

Apparent speed and speed sensitivity during adaptation to motion

Peter J. Bex

Department of Psychology, University of Essex, Wivenhoe Park, Colchester, Essex C04 3SQ, UK

Samantha Bedingham and Stephen T. Hammett

Department of Psychology, University of Glasgow, 58 Hillhead Street, Glasgow G12 8QF, UK

Received December 17, 1998; revised manuscript received May 3, 1999; accepted June 28, 1999

Adaptation, a change in response to a sustained stimulus, can be demonstrated in motion perception by velocity aftereffects—changes in the apparent speed of a moving pattern following adaptation. We measured changes in the apparent speed of sinusoidal gratings drifting at 4 or 7.5 deg/s during 30 s of adaptation followed by 30 s of recovery. The apparent speed of the patterns fell to approximately half the unadapted apparent speed, and the time constants of adaptation were much faster (5 s) than for recovery (22 s). Part of the loss of apparent speed (approximately 12%) was related to a loss of apparent contrast with adaptation. Sensitivity to speed increments and speed decrements increased during adaptation and was well described by a Weber fraction based on apparent speed. The results suggest that adaptation to motion, like light adaptation, may serve to improve an observer's sensitivity to the prevailing environment. © 1999 Optical Society of America [S0740-3232(99)00612-2]

OCIS codes: 330.4150, 330.5510, 330.6790, 330.7320, 330.7310, 330.5020.

1. INTRODUCTION

After prolonged inspection of a moving pattern, a subsequently viewed static image can appear to move in the opposite direction to that of the adapting pattern. This phenomenon is called the motion aftereffect (MAE) and has been studied in considerable detail (for a review see Refs. 1 and 2). A somewhat less-well-studied phenomenon that can occur following adaptation to motion concerns a change in the apparent speed of a subsequently viewed moving pattern. This was first reported by Wohlgenuth,³ who showed that the apparent speed of a drifting black-and-white-striped belt was reduced following 30 s of adaptation. This effect is now known as the velocity aftereffect⁴ (VAE) and has been confirmed with several psychophysical techniques, including magnitude estimation,^{5–7} speed matching,^{4,8–12} and estimation of the time that it would take for a line to travel a particular distance.¹³

Many studies of VAE's have investigated combinations of adaptation and test speeds, directions, and contrasts. Several authors have reported that perceived velocity is reduced following adaptation to a stimulus moving faster than, and in the same direction as that of, the target.^{4,7–9,11,13} Adaptation to a pattern moving more slowly than, and in the same direction as that of, the test stimulus has been found to result in an increase in perceived speed for rotary patterns⁷ but no change or a small decrease for drifting vertical gratings.⁸ When adaptation is in the direction opposite to that of the target, perceived velocity has been reported to increase,¹⁴ to be variably affected,⁷ or to decrease,⁸ but only if the adaptation pattern moves as fast as or faster than the test pattern.⁹ Smith and Edgar¹⁰ have modeled this complex collection

of results with a ratio model of motion processing.¹⁵ The model is based on the antagonistic comparison of two temporal channels, one low pass and the second bandpass^{16–21} (cf. alternative results implicating three temporal channels^{22,23}). To account for both increases and decreases in apparent speed that can occur under certain conditions, the model assumes that the bandpass channel is more adaptable than the low-pass channel.

Psychophysical studies of the time course of motion adaptation and recovery from adaptation have concentrated on the conventional MAE. While there is some evidence of MAE's lasting up to three days for spiral patterns,²⁴ most studies of the time course of the MAE (Refs. 25–29) and the VAE (Ref. 12) have found much shorter time constants that are well fitted by exponential functions. The exponential buildup and decay of adaptation to motion compares well with physiological measures of neural response changes in area 17 of cats^{30–33} and in area H1 of flies.³⁴ Giaschi *et al.*³³ also recorded recovery rates, finding them to be somewhat slower than adaptation rates (approximately 8 s compared with 5 s). They also found an initial rapid decline in response rate, followed by a much slower steady decline that was best fitted by combined fast and slow exponential functions.

The aim of the present investigation was to measure the changes in apparent velocity of medium-speed and high-speed drifting sine-wave gratings during a 30-s adaptation period and the subsequent recovery of normal apparent speed. Recently, Clifford and Langley¹² measured sensitivity to sinusoidal oscillations in speed during speed adaptation. They found that subjects were able to detect oscillations after a few seconds of adaptation that they were unable to detect at the beginning of the adap-

tation period. We sought to confirm this result and to relate any changes in speed sensitivity to changes in apparent speed.

2. METHODS

One of the authors (PB) and a paid, naive volunteer (RW) served as observers. Stimuli were generated on a Macintosh 8600/200 using software adapted from the VideoToolbox routines³⁵ and were displayed on an Eizo Flexscan 6600 gray-scale monitor at a frame rate of 120 Hz and mean luminance (L_0) of 50 cd/m². The luminance of the display was linearized with pseudo-12-bit resolution³⁶ and calibrated with an OptiCal photometer. Pseudo-12-bit resolution in this case allowed the presentation of 2⁸ gray levels from a possible range of 2¹² levels. The display measured 20 cm horizontally (640 pixels) and 15 cm vertically (480 pixels) and was in a dark room 57 cm from the observer.

Stimuli in all cases were horizontal sinusoidal gratings [2 cycles per degree (c/deg)] drifting within stationary Gaussian windows ($\sigma_{x,y} = 1$ deg):

$$L_{(x,y)} = L_0 \{1 + C \exp[-(x^2 + y^2)/2\sigma^2] \sin(2\pi x/\lambda)\}, \quad (1)$$

centered at 2° to the left or the right of a central, black fixation cross.

A. Procedure

Each run consisted of 16 sessions, where each session was a 30-s adaptation period followed by a 30-s recovery period. There was a match interval every 3 s throughout adaptation and recovery. The adapting pattern was presented continuously throughout the adapting period, then for 1 s every 3 s throughout the recovery period. The match pattern was presented for 1 s every 3 s throughout the adaptation and recovery periods. The temporal frequency of the adapting pattern was 8 or 15 Hz (4 or 7.5 deg/s), and its location (left or right of fixation) and direction of motion (up/down) were randomized across sessions. The starting phases of the adapting and match gratings were randomized. The match pattern was presented on the opposite side of fixation to the adapting pattern, and its direction of movement was randomized from trial to trial to minimize the buildup of adaptation to the match pattern itself. The speed of the match pattern on any trial was controlled by an independent QUEST staircase.³⁷ There were 20 independent QUEST staircases, one for every test interval. Each QUEST was initialized with a random starting point and concentrated observations near the point of subjective speed equality for each match interval. The observer's task was to maintain steady fixation throughout each session and, following each match interval, to indicate whether the pattern to the left or the right of fixation had been moving faster. The observer was allowed a rest period of not less than 1 min between sessions before proceeding to the next adaptation and recovery session in the run. At least four but typically eight runs of 16 trials each were made for each condition, and all conditions were randomly interleaved.

B. Experiment 1: Apparent Speed Changes in Adaptation and Recovery

Figure 1 shows a typical psychometric function for the naive observer (RW) for speed matches of a 15-Hz standard at 21 s (out of 30 s) into the adaptation period; error bars show the binomial standard deviations. The binomial distribution is approximately normally distributed for large samples, and its standard deviation for each data point was estimated with standard methods³⁸ at

$$\pm(pq/n)^{0.5} + (1/2n), \quad (2)$$

where p = proportion correct, $r = 1 -$ proportion correct, and $1/2n$ = correction for continuity.

The raw data have been fitted (solid curve) by a cumulative normal function by a least χ^2 fit; dashed curves show the upper and lower 95% confidence fits, estimated with standard methods.³⁹ The match speed was taken as the speed at which observers indicated that the adapting pattern was faster on 50% of trials. For each observer 20 similar psychometric functions were collected at 3-s intervals throughout each run: ten during adaptation and ten during recovery.

Figure 2 shows speed matches (in log Hz) at 3-s intervals throughout the run for two observers [PB, Fig. 2(a); RW, Fig. 2(b)] for two standard speeds, 15 Hz (squares) and 8 Hz (circles). Error bars show 95% confidence intervals. The data have been fitted by exponential functions by a least-squares fit, weighted by the 95% confidence intervals. The exponential functions have the following form:

Adaptation:

$$(Sa) + (S - Sa)\exp(-t/\tau), \quad (3)$$

Recovery:

$$S - (S - Sa)\exp(-t/\tau), \quad (4)$$

where S is standard speed, a is proportion of speed attenuation, t is time in seconds, and τ is time constant of the exponential function for adaptation and recovery.

The adaptation functions are shown by the black curves, and the recovery functions are shown by the gray

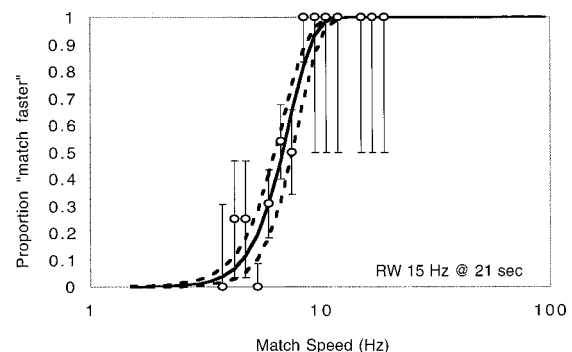


Fig. 1. Typical psychometric function for speed matching. The data are for the naive observer after 21 s of adaptation to a standard grating drifting at 15 Hz. The x axis shows the speed of the match pattern, and the y axis shows the proportion of observations in which the match appeared faster. Error bars show binomial standard deviations. The solid curve shows the best-fitting cumulative normal function, and the dashed curves show the upper and lower 95% confidence limits to the fit.

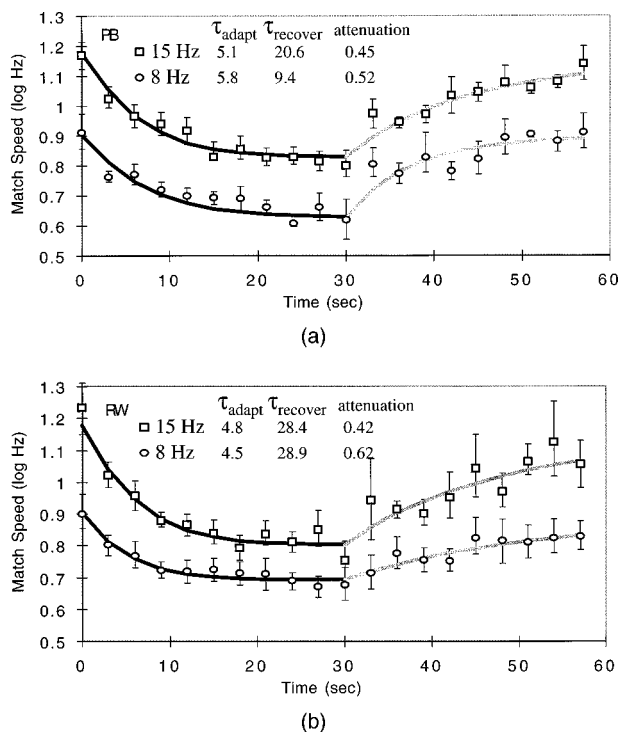


Fig. 2. Apparent speed as a function of adaptation and recovery duration for 8-Hz (circles) and 15-Hz (squares) adapting gratings for (a) one of the authors (PB) and (b) a naive observer (RW). The physical contrast of standard and match gratings was equal (50%). The observer adapted to continuous motion for the first 30 s and then recovered for 30 s; apparent speed matches were measured at 3-s intervals throughout. Error bars show 95% confidence intervals. The data have been fitted by exponential functions: black curves for adaptation and gray curves for recovery. The time constants and the proportions of attenuation for each function are also shown.

curves. The results show that the apparent speed of the adapting pattern slowed exponentially during adaptation with a time constant of approximately 5–6 s (mean = 5 s). Recovery was much slower, taking approximately 9–29 s (mean = 22 s). The magnitude of attenuation was slightly greater at 15 Hz, where adapted apparent speed fell to 44% of unadapted apparent speed (mean across observers), than at 8 Hz, where adapted apparent speed fell to 57% of unadapted levels.

C. Experiment 2: Apparent Contrast Changes in Adaptation and Recovery

Several researchers have shown that the apparent contrast of temporally modulated gratings can decrease with adaptation,^{40–42} the magnitude and the rate of contrast attenuation depending on the spatial frequency, the temporal frequency, and the contrast of the adapting pattern.⁴² It is also known that the apparent speed of slowly drifting gratings depends on contrast,^{43–45} although the results are inconclusive at higher temporal frequencies. While some studies report that apparent speed increases with contrast for temporal frequencies up to 10 Hz for 2- and 3-c/deg gratings,^{43,44} others report that apparent speed is invariant of contrast at 8 Hz for 1-c/deg gratings⁴⁵ and that the relationship reverses at 16 Hz for 1–8-c/deg gratings.^{43,44} It is therefore possible that a change in the apparent contrast of the adapting pattern

could contribute to its change in apparent speed. In experiments 2 and 3, we measured the contribution of the change in apparent contrast to the change in apparent speed during adaptation. The change in apparent contrast during adaptation and recovery was measured in experiment 2.

Stimuli and procedure were as in experiment 1, except that the adapting and match speeds were equal and the observer was required to indicate the pattern of higher contrast. The temporal frequencies of the adapting and match gratings were equal (8 or 15 Hz) throughout the 30-s adaptation and recovery periods. The contrast of the adapting grating was fixed (50%), and the contrast of the match grating for each matching interval was varied according to an independent QUEST staircase. Figure 3 shows the change in apparent contrast during a 30-s adaptation period followed by a 30-s recovery period, and the results are presented in the same format as that of the speed-matching results shown in Fig. 2. Adaptation contrast matches are again fitted by black curves, and recovery contrast matches are fitted by gray curves with functions of the form shown in expressions (3) and (4). The results show that the apparent contrast of the adapting grating decreased exponentially during adaptation, to approximately 70% of the physical contrast (mean

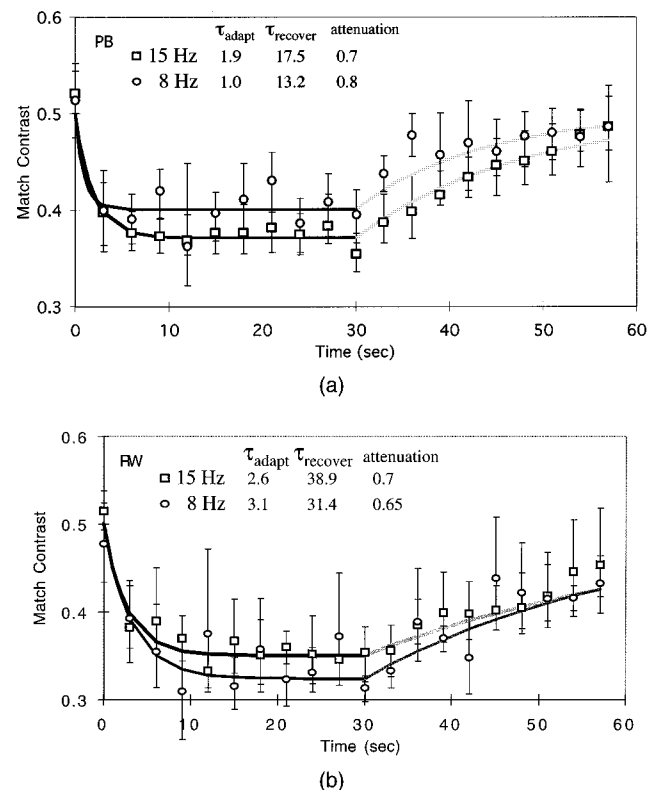


Fig. 3. Apparent contrast as a function of adaptation and recovery duration for 8-Hz (circles) and 15-Hz (squares) adapting gratings for (a) one of the authors (PB) and (b) a naive observer (RW). The speed of standard and match gratings was equal. The observer adapted to continuous motion for the first 30 s and then recovered for 30 s; apparent contrast matches were measured at 3-s intervals throughout. Error bars show 95% confidence intervals. The data have been fitted by exponential functions: black curves for adaptation and gray curves for recovery. The time constants and the proportions of attenuation for each function are also shown.

= 71.3%) with a time constant of approximately 1–3 s (mean = 2.2 s). Recovery was slower than adaptation with a time constant of between 13 and 39 s (mean = 25.3 s). Although there was little difference between the observers in the magnitude of contrast attenuation, there was greater variability in the time courses of adaptation and especially of recovery. The adaptation results are in very good agreement with similar conditions in a previous study of apparent contrast during adaptation for counterphase flickering gratings.⁴²

D. Experiment 3: Speed Matching II: Perceived Contrast Equated

The results of experiment 2 show the changes in apparent contrast for drifting gratings during 30 s of adaptation and recovery. In experiment 3 we repeated the speed-matching task of experiment 1 but simultaneously varied the *physical* contrast of the match grating so that their *apparent* contrasts were equal. The procedure was as in experiment 1, except that the contrast and the speed of the match grating were varied from trial to trial. The physical contrast of the adapting grating was fixed throughout all runs (at 50%, although its apparent contrast varied; see experiment 2). The physical contrast of the match grating was varied according to the best-fitting function (as shown in Fig. 3) that equated its apparent contrast to that of the adapting grating, and its speed was varied according to an independent QUEST staircase for each matching interval.

Figure 4 shows the change in apparent speed of a 15- and an 8-Hz drifting grating during a 30-s adaptation period followed by a 30-s recovery period for two observers [PB, Fig. 2(a); RW, Fig. 2(b)]. The results are presented in the same format as that of the speed-matching results shown in Fig. 2. For comparison, the best-fitting functions of the basic speed-matching task (physical contrast equated) are replotted from Fig. 2 as dashed curves. Adaptation contrast matches are again fitted by black curves, and recovery contrast matches are fitted by gray curves with functions of the form shown in expressions (3) and (4). The results show that the apparent speed of the adapting grating decreases exponentially during adaptation with a time constant of approximately 4–5 s (mean = 4.2 s). Recovery is once again slower than adaptation, with a time constant of between 9 and 24 s (mean = 17.3 s). The time constants of adaptation and recovery are similar to those recorded with physical contrast equated.

As in experiment 1, the magnitude of attenuation was slightly greater at 15 Hz than at 8 Hz. At 15 Hz, adapted apparent speed fell to 52% of unadapted apparent speed (compared with 44% in experiment 1), and so equating apparent contrast reduced the loss of apparent speed by 8%. At 15 Hz, adapted apparent speed fell to 72% of unadapted apparent speed (compared with 57% in experiment 1), and so equating apparent contrast reduced the loss of apparent speed by 15%. These results show that part of the loss of apparent speed is evidently attributable to a loss of apparent contrast, but there is a sizable speed loss that persists when this contrast-related speed change is eliminated.

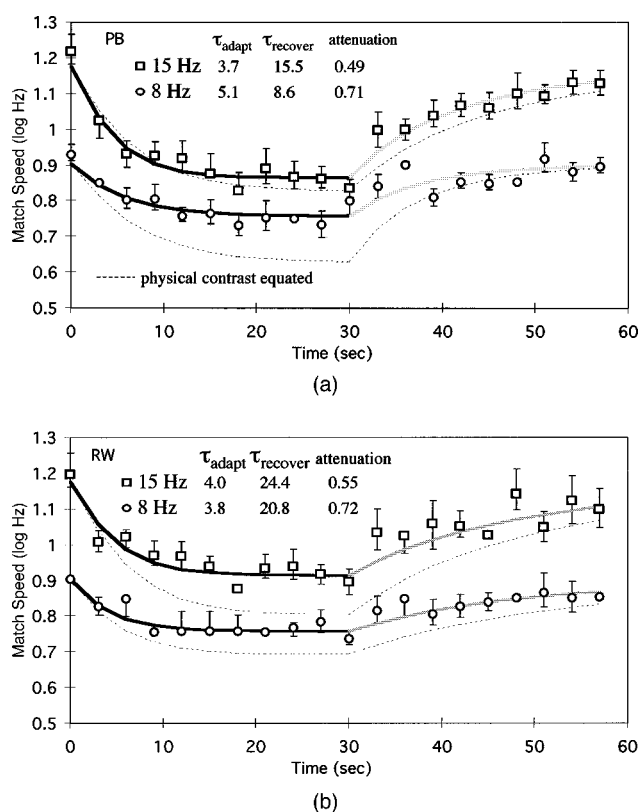


Fig. 4. Apparent speed as a function of adaptation and recovery duration for 8-Hz (circles) and 15-Hz (squares) adapting gratings for (a) one of the authors (PB) and (b) a naive observer (RW). The contrast of the standard grating was 50%, and the contrast of the match grating was varied (according to the function measured in experiment 3), so that it matched the *apparent* contrast of the standard. The observer adapted to continuous motion of the standard for the first 30 s and then recovered for 30 s; apparent speed matches were measured at 3-s intervals throughout. The data are plotted as in Fig. 2. Dashed curves show the data replotted from Fig. 2 for comparison.

E. Experiment 4: Speed Sensitivity in Adaptation and Recovery

The results of experiments 1–3 show that apparent speed decreases exponentially during adaptation and slowly returns to unadapted levels during recovery. In experiment 4 we measured changes in sensitivity to speed increments and decrements throughout the adaptation and recovery periods and compared Weber fractions for speed increments based on physical and apparent speed. Stimuli and procedure were similar to those of experiment 1, except that two adapting patterns were present throughout the adapting period and for 1 s every 3 s throughout the recovery period. As above, the patterns moved at 8 or 15 Hz and were 2 deg to the left and the right of the central fixation cross. The direction of motion of both patterns was fixed throughout each adaptation and recovery period but was randomized across the periods. Observers reported that it was easier to maintain steady fixation when the patterns moved in opposite directions on either side of fixation, and so we incorporated this constraint. This spatial configuration ($\uparrow + \downarrow$ or $\downarrow + \uparrow$) gave the appearance of rotational or shearing motion, and it has been shown that rotational configurations of motion can lead to elevated adaptation effects for

conventional MAE's.⁴⁶ However, control data for the experienced observer (PB) in the present task were unaffected by this constraint.

There was a test interval every 3 s throughout a session. During the test interval, one of the patterns (at random) increased in speed, then returned to the baseline adapting speed (8 or 15 Hz). To avoid temporal artifacts arising from abrupt speed changes, we smoothed the speed change within a Gaussian envelope with a standard deviation of 32 frames (27 ms). The observer was notified that a test interval was in progress because the fixation cross was switched to white, then back to black again at the end of the test interval. This signaled the observer to respond (with a button press) whether the pattern on the left or the right of fixation had changed speed. The size of the speed increment on any trial was varied from trial to trial according to an independent QUEST procedure that concentrated observations near a threshold of 75% correct for each testing interval.

Figure 5 shows a typical psychometric function for the naive observer (RW) for speed increment detection for a 15-Hz adapting pattern at 21 s (out of 30 s) into the adaptation period. The raw data have been fitted (solid curve) by a cumulative normal function by a least χ^2 fit, dashed curves show the upper and lower 95% confidence fits, and error bars show the binomial standard deviations. The speed increment threshold was taken as the speed at which observers identified the faster pattern on 75% of trials. For each observer 20 similar psychometric functions were collected at 3-s intervals throughout each run: ten during adaptation and ten during recovery.

Figure 6 shows speed increment thresholds at 3-s intervals throughout the run for two observers [PB, Fig. 6(a); RW, Fig. 6(b)] for two standard speeds, 15 and 8 Hz. Error bars show 95% confidence intervals. The data have been fitted by Weber fractions based on the apparent speed estimates for each observer, as shown in Fig. 2. The basic Weber fraction [expression (5): the lower threshold of motion, σ , plus a proportion of speed, k_1] provided an adequate fit to the data. However, superior fits were obtained with the addition of a second quadratic term [Eq. (6) below, where σ and k_1 are unchanged but a proportion of speed squared, k_2 , was included]:

$$\Delta v_{\text{thresh}} = \sigma + k_1 S_a, \quad (5)$$

$$\Delta v_{\text{thresh}} = \sigma + k_1 S_a + k_2 S_a^2, \quad (6)$$

where S_a = apparent speed, k_1 = standard Weber fraction, k_2 = quadratic term, and σ = lower threshold of motion.

For further comparisons between these Weber fractions for speed increments, see Fig. 1 of Simpson *et al.*⁴⁷ It can be seen that the data are well fitted by the predicted increment threshold from Weber's law based on apparent speed. Weber's law based on physical speed is a flat function that does not describe the data very well. For observer PB's speed increments, the best-fitting parameters for k_1 , k_2 , and σ were, respectively, 0.083, 0.012, and 0.039, and for observer RW they were 0.136 and 0.008 for k_1 and k_2 , and σ tended to 0. These param-

eters are higher than estimates of Weber fractions for speed in unadapted conditions, but this is perhaps not surprising given that speed change was smoothed in a Gaussian envelope in the present task. In adapted conditions, detection of speed oscillations approaches 100% correct for 16%–20% modulations¹² and are in broad agreement with our 75% thresholds of 8%–14% speed change.

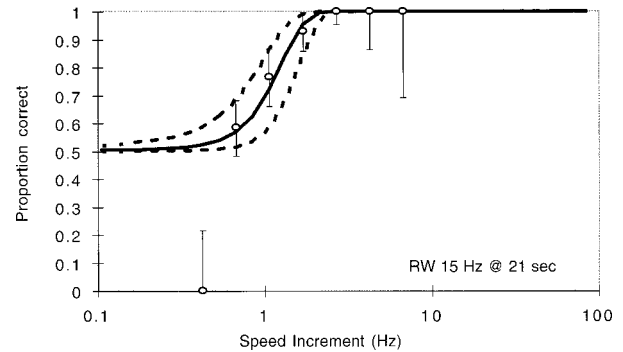


Fig. 5. Typical psychometric function for speed increment detection. The data are for the naive observer after 21 s of adaptation to a standard grating drifting at 15 Hz. The x axis shows the speed increment (Δv), and the y axis shows the proportion of observations in which the match appeared faster. Error bars show binomial standard deviations. The solid curve shows the best-fitting cumulative normal function, and the dashed curves show the upper and lower 95% confidence limits to the fit.

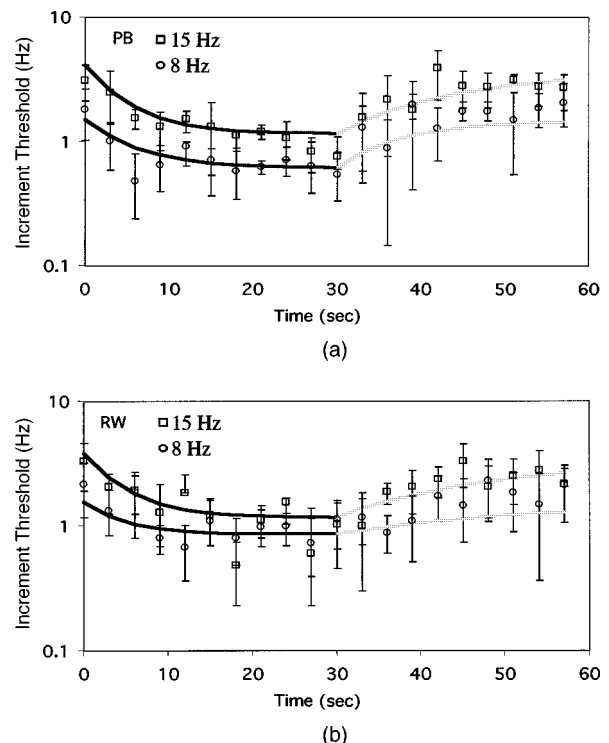


Fig. 6. Speed increment sensitivity as a function of adaptation and recovery duration for 8-Hz (circles) and 15-Hz (squares) adapting gratings for (a) one of the authors (PB) and (b) a naive observer (RW). Observers adapted to continuous motion for the first 30 s and then recovered for 30 s; speed increment sensitivity was measured at 3-s intervals throughout. Error bars show 95% confidence intervals. The data have been fitted by Weber fractions based on the apparent speed measured in experiment 2: black curves for adaptation and gray curves for recovery.

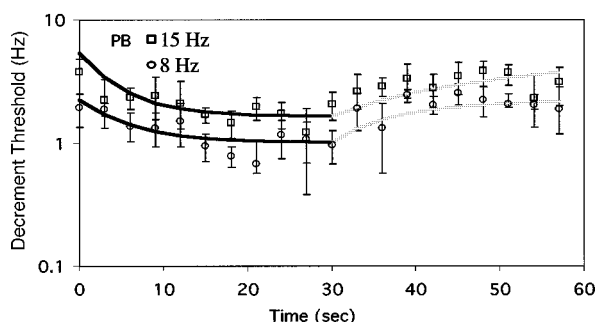


Fig. 7. Speed decrement sensitivity as a function of adaptation and recovery duration for 8-Hz (circles) and 15-Hz (squares) adapting gratings for one of the authors (PB). Data are plotted as in Fig. 6: black curves for adaptation and gray curves for recovery.

Figure 7 shows speed decrement thresholds at 3-s intervals throughout the run for observer PB at two adapting speeds, 8 and 15 Hz. Error bars show 95% confidence intervals. Once again the data are well fitted by the Weber function based on perceived speed. The best-fitting parameters for k_1 and k_2 were 0.19 and 0.011, and σ tended to 0. For both adapting speeds, decrement thresholds were higher than increment thresholds. We do not know why the observer is less sensitive to speed decrements.

3. DISCUSSION

A. Time Course of Speed Adaptation and Recovery

Adaptation, a change in response to a sustained stimulus, can be demonstrated in motion perception by the illusory motion of a static pattern [the motion aftereffect (MAE)] and by changes in the apparent speed of moving patterns [the velocity aftereffect (VAE)]. The magnitude and the time course of these aftereffects depend on the combination of adapting and test stimuli as well as the method employed to measure them (for a review see Refs. 1 and 2). Experiment 1 confirms the classic observation that the apparent speed of a drifting pattern is reduced during adaptation.³ The reduction in apparent speed was exponential with a time constant of approximately 5 s under the present conditions, and the magnitude was slightly greater at higher adapting speeds. Recovery from motion adaptation was also exponential but was much slower, with a mean time constant of approximately 22 s.

The results compare favorably with previous psychophysical and physiological studies of VAE's. For adapting gratings of somewhat lower spatial and temporal frequency (0.75 c/deg and 6.25 Hz), Clifford and Langley¹² reported slightly faster time constants of approximately 3 s, with adapted apparent speed falling to approximately only 75%–80% of unadapted apparent speed, compared with 38%–58% in the present conditions. However, aftereffects of the magnitude found in the present results are not atypical: In a fairly exhaustive study of VAE's for many combinations of adapting and match temporal frequencies, Thompson⁴ reported speed attenuation of this magnitude and as much as 80% attenuation in some conditions. The time constants of adaptation are in broad agreement with physiological measures of the time

course of changes in spike rates during adaptation to motion in other species (5 s in cats,³³ 1–2 s in flies³⁴). The results are also consistent with physiological studies of feline neurons showing that recovery from adaptation is slower than adaptation, but the absolute values differ considerably (8 s in cats³³ compared with 22 s in the present study).

B. Contribution of Contrast Attenuation to Speed Attenuation

Experiment 2 confirms that the apparent contrast of temporally modulated gratings rapidly decreases with adaptation^{40–42} ($\tau = 2$ s), and here we report that recovery of normal contrast perception is also exponential but with a much slower time constant (approximately 25 s). It is well-known that the apparent speed of a grating can depend on its contrast,^{43–45} suggesting that changes in apparent contrast could affect the match speed. In unadapted conditions the apparent speed of 8-Hz drifting gratings has been found to be invariant of contrast⁴⁵ or to decrease at low contrasts.^{43,44} The reduction in the magnitude of speed attenuation at 8 Hz is consistent with the latter results. At 16 Hz, apparent speed can increase at low contrasts near detection threshold and when there is a 3–5-fold difference in the contrast of standard and match gratings.^{43,44} This suggests that lowering the contrast of the match pattern (to equate the apparent contrast of adapting and match gratings) should increase its apparent speed, and therefore it should match the apparent speed of the adapting pattern at an even lower physical speed. However, experiment 3 shows that lowering the contrast of the match pattern (to equate apparent contrast) reduced the match speed. The effect of contrast at 15 Hz was much less than at 8 Hz, in the direction expected from studies of apparent speed and contrast in unadapted conditions.^{43,44} Also, the contrast of our stimuli was much higher (50% for the adapting grating and a minimum of 33% for the match grating), and the contrast differences were much lower, than in speed studies with no adaptation^{43,44} to motion. In general, experiment 3 shows that when the apparent contrasts of the adapted and unadapted drifting patterns are equated, the loss of apparent speed was reduced (by approximately 15% at 8 Hz and 8% at 15 Hz). In a similar speed-matching study, Thompson⁴ varied the physical contrast of the match grating so that the apparent contrasts of the adapting and match gratings were equal on some trials. He also found a small reduction in the magnitude of the VAE that was at most approximately 10%. Taken together, these results suggest that only approximately 12% of the loss of apparent speed is dependent on a loss of apparent contrast.

C. Enhanced Speed Sensitivity during Adaptation to Motion

In a final experiment, we examined sensitivity to speed change for patterns whose apparent speed had been attenuated by adaptation. We found that speed increment and speed decrement thresholds decreased during adaptation and steadily returned to unadapted levels during recovery. This result confirms that sensitivity to changes in speed can increase during adaptation to

motion.¹² As the physical speed of the stimulus did not change throughout the run (except for the small increments in the test intervals), Weber fractions for speed increment sensitivity based on the physical speed of the stimulus would be constant, but the data do not have this form. Together with the suggestions of an anonymous reviewer, we can offer three possible sources for the increase in speed sensitivity:

1. Sensitivity could be proportional to the stability of apparent speed. Thus, at the start of the adaptation period, apparent speed is varying more than it is later in the adaptation period, when the exponential function asymptotes and apparent speed is relatively stable. However, this possibility is unlikely because apparent speed is also relatively stable toward the end of recovery, but thresholds are higher in those conditions.

2. The Weber fraction is not constant throughout the run but varies with the level of adaptation.

3. A similar proposal to that of proposal 2 is that the Weber fraction is constant but the stimulus level is decreasing. Both these proposals mean that sensitivity to apparent speed effectively increases. We prefer this proposal because speed sensitivity can be compared with estimates of apparent speed determined in the speed-matching task, while it is difficult to test proposal 2. Experiment 4 shows that the speed increment and the decrement sensitivity calculated from the apparent speed in any test interval with a constant Weber fraction provide a very good fit to the data.

Several other groups have examined the effects of adaptation on increment sensitivity but for luminance and contrast. Adaptation mechanisms have been extensively studied for luminance coding that has a remarkable response range of approximately 8 orders of magnitude. Several adaptation mechanisms, including optical factors, photoreceptor nonlinearities, and synaptic adaptation, extend the luminance response range and help accommodate more information within a single cell. The net effect is a computationally advantageous removal of the background signal (for a discussion see Ref. 48).

Similarly, some studies of contrast increment sensitivity have shown that, under some conditions, contrast increment sensitivity can improve following adaptation. Greenlee and Heitger⁴⁹ compared unadapted contrast increment thresholds for a 2-c/deg grating with thresholds following adaptation to a high-contrast grating (80%). They found that the slope of the contrast discrimination function was reduced by adaptation and that thresholds for high-contrast gratings (greater than 50%) were significantly lower following adaptation. The results were described by a leftward shift in the contrast response function and were taken as evidence that adaptation serves to linearize the contrast response function of a mechanism in the region near the prevailing contrast level. Wilson and Humanski⁵⁰ measured contrast increment thresholds for a D6 stimulus (the sixth derivative of a Gaussian in x multiplied by a Gaussian in y) centered at 3 or 9 c/deg following adaptation to a high-contrast grating (99%). Adaptation reduced the slope of the contrast discrimination function. In some cases the adapted contrast discrimination function crossed the unadapted function at high ped-

estal contrasts (60%), indicating an improvement in contrast increment sensitivity. However, other researchers have been unable to replicate these findings. Ross *et al.*⁵¹ measured contrast increment sensitivity for a 2-c/deg grating following adaptation to a 40% contrast grating, and both gratings counterphase flickered at 8.8 Hz. They found that while adaptation and masking raised thresholds at low contrasts, they had no effect at higher contrasts. The failure to find a reduction in thresholds at higher contrasts was attributed to the lower contrast of the adapting pattern (40%) and the lower mean luminance of the display (15 cd/m² compared with 80–100 cd/m²). For 5-c/deg gratings Maattanen and Koenderink⁵² confirmed that contrast detection thresholds and apparent contrast were reduced but found that contrast discrimination thresholds remained unchanged following adaptation to a 50% contrast grating. Their failure to replicate Greenlee and Heitger's⁴⁹ findings was attributable to the lower stimulus contrasts—while the physical contrasts of the stimuli were comparable (75% and 80%), the spatial Gaussian windowing employed by Maattanen and Koenderink⁵² increased detection threshold and therefore reduced its multiple of contrast threshold.

With these reservations in mind, it is tempting to conclude that adaptation to motion serves to increase sensitivity to the prevailing speed, as has been suggested for luminance adaptation and in some studies of contrast adaptation.

ACKNOWLEDGMENTS

This research was supported by Royal Society grants to Peter J. Bex and Stephen T. Hammett. We thank Richard Watson for observing, Peter Thompson for sending extracts from his Ph.D. thesis, and two anonymous reviewers for their helpful comments. A subset of these results was presented at the 1998 meeting of the Association for Research in Vision and Ophthalmology.⁵³

Address correspondence to Peter J. Bex at the location on the title page or by e-mail, pbex@essex.ac.uk.

REFERENCES

1. N. J. Wade, "A selective history of the study of visual motion aftereffects," *Perception* **23**, 1111–1134 (1994).
2. G. Mather, F. A. J. Verstraten, and S. M. Anstis, *The Motion Aftereffect: A Modern Perspective* (MIT Press, Cambridge, Mass., 1998).
3. A. Wohlgenuth, "On the aftereffect of seen movement," *Br. J. Psychol.* **1**, 1–117 (1911).
4. P. G. Thompson, "Velocity after-effects and the perception of movement," Ph.D. thesis (University of Cambridge, Cambridge, UK, 1976).
5. J. J. Gibson, "Adaptation with negative aftereffect," *Psychol. Rev.* **44**, 222–244 (1937).
6. A. G. Goldstein, "Judgements of visual velocity as a function of length of observation," *J. Exp. Psychol.* **54**, 457–461 (1959).
7. J. Rapoport, "Adaptation in the perception of rotary motion," *J. Exp. Psychol.* **67**, 263–267 (1964).
8. P. Thompson, "Velocity after-effects: the effects of adaptation to moving stimuli on the perception of subsequently seen moving stimuli," *Vision Res.* **21**, 337–345 (1981).

9. A. T. Smith, "Velocity coding: evidence from perceived velocity shifts," *Vision Res.* **25**, 1969–1976 (1985).
10. A. T. Smith and G. K. Edgar, "Antagonistic comparison of temporal frequency filter outputs as a basis for speed perception," *Vision Res.* **34**, 253–265 (1994).
11. R. Muller and M. W. Greenlee, "Effect of contrast and adaptation on the perception of the direction and speed of drifting gratings," *Vision Res.* **34**, 2071–2092 (1994).
12. C. W. G. Clifford and K. Langley, "Psychophysics of motion adaptation parallels insect electrophysiology," *Curr. Biol.* **6**, 1340–1342 (1996).
13. V. R. Carlson, "Adaptation in the perception of visual velocity," *J. Exp. Psychol.* **64**, 192–197 (1962).
14. T. R. Scott, A. E. Jordan, and D. A. Powell, "Does the visual after-effect of motion add algebraically to objective motion of the test stimulus?" *J. Exp. Psychol.* **66**, 500–505 (1963).
15. M. G. Harris, "Velocity specificity of the flicker to pattern sensitivity ratio in human vision," *Vision Res.* **20**, 687–691 (1980).
16. A. B. Watson and J. G. Robson, "Discrimination at threshold: labelled detectors in human vision," *Vision Res.* **21**, 1115–1122 (1981).
17. P. Thompson, "Discrimination of moving gratings at and above detection threshold," *Vision Res.* **23**, 1533–1538 (1983).
18. B. Moulden, J. Renshaw, and G. Mather, "Two channels for flicker in the human visual system," *Perception* **13**, 387–400 (1984).
19. S. T. Hammett and A. T. Smith, "Two temporal channels or three? A re-evaluation," *Vision Res.* **32**, 285–291 (1992).
20. A. B. Metha and K. T. Mullen, "Temporal mechanisms underlying flicker detection and identification for red-green and achromatic stimuli," *J. Opt. Soc. Am. A* **13**, 1967–1980 (1996).
21. R. E. Fredericksen and R. F. Hess, "Estimating multiple temporal mechanisms in human vision," *Vision Res.* **38**, 1023–1040 (1998).
22. M. B. Mandler and W. Makous, "A three channel model of temporal frequency perception," *Vision Res.* **24**, 1881–1887 (1984).
23. R. F. Hess and R. J. Snowden, "Temporal properties of human visual filters: number, shapes and spatial covariation," *Vision Res.* **32**, 47–59 (1992).
24. M. Hershenon, "Thirty seconds of adaptation produce spiral aftereffects three days later," *Bull. Psychon. Soc.* **23**, 122–123 (1985).
25. M. M. Taylor, "Tracking the decay of the aftereffect of seen rotary movement," *Percept. Motor Skills* **16**, 119–129 (1963).
26. M. J. Keck and B. Pentz, "Recovery from adaptation to moving gratings," *Perception* **6**, 719–725 (1977).
27. M. Hershenon, "Duration, time constant, and decay of the linear motion aftereffect as a function of inspection duration," *Percept. Psychophys.* **45**, 251–257 (1989).
28. M. J. Keck, T. D. Palella, and A. Pantle, "Motion aftereffect as a function of the contrast of sinusoidal gratings," *Vision Res.* **16**, 187–191 (1976).
29. M. Hershenon, "Visual system responds to rotational and size-change components of proximal motion patterns," *Percept. Psychophys.* **42**, 60–64 (1987).
30. R. G. Vautin and M. A. Berkley, "Responses of single cells in cat visual cortex to prolonged stimulus movement: neural correlates of visual aftereffects," *J. Neurophysiol.* **40**, 1051–1065 (1977).
31. D. G. Albrecht, S. B. Farrar, and D. B. Hamilton, "Spatial contrast adaptation characteristics of neurones recorded in the cat's visual cortex," *J. Physiol. (London)* **347**, 713–739 (1984).
32. P. Hammond, G. S. V. Mouat, and A. T. Smith, "Neural correlates of motion aftereffects in cat striate cortical neurones: monocular adaptation," *Exp. Brain Res.* **72**, 1–20 (1988).
33. D. Giaschi, R. Douglas, S. Marlin, and M. Cynader, "The time-course of direction-selective adaptation in simple and complex cells in cat striate cortex," *J. Neurophysiol.* **70**, 2024–2034 (1993).
34. T. Maddess and S. B. Laughlin, "Adaptation of the motion sensitive neuron H1 is generated locally and governed by contrast," *Proc. R. Soc. London, Ser. B* **225**, 251–275 (1985).
35. D. G. Pelli, "The VideoToolbox software for visual psychophysics: transforming numbers into movies," *Spatial Vis.* **10**, 437–442 (1997).
36. D. G. Pelli and L. Zhang, "Accurate control of contrast on microcomputer displays," *Vision Res.* **31**, 1337–1350 (1991).
37. A. B. Watson and D. G. Pelli, "QUEST: a Bayesian adaptive psychometric method," *Percept. Psychophys.* **33**, 113–120 (1983).
38. G. W. Snedecor and W. G. Cochran, *Statistical Methods* (Iowa State U. Press, Ames, Iowa, 1967).
39. W. H. Press, A. A. Teukolsky, W. T. Vetterling, and B. P. Flannery, *Numerical Recipes in C*, 2nd ed. (Cambridge U. Press, Cambridge, UK, 1992).
40. C. Blakemore, J. P. J. Muncey, and R. M. Ridley, "Stimulus specificity in the human visual system," *Vision Res.* **13**, 1915–1931 (1973).
41. M. A. Georgeson, "The effect of spatial adaptation on perceived contrast," *Spatial Vis.* **1**, 103–112 (1985).
42. S. T. Hammett, R. J. Snowden, and A. T. Smith, "Perceived contrast as a function of adaptation duration," *Vision Res.* **34**, 31–40 (1994).
43. P. G. Thompson, "Perceived rate of movement depends on contrast," *Vision Res.* **22**, 377–380 (1982).
44. L. S. Stone and P. Thompson, "Human speed perception is contrast dependent," *Vision Res.* **32**, 1535–1549 (1992).
45. K. Gegenfurtner and M. J. Hawken, "Perceived velocity of luminance, chromatic, and non-Fourier stimuli: influence of contrast and temporal frequency," *Vision Res.* **36**, 1281–1290 (1996).
46. P. J. Bex, A. B. Metha, and W. Makous, "Enhanced motion aftereffect for complex motions," *Vision Res.* (in press).
47. W. A. Simpson, A. Newman, and W. Aasland, "Equivalent background speed in recovery from motion adaptation," *J. Opt. Soc. Am. A* **14**, 13–22 (1997).
48. S. B. Laughlin, "The role of sensory adaptation in the retina," *J. Exp. Biol.* **146**, 39–62 (1989).
49. M. W. Greenlee and F. Heitger, "The functional role of contrast adaptation," *Vision Res.* **28**, 791–797 (1988).
50. H. R. Wilson and R. Humanski, "Spatial frequency adaptation and contrast gain control," *Vision Res.* **33**, 1133–1149 (1993).
51. J. Ross, H. D. Speed, and M. J. Morgan, "The effects of adaptation and masking on incremental thresholds for contrast," *Vision Res.* **33**, 2051–2056 (1993).
52. L. M. Maattanen and J. J. Koenderink, "Contrast adaptation and contrast gain control," *Exp. Brain Res.* **87**, 205–212 (1991).
53. P. J. Bex, S. Bedingham, and S. T. Hammett, "Enhanced speed sensitivity during adaptation to motion," *Invest. Ophthalmol. Visual Sci. Suppl.* **39**, S229 (1998).