Different time scales of motion integration for anticipatory smooth pursuit and perceptual adaptation

Gerrit W. Maus

Department of Psychology,
University of California Berkeley, Berkeley, CA, USA
Smith-Kettlewell Eye Research Institute,
San Francisco, CA, USA

Elena Potapchuk

Smith-Kettlewell Eye Research Institute,
San Francisco, CA, USA

Scott N. J. Watamaniuk

Department of Psychology, Wright State University,
Dayton, OH, USA

Stephen J. Heinen

Smith-Kettlewell Eye Research Institute,
San Francisco, CA, USA

When repeatedly exposed to moving stimuli, the oculomotor system elicits anticipatory smooth pursuit (ASP) eye movements, even before the stimulus moves. ASP is affected oppositely to perceptual speed judgments of repetitive moving stimuli: After a sequence of fast stimuli, ASP velocity increases, whereas perceived speed decreases. These two effects—perceptual adaptation and oculomotor priming—could result from adapting a single common internal speed representation that is used for perceptual comparisons and for generating ASP. Here we test this hypothesis by assessing the temporal dependence of both effects on stimulus history. Observers performed speed discriminations on moving random dot stimuli, either while pursuing the movement or maintaining steady fixation. In both cases, responses showed perceptual adaptation: Stimuli preceded by fast speeds were perceived as slower, and vice versa. To evaluate oculomotor priming, we analyzed ASP velocity as a function of average stimulus speed in preceding trials and found strong positive dependencies. Interestingly, maximal priming occurred over short stimulus histories (~two trials), whereas adaptation was maximal over longer histories (~15 trials). The temporal dissociation of adaptation and priming suggests different underlying mechanisms. It may be that perceptual adaptation integrates over a relatively long period to robustly calibrate the operating range of the motion system, thereby avoiding interference from transient changes in stimulus speed.

On the other hand, the oculomotor system may rapidly prime anticipatory velocity to efficiently match it to that of the pursuit target.

Introduction

Stimulus history influences how current stimuli are perceived and acted upon. Adaptation is a ubiquitous phenomenon in sensory systems, reducing sensitivity to recently presented stimuli and thereby resulting in a recalibration of perceptual experience (Clifford et al., 2007; Kohn, 2007; Webster, 2011). In the case of visual motion, prolonged exposure to a stimulus moving in one direction results in a motion aftereffect: A stationary stimulus is perceived to move in the opposite direction of the adapting stimulus (Anstis, Verstraten, & Mather, 1998; Mather, Pavan, Campana, & Casco, 2008; Mather, Verstraten, & Anstis, 1998). Motion aftereffects build up over time (Hershenson, 1993), can last for tens of seconds (Anstis et al., 1998), and can be stored over relatively long periods without additional stimulation (Verstraten, Fredericksen, Grüsser, & van de Grind, 1994; Wiesenfelder & Blake, 1992). Even relatively short exposure times can lead to substantial motion aftereffects (Kanai & Verstraten, 2005; Pavan, Campana, Maniglia, & Casco, 2010).

Priming, on the other hand, results in response facilitation following repeatedly presented stimuli (Kristjansson & Campana, 2010; Maljkovic & Nakayama, 1994, 1996; Tulving & Schacter, 1990). After exposure to a similar stimulus, priming leads to faster responses in perceptual detection or identification of probes. Priming also occurs specifically for visual motion stimuli (Anstis & Ramachandran, 1987; Campana, Cowey, & Walsh, 2002; Kristjansson, 2009; Pinkus & Pantle, 1997). In the oculomotor system, priming is seen in anticipatory eye movements. Although smooth pursuit eye movements are generally possible only in the presence of a moving stimulus, for repeated stimulus presentations the oculomotor system initiates anticipatory smooth pursuit (ASP) eye movements before the start of stimulus movement (Kowler, 1989; Westheimer, 1954). These anticipatory eye movements increase in velocity when the target repeatedly moves in the same direction (Heinen, Badler, & Ting, 2005; Kowler, 1989; Kowler, Martins, & Pavel, 1984).

Although adaptation and priming effects work in opposite directions, they can occur simultaneously. Oftentimes, whether a stimulus causes priming or adaptation is dependent on specific presentation times of adaptor and test stimuli and interstimulus intervals (Kanai & Verstraten, 2005; Pavan, Campana, Guerreschi, Manassi, & Casco, 2009). In multistable perceptual phenomena, such as binocular rivalry, the perception of *ambiguous* stimuli is dependent on previously presented stimuli in a manner that shows both adapting and facilitating effects on subsequent perception (Pearson & Brascamp, 2008). In a recent example, when a dot lattice with an ambiguous orientation is viewed after an unambiguous dot lattice, both adaptation and priming can be seen in the response to the ambiguous stimulus (Schwiedrzik et al., 2014). The likelihood of perceiving a particular orientation in the ambiguous stimulus increases when the orientation of the unambiguous stimulus is the same (i.e., priming). However, when there is more evidence in favor of a particular orientation in the unambiguous stimulus (due to a more extreme aspect ratio), the ambiguous stimulus is more likely to be perceived as having a different orientation (i.e., adaptation).

Here we show that perceptual adaptation and priming of anticipatory eye movements can occur simultaneously, even for unambiguous stimuli. We presented observers with random dot stimuli that moved at different velocities, randomized from trial to trial. Random dot pursuit stimuli are known to induce ASP eye movements similar to a single moving dot as a pursuit target (Santos, Gnang, & Kowler, 2012) and are used here to minimize the occurrence of correcting saccades (Heinen & Watamaniuk, 1998). Observers pursued the stimuli with their eyes and, at the end of each trial, made perceptual judgements of stimulus speed. We did not use an explicit adaptor stimulus but instead reasoned that observers would continuously adapt to the stimulus with repeated motion presentations. We found a robust repulsive adaptation effect (i.e., perceptual judgments were biased "faster" after viewing stimuli that were on average slower, and vice versa). To verify that this finding generalizes to retinal motion in the absence of pursuit eye movements, we ran an additional experiment in which observers maintained steady fixation. Perceptual adaptation occurred regardless of whether observers pursued the stimuli (Experiment 1) or maintained fixation (Experiment 2). In addition, in Experiment 1, we found attractive oculomotor priming (i.e., stimuli that on average elicited slower anticipatory eye movements on subsequent trials, and vice versa). In additional control experiments, we established that the perceptual adaptation effect also occurs when using other psychophysical measurement methods.

Both priming and adaptation could in principle be based on a single shared internal representation of a stimulus speed that integrates the average of recently encountered speeds. Perceptually comparing this adapted internal standard with the current stimulus speed would lead to repulsive aftereffects. At the same time, the standard could be used to generate an anticipatory eye movement of appropriate velocity on the next trial. Our experimental design allowed for assessing the temporal integration window over which information from previous stimuli are collated for the adaptation and oculomotor priming effects. We found that perceptual adaptation and oculomotor priming integrate over different time scales, a finding that hints at different underlying mechanisms for each effect.

Materials and methods

Participants

Nine observers (five female; mean age 30.2 years, range 20–49 years) volunteered to participate in the study, including two of the authors. Five observers took part in Experiments 1 and 2, and four observers participated in each of the two control experiments. All participants (except the two authors) were naïve as to the purpose and hypotheses of the study. All participants had normal or corrected-to-normal visual acuity. The study was approved by the Institutional Review Boards of the Smith-Kettlewell Eye Research Institute and the University of California, Berkeley.
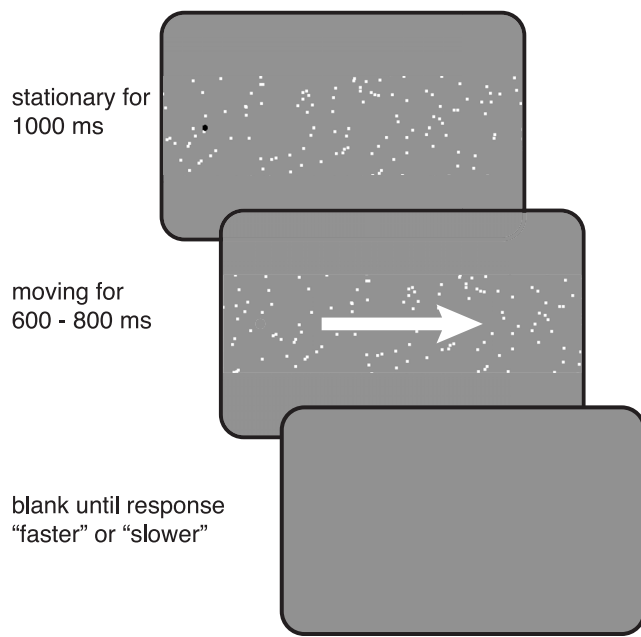
Figure 1. The stimulus consisted of random dots moving rightward across the screen after being presented stationary for 1 s. In Experiment 1, observers pursued the stimulus with their eyes; in Experiment 2, observers maintained fixation on a black fixation spot in the center of the screen throughout the trial.

Stimuli and procedure

Stimuli were generated using Matlab (MathWorks, Natick, MA) and the Psychophysics Toolbox (Brainard, 1997; Kleiner, Brainard, Pelli, Ingling, & Murray, 2007) and were presented on a 17-inch CRT monitor running at a 60-Hz refresh rate. The screen was viewed from a distance of 48 cm; the visible area subtended 36° × 27° of visual angle. The stimuli consisted of white dots (16.1 cd/m^2), initially positioned randomly on a gray background (3.81 cd/m^2). The dots moved within a horizontal stripe (height 10°) that extended the length of the screen (Figure 1). A black fixation spot (0.01 cd/m^2) was presented at the beginning of all trials.

In Experiment 1, the fixation spot was initially presented in a random position between 2° and 8° from the left edge of the screen. After 1.0 s, the fixation spot disappeared, and the random dots started moving rightward at one of seven speeds, randomly chosen from 5, 15, 18, 20, 22, 25, and 35°/s. This distribution had a large range of speeds to induce changes in the adaptive state of observers and was denser around the mean speed (20°/s), so that more measurements could be made in the crucial range for determining psychometric functions and to make the task challenging for observers. The dots moved for a random duration between 0.6 and 0.8 s. Observers were instructed to pursue the motion with their eyes and make a method-of-single-stimuli (MOSS) speed

judgement at the end of the trial, indicating with a button press whether the speed on the current trial was faster or slower than the mean speed of all trials. Observers performed two sessions of 224 trials (64 repetitions of each speed). The first 14 trials of each session contained two repetitions of each speed and were excluded from the analysis. This ensured that observers could first establish an implicit representation of the mean speed for the MOSS judgments (Morgan, Watamaniuk, & McKee, 2000). The advantage of MOSS is that it does not require an explicit comparison stimulus, as would be needed for a method-of-constant-stimuli two-interval forced-choice task. An explicit comparison stimulus might interfere with ongoing adaptation of the observer, whereas MOSS allows us to continuously acquire responses and test the adaptive state of the observer. In control experiments (described below), we also used different psychophysical methods to establish that adaptation can occur independently of the particular measurement method used.

In Experiment 2, participants performed the same judgement, but were instructed to keep their eyes stationary on the fixation point throughout the trial. In this experiment, the fixation spot was presented in the center of the screen and remained visible throughout the trial. The random dot stimulus was presented stationary for 1.0 s before moving rightward, as in Experiment 1. Observers again judged whether the speed on the current trial was faster or slower than the mean speed of all trials.

The same five observers participated in both experiments. Sessions of Experiments 1 and 2 were interleaved, and the order of which experiment was run first was counterbalanced between observers. Before each session, we calibrated the eye tracker with a nine-point calibration procedure. Before the first session of each experiment, participants performed about 100 trials for training purposes. These data were not included in the analysis.

Control experiments

In two control experiments, observers viewed the same stimuli but responded in different ways to establish the independence of our results from the specific psychophysical method used for observer judgments.

In the first control experiment, four observers rated the speed of the random dots on a nine-point scale. The stimuli and procedure were identical to the main experiment, but instead of doing a MOSS judgment, as in Experiments 1 and 2, observers rated the speed by pressing one of nine keys, the numbers 1 (slowest) to 9 (fastest) on the keyboard's number pad. This experi-

ment was run both with smooth pursuit eye movements (as in Experiment 1) and with steady fixation in the center of the screen (as in Experiment 2).

The second control experiment used an explicit standard stimulus in a two-alternative forced-choice (2AFC) task. We presented two additional stripes of random dots (height 3°) above and below the central stripe (gap to the central stripe 3°). The additional stripes were also stationary for 1.0 s at the start of each trial and started moving simultaneously with the central stripe. However, they always moved at the same speed of 20°/s, the mean speed of the central stripe, which was varied from trial to trial. All other aspects of the stimuli were identical to those in Experiments 1 and 2. By pressing one of two keys, four observers judged whether the central stripe moved faster or slower then the standard stripes, either while pursuing the motion (as in Experiment 1) or maintaining fixation (as in Experiment 2). Although the standard stimulus was presumably subject to the same adaptation mechanisms as the central stimulus, in the fixation condition the adapted state for those regions of the visual field should not change throughout the course of the experiment, because the standard stimulus always moved at the same speed. In the pursuit condition, the standard stimulus actually changed its retinal motion, depending on the difference in speed to the central pursuit stimulus, making the analysis of adaptation in this condition more difficult.

Analysis of psychophysical responses

Cumulative normal distributions were fitted to each participant's responses as a function of stimulus speed on the current trial, to estimate the point of subjective equality (PSE) of psychometric performance (Wichmann & Hill, 2001a, 2001b).

To estimate the amount of variance explained by the history of previous stimulus presentations (as opposed to the current stimulus), we binned trials according to the mean stimulus speed in k previous trials (for $1 \leq k \leq 42$) into five bins. Two separate analysis strategies were used. First, we fitted psychometric functions separately to trials from each bin, assessing how performance depends on speeds presented in recent stimulus history. In a second analysis, we determined the residuals of the response ratio in each bin from the ratio predicted by the psychometric function fit to all data. Summing the residual values from one bin provides a measure of how different responses were on trials with this particular stimulus history relative to the overall performance. The correlation of the mean preceding speed for each bin with the summed residuals is a measure for the effect of stimulus history on observers' responses.

For the first control experiment (magnitude estimation task), we fitted a simple linear regression line instead of a cumulative normal distribution to observers' responses. Analogous to the analysis above, we computed residuals from this linear function and used summed residuals to calculate correlations. The 2AFC judgments in the second control experiment were analyzed identically to the MOSS judgments in Experiments 1 and 2.

Analysis of eye movements

Eye position was sampled at 1000 Hz using a video-based Eyelink 1000 eye tracker (SR Research, Ottawa, Canada). The eye tracker was controlled using the EyeLink Toolbox for Matlab (Cornelissen, Peters, & Palmer, 2002). Prior to each block of trials, the eye tracker was calibrated by having observers fixate at a series of nine positions on the display (the center and eight surrounding peripheral positions). Forehead and chin rests maintained a constant viewing distance and stabilized the head for accurate eye tracking. Eye velocity was obtained by digital differentiation of eye position signals and filtered to reduce 60-Hz noise (two-pole Butterworth filter, cutoff at 50 Hz). Saccades were removed from the eye velocity traces by an automated saccade detection algorithm, using local variance and velocity thresholds (variance within a 10-ms window exceeding 150°/s or velocity exceeding 50°/s) and manual inspection. Eye velocity during saccades was replaced by linear interpolation of velocity before and after the saccade.

To quantify ASP velocity, we averaged eye velocity during a 100-ms period starting 50 ms before and ending 50 ms after the stimulus started to move. Eye velocity during this period is an internally generated anticipatory response that is not driven by the visual stimulus, because the typical latency for visually guided smooth pursuit is in the order of 100 ms (e.g., Krauzlis & Lisberger, 1994). To assess the influence of stimulus history on anticipatory eye velocity, we binarized anticipatory eye velocity by a median split (to create trials judged to be "faster" and "slower" based on eye velocity) and plotted the proportion of faster trials as a function of mean speed in the previous k trials. We then determined the correlation as a measure for the priming effect.

Confidence intervals

Confidence intervals for the correlation measures were calculated using a permutation procedure. We shuffled the temporal order of each participant's psychophysical responses and anticipatory eye veloc-

ities for 1,000 iterations, while leaving the trial sequence intact. This procedure leaves idiosyncratic observer characteristics such as response biases or biased distributions of eye velocities in place but destroys the relationship of psychophysical or motor responses with the actual stimulus sequence. We recalculated correlations using the unshuffled stimulus sequence and the 1,000 shuffled sequences of psychophysical and oculomotor responses. The resulting distribution of correlations represents a null distribution that would be expected if correlations did not depend on the specific stimulus history. The difference of the empirical correlations from these null distributions was used to construct confidence intervals.

Results

Psychophysics

Observers judged the speed of moving random dot stimuli while performing smooth pursuit eye movements (in Experiment 1) or while maintaining fixation at the center of the screen (in Experiment 2). Using MOSS, they judged whether the speed on the current trial was slower or faster than the mean speed on all trials. This method allowed us to avoid presenting explicit adaptor stimuli but rather let the observer adapt naturally to each stimulus as they occurred in the random sequence. The MOSS is similarly robust as a method-of-constant-stimuli two-interval forced-choice task, in which observers compare the speed of two subsequently presented stimuli (Morgan et al., 2000). Aggregate psychometric functions for the speed judgment in pursuit and fixation experiments are shown in Figure 2A, and individual observers' PSEs from psychometric function fits are shown in Figure 2B. The mean PSE in pursuit trials was 21.51°/s (*SEM* = 0.24°/s), indicating that observers judged speed accurately with a small bias to judge speed on any given trial to be slightly slower than the actual mean speed. During fixation, the mean PSE was 19.95°/s (*SEM* = 0.66°/s), indicating that, on average, the motion appeared slightly faster than during smooth pursuit, as has been found previously (Fleischl, 1882; Mack & Herman, 1972), although this difference was not significant, paired *t* test: $t(4) = 2.03$, $p = 0.11$, and not of crucial interest for the remainder of our analysis.

To investigate the influence of stimulus history on perceptual responses, we binned trials according to the mean speed in the previous *k* trials into five bins and fitted psychometric functions separately for each bin. Psychometric functions for $k = 15$ are shown in Figure
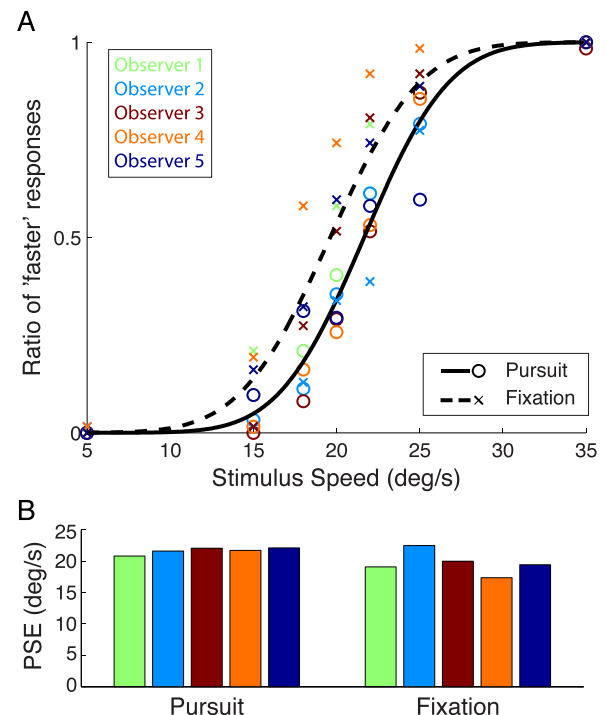

Figure 2. (A) Aggregate psychometric functions for pursuit (Experiment 1, solid line) and fixation (Experiment 2, dashed line). Different colored circles and crosses are individual observers' measurements for pursuit and fixation, respectively. (B) Individual observers' PSEs.

3A. Trials with a history of slower stimuli led to lower PSEs (meaning that perceived motion was on average faster), and vice versa. Individual observers' PSEs for each bin are plotted in Figure 3B. A two-way repeated-measures analysis of variance showed a significant effect of trial history on PSE, $F(4, 16) = 22.8$, $p < 0.001$, partial $\eta^2 = 0.85$, but no effect of fixation/pursuit, $F(1, 4) = 3.74$, $p = 0.13$, partial $\eta^2 = 0.48$, and no interaction, $F(4, 16) = 1.72$, $p = 0.20$, partial $\eta^2 = 0.30$. Linear regression revealed a significant correlation of the mean speed in the previous 15 trials and the PSE for each bin during pursuit ($r = 0.850$, $p < 10^{-7}$). The number of bins in this analysis (five) was chosen arbitrarily, but similar results were obtained for bin sizes between three and seven. Similar results were obtained for Experiment 2 (Figure 3C), when subjects maintained steady fixation ($r = 0.485$, $p = 0.014$).

Fitting psychometric functions to data from each bin separately has the disadvantage of decreasing the number of trials that are used to estimate each PSE. In an additional analysis, we used the psychometric function fit to all data and estimated the influence of stimulus history by analyzing the residuals of response ratios for each bin from the function fit. Figure 4A shows this analysis for one observer. Similar analyses of nonstationary observer behavior have recently been
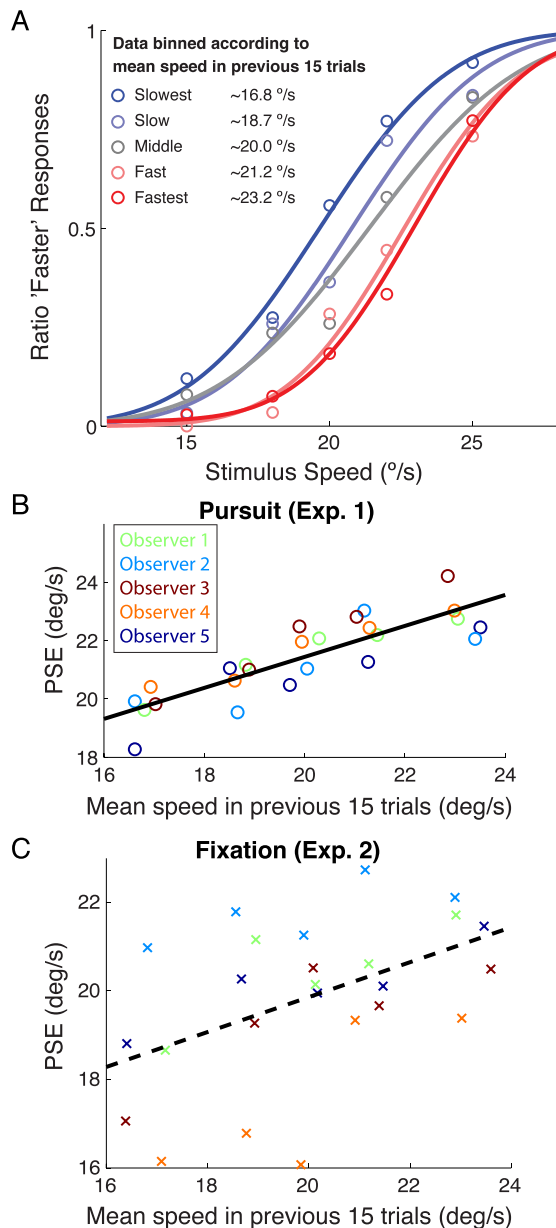
Figure 3. (A) Aggregate psychometric functions for pursuit with separate fits for trials binned according to stimuli presented in the 15 previous trials. (B) Individual PSEs for each bin as a function of the mean speed in the previous 15 trials for Experiment 1 (pursuit). (C) The same plot as in B for Experiment 2 (fixation).
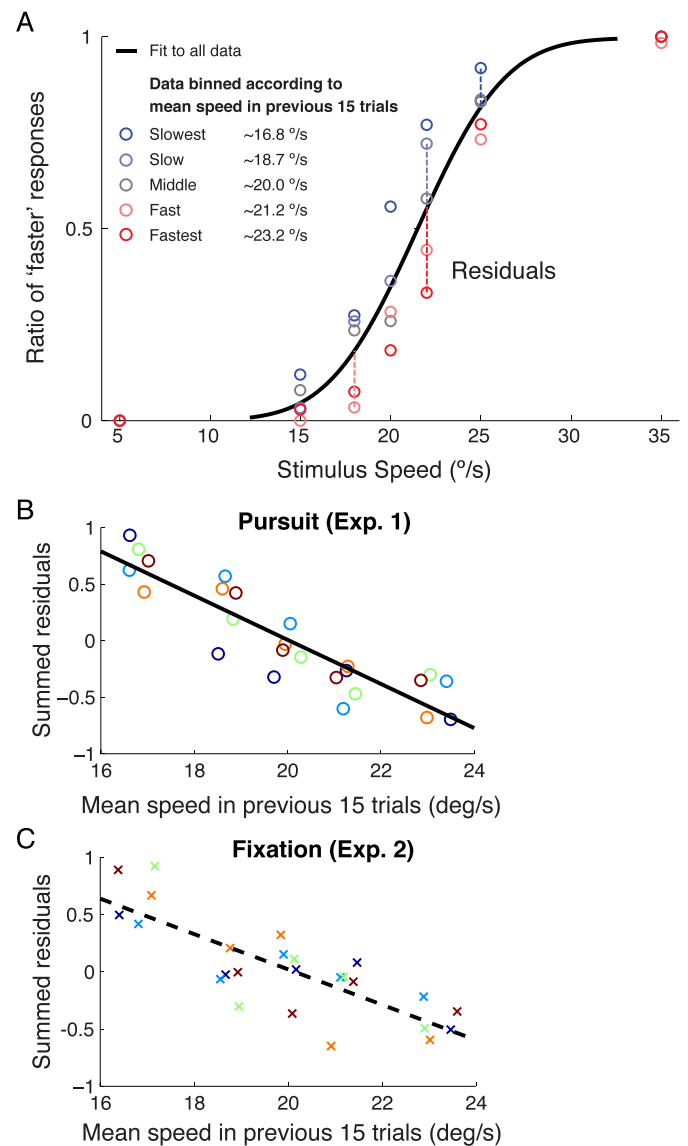

Figure 4. (A) Residuals were determined as the difference of response ratios in trials binned according to their stimulation history from the psychometric function fit to all data (here shown for aggregate psychometric function from all observers). (B) Summed residuals of individual observers as a function of mean speed in 15 previous trials for Experiment 1 (pursuit) and (C) the same plot as in B for Experiment 2 (fixation).

proposed (Fründ, Haenel, & Wichmann, 2011). Figure 4B shows the summed residuals for each bin as a function of the average previous stimulus velocity in Experiment 1. Linear regression revealed a highly significant negative correlation ($r = -0.896$, $p < 10^{-8}$), indicating that stimuli with on average faster preceding trials lead to fewer faster responses, and vice versa. Similar results were obtained for Experiment 2 (Figure 4C), when subjects maintained steady fixation ($r = -0.803$, $p < 10^{-5}$).

The value of $k = 15$ (i.e., taking a stimulus history of the last 15 trials into account) was chosen here because this value led to the maximal average correlation of stimulus history with response residuals. Correlations for other values of k are shown in Figure 5.

Eye movements

In each trial in Experiment 1, participants were instructed to pursue the motion of the random dot
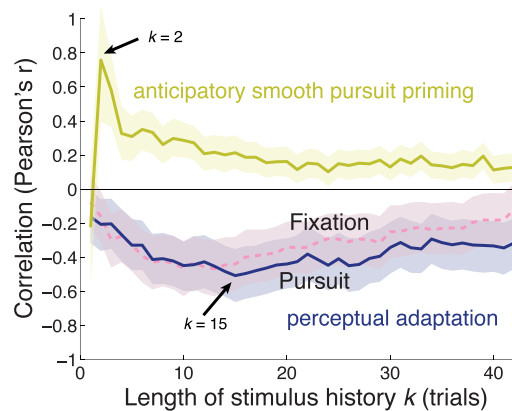
Figure 5. Mean correlation coefficients (and bootstrapped confidence intervals) for perceptual adaptation (Figure 4B/C) and ASP priming (Figure 6C) as a function of stimulus history length k.

stimulus with their eyes. The average eye velocity traces for one participant (Figure 6A) show that, in general, during the steady-state phase of pursuit, eye velocity matched stimulus velocity accurately. Note that eye velocity began to increase before the onset of visually guided pursuit at about 100 ms after stimulus motion onset. ASP is virtually always present at pursuit initiation and is more robust when target motion occurs at a predictable time (Heinen et al., 2005; Kao & Morrow, 1994; Kowler & McKee, 1987). ASP begins before stimulus motion and therefore does not vary as a function of stimulus speed on the current trial, as can be seen here. However, its magnitude is directly related to stimulus speed on preceding trials (Heinen et al., 2005; Kowler et al., 1984). To demonstrate the dependence of ASP on the stimulus speed in previous trials in our data, we show the eye velocity traces separated by the mean speed in the previous two trials in Figure 6B.

To characterize the influence of stimulus history on anticipatory pursuit, we analyzed mean eye velocity in a 100-ms window centered around the time of stimulus motion onset. We applied a median split to each observer's mean anticipatory eye velocity to make these data more comparable to the perceptual responses (i.e., we coded anticipatory eye velocity on a given trial as 1 if it was faster than the median velocity on all trials and 0 otherwise). Figure 6C shows anticipatory eye velocity as a function of the mean speed from the two previous trials ($k = 2$). No binning of data is necessary for this analysis. The correlations of stimulus speed on previous trials and anticipatory eye velocity are consistently positive. Averaged over all five observers, a history of two trials back ($k = 2$) showed the greatest correlation ($r = 0.580$, $SEM = 0.078$). Correlations for other values of k are shown in Figure 5.
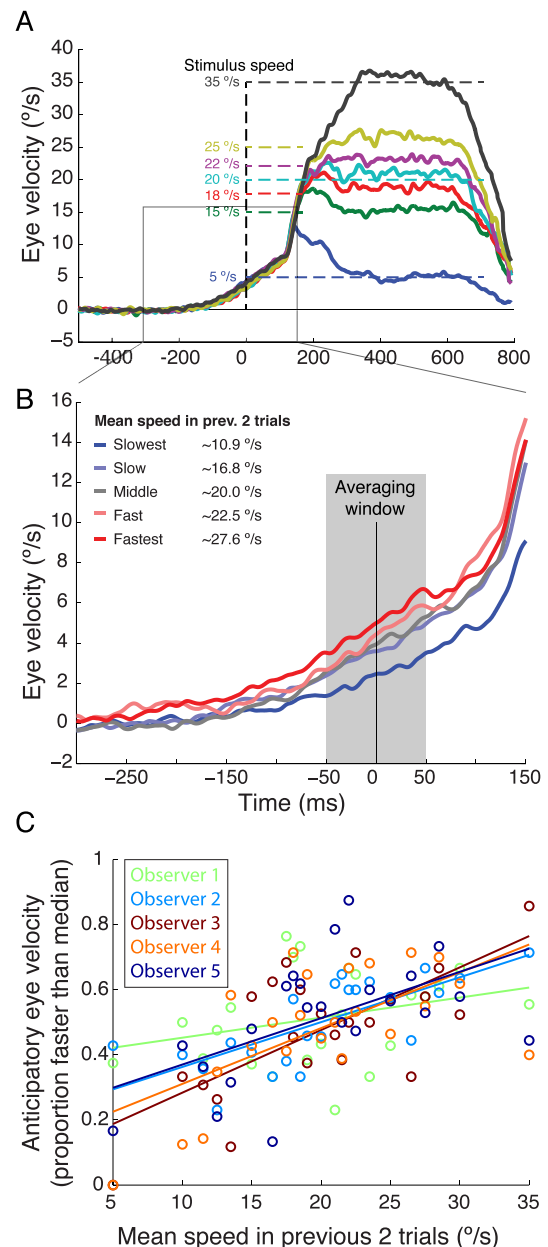

Figure 6. (A) Eye velocity traces of one participant, separated by stimulus speed on the current trial. Dashed lines show the velocity of the random dot stimulus. (B) Eye velocity traces separated by mean stimulus speed on the previous two trials (zoomed in on the time around stimulus motion onset). The shaded area (−50 to 50 ms around stimulus motion onset) was used to calculate anticipatory smooth pursuit (ASP) velocity. (C) Proportion of ASP eye velocity faster than median ASP as a function of the mean stimulus speed on the previous two trials.

Effect of stimulus history length on perception and eye movements

The effects of stimulus history on speed perception and ASP velocity were characterized by separate correlation measures. For the perceptual adaptation

effect, the summed residuals from the psychometric function fit were correlated with mean stimulus speed on k previous trials; for the oculomotor priming effect, ASP velocity was correlated with mean stimulus speed on k previous trials. Mean values for both correlations are shown as a function of trial history length k in Figure 5. The perceptual correlation is shown for both Experiment 1 (pursuit) and Experiment 2 (fixation). Correlations for perceived speed are negative, as expected from motion adaptation and a negative perceptual aftereffect. Correlations for anticipatory pursuit are positive, consistent with an oculomotor priming effect. Importantly, the maximum perceptual adaptation effect occurs for a stimulus history of ~15 trials for pursuit and ~13 trials for fixation. In contrast, the oculomotor priming effect peaks for a short stimulus history of only two trials.

Confidence intervals from a permutation procedure, in which the order of psychophysical and oculomotor responses were reshuffled with respect to the stimulus sequence, are shown as shaded areas in Figure 5. It should be noted here that progressively increasing stimulus history length k adds more trials from the increasingly distant past to the history being used to explain the current response, but it does not exclude more recent trials. Therefore, adding more trials increases the ability to explain variance in the responses up to the peak correlation value. The correlation values do not, however, converge toward zero as more trials are added to the stimulus history, because the more recent trials explaining most of the variance remain part of the stimulus history considered for higher values of k.

Control experiments with different psychophysical methods

In two control experiments, observers made different psychophysical judgments to evaluate whether the adaptation effect reported above might be an artifact of the MOSS judgment. Compared with other forms of visual motion adaptation (Kanai & Verstraten, 2005; Pavan et al., 2009; Pavan et al., 2010), our results have a relatively long-lasting perceptual effect, building up over tens of seconds and ~13 to 15 trials. On the other hand, MOSS judgments are known to be based on an internal implicit standard generated over roughly the same time period (Morgan et al., 2000). It is therefore possible that our long adaptation time simply represents the integration time for an implicit decision criterion for MOSS judgments. Therefore, in two additional control experiments, we aimed to establish whether similar adaptation can be found using different psychometric methods. In the first control experiment, observers performed a magnitude estimation of the

speed on each trial. In the second control experiment, observers performed a 2AFC judgment comparing the central motion stimulus to an explicit standard presented in separate locations of the visual field.

Figure 7A and B show data from the magnitude estimation task during fixation. The summed residuals for each bin from a linear regression fit to observers' responses correlate negatively with each bin's mean stimulus speed in the previous $k = 15$ trials ($r = -0.678$, $p = 0.001$). Mean correlations for other values of k for both pursuit and fixation are shown in Figure 7C, with confidence intervals calculated from a permutation procedure as described above. The correlation as a function of stimulus history follows a similar trend as in Experiments 1 and 2 (Figure 5), with maximal correlations for stimulus histories of between 10 and 15 trials. One obvious difference is a positive correlation for short stimulus histories ($k < 4$).

Figure 7D and E show data from the 2AFC task during fixation. The summed residuals for each bin from the cumulative normal fit to observers' responses also correlate negatively with each bin's mean stimulus speed in the previous $k = 15$ trials ($r = -0.789$, $p < 10^{-4}$). Mean correlation values for all values of k for both pursuit and fixation are shown in Figure 7F. Here, it seems that responses during pursuit lead to smaller correlation coefficients than during fixation. Although the correlations do not have distinct peaks for the same values of k as in Experiments 1 and 2 (Figure 5), correlations for all values of k are clearly negative (i.e., observers' responses exhibit a long-lasting negative aftereffect).

Discussion

Perceptual adaptation

We found that when observers repeatedly viewed a moving random dot field, the perception of speed exhibited a negative aftereffect consistent with motion adaptation (i.e., the perceived speed on the current trial was negatively correlated with speeds presented on previous trials). This effect occurred regardless of whether the stimulus was pursued or not, consistent with previous reports of allocentric motion aftereffects in the absence of retinal motion (Mack et al., 1987; Morgan, Ward, & Brussell, 1976; Moulden, Patterson, & Swanston, 1998).

In contrast to most studies on motion adaptation, our present experiments did not use explicit adaptation and test stimuli. Instead, observers adapted naturally while viewing a random sequence of relatively brief motion stimuli with different speeds. In other studies using brief adaptor stimuli, aftereffects decay rapidly
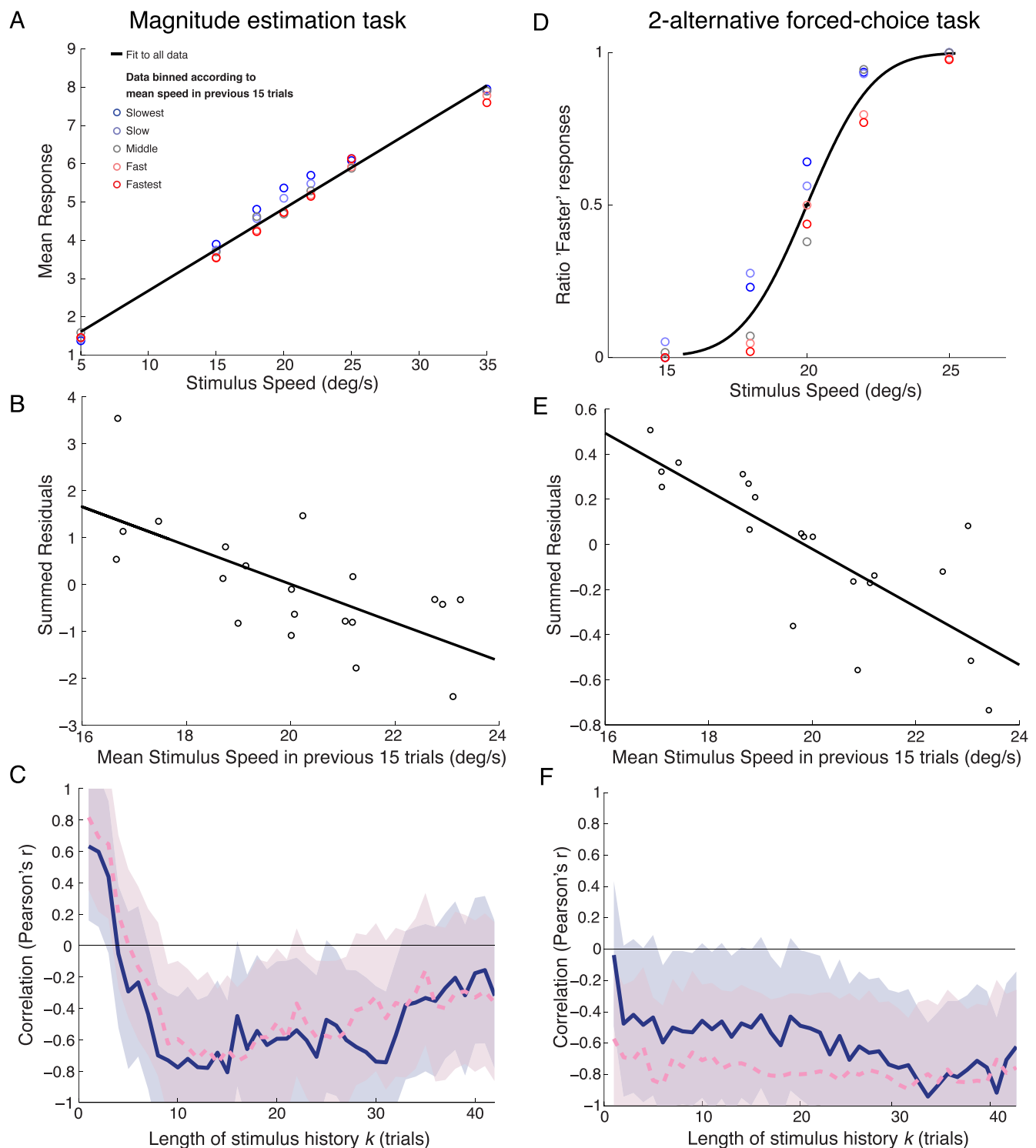
Figure 7. Results of the two control experiments. (A) Mean responses of four observers in the magnitude estimation task with fixation, binned by mean stimulus velocity in the previous 15 trials. The black line is a linear regression fit to all data. (B) Residuals of trials in each bin from the linear fit in A for each observer. The black line is a linear regression fit, whose correlation coefficient is used as a measure of the perceptual aftereffect. (C) Correlation coefficients for different values of stimulus history length k. Solid blue line is for sessions with pursuit eye movements; the dashed gray line is for fixation. (D) Same as A for the control experiment using a 2AFC task. Here, responses are fit by a cumulative normal fit as in Figure 4A. (E, F) Same as B and C for the 2AFC task.

within ~1 s (Kanai & Verstraten, 2005; Pavan et al., 2009; Pavan et al., 2010). The adaptation effects we measured last longer, or rather, they build up over a longer time period (~15 trials). It is likely that our paradigm, without explicit adaptor stimuli, allowed adaptation effects to accumulate over multiple trials and be stored over periods with either no stimulation (during responses) or static stimuli irrelevant to the task (at the beginning of each trial).

Using MOSS judgments allowed us to measure perceived speed continuously on each trial without using an explicit comparison stimulus. However, the MOSS has the potential disadvantage that the adaptation effect we measure is not due to perceptual adaptation, as classically measured in studies on the motion aftereffect, but rather to a cognitive recalibration of the internal response criterion used for the MOSS judgments. On this view, stimulus history would not influence the perception of speed on the current trial but rather the internal criterion to which the current speed is compared in order to make the perceptual judgment. Indeed, our finding that maximal correlations occur for a stimulus history of about ~13 to 15 trials is consistent with a recalibration of a MOSS decision criterion (Morgan et al., 2000). However, this recalibration might itself be a perceptual effect that is for all intents and purposes indistinguishable from perceptual adaptation.

In two control experiments, we confirmed that the adaptation effect does not depend on MOSS judgments, as it also occurs for different response methods, such as an explicit magnitude estimation task and a 2AFC task, in which observers directly compare the speed to another stimulus simultaneously visible on the screen. There are slight differences in the results of those experiments: In the magnitude estimation task, observers' responses exhibited a positive bias for short stimulus histories (up to ~four trials back; Figure 7C). This is reminiscent of previously reported positive serial dependencies in perception (Fischer & Whitney, 2014; Liberman, Fischer, & Whitney, 2014), in which observers viewed similar random stimulus sequences and also responded on a continuous scale. In the 2AFC task, judgments during smooth pursuit generally led to less adaptation than during fixation (smaller correlation values in Figure 7F). While pursuing the stimulus, the standard stimulus actually differed in retinal speed from trial to trial, depending on whether it moved faster or slower than the pursuit stimulus. The 2AFC judgment could be performed by judging the retinal motion of the standard stimulus. In this condition, adaptation might occur both in a retinal and an allocentric reference frame (for the peripheral standard and the central pursuit stimulus, respectively), making a straightforward interpretation of the results difficult. Furthermore, during both pursuit and fixation, there

were no clear *peaks* of stimulus history effects for ~13 to 15 trials.

Regardless of these differences, however, both control experiments showed clear perceptual adaptation of observers to the motion of the random dot field, including for stimulus histories of ~13 to 15 trials. Whereas in Experiments 1 and 2, a cognitive recalibration of an internal decision criterion for MOSS judgments might have contributed to the measured effects, the control experiments confirm that our stimuli also cause perceptual motion adaptation effects comparable to those in classical studies on the motion aftereffect.

Oculomotor priming

ASP eye velocity showed the opposite effect to the perceptual speed judgments: ASP velocity on the current trial correlated *positively* with the speeds presented in previous trials. Unlike the perceptual system, the oculomotor system exhibits a positive aftereffect—or a priming effect—in anticipatory responses. Other studies have shown that smooth pursuit eye movements adapt similarly to perception (i.e., both direction and speed of eye movements are repelled from direction and speed of an adapting stimulus; Gardner, Tokiyama, & Lisberger, 2004). However, here we analyzed the anticipatory phase of pursuit, which is not based on retinal input but on the expectation of stimulus motion.

Although seemingly paradoxical, the opposite signs of the two effects could in principle be implemented by a system with just one internal representation that keeps a running average of stimulus speeds from previous trials. This representation could then be used for (a) generating ASP eye movements that match the likely velocity required for initiation and maintenance of accurate smooth pursuit and (b) comparison with the current speed in order to maintain optimal sensitivity for detecting changes in an object's motion. A faster speed in the internal representation will lead to judgments biased in the "slower" direction and at the same time would trigger a relatively faster ASP to match the predicted stimulus speed for the next trial as closely as possible.

One crucial aspect of our results, however, makes a system with just one internal representation unlikely: The perceptual negative aftereffect and the motor priming of ASP operate over very different time scales. The perceptual responses correlate maximally with the mean speed of the last ~15 trials, whereas the motor priming is maximal for a trial history of just two trials. In other words, two different internal representations, each with a different temporal capacity, are being used for motor priming and

perceptual judgments. The perceptual representation is the result of integrating motion information over a large number of previous presentations. Integration over a longer perceptual history would filter out small, transient discrepancies in motion to maintain a more general awareness of how an object moves over time. The oculomotor representation, on the other hand, has a relatively short temporal integration time (Heinen et al., 2005), using information from only the last two trials. Use of a shorter history would facilitate quick changes to eye velocity to maintain accurate smooth pursuit.

Previous studies had investigated the temporal extent of storage of motion information for ASP (Wells & Barnes, 1998). There is evidence that ASP eye movements are generated even in situations in which target velocity or time of motion onset is randomized, and thus unpredictable, based on information from just the previous trial (Heinen et al., 2005). Our findings are consistent with the notion that the oculomotor system uses relatively short-term temporal information to generate anticipatory eye movements.

Stimulus history effects

Perceptual history can manifest as negative aftereffects or priming. Stimuli presented in the recent past bias the perception of a current stimulus by means of adaptation, resulting in a recalibration of perceptual sensitivity that leads to increased performance in detecting new stimuli (Kohn, 2007; Webster, 2011). A recent report of longer-term positive aftereffects (Chopin & Mamassian, 2012) is most likely due to an analysis artifact (Maus, Chaney, Liberman, & Whitney, 2013). Nonetheless, positive biases of perception with previous stimuli have been reported, showing that the visual system favors the temporal stability of objects (Burr & Cicchini, 2014; Fischer & Whitney, 2014; Liberman et al., 2014). Priming, on the other hand, facilitates detection or identification of a repeatedly presented stimulus (Kristjansson & Campana, 2010). Both facilitatory priming effects and perceptual negative aftereffects can occur for visual motion stimuli with only slight changes in presentation parameters (Kanai & Verstraten, 2005) and seem to be supported by the same neural substrates (Campana et al., 2002; Campana, Cowey, & Walsh, 2006; Campana, Maniglia, & Pavan, 2013). In the present study, priming and adaptation, measured via ASP eye movements and perceived speed, respectively, occur simultaneously for the same stimuli.

The seemingly opposing effects in our study might be explained by the different functions of the perceptual and motor systems. A perceptual system that needs to discern small changes but maintain a

general idea of the motion of a stimulus over time would likely operate under a longer time scale. The effects of adaptation make stimulus changes more obvious because adaptation serves to shift the effective operating range of perception (Webster, 2011), but a longer time scale filters out brief discrepancies from the general representation. The oculomotor system, however, needs to follow an object as closely and accurately as possible, and the short time scale of priming allows smooth pursuit to react to changes in stimulus motion quickly.

Conclusion

When moving stimuli are sequentially presented at a range of speeds, observers adapt to previous speeds and negatively bias their estimate of the current speed. At the same time, however, the velocity of ASP eye movements correlates positively with the speed of previous stimulus presentations. The present study for the first time directly compares the temporal extents of these two effects. Perceptual adaptation and oculomotor priming show vastly different time scales: Whereas the oculomotor priming effect uses information from only the last one to two trials, perceptual adaptation is based on the average of the last ~15 stimulus trials, indicating that both effects are based on independent temporal representations.

Keywords: adaptation, motion aftereffect, eye movements, anticipatory smooth pursuit, priming

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Corresponding author: Gerrit W. Maus.
E-mail: maus@berkeley.edu.
Address: Department of Psychology, University of California Berkeley, Berkeley, CA, USA.

References

Anstis, S., & Ramachandran, V. S. (1987). Visual inertia in apparent motion. *Vision Research, 27,* 755–764.

Anstis, S., Verstraten, F. A., & Mather, G. (1998). The

motion aftereffect. *Trends in Cognitive Sciences, 2,* 111–117.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10,* 433–436.

Burr, D., & Cicchini, G. M. (2014). Vision: Efficient adaptive coding. *Current Biology, 24,* R1096–R1098.

Campana, G., Cowey, A., & Walsh, V. (2002). Priming of motion direction and area V5/MT: A test of perceptual memory. *Cerebral Cortex, 12,* 663–669.

Campana, G., Cowey, A., & Walsh, V. (2006). Visual area V5/MT remembers "what" but not "where." *Cerebral Cortex, 16,* 1766–1770. doi:10.1093/cercor/bhj111

Campana, G., Maniglia, M., & Pavan, A. (2013). Common (and multiple) neural substrates for static and dynamic motion after-effects: A rTMS investigation. *Cortex, 49,* 2590–2594. doi:10.1016/j.cortex.2013.07.001

Chopin, A., & Mamassian, P. (2012). Predictive properties of visual adaptation. *Current Biology, 22,* 622–626. doi:10.1016/j.cub.2012.02.021

Clifford, C. W. G., Webster, M. A., Stanley, G. B., Stocker, A. A., Kohn, A., Sharpee, T. O., & Schwartz, O. (2007). Visual adaptation: Neural, psychological and computational aspects. *Vision Research, 47,* 3125–3131. doi:10.1016/j.visres.2007.08.023

Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments, & Computers, 34,* 613–617. doi:10.3758/BF03195489

Fischer, J., & Whitney, D. (2014). Serial dependence in visual perception. *Nature Neuroscience, 17,* 738–743. doi:10.1038/nn.3689

Fleischl, E. (1882). Physiologisch-optische Notizen. *Sitzungsberichte der Akademie der Wissenschaften, 86,* 17–25.

Fründ, I., Haenel, N. V., & Wichmann, F. A. (2011). Inference for psychometric functions in the presence of nonstationary behavior. *Journal of Vision, 11*(6):16, 1–19, http://www.journalofvision.org/content/11/6/16, doi:10.1167/11.6.16. [PubMed] [Article]

Gardner, J. L., Tokiyama, S. N., & Lisberger, S. G. (2004). A population decoding framework for motion aftereffects on smooth pursuit eye movements. *Journal of Neuroscience, 24,* 9035–9048. doi:10.1523/JNEUROSCI.0337-04.2004

Heinen, S. J., Badler, J. B., & Ting, W. (2005). Timing and velocity randomization similarly affect antici-patory pursuit. *Journal of Vision, 5*(6):1, 493–503, http://www.journalofvision.org/content/5/6/1, doi:10:1167/5.6.1. [PubMed] [Article]

Heinen, S. J., & Watamaniuk, S. N. (1998). Spatial integration in human smooth pursuit. *Vision Research, 38,* 3785–3794.

Hershenson, M. (1993). Linear and rotation motion aftereffects as a function of inspection duration. *Vision Research, 33,* 1913–1919.

Kanai, R., & Verstraten, F. A. J. (2005). Perceptual manifestations of fast neural plasticity: Motion priming, rapid motion aftereffect and perceptual sensitization. *Vision Research, 45,* 3109–3116. doi:10.1016/j.visres.2005.05.014

Kao, G. W., & Morrow, M. J. (1994). The relationship of anticipatory smooth eye movement to smooth pursuit initiation. *Vision Research, 34,* 3027–3036.

Kleiner, M., Brainard, D., Pelli, D., Ingling, A., & Murray, R. (2007). What's new in Psychtoolbox-3. *Perception, 36*(ECVP Abstract Supplement), 14.

Kohn, A. (2007). Visual adaptation: Physiology, mechanisms, and functional benefits. *Journal of Neurophysiology, 97,* 3155–3164. doi:10.1152/jn.00086.2007

Kowler, E. (1989). Cognitive expectations, not habits, control anticipatory smooth oculomotor pursuit. *Vision Research, 29,* 1049–1057.

Kowler, E., Martins, A. J., & Pavel, M. (1984). The effect of expectations on slow oculomotor control 4. Anticipatory smooth eye-movements depend on prior target motions. *Vision Research, 24,* 197–210.

Kowler, E., & McKee, S. P. (1987). Sensitivity of smooth eye movement to small differences in target velocity. *Vision Research, 27,* 993–1015.

Krauzlis, R. J., & Lisberger, S. G. (1994). A model of visually-guided smooth pursuit eye movements based on behavioral observations. *Journal of Computational Neuroscience, 1,* 265–283.

Kristjansson, A. (2009). Independent and additive repetition priming of motion direction and color in visual search. *Psychological Research, 73,* 158–166. doi:10.1007/s00426-008-0205-z

Kristjansson, A., & Campana, G. (2010). Where perception meets memory: A review of repetition priming in visual search tasks. *Attention, Perception, and Psychophysics, 72,* 5–18. doi:10.3758/APP.72.1.5

Liberman, A., Fischer, J., & Whitney, D. (2014). Serial dependence in the perception of faces. *Current*

Biology, 24, 2569–2574. doi:10.1016/j.cub.2014.09. 025

Mack, A., Goodwin, J., Thordarsen, H., Benjamin, D., Palumbo, D., & Hill, J. (1987). Motion aftereffects associated with pursuit eye movements. *Vision Research, 27,* 529–536.

Mack, A., & Herman, E. (1972). A new illusion: The underestimation of distance during pursuit eye movements. *Perception and Psychophysics, 12,* 471–473. doi:10.3758/BF03210937

Maljkovic, V., & Nakayama, K. (1994). Priming of pop-out: I. Role of features. *Memory & Cognition, 22,* 657–672.

Maljkovic, V., & Nakayama, K. (1996). Brief duration of pop-out priming. *Investigative Ophthalmology & Visual Science, 37,* 59.

Mather, G., Pavan, A., Campana, G., & Casco, C. (2008). The motion aftereffect reloaded. *Trends in Cognitive Sciences, 12,* 481–487. doi:10.1016/j.tics. 2008.09.002

Mather, G., Verstraten, F., & Anstis, S. M. (1998). *The motion aftereffect.* Cambridge, MA: MIT Press.

Maus, G. W., Chaney, W., Liberman, A., & Whitney, D. (2013). The challenge of measuring long-term positive aftereffects. *Current Biology, 23,* R438–R439. doi:10.1016/j.cub.2013.03.024

Morgan, M. J., Ward, R. M., & Brussell, E. M. (1976). The aftereffect of tracking eye movements. *Perception, 5,* 309–317.

Morgan, M. J., Watamaniuk, S. N. J., & McKee, S. P. (2000). The use of an implicit standard for measuring discrimination thresholds. *Vision Research, 40,* 2341–2349.

Moulden, B., Patterson, R., & Swanston, M. (1998). The retinal image, ocularity, and cyclopean vision. In G. Mather, F. Verstraten, & S. Anstis (Eds.), *The motion aftereffect: A modern perspective* (pp. 57–84). Cambridge, MA: Bradford Books.

Pavan, A., Campana, G., Guerreschi, M., Manassi, M., & Casco, C. (2009). Separate motion-detecting mechanisms for first- and second-order patterns revealed by rapid forms of visual motion priming and motion aftereffect. *Journal of Vision, 9*(11):27, 1–16, http://www.journalofvision.org/content/9/11/27, doi:10.1167/9.11.27. [PubMed] [Article]

Pavan, A., Campana, G., Maniglia, M., & Casco, C. (2010). The role of high-level visual areas in short- and longer-lasting forms of neural plasticity.

Neuropsychologia, 48, 3069–3079. doi:10.1016/j. neuropsychologia.2010.06.018

Pearson, J., & Brascamp, J. (2008). Sensory memory for ambiguous vision. *Trends in Cognitive Sciences, 12,* 334–341. doi:10.1016/j.tics.2008.05.006

Pinkus, A., & Pantle, A. (1997). Probing visual motion signals with a priming paradigm. *Vision Research, 37,* 541–552.

Santos, E. M., Gnang, E. K., & Kowler, E. (2012). Anticipatory smooth eye movements with random-dot kinematograms. *Journal of Vision, 12*(11):1, 1–20, http://www.journalofvision.org/content/12/11/1, doi:10.1167/12.11.1. [PubMed] [Article]

Schwiedrzik, C. M., Ruff, C. C., Lazar, A., Leitner, F. C., Singer, W., & Melloni, L. (2014). Untangling perceptual memory: Hysteresis and adaptation map into separate cortical networks. *Cerebral Cortex, 24,* 1152–1164. doi:10.1093/cercor/bhs396

Tulving, E., & Schacter, D. L. (1990). Priming and human memory systems. *Science, 247,* 301–306. doi:10.1126/science.2296719

Verstraten, F. A., Fredericksen, R. E., Grüsser, O. J., & van de Grind, W. A. (1994). Recovery from motion adaptation is delayed by successively presented orthogonal motion. *Vision Research, 34,* 1149–1155.

Webster, M. A. (2011). Adaptation and visual coding. *Journal of Vision, 11*(5):3, 1–23, http://www. journalofvision.org/content/11/5/3, doi:10.1167/11. 5.3. [PubMed] [Article]

Wells, S. G., & Barnes, G. R. (1998). Fast, anticipatory smooth-pursuit eye movements appear to depend on a short-term store. *Experimental Brain Research, 120,* 129–133.

Westheimer, G. (1954). Eye movement responses to a horizontally moving visual stimulus. *AMA Archives of Ophthalmology, 52,* 932–941.

Wichmann, F. A., & Hill, N. J. (2001a). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception and Psychophysics, 63,* 1293–1313.

Wichmann, F. A., & Hill, N. J. (2001b). The psychometric function: II. Bootstrap-based confidence intervals and sampling. *Perception and Psychophysics, 63,* 1314–1329.

Wiesenfelder, H., & Blake, R. (1992). Binocular-rivalry suppression disrupts recovery from motion adaptation. *Visual Neuroscience, 9,* 143–148.