Independent Effects of Adaptation and Attention on Perceived Speed

Katharina Anton-Erxleben[1,2], Katrin Herrmann[1], and Marisa Carrasco[1,2]
[1]Department of Psychology and [2]Center for Neural Science, New York University

Abstract

Adaptation and attention are two mechanisms by which sensory systems manage limited bioenergetic resources: Whereas adaptation decreases sensitivity to stimuli just encountered, attention increases sensitivity to behaviorally relevant stimuli. In the visual system, these changes in sensitivity are accompanied by a change in the appearance of different stimulus dimensions, such as speed. Adaptation causes an underestimation of speed, whereas attention leads to an overestimation of speed. In the two experiments reported here, we investigated whether the effects of these mechanisms interact and how they affect the appearance of stimulus features. We tested the effects of adaptation and the subsequent allocation of attention on perceived speed. A quickly moving adaptor decreased the perceived speed of subsequent stimuli, whereas a slow adaptor did not alter perceived speed. Attention increased perceived speed regardless of the adaptation effect, which indicates that adaptation and attention affect perceived speed independently. Moreover, the finding that attention can alter perceived speed after adaptation indicates that adaptation is not merely a by-product of neuronal fatigue.

At every moment, people are exposed to an overwhelming amount of information. However, because of limited neural resources, people cannot process all input equally well (Lennie, 2003). Several mechanisms, such as adaptation and attention, reduce the cost of cortical computation by shifting priority to relevant information.

Adaptation decreases sensitivity for stimuli that have been encountered repeatedly in the past, thereby increasing sensitivity to changes in the environment (Kohn, 2007). Adaptation is ubiquitous in sensory modalities; in vision, for example, people adapt to very diverse low- and high-level stimulus features, such as color, spatial frequency, motion, and contrast, as well as aspect ratio and facial expression (Webster, 2011). Although adaptation had long been viewed as a by-product of neuronal fatigue, in which the level of fatigue for a given neuron depends on the magnitude of its response to the adapting stimulus, it is now clear that adaptation may have functional benefits (Kohn, 2007; Webster, 2011). Adaptation adjusts the dynamic range of the system by shifting contrast-response functions to match contrast levels prevalent in the environment (Movshon & Lennie, 1979; Ohzawa, Sclar, & Freeman, 1982). Adaptation also shifts tuning curves for orientation (Jin, Dragoi, Sur, & Seung, 2005) and direction (Krekelberg, van Wezel, & Albright, 2006) to optimize processing of prevailing stimulus features. Thus, adaptation optimizes processing resources for recent stimulus conditions. A consequence of the selective change in sensitivity is an aftereffect—a change in the appearance of visual stimulus features, such as spatial frequency (Blakemore, Nachmias, & Sutton, 1970) and motion direction (Levinson & Sekuler, 1976). For a given feature, adaptation typically causes a repulsive shift in perception, either an over- or underestimation, away from the adaptor.

Attention is another mechanism by which sensory systems prioritize relevant information. Spatial attention enables people to dynamically concentrate processing resources at the location of interest, either overtly (by moving their gaze) or covertly (without moving their gaze toward the attended object). Spatial covert attention improves contrast sensitivity, spatial resolution, and processing speed for stimuli at the attended location, but it impairs performance at unattended locations (Carrasco, Giordano, & McElree, 2006; Carrasco, Penpeci-Talgar, & Eckstein, 2000; Giordano, McElree, &

Corresponding Author:
Katharina Anton-Erxleben, New York University, Department of Psychology, 6 Washington Place, New York, NY 10003
E-mail: katharina.antonerxleben@nyu.edu

Carrasco, 2009; Herrmann, Montaser-Kouhsari, Carrasco, & Heeger, 2010; Ling & Carrasco, 2006; Lu & Dosher, 1998; Luck et al., 1994; Montagna, Pestilli, & Carrasco, 2009; Pestilli, Viera, & Carrasco, 2007; Yeshurun & Carrasco, 1998). Spatial covert attention also changes the appearance of visual stimulus features (Abrams, Barbot, & Carrasco, 2010; Anton-Erxleben, Abrams, & Carrasco, 2010; Anton-Erxleben, Henrich, & Treue, 2007; Carrasco, Ling, & Read, 2004; Fuller & Carrasco, 2006; Gobell & Carrasco, 2005; T. Liu, Abrams, & Carrasco, 2009; T. Liu, Fuller, & Carrasco, 2006; Montagna & Carrasco, 2006; Störmer, McDonald, & Hillyard, 2009); for example, it leads to an overestimation of speed (Fuller, Park, & Carrasco, 2009; Turatto, Vescovi, & Valsecchi, 2007).

How Do Adaptation and Attention Interact?

It is established that attention during the adapting phase potentiates the effects of adaptation on a variety of visual phenomena (leading to, for example, motion, orientation, and contrast aftereffects; Alais & Blake, 1999; Lankheet & Verstraten, 1995; Ling & Carrasco, 2006; T. Liu, Larsson, & Carrasco, 2007; but see Hudson, Schiff, Victor, & Purpura, 2009). However, little is known about whether and how adaptation modulates the effects of attention. The magnitude of the attention effect on contrast sensitivity does not vary with adaptation state (Pestilli et al., 2007). However, in a texture-segmentation task, adaptation to high but not low spatial frequencies diminished the effects of attention on performance (Carrasco, Loula, & Ho, 2006). Thus, the interaction of attention and adaptation effects on performance can differ. Furthermore, attention can alter performance without altering appearance (Fuller & Carrasco, 2006), so effects on performance and appearance do not necessarily covary.

Altered stimulus appearance is a well-known consequence of both adaptation and attention, yet no researchers have investigated the combined effects of adaptation and attention on appearance. In the experiments reported here, we tested how the interaction of adaptation and attention affects the appearance of a visual stimulus. We used speed perception as a "model system," because the neural basis of speed perception and the effects of adaptation and attention on speed perception in isolation are well understood.

Additive Versus Nonadditive Combinations of Attention and Adaptation

We combined attention with adaptation and measured perceived speed using the method of constant stimuli (Fig. 1). Observers judged the speed of two moving Gabor patterns—a test pattern and a standard pattern—while covert spatial attention was drawn to one of the stimuli by an uninformative, exogenous cue; the other stimulus was uncued (Fuller et al., 2009; Turatto et al., 2007). An adaptor moving at one of two speeds, slow or fast, preceded either the cued or the uncued stimulus. Observers reported which stimulus they perceived as
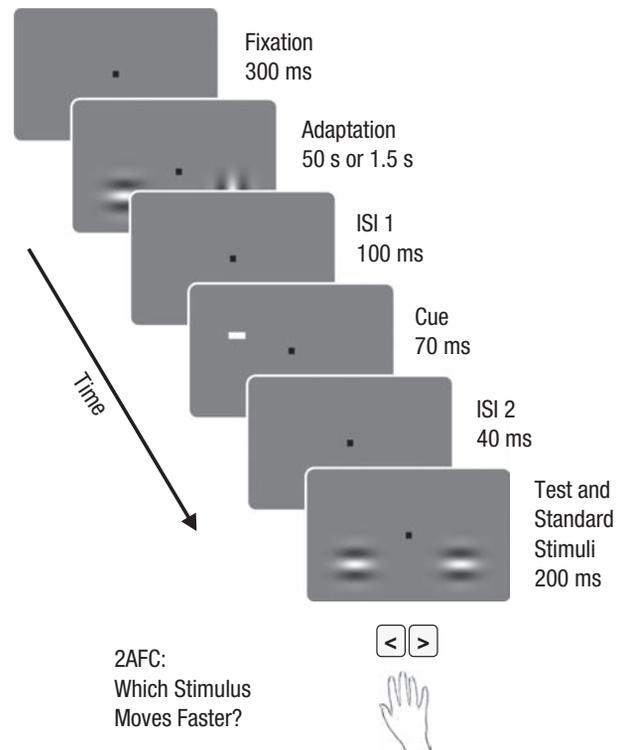

Fig. 1. Sample trial sequence in Experiment 1. After an initial fixation period, two Gabor patches were presented side by side in the lower half of the display. The grating in one patch (the adaptor) moved upward; the grating in the other patch (the control stimulus) moved rightward. In each block, these stimuli were presented for 50 s on the first trial and for 1.5 s on each subsequent trial. After an interstimulus interval (ISI), a cue was flashed either at fixation or, as shown here, 2.5° above the location of one of the previously presented Gabor patches. After another ISI, two new Gabor patches (the test and standard stimuli) were presented. The gratings of both patches moved upward, matching the adaptor. The speed of the standard stimulus was kept constant across trials, but the speed of the test stimulus varied across trials. In a two-alternative forced-choice (2AFC) task, observers reported either which stimulus was moving faster (Experiment 1) or which stimulus was moving slower (Experiment 2).

moving faster (Experiment 1) or which stimulus they perceived as moving slower (Experiment 2).

Figure 2 shows the predicted outcomes for additive and nonadditive effects. Throughout this article, we refer to a nonadditive combination as an interaction. Because the perceived speed of a stimulus is generally not greater after exposure to a slower adaptor (Smith, 1985; Thompson, 1981), we used a slow adaptor to measure a baseline attention effect. This allowed us to measure the magnitude of the attention effect with and without the influence of adaptation under the same conditions. The slow adaptor speed, which would yield no adaptation effect, was determined in preliminary testing. In this case, we predicted the point of subjective equality (PSE) in a neutral condition to be at the point of physical equality (PPE; equal test-stimulus and standard-stimulus speeds), independent of whether the location of the standard or the test stimulus was adapted (Fig. 2a). If attention increased perceived speed, cuing the test stimulus would lead observers to
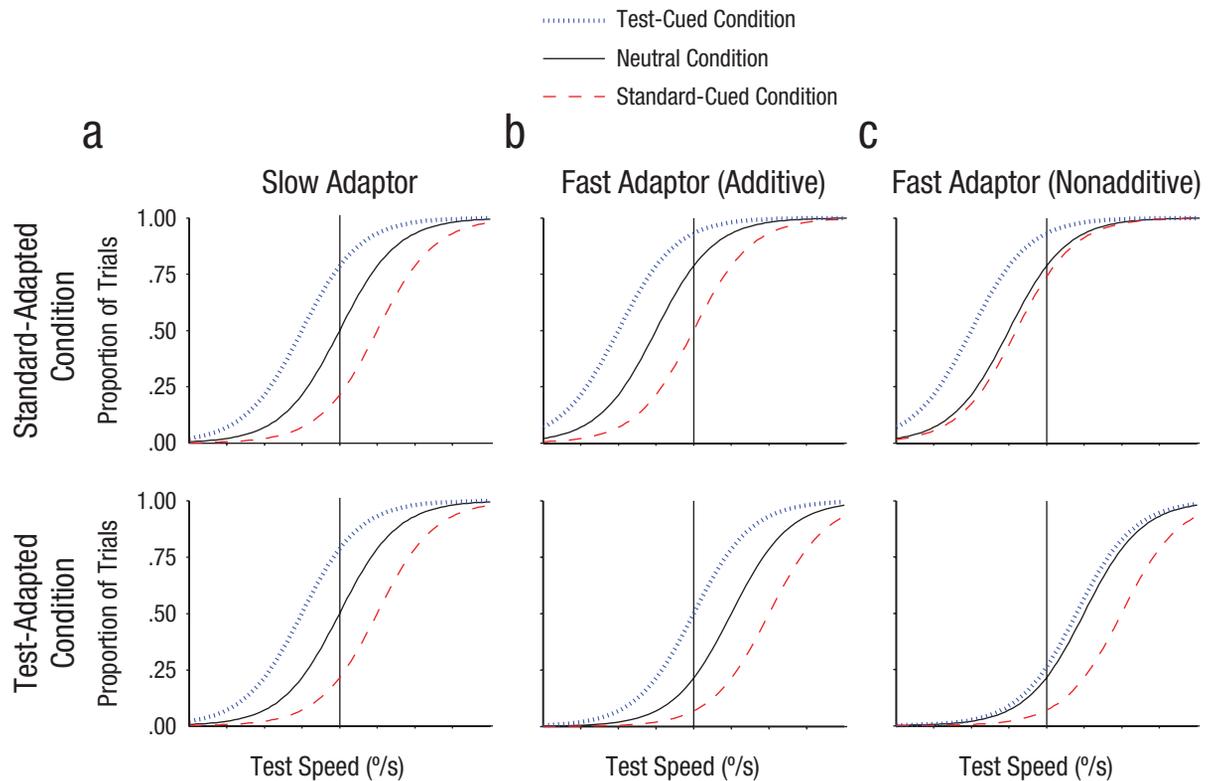
Fig. 2. Predicted proportion of trials in which observers would answer that the test stimulus was faster than the standard stimulus as a function of the test stimulus's speed and cuing condition. Predictions are shown for conditions of (a) a slow-moving adaptor and (b, c) a fast-moving adaptor. In the case of the fast-moving adaptor, predictions from both a model assuming additive effects and a model assuming nonadditive effects are shown. The top row shows predictions for trials on which the standard stimulus appeared at the same location as the adaptor; the bottom row shows predictions for trials on which the test stimulus appeared at the same location as the adaptor. The solid vertical lines mark the physical speed of the standard stimulus.

select it as faster than the standard stimulus more often, which would result in a leftward shift of the PSE: A physically slower test-stimulus speed would be perceived as equal to the standard-stimulus speed. Conversely, after cuing the standard stimulus, we expected the test stimulus to be selected as faster less often, which would result in a rightward shift of the PSE: A physically faster test-stimulus speed would be perceived as being equal to the standard-stimulus speed.

The fast adaptor was expected to decrease perceived stimulus speed (Smith, 1985; Thompson, 1981) and thus shift the neutral PSE to the left when the standard stimulus was adapted and to the right when the test stimulus was adapted (Figs. 2b and 2c). If adaptation and attention combined additively, attention would shift the PSE by the same amount as in the slow adaptor condition but relative to the shifted neutral PSE (Fig. 2b). Alternatively, if adaptation fatigued neuronal populations that mediate the attention effect, attention should not be able to exert its effect. In this case, adapting the standard location or the test location would reduce or cancel the effect of attention in the standard-cued condition or the test-cued condition, respectively (Fig. 2c).

Method

Observers

Eight observers (4 female, 4 male; mean age = 24.6 years, *SD* = 3.9) participated in Experiment 1, and 7 of the same observers participated in Experiment 2. Because the aim of these experiments was to investigate the interaction between adaptation and attention rather than to test the effect of attention per se, we selected observers who had a significant effect of attention on perceived speed in a preexperiment, in which we replicated the attention modulation of perceived speed (Fuller et al., 2009; Turatto et al., 2007). In Experiments 1 and 2, 4 observers, inexperienced in visual psychophysical tasks, were paid for their participation; the other 4 observers were lab members. All observers except 1 (one of the authors) were naive to the purpose of the study; all had normal or corrected-to-normal vision. Two observers in Experiment 1 and 1 observer in Experiment 2 were excluded from analysis because of large gaze deviations from fixation (> 1.5°; see Eye Positions in the Supplemental Material available online).

Apparatus

Experiments were performed in a dark room. Stimuli were presented on a calibrated, linearized CRT monitor (IBM P260, viewable area = 40 × 30 cm, resolution = 1 cm/° with 32 pixels/°, refresh rate = 85 Hz). Observers used a chin rest positioned 57 cm from the monitor. Experiments were run on an Apple Macintosh computer (iMac) using a custom MATLAB (The MathWorks, Natick, MA) script and the Psychophysics Toolbox extension (Brainard, 1997; Pelli, 1997). Eye positions were recorded using an infrared eye tracker (EyeLink CL, SR Research, Kanata, Ontario, Canada; see Eye Positions in the Supplemental Material).

Stimuli and procedure

Stimuli were presented on a gray background (~56 cd/m^2). Each trial started with the presentation of a dark (< 1 cd/m^2) fixation square (side length = 0.2°) at the center of the screen (Fig. 1). After 300 ms, an adaptor and a control stimulus were presented on opposite sides of the screen; each was 2° below and 5.5° to the left or right of fixation. The adaptor location (left or right) was constant within each block but alternated across blocks. The adaptor was a Gabor patch (1 cycle/°, Gaussian envelope of 1.24° diameter at half height, Michelson contrast = 60%) with its grating moving upward behind the Gaussian aperture at either 2.82°/s or 6.56°/s. The control stimulus was the same, but its grating moved rightward (i.e., orthogonal to the motion direction of the subsequent standard and test stimuli) to keep stimulation constant at both locations without influencing the perceived speed of the test or standard stimulus. In the first trial of each block, the adaptor stimulus and control stimulus were presented for 50 s; in each subsequent trial, they were presented for top-up adaptation for 1.5 s.

After an interstimulus interval (ISI) of 100 ms, a 70-ms stationary cue was flashed. This 0.3° × 0.7° cue was a bright (100% contrast) rectangle positioned 2.5° above the center of the test-stimulus location (test-cued condition), 2.5° above the center of the standard-stimulus location (standard-cued condition), or at the fixation point (neutral condition). After an ISI of 40 ms, test and standard stimuli were presented simultaneously for 200 ms at the same locations as the adaptor and control stimuli had been. The test and standard stimuli had the same characteristics, except for their speed. The standard stimulus's speed was 4.3°/s. The test stimulus's speed was randomly chosen from 7 to 13 levels, adjusted separately for each observer for each adaptation condition. The medium level corresponded to the PSE with five levels in the dynamic range of the psychometric function, defined as between the 10% and 90% threshold, in the corresponding adaptation condition in the training session. In the training session, the cue was always presented at fixation (neutral cue); the test stimulus's speed on each training trial was randomly chosen from 13 levels equally spaced around the standard stimulus's speed (logarithmic scale, 1.21–15.24°/s).

The locations of the cue, test, and standard stimuli were randomly and independently assigned on each trial. Thus, in a given trial, either the test or the standard stimulus could appear at the location where the adaptor had been presented (test-adapted and standard-adapted conditions, respectively) and could either be cued or not cued, so that all combinations of attention and adaptation conditions were counterbalanced.

Each observer completed 680 trials in a 1-hr training session and 2,720 or 3,400 trials of the main experiment in four or five 1-hr sessions. At the beginning of each block, observers received instructions on the screen, either "Please judge the stimuli in the second interval: Which stimulus moves faster?" (Experiment 1) or "Please judge the stimuli in the second interval: Which stimulus moves slower?" (Experiment 2). Observers pressed the left or right arrow key to indicate the left or the right stimulus, respectively (a two-alternative forced-choice, or 2AFC, paradigm). Observers were instructed to respond as accurately and quickly as possible, but response time was unlimited. Observers were instructed to maintain fixation throughout each trial, and the position of the right eye was recorded and analyzed off-line (see Eye Positions in the Supplemental Material). The New York University Institutional Review Board approved all procedures used in the experiment.

Results

Experiment 1

Figures 3a and 3b show the results for a representative observer. For each combination of adaptation speed, adaptation condition (standard adapted or test adapted), and cue condition, the proportion of trials in which the test stimulus was selected as faster was analyzed as a function of actual test speed. These data were fit with a logistic function to derive PSE and slope estimates using the psignifit toolbox (http://bootstrap-software.org/psignifit/), which implements the maximum-likelihood method described by Wichmann and Hill (2001). The mean R^2 was .96 (SD = ±.03) across all 12 conditions (2 adaptor speeds × 2 adaptation conditions × 3 cue conditions) for 6 observers (N = 72). For the slow adaptor speed, the PSE in the neutral condition did not differ from the PPE, either when the standard stimulus or the test stimulus was adapted. For the fast adaptor speed, the PSE in the neutral condition shifted away from the actual standard speed—to the left or to the right—when the standard or the test stimulus, respectively, was adapted. This finding is consistent with a decrease in perceived speed by adaptation. For both adaptor speeds, cuing the test-stimulus location shifted the PSE to the left of the neutral PSE, whereas cuing the standard-stimulus location shifted the PSE to the right of the neutral PSE, consistent with an increase in perceived speed by attention. These effects were consistent across observers for both adaptation (Fig. 3c) and attention (Fig. 3d).
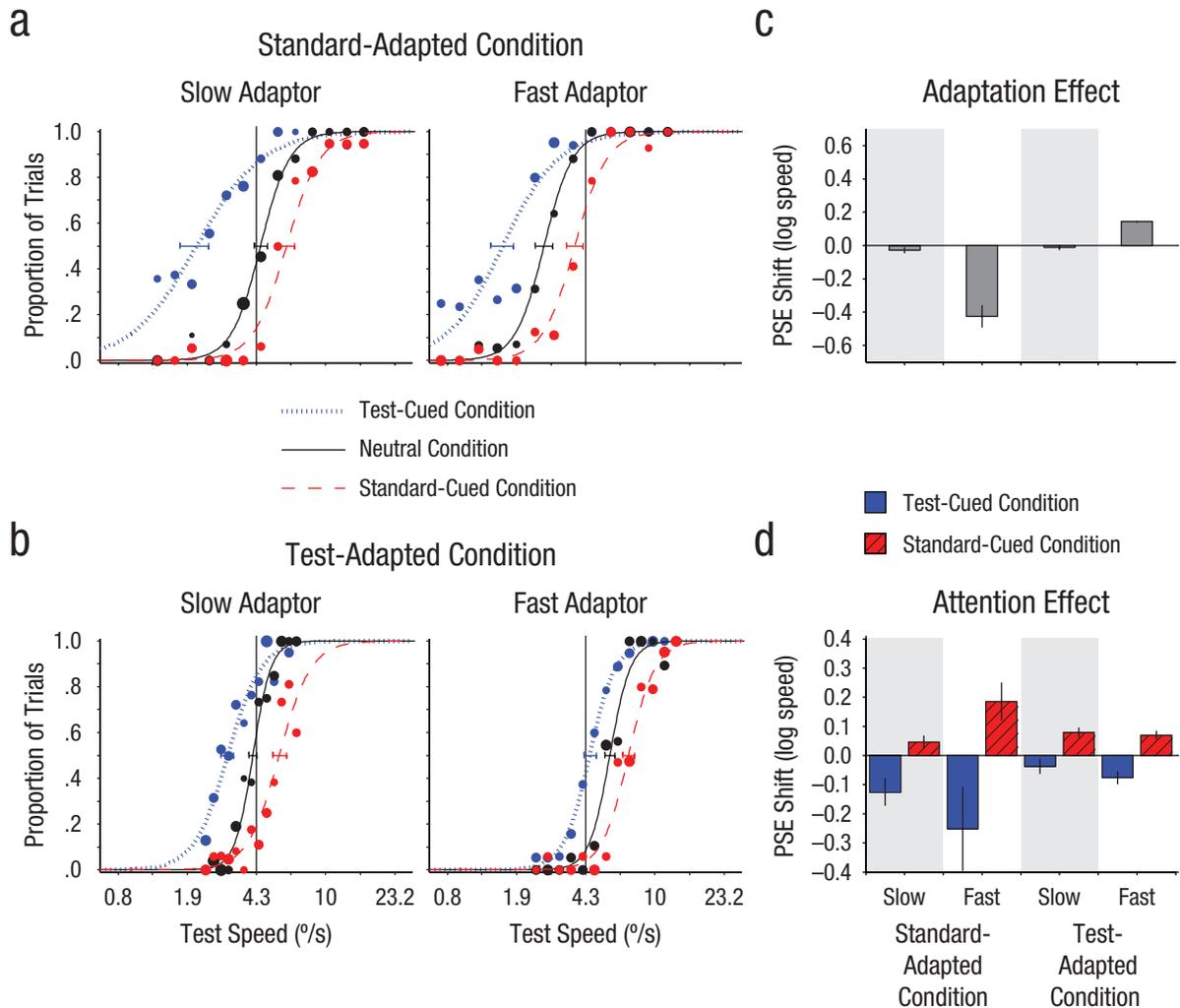
Fig. 3. Results from Experiment 1. The graphs in (a) and (b) show the proportion of trials on which a single observer reported the test stimulus as being faster than the standard stimulus as a function of the test stimulus's speed and cuing condition, separately for the slow and fast adaptors. The top row (a) shows results for trials on which the standard stimulus appeared at the same location as the adaptor; the bottom row (b) shows results for trials on which the test stimulus appeared at the same location as the adaptor. The size of the circles reflects the relative number of trials for each data point. The solid curves are best-fitting logistic functions. Error bars show 95% confidence intervals derived from bootstrapping. The solid vertical lines mark the physical speed of the standard stimulus. The bar graphs show (c) the average adaptation effect and (d) the average attention effect across observers ($n = 6$). In (c), the shift of the point of subjective equality (PSE) in the neutral condition relative to the physical speed of the standard stimulus is shown as a function of the adaptor speed and adaptation condition. In (d), the shift of the PSE in the test- and standard-cued conditions relative to the neutral condition is shown as a function of the adaptor speed and adaptation condition. Error bars show standard errors of the mean.

A three-way repeated measures analysis of variance (ANOVA; 2 adaptor speeds × 2 adaptation conditions × 3 cue conditions) on the PSE revealed main effects of adaptor speed, $F(1, 5) = 9.08$, $p < .05$, $\eta^2 = .65$, adaptation condition, $F(1, 5) = 65.87$, $p < .0001$, $\eta^2 = .93$, and cue condition, $F(1.06, 5.30) = 9.74$, $p < .05$, $\eta^2 = .66$.[1] Neither the three-way interaction, $F(1.08, 5.38) = 1.61$, $p > .1$, $\eta^2 = .24$, nor the interaction between adaptor speed and cue condition, $F(1.04, 5.22) = 1.57$, $p > .1$, $\eta^2 = .24$, was significant. There was a significant interaction between adaptor speed and adaptation condition, $F(1, 5) = 30.11$, $p < .005$, $\eta^2 = .85$; an adaptation effect was evident only

for the fast adaptor speed (Fig. 3c). There was a marginal interaction between adaptation condition and cue condition, $F(1.10, 5.49) = 4.19$, $p < .1$, $\eta^2 = .46$; the cue effect was more pronounced for the standard-adapted condition than the test-adapted condition (Fig. 3d).

Given that different predictions would be derived from a nonadditive-interaction hypothesis for trials in which the test location or the standard location had been adapted (Fig. 2c), we explored whether an interaction between adaptor speed and cue condition would emerge in either of these two cases. The interaction between adaptor speed and cue condition was

significant neither for the standard-adapted trials, $F(1.06, 5.28) = 1.58$, $\eta^2 = .24$, nor for the test-adapted trials, $F(1.05, 5.27) = 1.90$, $\eta^2 = .28$; both $ps > .1$.

Experiment 2

In principle, the effect of the cue in Experiment 1 could be explained by a bias of observers to select the cued stimulus. Such a response strategy would lead to the same shift of the psychometric function without implying a change in perceived speed. To control for response biases, we next performed an experiment in which observers reported the slower instead of the faster stimulus. If observers were biased to select the cued stimulus, we would expect them to select the cued stimulus more often, whether asked for the faster or for the slower stimulus. Such a bias would cause the PSE to shift in opposite directions for these two different instructions. In contrast, an attention increase in perceived speed would shift the PSE in the same direction independent of instruction. Thus, comparing the cue effect in these two tasks can be used to estimate the attention effect without any response-bias contribution (Anton-Erxleben et al., 2007; Carrasco et al., 2004; Fuller & Carrasco, 2006; Gobell & Carrasco, 2005; Ling & Carrasco, 2007; T. Liu et al., 2009; Montagna & Carrasco, 2006; Turatto et al., 2007).

Figures 4a and 4b show the results for a representative observer. Data were analyzed as in Experiment 1. The mean R^2 was .95 ($SD = \pm.06$) across all 12 conditions and 6 observers
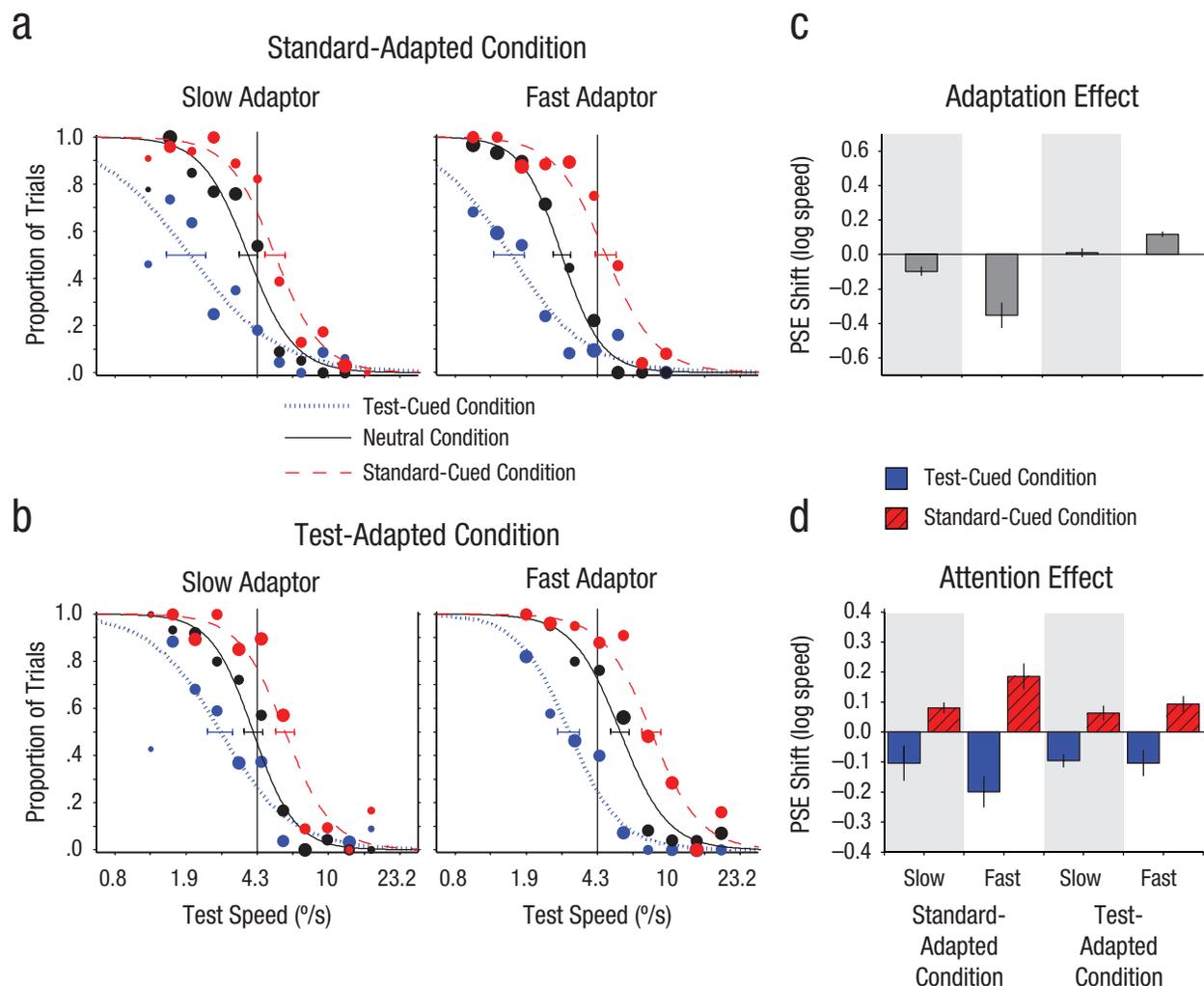

Fig. 4. Results from Experiment 2. The graphs in (a) and (b) show the proportion of trials on which a single observer reported the test stimulus as being slower than the standard stimulus as a function of the test stimulus's speed and cuing condition, separately for the slow and fast adaptors. The top row (a) shows results for trials on which the standard stimulus appeared at the same location as the adaptor; the bottom row (b) shows results for trials on which the test stimulus appeared at the same location as the adaptor. The size of the circles reflects the relative number of trials for each data point. The solid curves are best-fitting logistic functions. Error bars show 95% confidence intervals derived from bootstrapping. The solid vertical lines mark the physical speed of the standard stimulus. The bar graphs show (c) the average adaptation effect and (d) the average attention effect across observers ($n = 6$). In (c), the shift of the point of subjective equality (PSE) in the neutral condition relative to the physical speed of the standard stimulus is shown as a function of the adaptor speed and adaptation condition. In (d), the shift of the PSE in the test- and standard-cued conditions relative to the neutral condition is shown as a function of the adaptor speed and adaptation condition. Error bars show standard errors of the mean.

(N = 72). As in Experiment 1, the fast adaptor decreased perceived speed, but there was no evidence for an adaptation effect with the slow adaptor (Figs. 4a and 4c). For each adaptation condition, the cue shifted the PSE consistent with an increase in perceived speed by attention (Figs. 4a, 4b, and 4d).

A three-way repeated measures ANOVA (2 adaptor speeds × 2 adaptation conditions × 3 cue conditions) on the PSE revealed main effects of adaptation condition, $F(1, 5) = 23.89$, $p = .005$, $\eta^2 = .83$, and cue condition, $F(1.06, 5.32) = 29.84$, $p < .005$, $\eta^2 = .86$, but no main effect of adaptor speed, $F(1, 5) = 3.98$, $p > .1$, $\eta^2 = .44$. Neither the three-way interaction, $F(1.12, 5.61) = 1.48$, $p > .1$, $\eta^2 = .23$, nor the interaction between adaptor speed and cue condition, $F(1.11, 5.56) = 2.67$, $p > .1$, $\eta^2 = .35$, were significant. There was a significant interaction of adaptor speed and adaptation condition, $F(1, 5) = 14.67$, $p < .05$, $\eta^2 = .75$; an adaptation effect was only evident for the fast adaptor speed (Fig. 4c). There was also a significant interaction of adaptation condition and cue condition, $F(2, 10) = 4.23$, $p < .05$, $\eta^2 = .46$; the cue effect was more pronounced for the standard-adapted condition than for the test-adapted condition (Fig. 4d).

As in Experiment 1, we analyzed the interaction of adaptor speed and cue condition separately for standard-adapted and test-adapted trials. Again, the interaction between adaptor speed and cue condition was significant neither for standard-adapted trials, $F(1.06, 5.29) = 2.27$, $\eta^2 = .31$, nor for test-adapted trials, $F(2, 10) = 0.79$, $\eta^2 = .14$; both ps > .1.

To directly compare the magnitude of the attention effect between both experiments, we calculated the average shift between the standard-cued and test-cued PSE over all adaptation conditions for those observers whose data were included in both experiments. This average attention effect was not significantly different between the two experiments—two-tailed paired $t(4) = 0.57$, $p > .1$, Cohen's $d = 0.32$—which demonstrated that the cue effect cannot be explained by a response bias. (For the effects of adaptation and attention on the slopes of the psychometric functions, see Slope Analysis in the Supplemental Material.)

Discussion

The two experiments reported here showed that adaptation does not modulate the effect of attention on the perceived speed of a visual stimulus; this indicates, for the first time, that the effects of adaptation and attention on the appearance of stimulus features combine additively. In both experiments, the fast adaptor decreased perceived speed, whereas the slow adaptor had no effect on perceived speed. These findings are in line with the results of previous studies: Although, generally, adaptation to a particular stimulus feature shifts perception of similar stimulus features away from the adapted feature (Blakemore et al., 1970; Levinson & Sekuler, 1976); for speed, the effects can be asymmetric, so that speeds below the adaptor speed are further reduced, whereas higher speeds are not further increased (Smith, 1985; Thompson, 1981). Attention increased perceived speed, which is also consistent with

previous findings (Fuller et al., 2009; Turatto et al., 2007). Most important, the magnitude of this attention effect did not vary with adaptor speed. The additive combination of adaptation and attention could indicate that distinct neuronal populations or distinct mechanisms within the same population underlie each effect.

Which mechanisms mediate adaptation and attention effects on perceived speed?

The medial temporal (MT) area is a likely candidate for effects of adaptation and attention: Speed-selective cells are common in MT (Lingnau, Ashida, Wall, & Smith, 2009; J. Liu & Newsome, 2003; Priebe, Cassanello, & Lisberger, 2003), and the perception of speed is related to the firing of MT neurons (J. Liu & Newsome, 2005). Several computational models explain how perception of stimulus speed can be derived from population activity (for a review, see Burr & Thompson, 2011).

Changes in perception after adaptation have been associated with shifts in neuronal selectivity (Jin et al., 2005; Krekelberg et al., 2006; Levinson & Sekuler, 1976). Covert spatial attention is generally associated with enhanced neuronal activity (Beck & Kastner, 2009; Martinez-Trujillo & Treue, 2002; Reynolds, Pasternak, & Desimone, 2000; Williford & Maunsell, 2006). In a labeled-line framework, modulation of perceived speed is likely to involve a shift instead of a mere increase in neuronal population responses: Specifically, an increase of apparent speed might be correlated with enhanced activity in neuronal populations, which are tuned to a higher speed, or a relative decrease of activity of neurons preferring a lower speed. Similarly, attention has been suggested to modulate perceived spatial frequency (Abrams et al., 2010; Gobell & Carrasco, 2005) or perceived flicker rate (Montagna & Carrasco, 2006) by selectively changing the sensitivity of particular spatial-frequency channels or temporal-frequency channels, respectively, and thereby reweighting the population response.

The Bayesian model assumes that perceived speed is the product of a likelihood distribution, centered at the true stimulus speed, and a prior distribution, centered at zero speed, which biases perception toward slower speeds depending on signal strength (Weiss, Simoncelli, & Adelson, 2002). Neuronal populations can represent likelihoods by noisy spiking activity (Ma, Beck, Latham, & Pouget, 2006) and priors by the distribution of neurons' selectivity and tuning width according to the frequency with which certain stimulus properties are encountered in the environment (Ganguli & Simoncelli, 2010). A Bayesian decoder can combine prior and likelihood to get an estimate of the stimulus by computing a weighted average of preferred stimuli (Ganguli & Simoncelli, 2012), similar to vector-averaging mechanisms often employed in labeled-line models. The Bayesian model can explain the increase in perceived speed at higher contrasts and could explain the increase of perceived speed with attention: Given that attention has

been shown to enhance the stimulus representation (Carrasco, 2011; Reynolds & Chelazzi, 2004; Treue, 2003), from a Bayesian viewpoint, attention might enhance the signal-to-noise ratio of neurons tuned to the stimulus's speed by increasing their gain, so that perception is shifted away from a zero-motion prior. Thus, the labeled-line and the Bayesian frameworks that have been developed to account for speed perception in other contexts could also explain the effect of attention on perceived speed.

Interaction of adaptation and attention effects

In previous studies, researchers have investigated how attention affects the adaptation process (Alais & Blake, 1999; Hudson et al., 2009; Lankheet & Verstraten, 1995; Ling & Carrasco, 2006; T. Liu et al., 2007). However, only three studies have investigated how adaptation affects subsequent effects of attention on performance; these studies have revealed additive (Pestilli et al., 2007) and nonadditive effects (Barbot, Montagna, & Carrasco, 2011; Carrasco, Loula, & Ho, 2006) in different visual domains.

The present study is the first to investigate the interaction of adaptation and attention effects on appearance. By manipulating attention during different adaptation states, we found that adaptation and attention affect appearance independently. Thus, consistent with the contrast-sensitivity study (Pestilli et al., 2007), we provided converging behavioral evidence that adaptation is not merely a neuronal fatigue effect: If neuronal responses in the adapted state were saturated because of fatigue, attention should not be able to restore contrast sensitivity or perceived speed. Rather, it seems that attention can "reset" the system when adaptation is present: Here, adapting the standard stimulus's location shifted perception away from the physical speed of the standard stimulus, whereas allocating attention to the standard stimulus shifted perception back toward the physical speed of the standard stimulus (Figs. 3a and 4a). When the test stimulus's location was adapted, attention on the test stimulus shifted the PSE back to the test speed that was physically equal to the standard speed (Figs. 3b and 4b). Both of these effects are consistent with attention restoring the base-level speed perception after adaptation. Note, however, that this does not imply that attention leads to veridical perception: Without adaptation, attention leads to speed overestimation.

In contrast, the effects of adaptation on spatial resolution are more consistent with a fatigue explanation: In a texture-segmentation task, performance is determined by the proportional activation of low- and high-spatial-frequency filters. After adaptation to a high-spatial-frequency pattern, both performance and the attention effects on performance are modulated in accordance with a decreased availability of high-spatial-frequency filters, which suggests that attention enhances spatial resolution by shifting population sensitivity toward higher spatial frequencies (Barbot et al., 2011; Carrasco, Loula, & Ho, 2006).

Conclusion

In these two experiments, we showed, for the first time, that adaptation does not alter the effect of attention on perceived speed. Given that for spatial frequency, adaptation and attention effects on performance were not independent, it would be interesting in future studies to investigate how the adaptation state modulates the attention effect on spatial-frequency appearance. In line with previous research, our findings support the view that adaptation is not simply a neuronal fatigue effect. Instead, attention can "reset" the system in a dynamic fashion. Both adaptation and attention lead to relatively short-term plastic changes by which the visual system adjusts to current environmental demands related either to sensory history or to behavioral relevance, thereby prioritizing important over unimportant information. The finding that the effect of attention on perceived speed is not modulated by the adaptation state reveals independent effects of adaptation and attention, two adaptive mechanisms that help people allocate limited resources.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

Supplemental Material

Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

Note

1. In all cases in which Mauchly's test of sphericity indicated a violation of the assumption of sphericity, we report Greenhouse-Geisser-corrected *p* values.

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