

# Speed perception during acceleration and deceleration

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We have recently shown that stimulus acceleration affects subsequent preferred speed and tuning widths of macaque area MT neurons (A. Schlack, B. Krekelberg, & T. D. Albright, 2007). Given the close link between area MT and speed perception, this predicts that speed perception should depend on the acceleration context. Here, we show that this is indeed the case for both speed discrimination and speed perception. Specifically, speed discrimination thresholds improve in an acceleration context but absolute speeds are more underestimated than in a deceleration context. In line with our physiological data, these changes can be understood in terms of speed-dependent adaptation mechanisms in MT and do not require an explicit acceleration dependence of speed perception.

**Keywords:** speed perception, acceleration, deceleration, adaptation

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## Introduction

The perception of visual motion is one of the basic abilities that many species rely on for survival in an ever changing environment. Consider for instance a cheetah chasing its prey. It must constantly adjust its own velocity to the velocity of the prey to successfully hunt it down. From the point of view of the prey that cannot outrun the pursuer, the best survival strategy is to rapidly change direction and speed, such that the cheetah may misjudge the prey's movements. To effectively deal with this strategy, the cheetah must estimate the instantaneous speed of the prey whose speed continuously changes. This process—extracting speed information from a stream of continuously changing motion patterns—is what we investigated in this study.

It is well known that exposure to a moving pattern changes the perceived speed (and direction) of subsequent moving patterns. The influence of exposure to a constant speed on the estimation and discrimination of speed has been studied extensively (for a review, see Clifford & Ibbotson, 2002; Kohn, 2007). Behavioral studies have shown that long exposure to a constant speed typically leads to a reduction in perceived speed (Thompson, 1981) while adaptation at very low speeds can result in an increase of perceived speed (Hammett, Champion, Morland, &

Thompson, 2005). Hammett et al. (2005) modeled these behavioral effects by assuming that perceived speed is proportional to the ratio of a high- and low-speed channel. Exposure to a constant speed stimulus also leads to an improvement in the subject's ability to discriminate among speeds near that speed (Bex, Bedingham, & Hammett, 1999; Clifford & Langley, 1996; Clifford & Wenderoth, 1999; Huk, Ress, & Heeger, 2001; Krekelberg, van Wezel, & Albright, 2006a). At the neural level, two response properties of neurons in the middle temporal area of the macaque are relevant to these issues. First, after exposure to constant speeds MT responses are generally lower. Second, speed tuning curves become narrower (Krekelberg et al., 2006a). Using fairly general assumptions about the neural code for speed in MT, these neural properties can explain both changes in perceived speed and speed discrimination (Krekelberg et al., 2006a).

As the cheetah's predicament illustrates, however, real-life motion rarely stays constant for very long. The goal of the current study is therefore to investigate changes in speed perception and discrimination in the context of stimuli whose speed does not remain constant. For ease of reference, we will use the term “speed history” or “acceleration context” to refer to the stimulus speeds preceding the time at which speed sensitivity or perception is measured. This topic—the influence of speed history or acceleration context—has received much less

attention in the behavioral literature although there is anecdotal evidence that speed perception differs when a stimulus is preceded by an acceleration or deceleration (Bex et al., 1999). The current study was directly motivated by our recent findings that cortical visual area MT encodes not only speed but also acceleration signals and that the preferred speeds and the speed tuning widths of MT neurons depend on acceleration context. As abundant evidence shows that MT plays an important role in the perception of speed (Krekelberg et al., 2006a; Liu & Newsome, 2005; Orban, Saunders, & Vandembussche, 1995; Pasternak & Merigan, 1994; Rudolph & Pasternak, 1999), these findings lead to the prediction that acceleration context should influence speed perception both in terms of absolute perceived speed and speed discriminability. In the current study, we used human and monkey subjects to systematically test these predictions. By linking the behavioral measures obtained in human and monkey observers with the neuronal data obtained in macaque MT (Schlack, Krekelberg, & Albright, 2007), we provide further constraints on the readout mechanism that links MT activity with speed perception.

## Methods

### Subjects

Ten naive human subjects, one author, and one monkey subject (an adult male rhesus monkey; *Macaca mulatta*) participated in the psychophysical experiments. All subjects had normal or corrected-to-normal visual acuity. The human participants gave their informed consent, and all procedures were in accordance with international standards (Declaration of Helsinki) and NIH guidelines. Animal protocols were approved by the Salk Institute Animal Care and Use Committee and conform to U.S. Department of Agriculture regulations and to the National Institutes of Health guidelines for humane care and use of laboratory animals.

### General experimental setup

We used the CORTEX program to control the behavior of the subjects and the stimulus presentation as well as data recording (Laboratory of Neuropsychology, National Institute of Medical Health; <http://www.cortex.salk.edu/>). Eye position was monitored at a 60-Hz sampling rate using an infrared video-based system (IScan, Burlington, MA).

We generated all visual stimuli with in-house OpenGL software using a high-resolution graphics display controller (Quadro Pro Graphics card, 1024 × 768 pixels, 8 bits/pixel). For our monkey subjects, stimuli were displayed on a 21-in. monitor (Sony GDM-2000TC; 75 Hz,

non-interlaced; 1024 × 768 pixels); for our human subjects, stimuli were displayed on a 19-in. Sony Trinitron E500 monitor (75 Hz, non-interlaced, 1024 × 768 pixels). Both monkeys and humans viewed stimuli from a distance of 57 cm in a dark room (<0.5 cd/m<sup>2</sup>). During experiments, our monkey subjects were seated in a standard primate chair (Crist Instruments, Germantown, MD). Their head movements were constrained with the help of a head post (for details, see Krekelberg & Albright, 2005). Head movements of the human subjects were constrained by a chin rest.

### Visual stimuli

The basic visual stimulus used in all experiments consisted of random dots moving coherently in one direction within a 6° diameter circular aperture. The dots had unlimited lifetime and wrapped around after leaving the aperture. Each dot had a diameter of 0.15° and was 70% more luminous than the gray—5 cd/m<sup>2</sup>—background.

### Procedure

In all experiments, the trials were paced by the subject; once the subject responded (with a key-press), the next trial would commence after an intertrial interval of less than 0.5 s. All conditions were randomly interleaved, and in each trial the direction of motion was chosen randomly (either leftward or rightward). As a consequence, no systematic build-up of adaptation over trials was expected.

#### Experiment 1: Speed sensitivity

The goal of this experiment was to measure the threshold speed change that a subject could detect in an accelerating versus decelerating speed trajectory. The data were obtained from five naive human subjects and one author (subject “AS”). During the experiment, subjects fixated a small central point; trials in which eye-position deviated more than 2° from this point were discarded. Because subjects only had to detect a speed change, only one moving stimulus appeared on each trial. This stimulus appeared 250 ms after the start of each trial and was always presented 8° to the left of the fixation point.

Immediately following their appearance, the dots moved either to the left or to the right for 333 ms at a constant speed (0.001°/s for the acceleration condition, 64°/s for the deceleration condition). This brief initial period merely served to separate the subsequent acceleration or deceleration stage from the onset transients. After the initial constant speed, the speed changed linearly for a maximal duration of 8500 ms. The rate of change was 7.53°/s<sup>2</sup> in the acceleration condition and −7.53°/s<sup>2</sup>

in the deceleration condition. When the stimulus reached a speed of 4, 8, 16, or 32°/s, it suddenly increased (acceleration condition) or decreased (deceleration condition) with a larger step. Subjects were asked to hit the “l” key as soon as they detected such a sudden change in the otherwise smooth stimulus. If they did not perceive any such step, they pressed the “s” key at the end of the stimulus presentation. We used a staircase paradigm (three up, two down) to adjust the size of the sudden stimulus speed change to track the 70.7% correct point. The smaller the value, the more sensitive the subject was to a speed change at the tested speed.

In the [Results](#) section, we present only the data from the trials in which the speed step occurred at 32°/s. The reason for excluding the other test speeds from analysis is that these instantaneous speeds occur later in deceleration trials than acceleration trials. On the one hand, this may have increased the amount of adaptation for deceleration conditions; on the other, it placed the decision point closer to the offset transients at the end of the trial. Moreover, many of our subjects had thresholds above 4°/s; hence, an above-threshold decrease in speed at 4°/s was physically impossible. For completeness, we note that in all of these conditions, speed change thresholds were typically higher during deceleration than acceleration (just as we report for the 32°/s condition in the [Results](#) section). Given the confounds in the design, the former findings should be interpreted with caution.

### Experiment 2: Perceived speed: acceleration vs. deceleration

In this experiment, the goal was to determine how perceived speed depended upon speed context. For this reason, two patches of moving dots were presented on each trial. One stimulus appeared only briefly and served as a reference stimulus with only minimal speed context. For the other stimulus, we systematically varied the speed history that preceded the judgment of perceived speed. The data in this experiment were obtained from six naive human subjects and one monkey subject.

#### Human subjects

Each trial started with the appearance of a fixation target in the center of the screen. Subjects were required to fixate this target for the duration of the trial. The stimuli were random dots moving to the left or right in a 6° diameter aperture. The test stimulus was placed 8° to the left and the reference stimulus 8° to the right of the fixation point.

On each trial, a speed context was first established for the test stimulus by linearly increasing (“aRamp,” red line in [Figure 1](#)) or decreasing (“dRamp,” blue line in [Figure 1](#)) its speed over a period of 1000 ms. In the aRamp condition, the initial speed was 0.001°/s, in the dRamp condition 48°/s. Given the 24°/s<sup>2</sup> acceleration, the speed in the aRamp and the dRamp conditions at the end of this

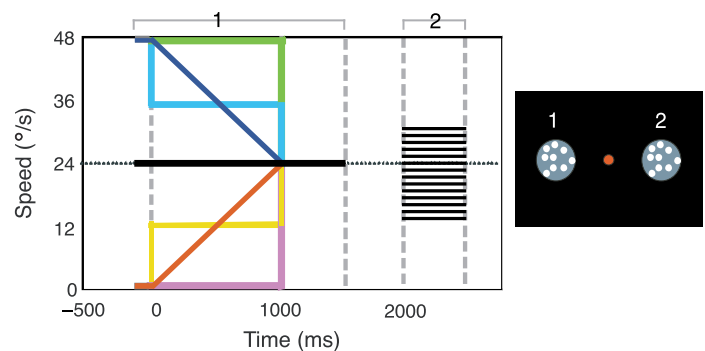


Figure 1. Stimulus for the “perceived speed” paradigms ([Experiments 2 and 3](#)). The panel on the right shows the spatial arrangement of the two stimuli (1 = test; and 2 = reference stimulus). The left panel shows the time courses and speed trajectories of the stimuli in the different conditions. Each test stimulus’ speed first followed one of seven speed trajectories (colored traces), after which it moved constantly at 24°/s (black line segment). After a 650-ms blank period, the reference stimulus appeared and moved at one of 14 constant speeds (dark gray lines, between 14.4°/s to 30°/s in 1.2°/s steps). [Experiment 2](#) (“acceleration vs. deceleration”) compared smoothly accelerating with smoothly decelerating stimulus motion (conditions: “aRamp” = red line and “dRamp” = blue line). [Experiment 3](#) (“speed trajectories”) investigated a wider range of speed trajectories. The five additional conditions were “aStart” (pink line), “aMean” (yellow line), “const” (black line), “dMean” (turquoise line), and “dStart” (green line). See text for details.

period both equaled 24°/s. To allow the subject to form a subjective estimate of this final speed, this constant speed was maintained for 500 ms after which the test stimulus was switched off.

After 650 ms without visual stimulation, we assessed the subject’s perceived final speed of the test stimulus by asking whether it was faster or slower than a reference stimulus that appeared on the opposite side of fixation and moved at one of 14 constant speeds (14.4, 15.6, 16.8, 18, 19.2, 20.4, 21.6, 22.8, 24, 25.2, 26.4, 27.6, 28.8, and 30.0°/s) for 500 ms. Subjects indicated their decisions with a key press (keys “l” and “s”).

#### Monkey subject

To determine whether speed history has a similar influence on perceived speed in humans and monkeys, we trained one monkey (M) to perform a speed comparison task. It proved difficult to train the animal on the paradigm used for the human subjects. We suspected that the animal’s slow progress on learning the task could be attributed to the temporally complex temporal nature of the paradigm. Because the discrimination and the reference appeared at different times, it may have been unclear to the animal which stimuli should be compared. To simplify the task for the animal, we therefore removed the temporal separation of the stimuli and instead presented the test and the reference stimulus simultaneously (8° left

and right of fixation) for the full 1500 ms duration of the trial. The animal quickly learned this modified task. In the final experiment, the test stimulus had a period of acceleration or deceleration preceding the speed judgment, while the reference stimulus always moved at a constant speed. After 1500 ms, both stimuli were switched off, and two saccade targets (red dots) appeared left and right of fixation. The monkey's task was to make an eye movement toward the saccade target at the location of the faster stimulus. The animal received a liquid reward (a drop of juice) for making a correct decision.

### Training procedure

We first trained the monkey on speed discrimination by using constant speeds for both test and reference stimuli. Once the monkey had learned this task (>80% correct for several days), we changed the task to include a period of acceleration or deceleration for the test stimulus. The test stimulus moved in an accelerating or decelerating manner for 1000 ms and then remained constant at 24°/s for the final 500 ms (just as in the human experiment). At first the comparison speeds (i.e. the constant speed of the reference stimulus) were 48°/s or 12°/s. From the human psychophysical experiments, we knew that these stimuli should be unambiguously faster or slower than the 24°/s stimulus, even if the latter was preceded by an acceleration or a deceleration. This allowed us to reward the monkey for veridical report; he was trained on this task for another 10 days until his performance was over 80% correct for several days in a row. Finally, we introduced a wider range of constant test speeds [5%, 10%, 20%, 40%, and 80% faster or slower than 24°/s] to measure the psychometric function in the range where perceived speed could be ambiguous. In trials in which the difference between test and reference speed was less than or equal to 10%, rewards were given on a random schedule, independent of the monkey's decision but proportional to his performance on the unambiguous trials (~75% of trials were rewarded). All other conditions were rewarded for veridical report.

### Experiment 3: Perceived speed: speed trajectories

Experiments 1 and 2 allowed a direct comparison of perceived speed with the physiological data previously obtained in area MT (Schlack et al., 2007). Those physiological data, however, also showed that much of the speed–history effects could be understood by looking at speed-specific adaptation and not the presence of smooth acceleration or deceleration per se. In Experiment 3, we investigated this idea psychophysically by adding five constant speed trajectories to our experiment. In these conditions, we replaced the smooth speed change present in the “aRamp” and “dRamp” conditions by different constant speeds. One stimulus (“aStart”) moved constantly at the start speed of the “aRamp” condition (0.001°/s). The second stimulus (“aMean”) moved constantly at the mean

speed of the “aRamp” condition (12°/s). Likewise, the third (“dStart”) and the fourth (“dMean”) moved at the initial (48°/s) and the mean speed (36°/s) of the “dRamp” condition. Finally, we added a condition (“const”) in which the stimulus moved at 24°/s for the whole stimulus duration.

## Data analysis

### Experiment 1: Speed sensitivity

For each of the four test speeds at which the sudden speed step could occur (4, 8, 16, and 32°/s), we determined the 70.7% correct point of detecting the speed change with an adaptive staircase paradigm. We used this as a measure of the speed sensitivity of the human subjects in the two conditions (acceleration vs. deceleration). To test for a consistent difference between the speed sensitivity in the two conditions, we compared this value over the population of six subjects with a Wilcoxon signed rank test.

### Experiments 2 and 3: Perceived speed

Separately for each combination of a reference and test stimulus, we calculated the percentage of trials in which subjects reported that the reference stimulus was faster. We used the `psignifit` Matlab toolbox (Wichmann & Hill, 2001) to fit the psychometric functions with cumulative Gaussians. This fit provided an estimate of the point of subjective equality (PSE) defined as the speed where the fitted curve crossed 50% “test faster.”

In Experiment 2, we compared the “aRamp” and “dRamp” conditions using a Wilcoxon signed rank test to determine whether there was a consistent effect of the stimulus condition on the perceived speed. The fit also provided us with a measure of the slopes (with confidence intervals) of the psychometric functions. A steeper slope of the psychometric function would indicate higher speed sensitivity.

In Experiment 3, we tested the hypothesis that perceived speed depended on the speed trajectory with an ANOVA on ranks across conditions.

## Results

We recently showed that speed tuning in MT depends on stimulus history. First, we found that MT neurons are more narrowly tuned for speed in an acceleration context than in a deceleration context. From this, we predicted that subjects would be more sensitive to speed changes when these occurred in an acceleration context as compared to a deceleration context. This hypothesis was tested in Experiments 1 and 2. Our second physiological finding was that the preferred speed of MT neurons shifted toward



higher speeds in an accelerating context and toward lower speeds in a decelerating context. These changes in preferred speed should lead to changes in perceived speed. Experiments 2 and 3 tested these predictions.

## Experiment 1: Speed sensitivity

We measured subjects' sensitivity to sudden speed changes during prolonged smooth accelerations and decelerations (see Methods for details). Figure 2 shows the speed-change thresholds of 6 subjects determined for acceleration (red bars) and deceleration (blue bars) measured at the instantaneous speed of  $32^\circ/\text{s}$ . Because the speed step at  $32^\circ/\text{s}$  occurred at the same time during acceleration and deceleration trials, threshold differences in this condition must be attributed to the acceleration context and cannot be due to differences in the duration of the preceding adaptation. Confirming our prediction based on the electrophysiological data, the detection thresholds in the acceleration context were smaller than those in the deceleration context. This effect was significant across subjects (Wilcoxon signed rank test,  $p < 0.001$ ).

## Experiment 2: Perceived speed

### Human subjects

We measured subjects' perceived speed by asking them to report whether a constant speed of  $24^\circ/\text{s}$  following an accelerating or decelerating speed was faster or slower than a reference stimulus that always moved at a constant speed (see Methods for details).

Figure 3 shows the psychometric functions measured for one subject in our speed comparison task with acceleration (red curve) vs. deceleration (blue curve) speed history. In both conditions, the psychometric

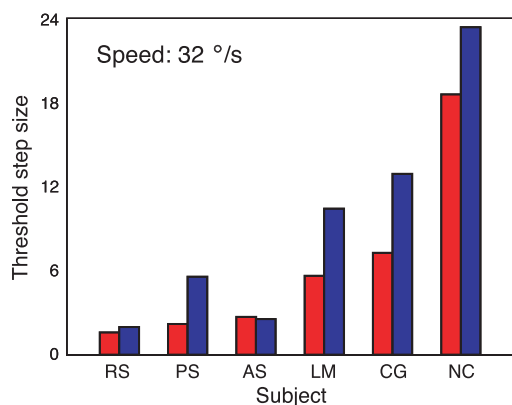


Figure 2. Detection thresholds for 6 subjects for the acceleration (red) vs. deceleration (blue) condition at a speed of  $32^\circ/\text{s}$ . The plot shows that for all subjects except the non-naïve subject AS (one of the authors), the detection threshold was higher in a deceleration context than an acceleration context.

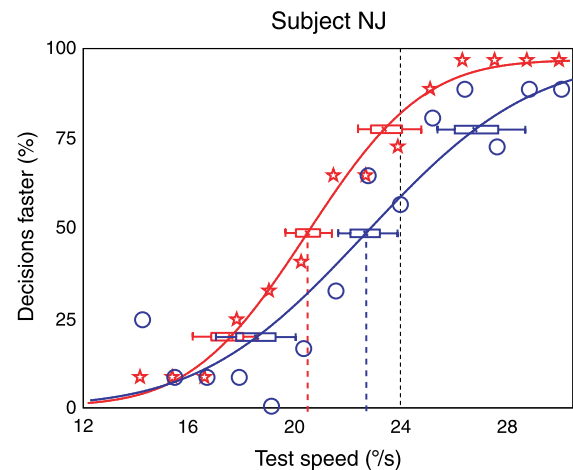


Figure 3. Perceived speed with acceleration vs. deceleration history (single subject). Each symbol (red stars for the acceleration condition, blue circles for the deceleration condition) corresponds to the percentage of perceived faster decisions of the subject at a particular test speed. Solid lines are fitted cumulative Gaussians to the data. Error bars indicate the confidence intervals at  $-2$ ,  $-1$ ,  $1$ ,  $2$  standard deviation. The PSEs for both conditions (red and blue dashed vertical lines) are shifted toward the left from the real speed of the probe (black dashed line at  $24^\circ/\text{s}$ ), indicating that the speed in both conditions is perceived slower than the real speed. The red curve (acceleration history) is located left from the blue curve (deceleration). This subject thus perceived speeds slower in an acceleration than in a deceleration context.

functions and thus the points of subjective equality (PSE) were shifted to the left, indicating that speeds were perceived as slower than the actual speed presented ( $24^\circ/\text{s}$ , vertical black dashed line). This is not surprising; it is well known that adaptation to visual motion leads to an underestimation of perceived speed (Goldstein, 1957).

Interestingly, however, there was a significant difference between the perceived speed between the acceleration and deceleration condition. Speeds were perceived as slower in the acceleration context than in the deceleration context. In addition to this change in perceived speed, the slope of the psychometric function around the PSE was significantly steeper for the acceleration compared to the deceleration context. This slope difference confirms the findings of the previous section; sensitivity in an acceleration context is higher than in a deceleration context.

The findings for this subject were typical for the population. Figure 4 shows the shift in PSE for the two conditions for six naïve subjects. The exposure to either acceleration or deceleration typically led to an underestimation of speed (subject CK was the sole exception). This underestimation was always more pronounced for accelerations than for decelerations. At the level of individual subjects, the difference between acceleration and deceleration was small compared to the subject's sensitivity (see confidence intervals in Figure 4), but the

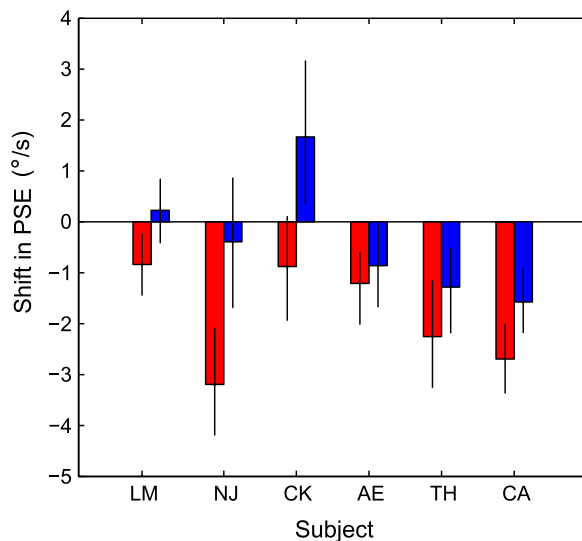


Figure 4. Changes in perceived speed in an acceleration vs. a deceleration context ( $N = 6$ ). The real speed of the stimulus was  $24^\circ/\text{s}$ . Red bars: acceleration; blue bars: deceleration. Error bars show 95% confidence intervals. Perceived speed was reduced more after exposure to accelerations than to decelerations.

consistency across subjects nevertheless allowed us to conclude that this difference was statistically significant (Wilcoxon signed rank,  $p < 0.05$ ). We also investigated the steepening of the psychometric curve; in four of six subjects, sensitivity during acceleration was higher than during deceleration.

### Monkey subject

Because our goal was to interpret the behavioral data in the context of our physiological findings, we needed to make sure that the changes in speed perception were not species specific. We trained one monkey subject on a comparable speed discrimination task and observed the effect of speed history on his perception of speed. The results for monkey M are shown in Figure 5.

The monkey reported speeds in an acceleration context as being slower than in a deceleration context. (This effect was significant on each day we repeated the experiment. Figure 5 pools all data over all sessions.) Additionally, the monkey's psychometric curve for acceleration contexts was significantly steeper than that for deceleration contexts. Hence, we conclude that changes of speed perception and sensitivity evoked by changes in temporal stimulus context are qualitatively the same in humans and monkeys. This provides further support for the use of macaque monkeys as ideal animal subjects to test hypotheses concerning the relationship between neural activity and perception.

One apparent difference with the human data is that the monkey did not show an underestimation of perceived speed for both conditions (Figure 3). Rather, the monkey reported the stimulus in the acceleration context as slower

and in the deceleration context as faster than a constant speed stimulus. This discrepancy is most likely due to a difference in the experimental design; the monkey was trained on a 2AFC in which both the constant speed stimulus and the changing speed stimulus were on the screen at the same time. As a consequence, *both* patches underwent the usual motion adaptation and the reduction in perceived speed resulting from this canceled out in the comparison. Human subjects saw the reference stimulus only briefly, after the test stimulus had disappeared. Therefore, the reference stimulus had not undergone significant adaptation, and as a result, all test stimuli appeared slower than the reference stimulus. (See also Figure 7, Compare “aRamp” and “dRamp” with “Const” for a condition in the human experiments that more closely mimics the situation in the monkey experiments.)

### Experiment 3: Speed trajectories

Our physiological data led to the view that the neural response changes in MT are not specific to accelerations or decelerations. Rather, we showed that the response changes could be understood as the consequence of an adaptation process in which the rate of adaptation was speed dependent. This hypothesis predicts that much of the perceptual effect for a given acceleration trajectory could be explained on the basis of adaptation to the speeds that necessarily make up an acceleration trajectory. In other words, the large effect on perceived speed of accelerations should be reflected in a large effect of low stimulus speeds

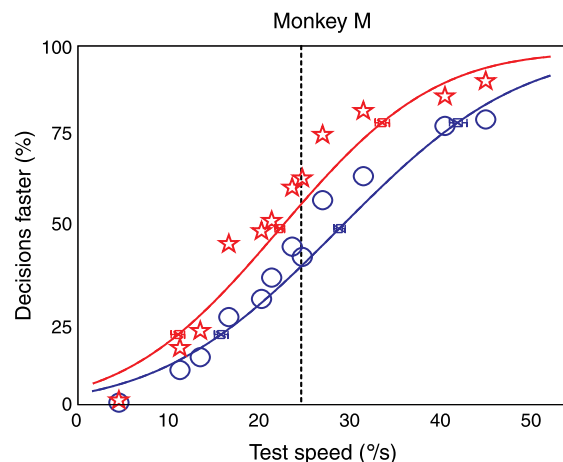


Figure 5. Perceived Speed with acceleration (red) vs. deceleration (blue) history (monkey subject). Same conventions as in Figure 3. The plot summarizes data from 17 sessions, 16149 trials in total. The curves were significantly shifted with respect to each other. The monkey reported the  $24^\circ/\text{s}$  speed stimulus as being  $21.5^\circ/\text{s}$  in the acceleration condition and  $29.1^\circ/\text{s}$  in the deceleration condition. The slopes of the two curves were also significantly different with the acceleration slope being significantly steeper than the deceleration slope.

(without acceleration). To test this, we added five conditions with different constant adaptation speeds. In these conditions, the stimulus moved at one of five constant speeds: the speed with which the stimulus in the acceleration condition starts to move (“aStart”), the mean speed of the stimulus in the acceleration condition (“aMean”), the final speed of 24°/s (“const”) of both the acceleration (“aRamp”) and deceleration (“dRamp”) stimulus, the mean speed of the deceleration condition (“dMean”), and finally the start speed of the deceleration condition (“dStart”) (see [Methods](#) and [Figure 1](#) for details).

[Figure 6](#) shows the result for one human subject, which broadly confirms our hypothesis. For instance, the largest effect on perceived speed was found for constant speeds below the final testing speed of 24°/s. This explains why an acceleration trajectory—that necessarily consists of many short phases of these slower speeds—would cause a bigger perceptual effect than a deceleration trajectory.

[Figure 7](#) summarizes the results averaged over six naive subjects. To normalize for individual differences, this figure shows average speed rankings, not perceived speed. The average changes in perceived speed across subjects were similar to those shown for the single subject in [Figure 6](#) (from 0 to 25%). This graph confirms the trends that are visible in the single subject of [Figure 6](#); speeds in all conditions were perceived as slower than the veridical speed. Clearly, however, the lowest constant speeds led to

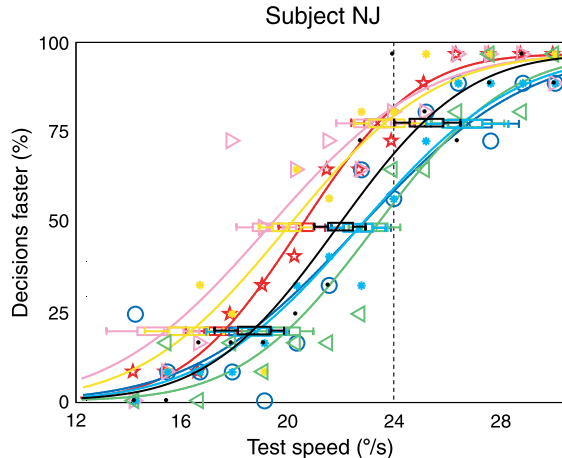


Figure 6. Perceived speed depends on speed history (single subject). Same conventions as [Figure 3](#). The plot shows the psychometric functions determined with stimuli with different speed histories (see [Methods](#) for details). Pink data points and curves correspond to the “aStart” condition, yellow to the “aMean” condition, red to the acceleration (“aRamp”) condition, black to the “const,” blue to the “dRamp,” turquoise to the “dMean,” and green to the “dStart” condition. For all conditions, the 50% (PSE) points are shifted to the left relative to the veridical speed (vertical dashed line), i.e. speeds were all perceived as being slower than they actually were. The stimulus in the “aStart” context is perceived as being slowest, followed by “aMean,” “aRamp,” “const,” “dMean,” “dRamp,” and finally “dStart.”

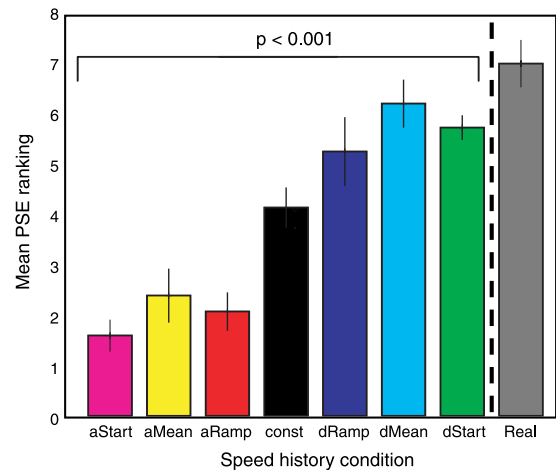


Figure 7. Speed perception with different speed trajectories. The figure shows the mean ( $\pm$  standard error) ordering of the perceived speed of the 24°/s stimulus over the different speed history conditions across the 6 subjects relative to the real speed of the stimulus (gray bar). There was a significant effect of speed history on the perceived speed (Kruskal–Wallis analysis:  $p < 0.001$ ). All conditions tended to be perceived as being slower than the real speed. This effect was most pronounced for the conditions containing slower speeds (“aStart,” “aMean,” “aRamp”), which accordingly got the lowest rankings. The smallest slowing down effect could be observed for the 3 conditions containing higher stimulus speeds (“dRamp,” “dMean,” and “dStart”). The speed of the stimulus in the “const” condition was perceived as being in between these two main groups.

much larger reductions in perceived speed than the highest constant speed. Because the decelerating ramp necessarily includes the highest constant speeds, this fact alone (i.e. without assuming any deceleration specific adaptation) will lead to a smaller adaptation effect for deceleration ramps.

These data are consistent with the idea that speed-specific adaptation changes the speed percept and one need not assume acceleration- or deceleration-specific mechanisms. In this view, the reduction in perceived speed that follows exposure to the “aRamp” is simply the cumulative effect of many short duration adaptation phases like those represented by the “aStart” and “aMean” conditions. This is similar to what we found in our electrophysiological data (Schlack et al., 2007) in which an accurate description of the speed tuning changes during acceleration and deceleration could be calculated from the speed dependent adaptation profiles of the neurons.

## Discussion

In a previous electrophysiological study, we showed that most MT neurons’ speed tuning curves were significantly altered by the speed stimulus history

(Schlack et al., 2007). Our current study confirms the resulting hypothesis that stimulus history affects speed perception. Specifically, we showed that an acceleration context leads to increased speed discriminability but also a larger underestimation of veridical speed than a deceleration context. Our analysis of the physiological and behavioral data suggests that these effects are not specific to acceleration trajectories. They can be explained more parsimoniously by differences in adaptation at each of the constant speeds that make up an acceleration or deceleration trajectory. In the following, we will discuss our behavioral findings and their link with the neuronal data in more detail.

## The neural code for speed and acceleration

There is increasing evidence that activity in area MT is linked with the perception of the speed of visual motion. First of all, the information necessary for speed perception is represented in area MT: cells in this area are tuned to the speed of visual motion (Maunsell & Van Essen, 1983; Rodman & Albright, 1987). Secondly, there is also more direct evidence that activity in area MT and speed perception are linked: many MT neurons have significant choice probabilities for speed discrimination (Liu & Newsome, 2005), microstimulation in area MT can change perceived speed of visual motion stimuli (Liu & Newsome, 2005), and lesions in area MT impair speed perception (Orban et al., 1995; Pasternak & Merigan, 1994; Rudolph & Pasternak, 1999). Studies like ours that aim to link systematic changes in the neuronal activity to systematic changes in speed perception are useful to gain new insights into how the information in area MT is read out and used to shape perception.

The representation of acceleration information appears to be largely implicit in the response of motion sensitive neurons. Several studies have now shown that MT neurons (Lisberger & Movshon, 1999; Price, Ono, Mustari, & Ibbotson, 2005) do not have bell-shaped tuning curves for acceleration. Very similar properties have been observed in V1, V2, and PMLS of the cat visual cortex (Price, Crowder, Hietanen, & Ibbotson, 2006). The absence of an explicit representation, however, does not mean that acceleration information is not represented. Schlack et al. (2007), for instance, showed that a linear classifier can extract veridical acceleration signals from the MT population response. What remains uncertain, however, is the neural mechanism that the brain uses to extract this information.

## Speed sensitivity

In our previous study (Schlack et al., 2007), we showed that neurons had narrower tuning curves for speed in acceleration as compared to a deceleration context. In our

current psychophysical study, we found that both human and monkey subjects were more sensitive to speed changes in an acceleration context than in a deceleration context. Under the assumption that these two findings are causally related, this provides insight into the code used to read out MT activity.

Pouget, Deneve, Ducom, and Latham (1999) showed that an optimal readout mechanism (as quantified by the Fisher information present in a population of neurons) only improves with a narrowing of the tuning curves provided there is no concomitant change in the level of noise. In our case, this would imply that the sharpening could not result from a computation in a fixed network of neurons but would require the recruitment of additional neurons. This is an interesting scenario, in which some speed-sensitive neurons only become part of the population code during acceleration.

An alternative explanation, however, is that the readout of the MT population is not optimal to begin with. Once optimality is no longer required, there are very few general statements one can make about the influence of sharpening. For a specific non-optimal decoder such as the center-of-mass, however, it has been shown that narrower tuning curves actually hurt performance (Pouget et al., 1999). Hence, it seems unlikely that the neural code for speed relies on such a decoder.

## Perceived speed

Changes in speed history that led to changes in neural responses, also led to changes in perceived speed. Moreover, our physiological data could be well explained by speed-dependent adaptation without explicit acceleration/deceleration dependent signals. This appears consistent with the limited effect that the detailed speed trajectories had on the final percept. We take these findings as further evidence that neural changes in MT are linked to perceptual changes.

What this link is, however, remains an open question. An intuitive view of how information is coded and read out in the visual system is by the use of a labeled line code. The main idea is that each neuron has a preferred stimulus feature, e.g., a certain stimulus speed. This corresponds to the label of the cell; whenever the cell fires, it biases the percept into the direction of the label. In our physiological data set, we observed that, in an acceleration context, MT neurons respond optimally to stimuli that are slower than their preferred stimulus. As a result, whenever that slower stimulus is shown, the cell provides the strongest bias toward perceiving the preferred stimulus. This should lead to an overestimation of stimulus speed during acceleration and is in direct contradiction with our behavioral data. We interpret this as further evidence against the labeled line model (for a detailed critique using a different visual illusion of speed, see Krekelberg, van Wezel, & Albright, 2006b).



Hietanen, Crowder, and Ibbotson ([in press](#)) recently investigated how adaptation at one speed affects perceived speed at different test speeds. Consistent with what we report here, they found that adaptation at a given stimulus speed typically leads to an underestimation of perceived speed for stimuli with the same or higher speeds. Additionally, however, they report that adapting at low speeds (e.g.,  $2^\circ/\text{s}$ ) led to an overestimation of the highest speeds (e.g.,  $26^\circ/\text{s}$ ). For the stimulus condition that is closest to this situation in our paradigm (“aStart”), we found a reduction in perceived speed. One reason for this could be that our paradigm always included a final 500-ms period of  $24^\circ/\text{s}$ . If this period had a disproportionate influence on the perceived final speed, Hietanen et al.’s results also predict a reduction in perceived speed. Moreover, it is possible that the near absence of motion in our aStart condition ( $0.001^\circ/\text{s}$ ) changed the involvement of motion-specific adaptation mechanisms. Finally, Hietanen et al. used a top-up paradigm for adaptation which presumably activated mechanisms that act on much longer time scales and may have different properties from the short-term adaptation that we investigated. Taken together, our data and those of Hietanen et al. reinforce the view that adaptation is a complex process that depends on the properties of the adapter, the test stimulus, and the time scale of adaptation (Krekelberg, Boynton, & van Wezel, [2006](#)).

## Adaptation

Adaptation—defined neutrally as behavioral or neural changes in response to the exposure of an ongoing stimulus—likely involves multiple mechanisms and may have partially conflicting goals. One goal may be to conserve energy by representing only aspects of the environment that change. This goal fits well with the commonly observed reduction in neural firing after exposure to a constant stimulus, but it cannot explain why firing is also reduced when the stimulus changes (Schlack et al., [2007](#)) or why the reduction in firing depends critically on both the adaptation and the test stimulus (Kohn & Movshon, [2004](#); Krekelberg et al., [2006a](#)). A second goal may be to zoom in on the currently relevant stimulus properties; the enhanced speed discrimination we report here extends previous findings that also support this view (Bex et al., [1999](#); Clifford & Langley, [1996](#); Clifford & Wenderoth, [1999](#); Krekelberg et al., [2006a](#)). A third goal could be to anticipate a future stimulus on the basis of the stimulus history. In our data, only a single subject (CK; [Figure 4](#)) overestimated speeds in an acceleration context and underestimated speeds in a deceleration context. It is possible that such anticipatory behavior could become more prominent if the subject’s task required it. However, even in a task where subjects were instructed to intercept accelerating and decelerating objects, their performance showed evidence of temporal averaging, not extrapolation

(Port, Lee, Dassonville, & Georgopoulos, [1997](#)). This may reflect the importance of a fourth goal of adaptation that is to use temporal integration to improve estimates of stimulus properties. Such a process is useful in natural environments that tend to be noisy; not all small changes in the signal are meaningful and therefore should not lead to a change of the percept. Temporal integration explains why perceptual inertia, or the tendency to average, is often reported in human motion perception (Hock, Kelso, & Schöner, [1993](#); Krekelberg, [2001](#); Krekelberg & Lappe, [2000](#); Simpson, [1994](#); Watamaniuk & Duchon, [1992](#)). However, while inertia fits with our findings during acceleration, inertia also predicts that the speed of decelerating stimuli should be overestimated; only subject CK reported this in our study.

Some of the discrepancies between functional goals and the data in our and others studies can certainly be understood by assuming that the behavior reflects the trade-off among multiple goals of adaptation. This, however, begs the question how the visual system determines the trade-off of one goal versus another, whether these trade-offs are constant, vary per subject, or even per task.

## Conclusions

We showed that recent stimulus history affects speed perception of humans and monkeys. This demonstrates that the entire temporal context in which a moving stimulus is presented affects its neural representation and its perceptual consequences. While our psychophysical and physiological data are consistent with the view that changes in neural activity in area MT underlie these perceptual changes, no adequate model to link the two in a quantitative manner currently exists.

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