular disparity [5, 10], which is important for stereoscopic depth perception.

Area MT receives a direct input from the primary visual cortex (V1), mostly from layer 4B [11]. Receptive fields of MT neurons are about 10 times larger in area than the receptive fields of V1 neurons and the receptive field diameter approximately matches the receptive field eccentricity [14, 26, 13]. As most of the visual areas, MT is organized retinotopically and contains a nearly complete map of the contralateral visual hemi-field, where this representation is biased for fovea and the lower quadrant of the visual field [26].

3.2.2 Tuning for motion speed in area MT

The motion of an object on the retina is a vectorial measure with two major components: the direction and the rate of motion, where the latter is referred to as speed. The measurement of the speed of a moving object can be achieved by measuring its positions at two different spatial locations and at two different times. The ratio between the position difference and the time difference will be equal to the speed of the object. Therefore, the speed of visual motion can be described as the rate of change in retinal position over time.

In functional magnetic resonance and positron emission tomography studies, the (hMT+) complex in human subjects is shown to be more active during a speed discrimination task than during other discrimination tasks [3, 9, 17].

Electrophysiological recordings in monkeys showed that most of the directionally selective neurons in MT are also selective for stimulus speed [27, 40]. Their activity is modulated by speed, which means, they fire at a peak firing rate for a certain speed and for higher or lower speeds they fire less or their activity does not change from the spontaneous activity.

Recently, responses of speed tuned neurons in area MT have been shown to be directly linked to perceptual judgments [25]. Liu and Newsome showed this link (1) by looking at the correlation between activity of single neurons and monkey's speed discrimination, (2) by inducing a bias in monkey's perception through micro-stimulation of area MT.

One of the strongest evidences for MT's role in speed coding is its selective responses to speed. The responses of MT neurons are tuned for stimulus speed, which means their response shows a modulation as a function of speed. On a linear scale, this tuning is skewed toward higher speeds, meaning that if neurons response is plotted as a function of speed, the tail of the response distribution for the higher speeds will be the longer one. On a logarithmic scale for speed, these tuning curves are symmetrically bell-shaped and can be well fitted with a log-Gaussian [23]. The speed evoking the highest response is called the preferred speed and although the spectrum of preferred speeds in MT appears to be unimodal [27], speed selective MT neurons can be subdivided in three main filter categories according to their tuning profile: low-pass, band-pass and high-pass [40]. Maunsell tested speeds

ranging from 0.5 to 512 °/s with moving light slits of variable length and direction (matching the preferences of the neurons) and observed that the preferred speeds of the recorded sample had a single peak at 32 °/s [27]. This peak in the population selectivity matches well with the psychophysical finding of Orban [30] that human speed discrimination thresholds are lowest for speeds around 4-32°/s.

In non-primate mammals motion sensitivity, more precisely, direction selectivity already starts at the retinal level with ganglion cells [2], however, these cells are invariant to stimulus speed and temporal frequencies. Primate retinal ganglion cells are not selective for motion direction, instead, in ensembles of cells they convey information about spatiotemporal structure of the stimulus through the timing of their action potentials. The output of retinal direction selective cells passes through thalamus as the most of the sensory information on the way to cortex, and arrives in V1. V1 neurons are the first cortical cells with a speed selectivity to some extent. However, the proportion of speed tuned cells in V1 [37] is not as high as in MT [33]. It has been reported that above 80% of the directionally selective cells in MT are speed tuned as well [27, 24]. In addition to the evidence about MT's speed tuning described as the modulation of response as a function of speed, there has been a debate about the invariance of speed tuning in MT to the spatial composition of the stimulus. Perrone and Thiele has reported that approximately 60% of MT neurons showed the same response, regardless of the spatial frequencies of the sine wave grating stimuli moving in their receptive field, as long as the speed was the same [33].

3.2.3 Computational models for coding of speed

Our understanding about how visual speed might be coded as neuronal activity, will much likely come from computational models, which account for experimental data and combine knowledge about neurophysiological and psychophysical findings. Various models were suggested for the coding of velocity, that is, motion direction and speed.

A basic yet prominent model for the detection of motion is the so-called Reichardt detector [38], which exemplifies a simple motion detecting mechanism made of two receptors separated in space, two temporal filters and a detector receiving input

from the temporal filters. The output of one receptor is delayed via an internal delay filter, therefore, maximum facilitation of the detector will depend on the suitable temporal frequency input. If the activation of receptors are separated in time, with a delay matching the internal temporal filter of the detector, then the outputs of the receptors will arrive at the detector about at the same time.

For the coding of motion speed from the activities of speed tuned neurons, independent from direction information, a number of models were suggested. In the following, we will briefly introduce three of the currently discussed models of speed perception. Within the framework of this thesis, we collected electrophysiological data, with which we could test the vector average model of speed coding.

The vector average model

The vector average model is based on the principle of labeled lines. Each neuron is labeled with a speed (which may be considered as neuron's preferred speed). This model assumes that, activated by a stimulus, each speed tuned neuron will be voting for its label speed, and this vote will be weighted by the firing rate of the neuron. Perceived speed will correspond to the weighted average of all labels.

The ratio (two-channel) model

Thompson suggested a model for the coding of speed, based on the relative activity of two speed selective channels [46, 32], in compliance with his psychophysical studies about the effects of contrast on perceived speed. The ratio model states that perceived speed will be correlated to the ratio between the activities of neurons in one channel preferring higher speeds and of neurons in another channel preferring lower speeds. According to this model, for a given stimulus speed, neurons would vote for their label and the ratio of the overall activity of each channel would make up the perceived speed.

The Bayesian model

Weiss, Simoncelli and Adelson proposed a Bayesian model for speed perception [50], in which the perceived speed is the product of a likelihood distribution based on

the measurement of the stimulus velocity (centered at stimulus speed) and a prior distribution (centered at zero speed) which is biasing the product toward slower speeds. This model is shown to account for the effect of contrast on perceived speed [19].

3.2.4 Aim of this study

Understanding visual illusions might provide us powerful information about the functioning of the visual system. Given the psychophysical finding that a decrease in stimulus size increases perceived speed [41] and given the electrophysiological findings suggesting MT is directly involved in speed perception [25], we aimed to find a correlation between stimulus size and neuronal responses, which could help for choosing between the different models of speed perception.

3.3 Electrophysiological Methods

3.3.1 Surgery and Maintenance of the Monkeys

Animals. Two awake, behaving, male rhesus macaque monkeys (*Macaca mulatta*) of six years of age were trained for a visual fixation task. After an initial training, the animals were surgically implanted with a head-post to be able to prevent head movements during experimental sessions. Following the fixation training, 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 left hemisphere in monkey D). All surgical procedures and experiments were approved by the appropriate authorities. Head-posts and recording chambers were implanted using standard surgical techniques under isoflurane anesthesia [15].

Monkeys were deprived of fluid on training and recording days and received fluid reward during experimental sessions. Routinely, monkeys had access to unlimited fluid in form of water, juice, fresh fruits and vegetables, on two days of a week.

3.3.2 Apparatus

Monkeys were seated in a custom-made primate chair in a dimly lit separate experimental room during the experiments, at a distance of 57 cm to a computer monitor. The monitor had a resolution of 1200 pixels in the vertical and 1600 pixels in the horizontal and covered a visual field of $30 \times 40^\circ$ of visual angle. The refresh rate of the monitor was 75Hz, meaning that the display was refreshed every 13.3 ms.

3.3.3 Electrophysiological Recordings

Extracellular action potentials of single-units in the macaque middle temporal area (MT) were recorded with tungsten microelectrodes ($4M\Omega$ at 1 kHz, FHC, Bowdoinham, ME) controlled by a hydraulic micropositioner (David Kopf Inst., Tujunga, CA). Neuronal signals were processed and recorded with the Plexon (Plexon Inc., Dallas, TX) data acquisition system. The electrode was inserted through the dura with the help of a custom made guide tube. Area MT was identified by its

anatomical position, the typical activity and silence pattern (layers of gray and white matter) along the electrode track, the high proportion of direction selective units, that were less selective for complex motion (i.e. expansion and contraction), selectivity for speed and the ratio of receptive field size and eccentricities.

Eye positions were sampled by an infrared video monitoring system at 226 fps. (ET-49, Thomas Recording, Giessen, Germany). An infrared light source was reflected on one of the corneas (contralateral in monkey Z and ipsilateral in monkey D) to monitor the pupil, of which the center was computed as the eye position.

3.3.4 Visual Task

Monkeys performed the same fixation task both for the initial investigation of direction and speed selectivity and for the following speed tuning experiment. Figure 3.1 on page 51 describes the visual task. The animals were trained to fixate a small square ($0.15^\circ \times 0.15^\circ$) on the display throughout a variable trial duration of 4 to 6 seconds. A trial was considered as a hit as long as the animals kept their gaze within the fixation area (1.25° radius) and released a lever upon a change in the luminance of the fixation point, the so called response event. Fixation breaks aborted the trials. Following the response event, a lever release before a defined latency of 170 ms or after the response time window of 400 ms duration aborted the trials as well. Only hit trials were analyzed. The animals received fluid reward immediately following each hit trial. After aborted trials, the monkey had to wait for at least 300 ms to start another trial.

3.3.5 Stimulation

After isolating each unit, the classical receptive field sensitive to motion stimulus was mapped with a mouse-controlled bar or a random dot pattern of variable size. To investigate the direction and speed selectivity of the units, random dot patterns moving in one of 12 different directions (0, 30, 60, 90, 120, 150, 180, 210, 240, 270, 300, 330°) and at one of the 8 different speeds (0.5, 1, 2, 4, 8, 16, 32, 64°/s) were presented in the receptive field. In all electrophysiology experiments, the dot density of RDPs was 10 dots/deg². The size of the dots was kept constant at

0.01deg². Background luminance was set to 25.34 cd/m² and the luminance of the dots was 85.62 cd/m².

In experiment I, stimulus size and motion direction were adjusted to the preferences of each unit. The directions evoking the highest response from the unit (preferred direction) and the direction set 180° apart from this direction (null direction) were used. In each trial, stimuli moved repeatedly in preferred and the null direction in succession (e.g. 0° and 180°). The speed of each stimulus was randomly picked from the eight speeds mentioned above. The duration of each RDP stimulus was 800 ms and there was no blank interval between the successive presentations. A trial contained up to 7 successive stimulus presentations, the number of presentations in a given trial depended on the random timing of the response event. For each unit, stimuli in three sizes were used. The largest stimulus nearly covered the receptive field, whereas the diameter of the medium and small stimuli had 1/2 or 1/4 diameter of the largest stimulus. The size of the stimuli used for different units ranged from 2° to 16° in diameter, where in some cases receptive fields were larger than the biggest stimuli. For these recordings, stimuli were placed on the most active part (the “hot-spot”) of the receptive field.

In experiment II, the same visual task and the same visual stimuli were used in a different paradigm. Here, the stimuli in various sizes were presented over a large number of trials (at least 30, typically 40-50 trials) in order to obtain firing rate statistics from the unit. The collection of such a large number of trials at each data point of the speed tuning curves would demand a very large number of total trials, that could not be performed by the monkey in the course of daily recordings. Therefore, for each recording site, all stimuli were presented at a constant speed, which was chosen from the steepest part of the speed tuning curve for a stimulus approximately matching the size of the receptive field.

3.3.6 Data Acquisition and Analysis

Online analysis of neural activity was accomplished with a C-based custom software. Further data analyses and statistics were performed with scripts written in MATLAB (MathWorks, Natick, MA).

The average number of spikes a unit fired in a second of stimulus presentation was

computed as the firing rate. In experiment I, the firing rate was determined based on at least four repetitions (typically about eight) of identical stimulus presentations in different trials.

Speed tuning curves consisting of at least seven data points were then fit by a four parameter log-Gaussian with the formula:

$$f(x) = A + B \exp\left(-\frac{1}{2} \frac{(\log x - \log x_0)^2}{(\log \sigma)^2}\right) \quad (3.1)$$

where A denotes the baseline firing rate, B is the peak tuning amplitude, x_0 represents the speed at the peak position of the log-Gaussian, and $\log \sigma$ is the standard deviation of the log-Gaussian distribution.

The log-Gaussian, was fit with the Levenberg-Marquardt routine [35]. The peak of the fitted log-Gaussian was considered as the preferred speed for a given stimulus size. To test the changes in tuning width, the standard deviation of log-Gaussians were compared. The amplitude, which was equal to the difference between maximum and minimum response extracted from the log-Gaussian, was used as a measure of responsiveness and was compared for different sizes of stimuli as well.

A speed tuning index was computed for each speed tuning curve, where the amplitude (maximum - minimum) of the log-Gaussian was divided by the standard deviation. Units with poor speed tuning (i.e. units with too low or too high speed tuning indices) and visibly not well fit by the log-Gaussian curve were excluded from the analyses. Additionally, units with preferred speeds higher than $64^\circ/\text{s}$ were excluded from the data, since the stimulus speeds used did not exceed $64^\circ/\text{s}$ and it is not clear whether a unit with a higher preferred speed still can be considered as well fit with a log-Gaussian.

ROC curves in experiment II. For the analyses in the second experiment, receiver operating characteristics (ROC) curves were computed. They have been widely used in signal detection theory [16] and medical diagnostics, as well as in choice probability analyses, seeking a correlation between neuronal activity and psychophysical data [6, 25]. In this study, ROC curves are used to measure the

separation between distributions of firing rates measured with different stimulus sizes. Therefore, this analysis serves as a statistical method for analyzing the similarity of the firing rates for differently sized stimuli. For this purpose, after mapping the receptive field and determining the preferred direction, the speed tuning curve was measured with a stimulus covering the receptive field, which was to be used as the largest stimulus in experiment II. After fitting speed tuning curves with log-Gaussians, the two steepest parts of each tuning curve were computed in the linear speed space: one on the ascending and the other on the descending arm, using an equation of the following form:

$$g(x) = V_0 \exp\left(\frac{-\log \sigma^2}{2}\right) \exp\left(\frac{\pm \log \sigma \sqrt{\log \sigma^2 + 4}}{2}\right) \quad (3.2)$$

For clarity, the speeds corresponding to these two high slope points of the tuning curve are termed as the lower (for the ascending arm) and the higher (for the descending arm) critical speed. One of these two speeds is taken as the constant stimulus speed of experiment II. The choice of the critical speed depended on the speed tuning profile and the overall responsiveness of the unit. In general, the lower critical speed was used for high-pass and band-pass units and the upper critical speed was used for low-pass units. The division between high-pass and low-pass units was kept flexible and there was no strict criterion, since for some band-pass units with low firing rates, the lower critical speed evoked a very weak response. Stimuli moving at this speed would elicit firing rates near zero. Therefore, although such units were not low-pass per se, the upper critical speed was used as well. After repeated presentations of random dot patterns in different trials, firing rates for three sizes of the stimuli were computed. For each stimulus size, the histograms of firing rates were computed with a bin size of 2.5 spikes/s. The frequencies in each bin were then summed cumulatively and the cumulative sums were plotted in pairs (i.e. stimulus covering 50% of the receptive field vs stimulus covering 100% of the receptive field.) The resulting curve corresponded to the ROC curve and the area under this curve was computed for further analysis as described in results

of the experiment II.

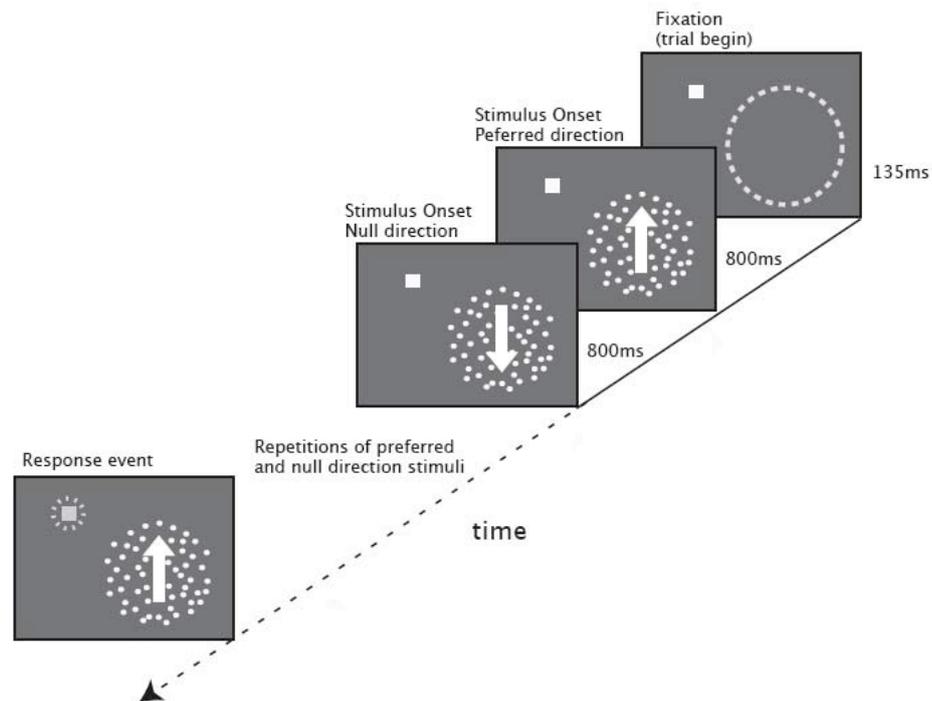


Figure 3.1: Visual fixation task. The monkeys were trained to keep their gaze on the fixation square throughout the trial. Each trial consisted of presentations of random dot patterns (RDP) moving in two opposite directions of the same motion axis. The figure depicts the upward direction as the preferred and the downward direction as the null direction. Each stimulus lasted for approximately 800 ms and moved at a speed randomly picked from a speed table (0.5, 1, 2, 4, 8, 16, 32 or $64^\circ/\text{s}$).

3.4 Results

We recorded from a total number of 86 single units, 66 units were from monkey Z and 20 units were from monkey D. 59 of these units were used in the analyses of experiment I, and the remaining 27 were recorded for experiment 2. The majority of our sample consisted of single units with distinct and well isolated waveforms ($\sim 89\%$).

Area MT is neighboured by area MST, which shows similar response properties to motion stimuli, such as direction and speed tuning [48]. However, area MST has a higher receptive field to eccentricity ratio [48]. To ensure that our single unit data is collected from area MT, we first analyzed the relationship between the classical receptive field size and receptive field eccentricity in the population of units we recorded from. The ratio of these two parameters in our sample was 0.99 ± 0.05 , indicating that recordings were in area MT. Another difference between these two areas is that MST units are tuned for complex motion such as expansion and contraction [42], whereas MT units are responsive but not necessarily tuned for such motion [12]. After isolating most of the motion responsive single units, we tested the responses to complex motion but observed no tuning in the spiral motion space, although most of the units displayed some nonselective response.

In the following sections, we summarize our results from two separate experiments. Experiment I investigates the stimulus size related changes in tuning preferences of MT units. Experiment II applies a signal detection theory quantifying the changes in firing rates of MT units, with regard to stimulus size. The data for these two experiments derive from different recordings, therefore, two different populations from the same two monkeys contribute to these results.

3.4.1 Experiment I: Effects of stimulus size on speed tuning preferences

To test the effects of stimulus size on speed tuning preferences, we analyzed the changes in the following parameters of the speed tuning curves: preferred speed, tuning width and tuning amplitude. 59 units (monkey Z: 46 units, monkey D: 13 units) contributed to the data of these experiments. The results of these analyses are summarized below.

The main plots in figure 3.2 show the speed tuning curves of two sample units. These curves show a characteristic bell-shaped modulation of the response as a function of stimulus speed on a logarithmic scale. In each plot, there are three curves plotted in different grays obtained for three sizes of stimulus. Both units demonstrate a band-pass type of speed selectivity, since their activity is highest for a range of speeds and since they do not prefer only slow or only high speeds behind a cutoff speed. The preferred speed for a given stimulus size is the speed for which the tuning curve reaches its maximum. The amplitude of each curve is the difference between the peak and the baseline of the fit.

Stimulus size dependent changes in preferred speed of MT neurons

To see whether there is a systematic effect of stimulus size on preferred speed, for each unit we first normalized the preferred speeds by the preferred speed for the middle size stimulus. Inset plots in figure 3.2 show normalized preferred speeds of the sample units. as a function of stimulus diameter normalized to the receptive field diameter We then fitted a straight line through the normalized preferred speeds to visualize any systematic increase or decrease with a single measure. This measure was the sign and the slope of the fitted line. The slope of this line was positive for the majority of the units (42 of 59 units, 71% of the population). Figure 3.3 shows the distribution of these slopes within the population. The mean slope was significantly different from zero (mean= 0.30 ± 0.09 , $p < 0.01$, two-sided t-test), meaning that a decrease in RDP size resulted in a decrease in preferred speed. Although not all units showed a monotonous decrease in preferred speed following the decrease in stimulus size, the slope we measured showed a tendency

for decreasing preferred speeds, which was consistent across the population.

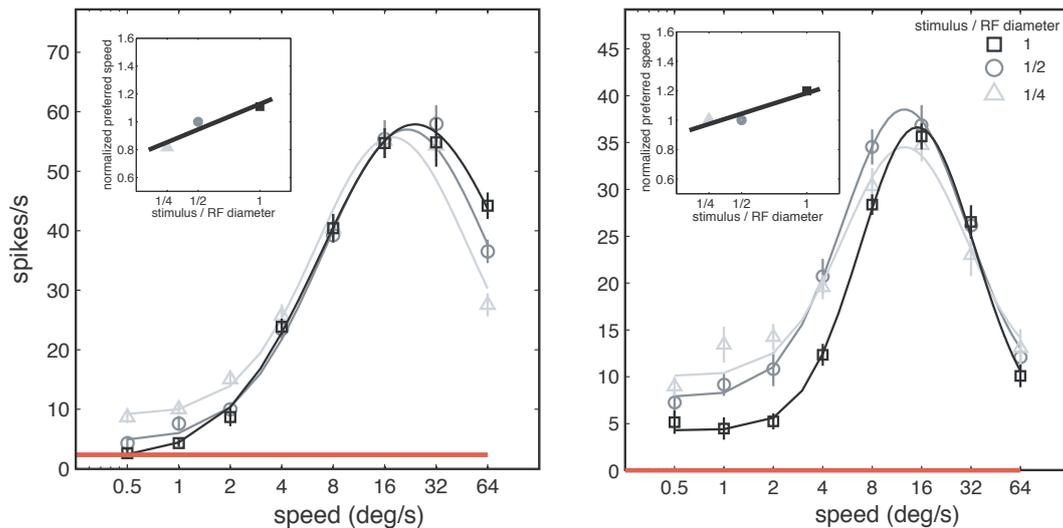


Figure 3.2: Sample speed tuning data of two single-units. Main plots display the speed tuning curves for three sizes of stimulus. Data points are mean firing rates for each speed and size combination. Smooth lines are the fitted log-Gaussians. Inset plots show the change in preferred speed of each unit as a function of stimulus size. Data points denote the preferred speeds and the straight line (a polynomial of first order) is fitted through the three preferred speeds. Red lines indicate the spontaneous firing rate of the units.

Stimulus size dependent changes in tuning width and tuning amplitude of MT neurons

We investigated the effects of stimulus size on the tuning width of MT units, by directly comparing the standard deviation of the fitted log-Gaussians. In figure 3.4a, each different mark represents the comparison of tuning width for a smaller size stimulus with tuning width for a larger size stimulus. We observed no significant difference in tuning width obtained from the presentations of three different stimulus sizes (repeated measures one-way ANOVA, $p > 0.05$).

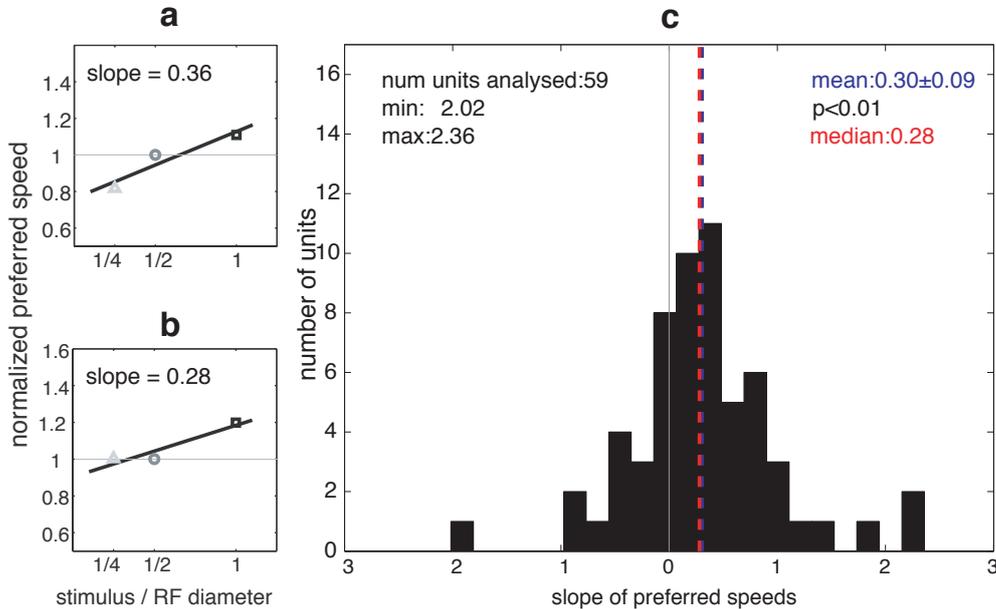


Figure 3.3: The effect of stimulus size on preferred speeds. (a) and (b) show normalized preferred speeds of the same two sample units as in figure 3.2. Three different symbols are used for the normalized preferred speeds obtained for different RDP sizes. The black line is a polynomial of the first order fit through these data points. In (c) the slope of the fitted lines from the recorded neurons is plotted in a histogram. Speed tuning curves shift toward slower speeds with decreasing RDP aperture size.

On the other hand, amplitudes increased significantly with stimulus size (repeated measures one-way ANOVA, $p < 0.001$). As seen in figure 3.4b the majority of the data points lie above the diagonal, denoting that tuning amplitude of MT neurons increased with stimulus size. This observation is not very surprising, since most of the MT neurons display an inhibitory surround and are size tuned, that is, at a given stimulus speed, their response will be the highest for stimuli almost covering their receptive field, but will be modest for stimuli larger or much smaller than the receptive field. The decrease in the tuning amplitude for smaller stimuli was therefore expected. The data points showing the comparison between the amplitudes for largest and middle stimuli (cross marks) are above the diagonal, as

also indicated by the mean (red cross), meaning that the response for the largest stimulus was the highest and the data are not influenced by the inhibitory surround. This is also not surprising given that we selected the largest stimulus size to still fit within the classical RF. This increase in tuning curve amplitudes with stimulus size is in accordance with the knowledge about the area summation property of MT neurons, meaning that a stimulus covering the classical receptive field would elicit the highest response. If the size of the stimulus would be further increased, this would activate the inhibitory surround and the resulting activity would decrease.

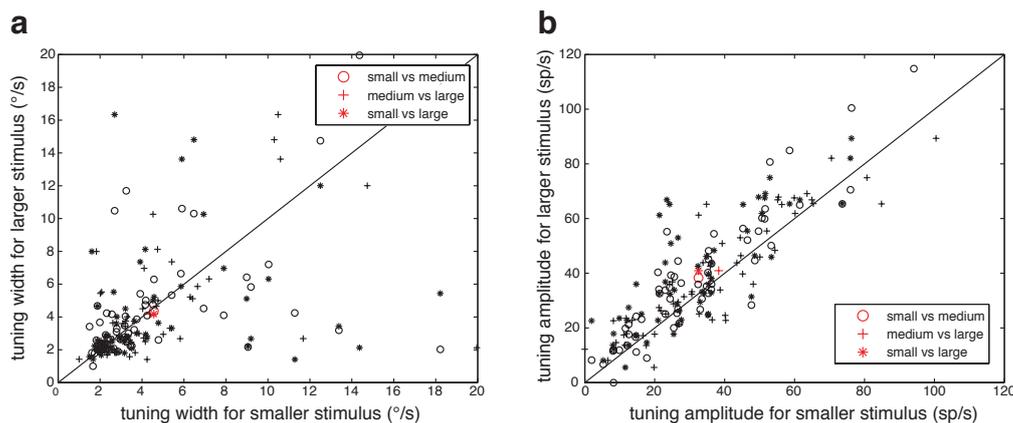


Figure 3.4: Analysis of speed influences on tuning width and tuning amplitude. (a) Scatter plot of tuning width shows that speed tuning width does not change depending on stimulus size. It is visible that standard deviations of log-Gaussians are widely distributed on both sides of the diagonal and show no systematic distribution. The means are on the diagonal, indicating that tuning width did not change with stimulus size. (b) This plot of tuning amplitudes for small and large stimuli demonstrates that tuning amplitude increases with the size of the RDP moving in the receptive field. Each unit contributed three times to each plot (see text). Red markers are the mean values of each data set.

3.4.2 Experiment II: Signal detection analysis of MT responses

In this part of the study, we investigated the direct influence of stimulus size on firing rate statistics, when the stimuli were moving at the same speed. Our approach here is based on signal detection theory. Therefore, for each stimulus condition at least 30 trials are collected. Such a large number of trials for each data point along a speed tuning curve would demand recording sessions of a duration, which cannot be accomplished by the monkey. Therefore, we concentrated on only a single point of the tuning curve. For this purpose, we adapted a choice probability analysis method, which was previously used to investigate the correlation between speed perception and neural activity in area MT [25].

The steepest part of a bell-shaped tuning curve is the stimulus value where the neuron is the most sensitive to a change in the stimulus value, because here a small change in this value results in the largest change in neuronal firing rate [43, 8]. From this point of view, a stimulus evoking the response at the highest slopes of the tuning curve, will be easier to discriminate from nearby stimuli than stimuli evoking responses at the peak of the tuning curve.

Figure 3.5 illustrates our analytical approach in two single units. As described in the methods section, for each stimulus size, the responses from at least 30 independent trials were recorded for three sizes of stimuli using the described critical speed (figure 3.5a). We compared two-by-two these three firing rate distributions (figure 3.5b) by computing the area under the ROC curve (AUC, figure 3.5c).

The area under the ROC curve (AUC) is a measure for discriminability and separation between two distributions: a distribution of responses to a larger stimulus and a distribution of responses to a smaller stimulus. The AUC has a value between 0 and 1. For two distributions that are totally separated, the AUC value is either 1 or 0. As the degree of overlap between the two distributions increases, the AUC approaches 0.5. The outcome will depend on the relative positioning of the distributions, if one is taken as the reference (for instance being the distribution on the x axis of the ROC plot).

If single MT neurons would respond to a decrease in stimulus size in the same way as they would respond to an increase in stimulus speed, this behavior would

cause a decrease in firing rates of low-pass units and an increase in firing rates of high-pass units, meaning that the divergence of distributions would have two different signs for the two different speed selectivity types.

Therefore, the AUC values of low-pass units were subtracted from 1 in order to make the separation between response distributions of such units and high-pass units comparable. The resulting AUC values were called *adjusted AUC* together with the AUC values from the band-pass and high-pass units, which were not subtracted from one.

A mean AUC value higher than 0.5 (as the mean of our sample) indicates that band-pass and high-pass units increase their firing rate and low-pass units decrease their firing rate for a smaller stimulus. This respective increase or decrease in the firing rate is ambiguous and is occurring in the same direction along the tuning curve as an increase in the stimulus speed. The results of this experiment are summarized in figure 3.6 as a histogram of all adjusted AUC values obtained from 27 units. The histogram contains three adjusted AUC values from each unit for each comparison between the three stimuli. The mean AUC of the sample was 0.56 ± 0.03 . This value was significantly different than 0.5 ($p < 0.01$, two-tailed ttest, $n=81$). In other words, the sampled units changed their firing rates as if they were responding to a faster stimulus, regardless of their specific speed tuning profile (i.e. low-pass or high-pass).

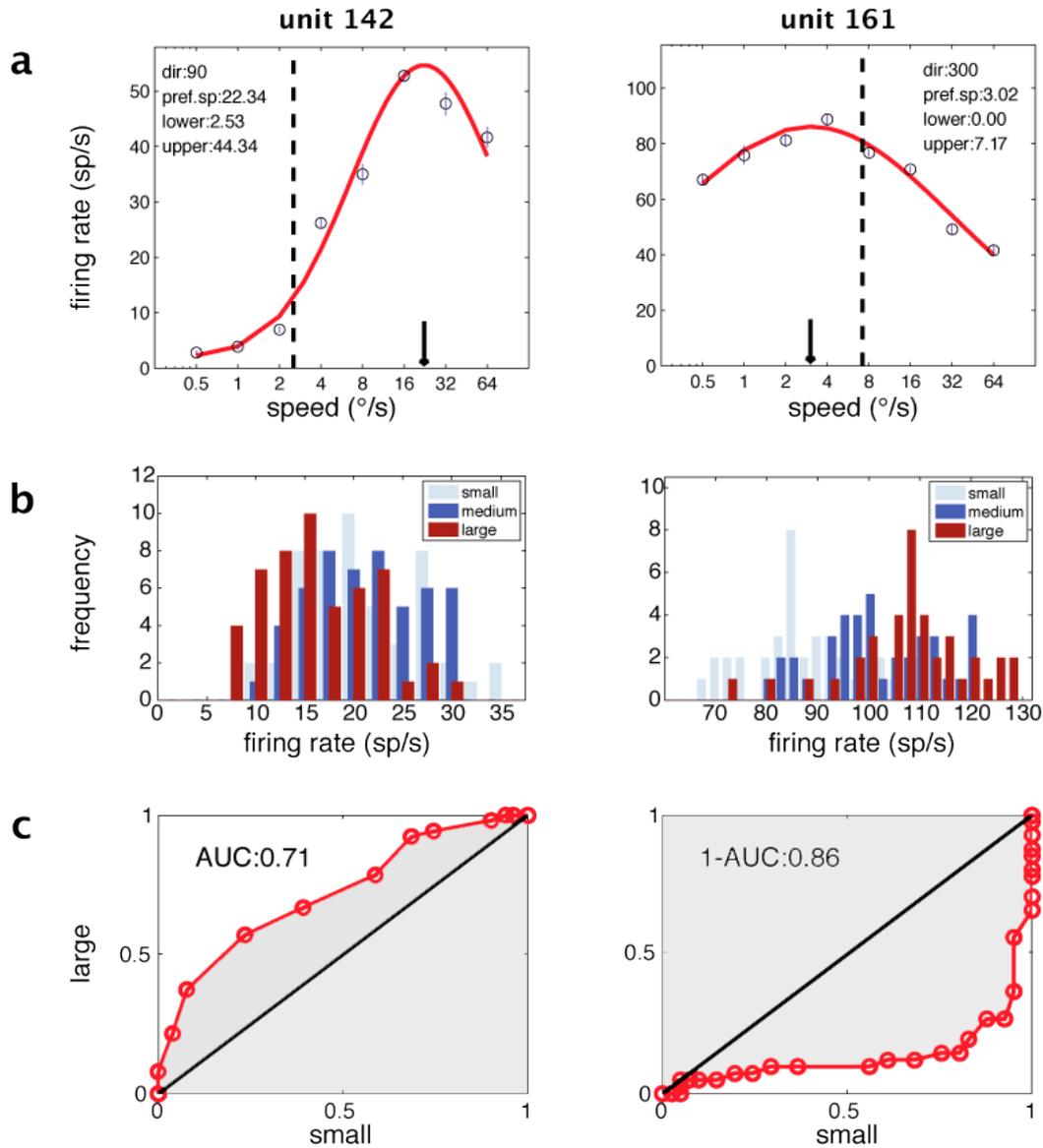


Figure 3.5: Computation of ROC curves for two main types of speed tuning in two sample units from the choice probability experiment. (a) Both panels show speed tuning curves measured with stimuli covering the receptive field of two sample units. Dashed lines mark the ascending or descending high-slope regions. (b) Histograms of the frequency of obtaining particular individual firing rates obtained from respective trials for three stimulus sizes. (c) Sample receiver operating characteristics curves. For each unit three ROC curves comparing firing rates for three sizes were acquired. AUC denotes the area under the ROC curve and serves as a measure for the separation between the two distributions compared.

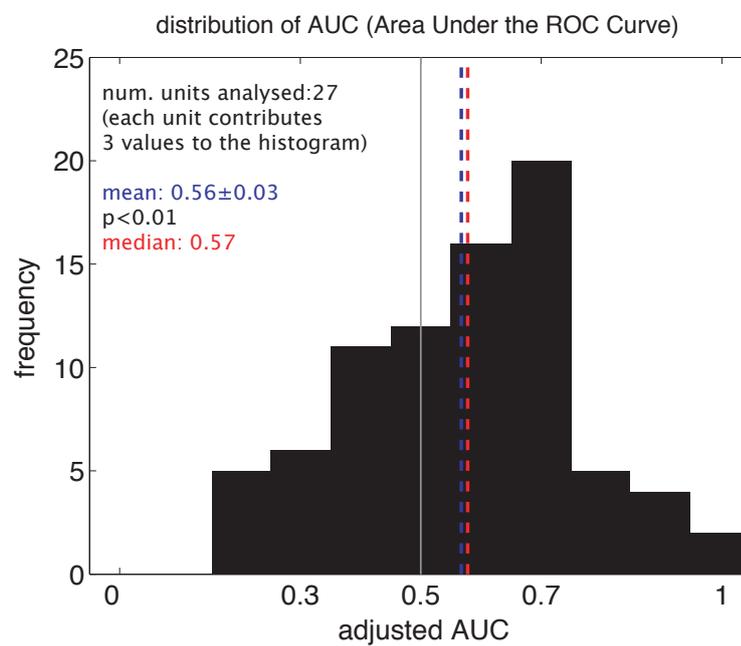


Figure 3.6: Distribution of the adjusted AUC throughout the population. Each unit contributes three adjusted AUC values to the histogram. Mean adjusted AUC is significantly larger than 0.5 ($p < 0.01$, two-tailed ttest, $n=81$), indicating that single units responded to a decrease in stimulus size in the same way as to an increase in stimulus speed.

3.5 Discussion

Stimulus size related changes in speed preferences of MT neurons suggest a vector averaged coding of stimulus speed

Our electrophysiological results from experiment I showed that a decrease in stimulus size caused a change in speed tuning preferences of speed selective MT neurons. As we decreased the stimulus size keeping other parameters constant, speed tuning curves shifted toward slower speeds, meaning that for a smaller stimulus, neurons preferred a lower speed. Since tuning widths did not change with stimulus size, a decrease in preferred speed was presumably a direct result of shifts in tuning curves.

This observation suggests that speed preference of MT units varies with stimulus size, and it matches the psychophysical findings with human subjects [41] as explained below.

Figure 3.7 explains our hypothesis schematically. The labeled line principle of sensory systems states that each receptor will be best activated by a particular value of a stimulus feature (e.g. a particular stimulus direction) and this activation will in turn result in a certain sensation of the stimulus feature. By definition, a speed tuned MT neuron will be most active and respond at its peak firing rate, when its preferred speed is present in the receptive field. Therefore, if perceived speed would depend on the activation of this single neuron, then the peak activation of the neuron would mean that the stimulus is moving at its preferred speed. A change in the preferred speed of this neuron would change the perceived speed, since the neuron would decrease neuron's activity for the same stimulus. The same assumption could also be passed on to the coding of perceived speed on population level. As a stimulus is moving at a certain speed in the visual field, not a single neuron but a population of neurons with a corresponding receptive field, will be active. The most active neurons of the population will be the ones with a preferred speed close to the stimulus speed.

If stimulus speed is represented in area MT as the output of a vector-average computation (figure 3.7a) , then the population of MT neurons, which are acti-

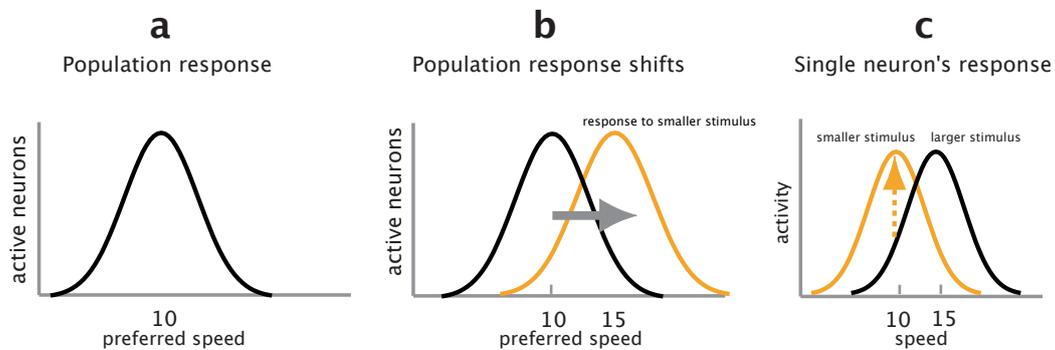


Figure 3.7: The Hypothesis. This figure illustrates the compatibility of shifts in tuning curves with a vector average model. (a) Perceived speed is the vector average of population. (b) Increasing the population average increases perceived speed. (c) This could be possible if single neurons decrease their preferred speed under specific circumstances (e.g. with decreased stimulus size).

vated by the stimulus will contribute to this computation by giving their vote for their preferred speed (or label speed). Therefore, most active neurons of the population will be the ones preferring the stimulus speed. On the other hand, neurons with a preferred speed higher or lower than the stimulus speed will show a weaker response. The vector average of such a population will be the estimate of the stimulus speed.

Hypothetically, to change the perceived speed of a moving stimulus, one has to change the vector average of the population. A shift in the average population response would cause a shift in the perceived speed in the same direction (figure 3.7b). Perceived speed would increase for a smaller stimulus size, when more neurons with higher preferred speeds would become active. This is possible, if single neurons of the population tend to decrease their preferred speed (figure 3.7c). At a given speed, for a smaller stimulus the responses of those neurons will increase, which prefer higher speeds for larger stimuli. The population response will be biased toward higher speeds depending on the high speed labels of these neurons. Our finding that speed tuning curves shift toward slower speeds with decreasing stimulus size validates this hypothesis.

A direct link between responses of MT single units and a speed misperception

In experiment II, we addressed the question, whether there is a link between MT responses and stimulus size for a given stimulus speed, in a different approach. In a large number of independent trials, we collected firing rates for different stimulus sizes at a specific speed and tested the differences between firing rate distributions using an ROC analysis. When we decreased the size of the stimulus, we observed that firing rates of speed selective MT single units changed in the same way, as though these were responding to a faster speed, regardless of the speed tuning type of the unit.

Although these changes in the firing rate pattern of single units would already directly account for the field-size related speed misperception, it also holds for the results and the hypothesis of the first experiment. That is, if a high-pass unit is increasing its firing rate for a smaller stimulus, which moves at a speed from the *ascending* slope, this hints to a shift of the tuning curve toward slower speeds. Similarly, if a low-pass unit is decreasing its firing rate for a smaller stimulus moving at a speed from the *descending* slope, this might be a result of the shift in the tuning curve, again toward slower speeds. Therefore, our results from both experiments match each other and support the vector average model of perceived speed.

In a recent study, Krekelberg et al.[23] followed a similar approach to investigate the correlation between another speed misperception and the activity of speed selective MT neurons, with the difference that the authors focus on another stimulus feature, namely the luminance contrast. As the contrast decreases, perceived speed decreases as well [46], a speed misperception, which we investigated in detail in the first chapter of this thesis. Krekelberg et al. reproduced the effect of contrast with human subjects, nevertheless, the electrophysiological data did not account for any of the current models of perceived speed. In fact, contrast related changes (i.e. shifts in speed tuning curves) in neuronal responses were in the opposite direction of what a vector-average model would suggest. Also Pack et al. [31] presented similar results. Therefore, the vector average model of speed perception does not seem to work for stimulus contrast. However, as our results suggest that the model

clearly accounts for stimulus size related changes in perceived speed.

Bibliography

- [1] ALLMAN, J., AND KAAS, J. A representation of the visual field in the caudal third of the middle temporal gyrus of the owl monkey (*aotus trivirgatus*). *Brain Research* 31, 1 (August 1971), 85–105.
- [2] BARLOW, H., AND HILL, R. Evidence for a physiological explanation of the waterfall phenomenon and figural after-effects. *Nature* 200 (December 1963), 1345–7.
- [3] BEAUCHAMP, M. S., COX, R. W., AND DEYOE, E. A. Graded effects of spatial and featural attention on human area MT and associated motion processing areas. *Journal of Neurophysiology* 78 (1997), 516–520.
- [4] BLAKEMORE, M., AND SNOWDEN, R. The effect of contrast upon perceived speed: a general phenomenon? *Perception* 28, 1 (1999), 33–48.
- [5] BRADLEY, D. C., AND ANDERSEN, R. A. Center-surround antagonism based on disparity in primate area mt. *Journal of Neuroscience* 18 (1998), 7552–7565.
- [6] BRITTEN, K. H., SHADLEN, M. N., NEWSOME, W. T., AND MOVSHON, J. A. The analysis of visual motion: a comparison of neuronal and psychophysical performance. *Journal of Neuroscience* 12, 12 (1992), 4745–4765.
- [7] BROWN, J. The visual perception of velocity. *Psychologische Forschung* 14 (1931), 199–232.
- [8] BUTTS, D. A., AND GOLDMAN, M. S. Tuning curves, neuronal variability, and sensory coding. *PLoS Biology* 4, 4 (2006), e92.

- [9] CORBETTA, M., MIEZIN, F. M., DOBMEYER, S., SHULMAN, G. L., AND PETERSEN, S. E. Attentional modulation of neural processing of shape, color, and velocity in humans. *Science* 248, 4962 (1990), 1556–1559.
- [10] DEANGELIS, G. C., AND NEWSOME, W. T. Organization of disparity-selective neurons in macaque area mt. *Journal of Neuroscience* 19 (1999), 1398–1415.
- [11] DUBNER, R., AND ZEKI, S. M. Response properties and receptive fields of cells in an anatomically defined region of the superior temporal sulcus in the monkey. *Brain Research* 35 (1971), 528–532.
- [12] DUFFY, C. J., AND WURTZ, R. H. Sensitivity of mst neurons to optic flow stimuli. i. a continuum of response selectivity to large-field stimuli. *Journal of Neurophysiology* 65 (1991), 1329–1345.
- [13] FELLEMAN, D. J., AND KAAS, J. H. Receptive-field properties of neurons in middle temporal visual area (mt) of owl monkeys. *Journal of Neurophysiology* 52 (1984), 488–513.
- [14] GATTASS, R., AND GROSS, C. G. Visual topography of striate projection zone (MT) in posterior superior temporal sulcus of the macaque. *Journal of Neurophysiology* 46, 3 (1981), 621–638.
- [15] GIBSON, J. R., AND MAUNSELL, J. H. R. Sensory modality specificity of neural activity related to memory in visual cortex. *Journal of Neurophysiology* 78 (1997), 1263–1275.
- [16] GREEN, D. M., AND SWETS, J. A. *Signal detection theory and psychophysics*. Wiley, New York, 1966.
- [17] HUK, A., AND HEEGER, D. J. Task-related modulation of visual cortex. *Journal of Neurophysiology* 83 (2000).
- [18] HURLIMANN, F., KIPER, D. C., AND CARANDINI, M. Testing the bayesian model of perceived speed. *Vision Research* 42 (2002), 2253–2257.

- [19] HÜRLIMANN, F., KIPER, D. C., AND CARANDINI, M. Testing the bayesian model of perceived speed. *Vision Research* 42, 19 (2005), 2253–2257.
- [20] JOHNSTON, A., BENTON, C. P., AND MORGAN, M. J. Concurrent measurement of perceived speed and speed discrimination threshold using the method of single stimuli. *Vision Research* 39 (1999), 3849–3854.
- [21] KAERNBACH, C. Simple adaptive testing with the weighted up-down method. *Perception & Psychophysics* 49, 3 (1991), 227–229.
- [22] KREKELBERG, B., VAN WEZEL, R. J., AND ALBRIGHT, T. D. Adaptation in macaque MT reduces perceived speed and improves speed discrimination. *Journal of Neurophysiology* 95, 1 (2006), 255–270.
- [23] KREKELBERG, B., VAN WEZEL, R. J. A., AND ALBRIGHT, T. D. Interactions between speed and contrast tuning in the middle temporal area: Implications for the neural code for speed. *Journal of Neuroscience* 26, 35 (2006), 8988–8998.
- [24] LIU, J., AND NEWSOME, W. T. Functional organization of speed tuned neurons in visual area MT. *Journal of Neurophysiology* 89, 1 (2003), 246–256.
- [25] LIU, J., AND NEWSOME, W. T. Correlation between speed perception and neural activity in the middle temporal visual area. *Journal of Neuroscience* 25, 3 (2005), 711–722.
- [26] MAUNSELL, J., AND VAN ESSEN, D. The connections of the middle temporal visual area (mt) and their relationship to a cortical hierarchy in the macaque monkey. *Journal of Neuroscience* 3 (1983), 2563–2586.
- [27] MAUNSELL, J. H., AND VAN ESSEN, D. C. Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. *Journal of Neurophysiology* 49, 5 (1983), 1127–1147.

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- [28] MCKEE, S. P., SILVERMAN, G. H., AND NAKAYAMA, K. Precise velocity discrimination despite random variations in temporal frequency and contrast. *Vision Research* 26 (1986), 609–619.
- [29] MOULDEN, B., KINGDOM, F., AND GATLEY, L. F. The standard deviation of luminance as a metric for contrast in random-dot images. *Perception* 19, 1 (1990), 79–101.
- [30] ORBAN, G. A., DE WOLF, J., AND MAES, H. Factors influencing velocity coding in the human visual system. *Vision Research* 24 (1984), 33–39.
- [31] PACK, C. C., HUNTER, J. N., AND BORN, R. T. Contrast dependence of suppressive influences in cortical area mt of alert macaque. *Journal of Neurophysiology* 93, 3 (2005), 1809–1815.
- [32] PERRONE, J. A. Economy of scale: A motion sensor with variable speed tuning. *Journal of Vision* 5 (2005), 28–33.
- [33] PERRONE, J. A., AND THIELE, A. Speed skills: measuring the visual speed analyzing properties of primate MT neurons. *Nature Neuroscience* 4, 5 (2001), 526–532.
- [34] POST, R., AND LEIBOWITZ, H. A revised analysis of the role of efference in motion perception. *Perception* 14, 5 (1985), 631–643.
- [35] PRESS, W. H., TEUKOLSKY, S. A., VETTERLING, W. T., AND FLANNERY, B. P. *Numerical Recipes in C: the Art of Scientific Computing*, 2nd ed. Cambridge University Press, Cambridge, UK, 1992.
- [36] PRIEBE, N. J., CASSANELLO, C. R., AND LISBERGER, S. G. The neural representation of speed in macaque area MT/V5. *Journal of Neuroscience* 23, 13 (2003), 5650–5661.
- [37] PRIEBE, N. J., LISBERGER, S. G., AND MOVSHON, J. A. Tuning for spatiotemporal frequency and speed in directionally selective neurons of macaque striate cortex. *Journal of Neuroscience* 26, 11 (2006), 2941–2950.

- [38] REICHARDT, W. *Autocorrelation, a principle for the evaluation of sensory information by the central nervous system*. In: *Principles of Sensory Communications*, Ed. W.A. Rosenblith, New York, 1961.
- [39] REISBECK, T., AND GEGENFURTNER, K. R. Velocity tuned mechanisms in human motion processing. *Vision Research* 39 (1998), 3267–3285.
- [40] RODMAN, H. R., AND ALBRIGHT, T. D. Coding of visual stimulus velocity in area MT of the macaque. *Vision Research* 27, 12 (1987), 2035–2048.
- [41] RYAN, J., AND ZANKER, J. What determines the perceived speed of dots moving within apertures? *Experimental Brain Research* 141, 1 (November 2001), 79–87.
- [42] SAITO, H., YUKIE, M., TANAKA, K., HIKOSAKA, K., FUKADA, Y., AND IWAI, E. Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. *Journal of Neuroscience* 6, 1 (1986), 145–157.
- [43] SEUNG, H., AND SOMPOLINSKY, H. Simple models for reading neuronal population codes. *Proceedings of the National Academy of Sciences* 90 (1993), 10749–10753.
- [44] SMITH, A. T., AND EDGAR, G. The influence of spatial frequency on perceived temporal frequency and perceived speed. *Vision Research* 30, 10 (1990), 1467–1474.
- [45] SNOWDEN, R. J., STIMPSON, N., AND RUDDLE, R. Speed perception fogs up as visibility drops. *Nature* 392, 6675 (April 1998), 450.
- [46] THOMPSON, P. Perceived rate of movement depends on contrast. *Vision Research* 22 (1982), 377–380.
- [47] THOMPSON, P., BROOKS, K., AND HAMMETT, S. T. Speed can go up as well as down at low contrast: Implications for models of motion perception. *Vision Research* 46 (2006), 782–786.

- [48] UNGERLEIDER, L. G., AND DESIMONE, R. Cortical connections of visual area mt in the macaque. *Journal of Comparative Neurology* 248, 2 (June 1986), 190–222.
- [49] WANG, L., KANEOKA, Y., AND KAKIGI, R. Spatiotemporal separability in the human cortical response to visual motion speed: a magnetoencephalography study. *Neuroscience Research* 47 (2003), 109–116.
- [50] WEISS, Y., SIMONCELLI, E. P., AND ADELSON, E. H. Motion illusions as optimal percepts. *Nature Neuroscience* 5, 6 (2002), 598–604.

Abbreviations

FR:Firing Rate

ISI:Interstimulus Interval

MST:Medial Superior Temporal Area

MT:Medial Temporal Area

PPE:Point of Physical Equality

PSE:Point of Subjective Equality

RDP : Random dot Pattern

RF:Receptive Filed

RS:Reference Speed

SW: Sine Wave Grating

Curriculum Vitae

Pınar Boyraz

Education

- Graduate
 - 2001-2003: Master's Degree in Neuroscience, International Max-Planck Research School for Neuroscience, Gttingen, Germany, upon submission of the thesis Visual Perception and Illusions of Speed of Motion in Human Subjects at the German Primate Center
 - since 2003: PhD project entitled Visual Perception of Visual Motion in Man and Monkey, German Primate Center
- Undergraduate
 - 1996-2000 B. Sc. in Medical Biology, Cerrahpasa Medical Faculty of Istanbul University, Istanbul, Turkey

PhD Project Details

- Psychophysics projects
 - Quantification of the effects of aperture size, luminance contrast and transience of random dot patterns on perceived speed in human subjects
 - The effect of contrast on perceived speed tested with random dot patterns and sine wave gratings
 - The change in point of subjective equality as a function of speed in illusory conditions
 - The effect of perceptual training on a speed misperception
- Electrophysiology projects

- Comparison of speed tuning curves of MT units for stimuli in various size and contrasts
- Choice Probability analysis on the response bias of MT single units
- Trial by trial correlation between monkey's behavioral bias and neuronal response bias during speed misperceptions

Laboratory Experience

- 1997-1998: Student projects at the Laboratory for Reproduction and Experimental Use of Laboratory Animals, at the Cerrahpasa Medical Faculty, Istanbul University, Turkey
- 1999: Cell culture and gene transfer techniques during a summer project about neuronal cytoskeleton under the supervision of Roland Brandt, at the Interdisciplinary Center for Neurosciences, Heidelberg, Germany
- 2002: Lab rotation project at the Functional Magnetic Resonance Imaging (BiomedNMR) Laboratory under supervision of Jens Frahm, Max Planck Institute for Biophysical Chemistry, Goettingen.
- 2002 - current: Psychophysical methods with human subjects; monkey training for a visual speed discrimination task, extracellular single unit recordings from the medial temporal area of macaque monkeys

Teaching Experience

Supervision of various projects of Lab Rotation Students enrolled in the Graduate Program Neurosciences, Goettingen

Conference Abstracts

- A neural correlate of speed illusions in area MT of the macaque monkey, SfN Meeting, 2005, Washington DC
- ROC analysis reveals neural correlates of speed illusions in area MT of the macaque monkey, SfN Meeting, 2006, Atlanta GA
- Neural correlates of speed illusions in area MT of the macaque monkey, Submitted to the 7th Meeting of German Neuroscience Society, 2007, Goettingen

Stipends and Fellowships

- 1999: Guest Scientist Fellowship at the ICN, Heidelberg, Germany
- 2003-2004: Georg-Christoph-Lichtenberg Stipend for PhD Students of the State of Lower Saxony, Germany

Manuscripts in Preparation

- Truthful speed perception for complex patterns of different contrast.
P. Boyraz, T. Tzvetanov, S. Treue

- Neural correlates of speed illusions in area MT of the macaque monkey.
P. Boyraz, S. Treue