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Increased sensitivity to speed changes during adaptation to first-order, but not to second-order motion

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Abstract

Observers adapted to drifting patterns varying either in luminance (first-order pattern), or in contrast (second-order pattern). Sensitivity to increases or decreases in the speed of the first-order pattern increased sharply as adaptation time increased, but sensitivity to speed changes of the second-order pattern remained unchanged throughout the adaptation time. Adaptation of first-order motion mechanisms seems thus to mediate increased sensitivity to variations in speed around the adapting speed. No evidence was found for such effects of adaptation to second-order motion. The observed differences in the effects of adaptation accord well with reports of fundamental differences between after-effects to drifting first- and second-order patterns and are in harmony with models of motion perception emphasizing different mechanisms for the detection of first- and second-order motion.

Keywords: Motion; Adaptation; Aftereffect; Second-order motion

1. Introduction

After prolonged viewing of a drifting pattern, observers often report that the apparent speed of the pattern decreases (Gibson, 1937; Goldstein, 1959; Thompson, 1981; Ledgeway & Smith, 1997; Clifford & Wenderoth, 1999). If the pattern stops, the now stationary pattern appears to drift in the direction opposite to the adapting motion (see Anstis, Verstraten, & Mather, 1998 for a review of the motion after-effect). What might be the usefulness of such adaptation for the visual system? It has been suggested that adaptation to motion increases sensitivity to velocities near the adapting velocity (Gibson, 1937; Barlow, 1990; Clifford & Langley, 1996; Bex, Beddingham, & Hammett, 1999). Wainwright (1999), (see also, Clifford, 2000), suggested that adaptation adjusts sensitivity to the characteristics of the input (in this case motion) for optimal information transmission. Consistent with this, Clifford and Langley (1996), (see also Bex et al.), reported that not only did the apparent speed of a drifting grating decrease during adaptation, but also that observers sensitivity to variations in speed around the adapting speed increased. Clifford and Wenderoth (1999) suggested that adaptation increases sensitivity to speed around the adapting level at the expense of an accurate representation of the absolute speed.

The visual system seems to be surprisingly insensitive to both stepped changes in speed (Snowden & Braddick, 1991; Mateeff, Dimitrov, & Hohnsbein, 1995; Mateeff & Hohnsbein, 1996) as well as to gradual accelerations and decelerations of a moving stimulus (Schmerler, 1976; Werkhoven, Snippe, & Toet, 1992). If adaptation to visual motion increases sensitivity around the speed of the adapting stimulus, this apparent lack of sensitivity might thus be overcome with sufficient adaptation.

1.1. Adaptation to drifting second-order patterns

Second-order patterns do not contain any changes in luminance (Cavanagh & Mather, 1989; Chubb & Sperling, 1988) that are accessible to neural units tuned to motion energy (Reichardt, 1961; Adelson & Bergen, 1985; Watson & Ahumada, 1985). The effects of adaptation to such patterns are of interest since they can provide important information about the hierarchical

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structure of the systems sensitive to visual motion (Nishida & Ashida, 2000). Some studies have reported no motion after-effect of adaptation to such patterns (Derrington & Badcock, 1985; Cropper & Hammett, 1997), while others have found robust after-effects to second-order motion, but only if the test stimulus is a dynamic stimulus such as a counterphasing version of the adapting stimulus (Ledgeway, 1994; Nishida & Sato, 1995). Many researchers have thus speculated that there are separate detection mechanisms for first- and second-order motion (e.g. Cavanagh & Mather, 1989; Ashida & Osaka, 1995; Lu & Sperling, 1995; Verstraten, Fredericksen, van Wezel, Lankheet, & van de Grind, 1996; van der Smagt, Verstraten, Vaessen, van Londen, & van de Grind, 1999). Seiffert and Cavanagh (1998, 1999) have suggested that the motion system most sensitive to slowly drifting second-order stimuli tracks changes in position over time, and does not perceive velocity directly. Consistent with this distinction, Allen, Ukkonen, and Derrington (2000), found that there were no direction specific effects on contrast detection thresholds, of adapting to drifting contrast defined (second-order) stimuli like they found for luminance (first-order) defined stimuli.

Given the differences in the characteristics of the motion after-effect for first- and second-order motion an interesting question is whether there are differences in the effects of adaptation to first- and second-order motion on the discrimination of changes in speed of the adapting patterns themselves. Many have argued that the visual system attaches more importance to the detection of changes in the environment than to maintaining an accurate representation of the absolute levels of stimuli (e.g. Attneave, 1954; Cornsweet, 1970; Kingdom & Moulden, 1988; Purves, Shimpi, & Lotto, 1999). Adaptation may be one way in which organisms achieve this goal (Wainwright, 1999). In the experiment reported here I investigate whether this holds for motion perception, both for a drifting first-order pattern (defined by sinusoidal changes in luminance, see Fig. 1a), and a drifting second order pattern (defined by sinusoidal changes in the contrast of a horizontal square-wave pattern, see Fig. 1c). The experiment measures the effects of adaptation to drifting first- and second-order patterns on the detection of velocity increments and decrements of the adapting pattern itself. It addresses whether adaptation serves to increase the

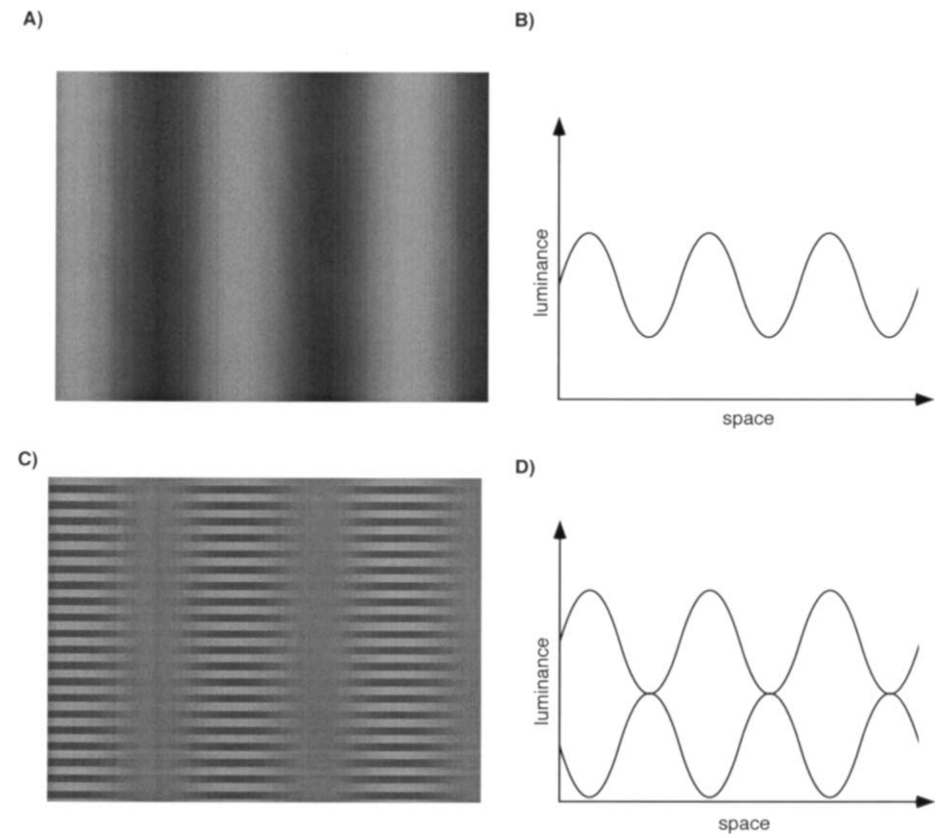

Fig. 1. Panel A shows the first-order stimulus, a luminance modulated vertical sine-wave grating, and panel B shows how its luminance varies sinusoidally as a function of space. Panel C shows a detail of the second order stimulus, a vertically contrast modulated horizontal square-wave grating. The pattern is constructed by alternating two horizontal sine-wave gratings of the same contrast that have a different mean luminance such that the trough of the high luminance grating has the same luminance as the peak of the low luminance grating. The high luminance grating is phase-shifted by 180° so its trough is aligned with the peak of the low-luminance grating. This is shown in the graph in panel D which shows the luminance of two bands of the horizontal square wave pattern as a function of space.

sensitivity to variations in speed around the speed of the adapting pattern. If that is the case, an increase in sensitivity to speed changes should be observed following adaptation to motion.

2. Method

2.1. Stimuli

The first order stimulus (see Fig. 1a–b) was a sinusoidal grating pattern that varied in luminance around a mean brightness of 15.6 cd/m^2. The Michelson contrast of the grating was 60 or 6% on different blocks of trials. The second order pattern (see Fig. 1c–d) which was adapted from the one used by Seiffert and Cavanagh (1998), was a vertically contrast modulated horizontal square wave pattern constructed by alternating narrow bands of horizontal luminance sine wave gratings. The mean contrast of the gratings alternated such that the peak of the lower-mean grating equaled the trough of the higher mean grating. The two alternating gratings were of the same spatial frequency but differed by 180° in phase so that when the two alternated vertically the peak of the lower-mean grating coincided spatially with the trough of the higher-mean grating (see Fig. 1d). This procedure results in a vertically contrast modulated, horizontal square-wave pattern (see Fig. 1c–d). The spatial frequency of the fundamental component of the horizontal square wave in the second-order pattern was 16 cd. The maximum contrast of the pattern was 60%. The spatial frequency of the first-order pattern and the sinusoid used for the contrast modulation of the square-wave (second-order) pattern was 0.52 cd. The adapting velocity was 7°/s, and 3.5°/s on one test session with the second-order pattern for observer ATL.

To test for perceptual equiluminance of the second-order patterns the ‘minimum-motion’ test adapted from Cavanagh, MacLeod, and Anstis (1987), was used. It consists of alternating the second order stimulus with a sinusoidal luminance grating of equal spatial frequency as the second order pattern, but displacing the patterns by a quarter cycle to the left on each presentation. If the second order pattern is completely equiluminant no motion is seen since the net direction of motion is ambiguous, but if the pattern is not equiluminant, motion is seen to the left. The parameter values obtained through this procedure were used to generate the second-order pattern for each observer.

The dots of the dynamic random dot pattern that followed each trial were either white (50.9 cd/m^2) or black (0.5 cd/m^2) and subtended 6.6 arc min. The pattern consisted of random dot arrays that were randomly reshuffled every 13 ms. While the drifting gratings were presented, the rest of the screen was covered by a similar but static random dot pattern. The angular subtense of the drifting gratings was 15° (vertical) by 49° (horizontal). A fixation point was present at the center of the screen throughout the experiment.

2.2. Apparatus

The stimuli were generated with color look-up table animation by placing a grayscale in an 8-bit look-up table on a G3 Macintosh computer. The VisionShell programming library was used to generate the stimuli (for info go to http://www.kagi.com/visionshell) which were presented on a CRT display with a refresh rate of 75 Hz.

2.3. Procedure

At a distance of 35 cm from the screen observers viewed the drifting patterns for a variable amount of time (adaptation period) before the speed of the pattern either increased or decreased. The task was to indicate by key press whether the speed of the pattern increased or decreased. The speed of the patterns could increase or decrease by 0.3, 0.6, 0.9, 1.2 or 1.5°/s from the adapting velocity. The increase or decrease in speed happened at an unpredictable time (1, 4, 8, 12 or 16 s, depending on the condition) after the onset of the drifting pattern. If observers had not responded 4 s after the speed change (a ‘miss’) the trial ended, and the response was coded as incorrect. The dynamic random dot pattern was presented for 8 s after each trial in an attempt to minimize any residual after-effect from the ending trial. The direction of the moving pattern was changed randomly (either leftwards drifting or rightwards drifting) from trial to trial. Each datapoint in the graphs in this paper represents at least 12 trials. If observers responded before the pattern changed speed (‘false alarms’) the trial was aborted and the data was not used for the analysis but the trial was repeated at the end of the testing session. Two different contrast levels of the first order stimulus were tested for observer AK (6 and 60%), whereas ATL was tested at 60% contrast only. Two different drift rates of the contrast modulated pattern (7 and 3.5°/s), and one for the first-order pattern (7°/s) were tested for observer ATL, but AK was tested at 7°/s only, for both first, and second order patterns.

The motion after-effect to the drifting patterns was measured after 16 s of adaptation for both first- and second-order patterns. The test stimulus in both cases was a counterphasing version of the adaptation stimulus. Observers indicated by keypress when they stopped seeing an after-effect. The mean duration of the after-effect was 8.2 s for the first order stimulus and 6.3 s for the second-order stimulus. Observers also reported that

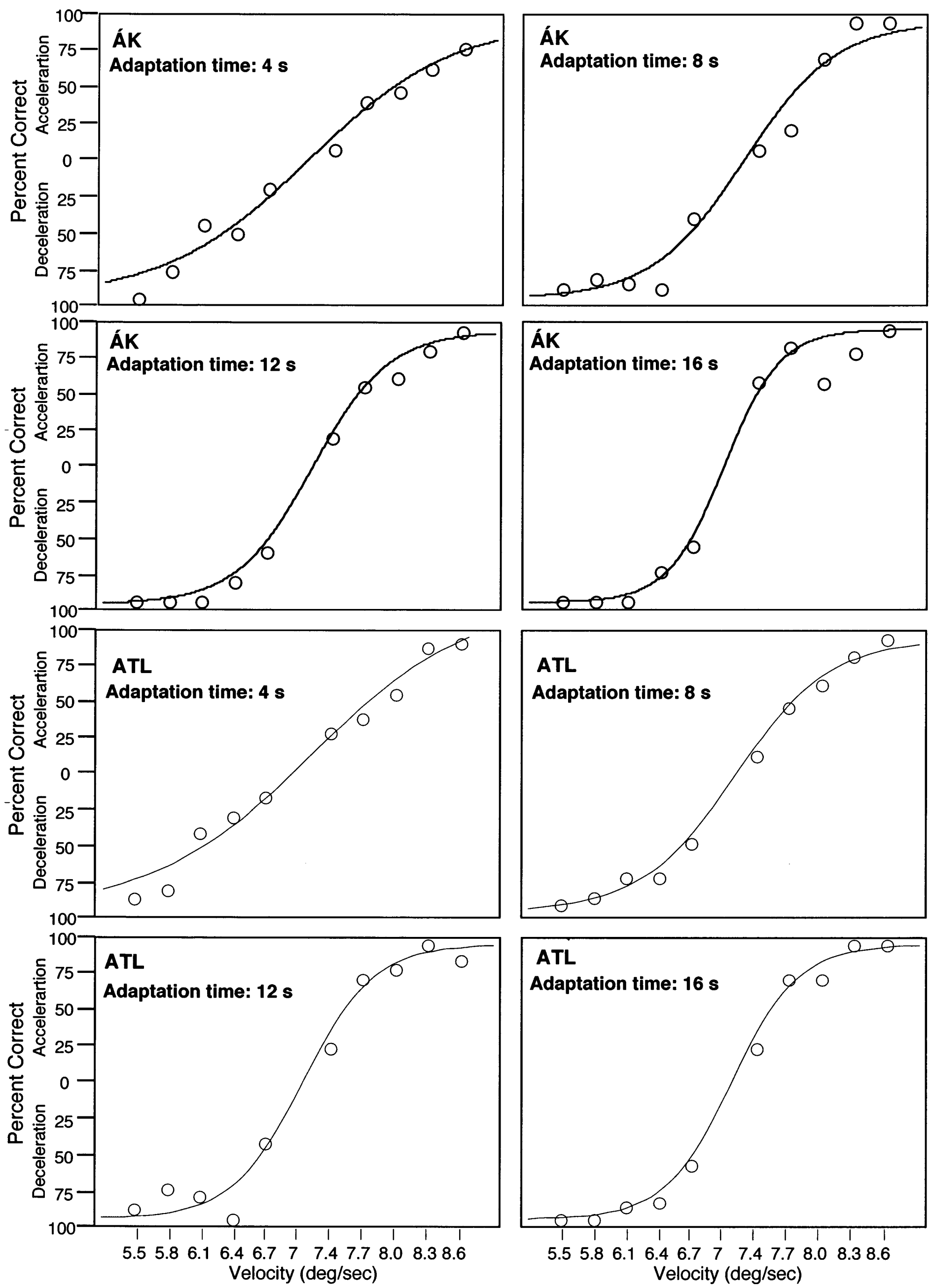

Fig. 2. The psychometric functions (see text) superimposed on the data for the discrimination of increases and decreases in the speed of the luminance (first-order) gratings, for both observers. Note how performance of both observers improves as adaptation is longer.

the apparent speed of the adapting patterns decreased with adaptation.

2.4. Data analysis

Psychometric functions were fit to the speed discrimination data using the logistic function $1/(1+e^{-\alpha(x-\beta)})$ where x denotes the speed, $\alpha/4$ is the slope of the function and β the transition point. To enable logistic curve fitting the data were transformed with the function $0.5+(\rho/2)$ for the speed-ups and $0.5-(\rho/2)$ for the slow-downs where ρ is the proportion correct. The curve fitting generates a slope parameter (α) that indicates how well speed-ups and slow-downs can be discriminated. In the graphs in Fig. 2 and Fig. 3 the fitted curves have been transformed (the reverse transform of the one for the actual data) to correspond to the scales presented on the left vertical axis. The R^2 for the curve fitting ranged from .91 to .98.

2.5. Observers

Observers were myself (ÁK) and observer ATL who is an experienced psychophysical observer but was unaware of the goals of the experiment. Both observers were 29 years old and had normal or corrected to normal vision.

3. Results

Fig. 2 presents the results and the psychometric functions for each of the four adaptation times at which the speed of the drifting patterns could increase or decrease, for the first-order pattern at 60% contrast, and drifting at 7°/s. Fig. 3 presents similar data for the second-order pattern drifting at 7°/s. The results for the two patterns are quite different. While sensitivity to speed changes around the adapting speed increases sharply as a function of adaptation time for the first-order pattern, no such increase was observed for the second-order pattern. It is important to note that this result is not due to the lack of adaptation to the second-order pattern since robust after-effects were found for the second-order pattern tested with a flickering test stimulus, and both observers noted that the

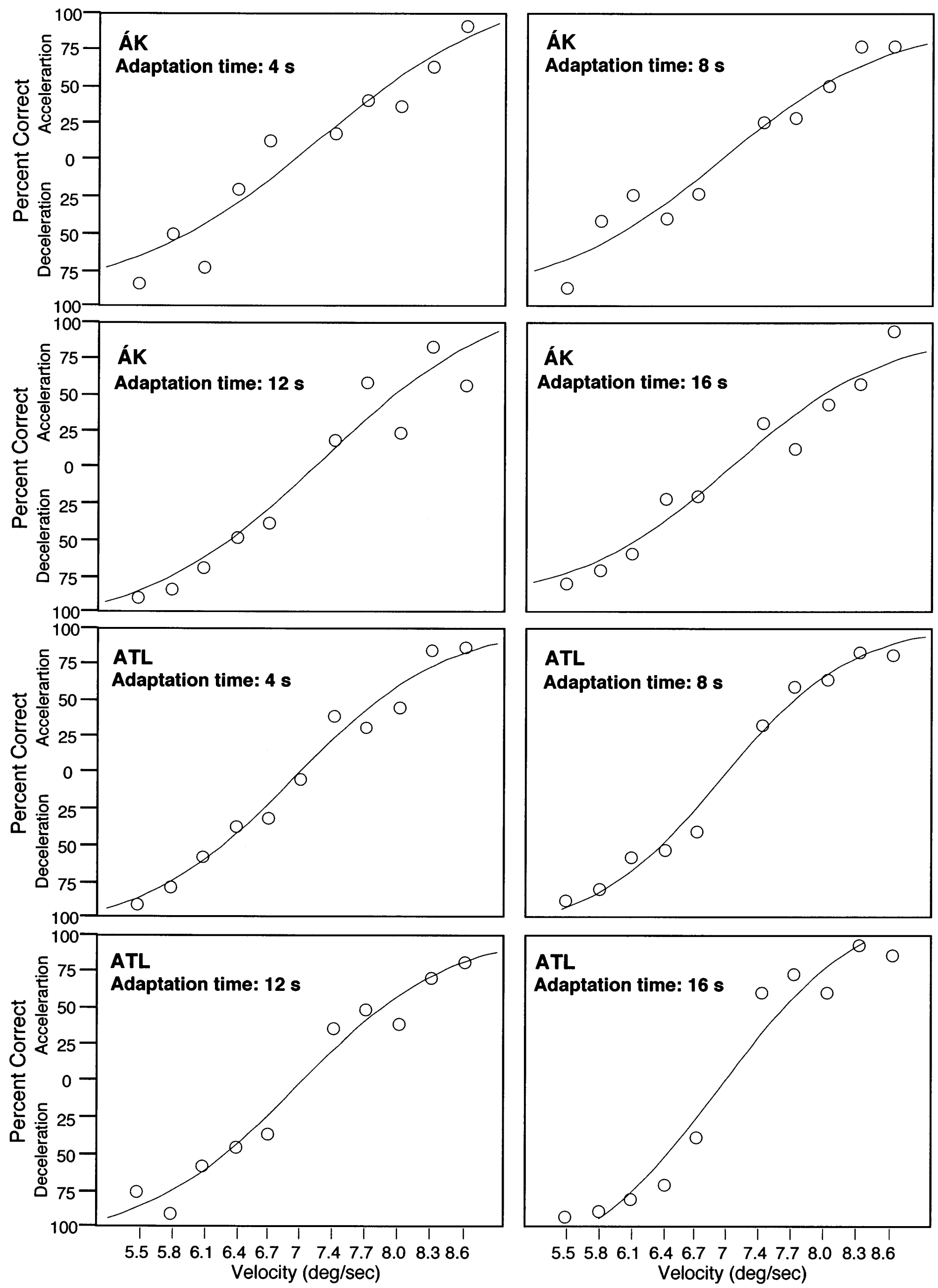

Fig. 3. The psychometric functions (see text) superimposed on the data for the discrimination of increases and decreases in the speed of the contrast modulated square wave (second-order) pattern, for both observers. Note how performance does not improve as a function of adaptation time.

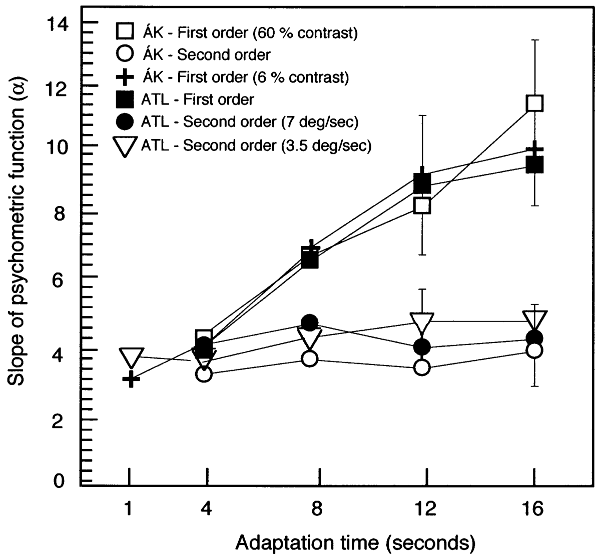

Fig. 4. The slopes of the psychometric functions for each of the adaptation times for the first- and second-order stimuli. The drift rate was 7°/s for all patterns for observer AK and all but one test of the second-order pattern drifting at 3.5°/s for observer ATL. Two different contrast levels of the first-order pattern (6 and 60%) were tested for observer AK. Note the increase in slopes as a function of adaptation times for the first order patterns, and that there is no such increase in slopes for the second-order patterns. The error bars show the largest 95% confidence intervals for the slopes for each condition.

apparent speed of the pattern decreased after prolonged viewing (see Section 2.3). This difference between first-order and second-order stimuli was also observed for the other patterns tested (not shown here). As a control, performance was also tested on a luminance sine wave pattern with a horizontal square wave carrier (a first-order pattern more similar in appearance to the second-order pattern that was used) with similar results.

Fig. 4 presents the slope parameter (α) for the fitted logistic function for each of the adaptation times for all the conditions tested. This slope parameter increases sharply as a function of adaptation time for the first order-patterns, but that is not the case for the second-order patterns. This indicates that increases and decreases in speed become more easily discriminated with adaptation for the first-order stimulus but not the second-order stimulus. The fact that the slopes are about the same for the adaptation time of 1000 and 4000 ms for the two patterns also indicates that at first, the speed changes of the two patterns are approximately equally discriminable, while the discriminability increases for the first-order, but not the second-order pattern. Thus it appears that adaptation to motion increases sensitivity to variations around the adapting speed, but only if the motion is defined by spatiotemporal changes in luminance (the first-order statistics of the stimulus). Furthermore, differences in apparent contrast between the first- and second-order patterns are unlikely to account for the results since the effects of adaptation are essentially the same for the two different contrast levels of the first-order stimulus that were tested (6 and 60%).

4. Conclusions

Following adaptation to second-order motion an after-effect is only seen with a dynamic test pattern (Ledgeway, 1994; Nishida & Sato, 1995). The results in this paper indicate that the adaptation uncovered with such after-effects is fundamentally different from the adaptation to motion revealed with a static test pattern in that the sensitivity to increments and decrements in speed does not increase with prolonged viewing even though there is clearly adaptation to the pattern since observers reported seeing clear motion after-effects after viewing the second order pattern. The results may thus shed some light on the debate over after-effects to drifting second-order patterns. The results are consistent with the idea that first-order motion is at least partly detected by a mechanism sensitive only to luminance based motion. This mechanism is likely to be the one that mediates the increased sensitivity to changes in speed with adaptation to a drifting luminance grating. This is consistent with the proposal that motion after-effects tested with a dynamic pattern reflect adaptation at multiple sites in the visual system, whereas the 'static' motion after-effect reveals low-level processing only (Nishida & Ashida, 2000). Particularly interesting in this context is that separate motion after-effects to first- and second-order motion can be induced at the same time (Nishida & Sato, 1995). Further differences between the two after-effects have been found, for example, the static after-effect is dependent on temporal frequency (Pantle, 1974), but the flicker after-effect is dependent on velocity (Ashida & Osaka, 1995), possibly reflecting adaptation at different levels in the visual system.

4.1. The functional benefits of motion adaptation

Müller and Greenlee (1994) found that adaptation to a slowly drifting luminance grating shifted the point where the grating appeared stationary towards higher velocities in the adapted direction. A possible conclusion from this and the present results is that adaptation to luminance based motion decreases the perceived speed of the adapting pattern, but at the same time increases the sensitivity to variations in speed around the adapting speed. This increase in sensitivity around the mean speed was not observed for second-order motion, however. Thus it seems that the claim that adaptation increases sensitivity to variations around the adapting stimulus (Clifford & Langley, 1996; Bex et al., 1999; Wainwright, 1999) holds, but only for luminance defined motion. A possible reason is that the second-order motion system tracks changes in position over time (Seiffert & Cavanagh, 1998) whereas the important input to sensors of luminance defined motion seems to be velocity (Nakayama & Tyler, 1981).

It seems reasonable that effectively coding increases and decreases in the speed of a stimulus that is actually present is of great importance for organisms. This is exactly what seems to happen during adaptation to first-order motion. The experiments reported here may reflect the workings of a gain control mechanism for luminance based motion perhaps designed to effectively code changes in the speed of a behaviorally important stimulus. On the other hand, no evidence for such a mechanism for second-order motion was found.

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References

Adelson, E. H., & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America*, *2*(2), 284–299.

Allen, H. A., Ukkonen, O. I., & Derrington, A. M. (2000). No direction specific adaptation effects from moving contrast-modulated gratings. *Investigative Opthalmology and Visual Science*, *41*(4), S4202.

Anstis, S., Verstraten, F., & Mather, G. (1998). The motion after effect. *Trends in Cognitive Sciences*, *2*, 111–117.

Ashida, H., & Osaka, N. (1995). Motion aftereffect with flickering test stimuli depends on adapting velocity. *Vision Research*, *35*, 1825–1833.

Attneave, F. (1954). Some informational aspects of visual perception. *Psychological Review*, *61*(3), 183–193.

Barlow, H. (1990). A theory about the functional role and synaptic mechanism of visual after-effects. In C. Blakemore, *Coding and efficiency* (pp. 363–375). Cambridge: Cambridge University Press.

Bex, P. J., Beddingham, S., & Hammett, S. T. (1999). Apparent speed and speed sensitivity during adaptation to motion. *Journal of the Optical Society of America*, *16*(12), 2817–2824.

Cavanagh, P., & Mather, G. (1989). Motion: the long and short of it. *Spatial Vision*, *4*, 103–129.

Cavanagh, P., MacLeod, D. I., & Anstis, S. M. (1987). Equiluminance: spatial and temporal factors and the contribution of blue-sensitive cones. *Journal of the Optical Society of America (A)*, *4*, 1428–1438.

Chubb, C, & Sperling, G. (1988). Drift-balanced random stimuli: a general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America (A)*, *5*, 1986–2007.

Clifford, C. W. G. (2000). A theory of adaptation in visual cortex. *Investigative Opthalmology and Visual Science*, *41*(4), S4243.

Clifford, C. W. G., & Langley, K. (1996). Psychophysics of motion adaptation parallels insect electrophysiology. *Current Biology*, *1*(6), 1340–1342.

Clifford, C. W. G., & Wenderoth, P. (1999). Adaptation to temporal modulation can enhance differential speed sensitivity. *Vision Research*, *39*, 4324–4332.

Cornsweet, T. N. (1970). *Visual perception*. New York: Academic.

Cropper, S. J., & Hammett, S. T. (1997). Adaptation to motion of a second-order pattern: the motion aftereffect is not a general result. *Vision Research*, *37*, 2247–2259.

Derrington, A. M., & Badcock, D. R. (1985). Separate detectors for simple and complex grating patterns? *Vision Research*, *25*, 1869–1878.

Gibson, J. J. (1937). Adaptation with negative aftereffect. *Psychological Review*, *44*, 222–224.

Goldstein, A. G. (1959). Judgements of visual velocity as a function of length of observation. *Journal of Experimental Psychology*, *54*, 457–461.

Kingdom, F., & Moulden, B. (1988). Border effects on brightness: a review of findings, models and issues. *Spatial Vision*, *3*, 225–262.

Ledgeway, T. (1994). Adaptation to second-order motion results in a motion aftereffect for directionally-ambiguous test stimuli. *Vision Research*, *34*, 2879–2889.

Ledgeway, T., & Smith, A. T. (1997). Changes in perceived speed following adaptation to first-order and second-order motion. *Vision Research*, *37*(2), 215–224.

Lu, Z. L., & Sperling, G. (1995). The functional architecture of human visual motion perception. *Vision Research*, *35*, 2697–2722.

Mateeff, S., Dimitrov, G., & Hohnsbein, J. (1995). Temporal thresholds and reaction time to changes in velocity of visual motion. *Vision Research*, *35*, 355–363.

Mateeff, S., & Hohnsbein, J. (1996). Perception of visual motion with modulated velocity: Effects of viewing distance and aperture size. *Vision Research*, *36*, 2873–2882.

Müller, R., & Greenlee, M. W. (1994). Effect of contrast and adaptation on the perception of the direction and speed of drifting gratings. *Vision Research*, *34*, 2071–2092.

Nakayama, K., & Tyler, C. W. (1981). Psychophysical isolation of movement sensitivity by removal of familiar position cues. *Vision Research*, *21*, 427–433.

Nishida, S., & Sato, T. (1995). Motion aftereffect with flickering test patterns reveals higher stages of motion processing. *Vision Research*, *35*, 477–490.

Nishida, S., & Ashida, H. (2000). A hierarchical structure of the motion system revealed by interocular transfer of flicker motion aftereffects. *Vision Research*, *40*, 265–278.

Pantle, A. (1974). Motion aftereffect magnitude as a measure of the spatio-temporal response properties of direction-sensitive analyzers. *Vision Research*, *14*, 1229–1236.

Purves, D., Shimpi, A., & Lotto, R. B. (1999). An empirical explanation of the Cornsweet effect. *Journal of Neuroscience*, *1*(19), 8542–8551.

Reichardt, W. (1961). Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. In W. A. Rosenblith, *Sensory communication*. New York: Wiley.

Schmerler, J. (1976). The visual perception of accelerated motion. *Perception*, *5*, 167–185.

Seiffert, A. E., & Cavanagh, P. (1998). Position displacement, not velocity, is the cue to motion detection of second-order stimuli. *Vision Research*, *38*, 3569–3582.

Seiffert, A. E., & Cavanagh, P. (1999). Position-based motion perception for color and texture stimuli: effects of contrast and speed. *Vision Research*, *39*, 4172–4185.

Snowden, R. J., & Braddick, O. J. (1991). The temporal integration and resolution of velocity signals. *Vision Research*, *31*, 907–914.

Thompson, P. (1981). Velocity aftereffects: the effects of adaptation to moving stimuli on the perception on subsequently seen moving stimuli. *Vision Research*, *21*, 337–345.

van der Smagt, M. J., Verstraten, F. A., Vaessen, E. B., van Londen, T., & van de Grind, W. A. (1999). Motion aftereffect of combined first-order and second-order motion. *Perception*, *28*, 1397–1411.

Verstraten, F. A., Fredericksen, R. E., van Wezel, R. J., Lankheet, M. J., & van de Grind, W. A. (1996). Recovery from adaptation for dynamic and static motion aftereffects: evidence for two mechanisms. *Vision Research*, *36*, 421–424.

Wainwright, M. J. (1999). Visual adaptation as optimal information transmission. *Vision Research*, *39*, 3960–3974.

Watson, A. B., & Ahumada, A. J. (1985). Model of human visual-motion sensing. *Journal of the Optical Society of America A*, *2*(2), 322–341.

Werkhoven, P., Snippe, H. P., & Toet, A. (1992). Visual processing of optic acceleration. *Vision Research*, *32*, 2313–2329.