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The Functional Benefits of Tilt Adaptation

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Abstract

Many have argued that effects of adaptation, such as aftereffects from motion or tilt, reflect that the visual system hones its responses in on the characteristics of the adapting stimulus. This view entails that on average, the discrimination of the characteristics of an adapting stimulus should become easier as viewing time increases since the variation in the response gradually adapts to the range and variation in the stimulus. Here this was tested for adaptation to tilt. Observers viewed a Gabor patch which varied in contrast from 0 to 74% at a rate of 0.6 Hz, for 4, 8, 16 or 32 s, after which the Gabor patch changed orientation (at the point when contrast was 0). The results show that the longer the observers adapt to the dynamic Gabor, the better they become at discriminating between clockwise (CW) or counterclockwise (CCW) changes in tilt (orientation) of the same patch. Experiment 2 confirms that both the direct and indirect tilt aftereffects are seen with this contrast varying Gabor patch and Experiment 3 shows that the aftereffects are only slightly smaller than in other studies with stimuli such as lines and sinusoidal gratings. These results show that adaptation to tilt leads to better discrimination around the orientation of the adapting stimulus itself, and that discrimination performance improves steadily with increased adaptation time. The results support proposals that the visual system adjusts its response characteristics to the properties of the visual input at a given time.

Keywords

Tilt aftereffect, adaptation, spatial vision, priming

1. Introduction

Our visual system constantly changes its operating characteristics depending on the surroundings at a given time. One example is that as ambient light in our environment increases, our pupils contract. In a darkened theatre they expand to let in more light.

But adaptation to environmental characteristics can be more subtle than this. We are all aware of various aftereffects of vision: when viewing a green pattern on a white background we see a ghostlike red pattern when the green one disappears

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(Hurvich, 1981). Or when viewing a pattern drifting in one direction, it appears to drift in the other when stopped (Anstis *et al.*, 1998; Gibson, 1937; Thompson, 1981). Are such aftereffects following adaptation meaningless consequences of neural stimulation indicating 'neural fatigue' (see, e.g., Graham, 1989), or could the observed adaptation be strategic? Many have, indeed, argued that adaptation reflects 'optimal coding' in the visual system (Barlow and Földiák, 1989; Clifford *et al.*, 2000; Clifford *et al.*, 2007; Ullman and Schechtman, 1982; Wainwright, 1999; see also discussion in Mather and Harris, 1998). Clifford *et al.* (2000) argued that adaptation to, for example, motion, tilt or even faces (Rhodes *et al.*, 2010), serves to hone the visual systems responses in on a particular range, a process Clifford called *centering*, and that the visual system also adapts to the variability in the stimulus, what Clifford referred to as *scaling*. Rather poetically, this has been called 'fitting the mind to the world' (Clifford and Rhodes, 2007; see also Durgin, 1996 and Helson, 1947; 1964a for some early theoretical developments). Such adaptation has been shown to occur for various types of visual stimuli, and Wainwright *et al.* (2002) showed how adaptation effects, measured both psychophysically and physiologically, fit with a model where response properties are modified according to the image statistics of recent visual input.

If our sensory systems map attributes of the surroundings onto the neural responses in a dynamic way, a clear prediction is that sensitivity to changes in the stimulus might increase if the neural mechanisms are tuned not only to the actual level of the stimulus, but also to variations around a 'mean' value determined by the level of a particular stimulus property at a given time. An example of this is that the perceived velocity of a drifting grating varying spatially in luminance appears to decrease with prolonged viewing (Goldstein, 1959; Thompson, 1981), but at the same time sensitivity to variation in speed around the adapted level increases (Bex *et al.*, 1999; Clifford and Langley, 1996; Kristjánsson, 2001). As an example, Kristjánsson (2001) showed that sensitivity to increases or decreases in the speed of a drifting grating varying sinusoidally in luminance increased sharply as adaptation time increased (from 4 to 16 s). Adaptation of first-order motion mechanisms appears to mediate increased sensitivity to variations in speed around the adapting velocity.

Such ideas entail that adaptation is not simply a relatively uninteresting consequence of neuronal firing, but an active mechanism serving the purpose of increasing our sensitivity to a given range, just as brightness adaptation increases both our sensitivity to low luminance levels, but also increases our sensitivity to variations that might go unnoticed under higher luminance levels, in other words the mechanisms of centering and scaling as discussed by Clifford *et al.* (2000). This may come at the cost of an accurate representation of the absolute levels of stimulation, however.

1.1. Adaptation to Orientation

Gibson and Radner (1937) studied adaptation to orientation (see also Ware and Mitchell, 1974). They found that extended exposure to a tilted line caused changes in the sensitivity of the visual system such that a subsequently presented vertical pattern appeared to be tilted in the direction opposite to the adapting pattern, for relatively small differences in angle (less than ∼50°). They also observed the so-called *indirect* tilt aftereffect where stimuli oriented perpendicular to the adapting stimulus seem to be attracted to the orientation of the adapting pattern. The *direct* and indirect tilt aftereffects may reflect the operation of different visual mechanisms (Wenderoth and Johnstone, 1988; see also Clifford *et al.*, 2001).

Note that as with the motion-aftereffect, neural fatigue (see, e.g., Blakemore *et al.*, 1973; Graham, 1989) cannot explain the effects of adaptation to tilt (Clifford, 2007; Wolfe, 1984). Neural fatigue typically refers to the possibility that neurons sensitive to a given characteristic such as leftwards motion gradually decrease their firing during adaptation to a leftwards drifting pattern so that spontaneous activity of neurons sensitive to motion in the other direction causes perceived movement. Wolfe and O'Connell (1986) observed, for example, a short-term TAE and a longer term one, arguing that the two reflect the operation of different mechanisms, the longer-term one not easily explained with fatigue. Also, the tilt aftereffect shows strong similarities with the simultaneous tilt illusion (O'Toole and Wenderoth, 1977; Wenderoth and van der Zwan, 1989), an effect which fatigue cannot, by definition, explain.

1.2. Current Experiments

Kristjánsson (2001), showed that with increased adaptation to luminance defined motion, sensitivity to stepped changes in velocity of the adapting pattern itself increased. Discrimination of whether a drifting grating varying sinusoidally in luminance increased or decreased its speed became more accurate with increased adaptation time. In Experiment 1 similar questions were addressed, for the first time, for adaptation to orientation (but see Regan and Beverley, 1985 for related findings). If it is indeed true that adaptation serves to increase sensitivity to the current image statistics, a clear prediction is that sensitivity to changes in the orientation of an adapting Gabor patch would increase, the longer the adaptation time, perhaps reflecting the operation of mechanisms with operating characteristics comparable to the centering and scaling proposed by Clifford *et al.* (2000). The observers viewed a dynamic Gabor patch for 4, 8, 16 or 32 s. To try to isolate any effect of tilt, the Gabor pattern varied in Michelson contrast from 0 to 74% at 0.6 Hz. Furthermore, at each timepoint where contrast = 0, the pattern was phase shifted by 90°. This was done to avoid any effect of local difference in contrast variation. Experiment 2 was conducted to see whether adaptation to a contrast and phase varying Gabor patch like the one that was used in Experiment 1 would result in similar tilt aftereffects (both direct and indirect, Gibson and Radner, 1937; Wenderoth and Johnstone, 1988) as seen for other stimulus patterns. Experiment 3 was designed to asses the size of any aftereffect.

2. Experiment 1

2.1. Methods

2.1.1. Observers

Three experienced psychophysical observers participated. Two (ATL and GA) were unaware of the aim of the experiments, while the third (AK) was the author. All were students at Harvard University, and had normal vision, or normal vision when corrected with lenses. The method of constant stimuli was used, where all observers participated in 6000 trials each, with roughly equal numbers of trials for each threshold estimate.

2.1.2. Apparatus

The stimuli were generated with color look-up table animation on a G3 Macintosh computer, and appeared on a CRT display with a refresh rate of 75 Hz. The custom made stimulus presentation software was programmed in C using functions from the Vision Shell library.

2.1.3. Procedure

When observes view a line or a grating for a prolonged period of time, other adaptation effects, apart from tilt adaptation, may simultaneously occur potentially contaminating the measured results. As an example, local brightness adaptation might affect perception of change in tilt angle. For this reason, a dynamic Gabor patch was created where contrast and phase varied throughout, while orientation remained constant until a critical time following adaptation (see Fig. 1). This was done to avoid any confounding or contaminating afterimages from local brightness adaptation or local adaptation to contrast variation. The only aspect of the Gabor patch that did not vary was its orientation and spatial frequency. This procedure eliminates any potential apparent motion when the change in tilt is introduced, since the change occurs when contrast is zero (see Fig. 1). The adapting orientation was randomly determined on each trial.

At an unpredictable time following presentation of the dynamic Gabor (4, 8, 16 or 32 s), its orientation changed either clockwise or counter-clockwise by 1, 2, 4, 6 or 8 arc deg. Psychometric functions (see Note 1) were plotted on the proportion of CW responses for each tilt angle as a function of the different adaptation times, for each observer. The psychometric function provides a measure of the discriminability of tilt changes as a function of adaptation time, when the difference between the 25% CW 75% CW points is taken and divided by two, yielding an estimate of the discrimination threshold at each adaptation time.

The observers watched a large Gabor patch (a sinusoidal grating convolved with a Gaussian patch) on a computer screen (see Fig. 1), at a viewing distance of 67 cm. The absolute size of the Gabor patch was 15° (at 7.5° in any direction from screen centre the luminance was equal to the background). The standard deviation of the Gabor was 3.7°. Michelson contrast varied sinusoidally from 0 to 74% at 0.6 Hz, around a mean luminance level of 15.8 cd/m^2 while spatial frequency remained

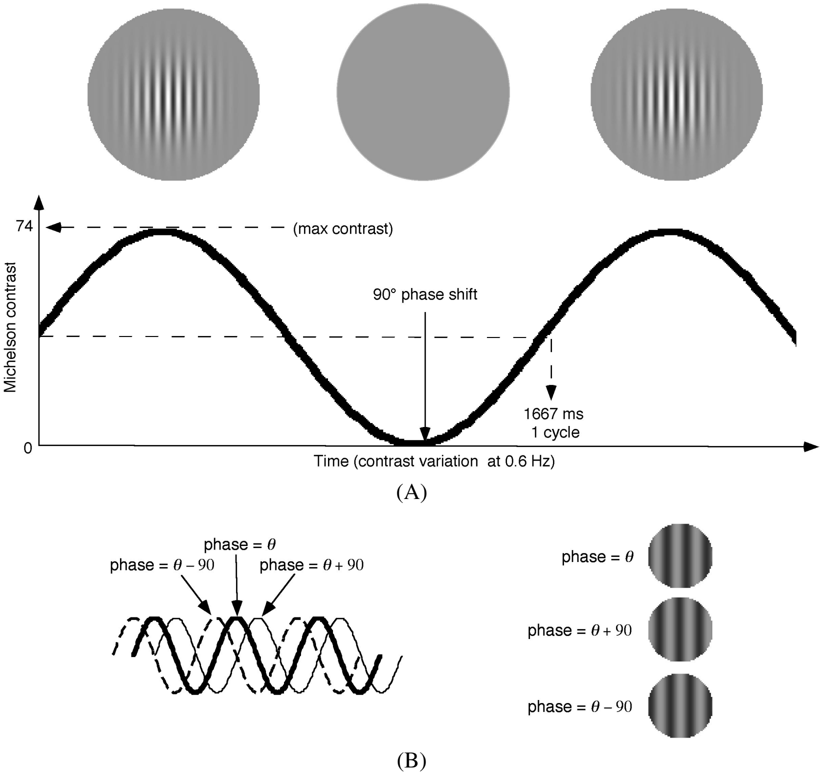


Figure 1. The stimulus sequence in Experiment 1. Panel (A) The observers viewed a randomly oriented Gabor patch which varied sinusoidally in Michelson contrast in time between 0 and 74%, at rate of 0.6 Hz, so that a cycle from peak contrast to the next instance of peak contrast was 1667 ms. The mean luminance was 15.8 cd/m^2. Panel (B) At the point where contrast was zero the Gabor patch was phase shifted to the left or right by 90° (randomly decided). Following 4, 8, 16 or 32 s viewing, the tilt changed slightly (by 1, 2, 4, 6 or 8°) and 3 s following this, the observers were prompted to respond whether the Gabor had tilted clockwise or counterclockwise, had they not already responded. Crucially the tilt change was introduced at the point where contrast was equal to zero to avoid any apparent motion.

constant at 0.9 cpd. This means that 1667 s passed between successive contrast peaks. When contrast was $= 0$, the Gabor patch was phase shifted by 90° to prevent any contaminating effect of adaptation to local variation in brightness, since the aim was to isolate any effect of adaptation to orientation. At the start of the trial, the Gabor patch was presented at random phase of the sinusoidally varying contrast function. The only property of the Gabor patch that remains constant is its orientation and spatial frequency. The observers were told to freely view the pulsating Gabor and to indicate by key-press when they noticed a change in tilt (or orientation) of the Gabor, where they pressed 2 (for CCW) or 4 (for CW) on the numeric keypad of a standard keyboard. Three seconds following the orientation change they were prompted for response had they not already responded. This was a 2AFC task and the observers were told to guess if they were unsure about the direction of the tilt change.

2.2. Results and Discussion

The results of Experiment 1 are presented in Fig. 2. The figure plots discrimination thresholds for the different adaptation times. The thresholds decreased sharply, by 8 to 13 arc min for each added second's adaptation for all three observers. The thresholds ranged from 4.3 to 5.7 arc deg for the 4 s viewing time to 1.2 to 2.1 arc deg for the 32 s viewing time.

The results of Experiment 1 show that adaptation to a dynamic Gabor patch of a given orientation leads to increased sensitivity to changes in the tilt of that stimulus, and this benefit increases sharply with increased viewing time. This pattern was quite clear for all the participating observers. This is consistent with the proposal that adaptation to a dynamic Gabor results in increased sensitivity to slight changes in orientation around the adapting orientation. Although the longest adaptation time tested was 32 s, one can clearly speculate, by the evidence from Fig. 2, that the thresholds will continue to decrease with longer viewing.

This falls in line with the argument that the visual system adjusts its operating characteristics to fit the visual input at any given time. This has previously been shown to occur for luminance defined motion but is shown here, for the first time, to occur for adaptation to tilt. This effect from adaptation applies to the adapting stimulus itself, suggesting ecological benefits of prolonged viewing. Note also that neither local brightness adaptation nor local adaptation to contrast variation can explain the increased sensitivity because of the contrast varying, phase shifting Gabor patch that was used. The measured orientation discrimination thresholds might

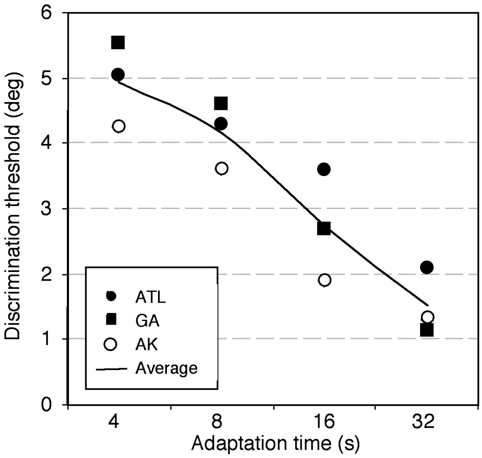


Figure 2. The results of Experiment 1. The graph shows the orientation discrimination threshold estimated by halving the difference between the 25% CW and 75% CW points on the psychometric function for each observer at each individual adaptation time. The smoothed line traces the average of the threshold estimates for the different observers at each adaptation time.

be considered high compared to other estimates (see, e.g., Heeley and Buchanan-Smith, 1990; Regan, 2000) but a likely reason for this is that orientation judgments are relatively difficult for this particular stimulus, certainly outside any hyperacuity range.

3. Experiment 2

Tilt adaptation results in a repulsive (direct) and attractive (indirect) aftereffect (Gibson and Radner, 1937; Wenderoth and Johnstone, 1988). The direct aftereffect involves post-adaptation repulsion of perceived orientation of a test relatively close in orientation to the adaptor, while the indirect effect involves perceived attraction of orientation of a perpendicular test stimulus towards the adapting orientation. The indirect aftereffect is typically smaller (by approximately 1–2 arc deg) than the direct aftereffect.

Experiment 2 was performed to test whether the pulsating Gabor adapt/test stimulus used in experiment 1 would lead to a similar tilt aftereffect as seen for stimuli used before, such as lines (Gibson and Radner, 1937; Wolfe, 1984) circular gratings (Wenderoth and Johnstone, 1988) or counterphasing Gabor patches (Clifford *et al.*, 2001). This was done to see how well the current results can be compared with previous results on orientation adaptation and discrimination. The observers adapted to the dynamic Gabor patch, which was oriented slightly CW or CCW from vertical by 5, 8, 11 or 14°, for 24 s, after which a vertical or horizontal test Gabor was presented. The observers were told that the test would either be oriented slightly clockwise or counter-clockwise to vertical and they had to decide which by pressing the appropriate key.

3.1. Methods

3.1.1. Observers

The two naïve observers (ATL and GA) tested in Experiment 1 participated. Each observer participated in 480 trials.

3.1.2. Procedure

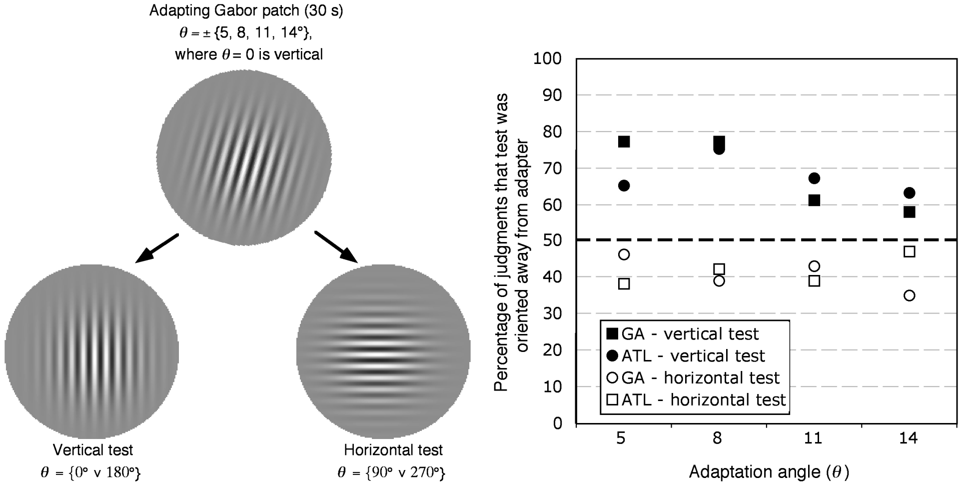
Observers viewed a dynamic Gabor patch of the same size as in Experiment 1 for 24 s. The patch was oriented 5, 8, 11 or 14° in either direction from vertical ($\theta = \pm\{5, 8, 11, 14\}$, where $\theta = 0$ is vertical). The test Gabor patch presented for 3 s following adaptation was vertical ($\theta = \{0 \vee 180\}$), or horizontal ($\theta = \{90 \vee 270\}$), with a 1 s blank screen (mid gray; 15.8 cd/m^2) presented in between. The observers were not aware that the test Gabors were either vertical or horizontal, and were told that they would always be oriented slightly clockwise or counterclockwise relative to horizontal or vertical. They were instructed to assess whether the Gabor was oriented CW or CCW to horizontal or vertical (depending on the orientation of the test). Again this was a 2AFC task, so the observers were told to guess if they were unsure whether the orientation of the test was CW or CCW. Otherwise methods were similar to Experiment 1.

3.2. Results and Discussion

In Fig. 3B the percentage of judgments that the vertical or horizontal test was of an orientation opposite (pooled over CW or CCW) to that of the adaptor is plotted for the two naïve observers. Chance level (50%) is indicated by the dotted line. So, in other words, a direct tilt aftereffect would be reflected by percentages higher than the 50% chance level (the test is perceived as oriented away from the adapting pattern — a repulsive effect). The indirect aftereffect would be reflected by a bias towards lower percentages than the chance level (the test pattern is perceived as being oriented towards the adapting orientation — an attractive effect). According to the results, if the adaptor is, for example, oriented clockwise by 5 arc deg, a vertical test will be judged to be counterclockwise 65–77% of the time, while a horizontal test is judged as counterclockwise 39–46% of the time.

There was a strong direct TAE as demonstrated by a strong bias to perceive the vertical test Gabor as oriented counterclockwise to the adaptor. Conversely, a smaller, but notable indirect tilt aftereffect was also seen, where a horizontal test Gabor was more likely to be judged as oriented towards the adapting Gabor.

The results of Experiment 2 show that traditional direct and indirect tilt aftereffects are seen with the dynamic contrast varying and phase shifting Gabor patch used here. This shows that the effects of adaptation observed in Experiment 1, where sensitivity to small changes in orientation increases with increased adap-



(A) (B)

Figure 3. The design and the results of Experiment 2. Panel (A) shows the adapting Gabor patch of orientations 5, 8, 11 or 14° CW or CCW away from vertical, presented for 24 s. The tests were either vertical or horizontal, presented for 3 s, following a 1 s blank screen. Panel (B) shows the results. The filled symbols show the percentage of trials where the vertical test Gabor was judged as being oriented in the other direction to the adapting Gabor (a repulsive effect), while the open symbols show the ‘indirect effect’ the percentage of time that the horizontal Gabor was judged as being oriented in the other direction relative to the adapting Gabor (an attractive effect).

tation time, can be discussed in the same context as other ‘standard’ findings on the tilt aftereffect.

4. Experiment 3

While the results of Experiment 2 show that both direct and indirect tilt aftereffects are seen with the contrast varying Gabor used in Experiment 1 they do not provide a measure of their size. Experiment 3 was aimed at directly testing the size of the tilt-aftereffect by using the method of adjustment. Following 24 s adaptation the observers adjusted a test grating to its perceived vertical or horizontal.

4.1. Methods

The observers adapted for 24 s to the contrast varying Gabor patch. The only difference from previous experiments is that in this case the Gabor was presented on an 85 Hz CRT display controlled by a G4 Macintosh computer. The observers adapted for 30 s to the Gabor at various orientations (see below) and were then presented with horizontal or vertical static test Gabors, and adjusted their orientation (by keypress; ‘4’ for CCW tilt and ‘6’ for CW tilt, in steps of 15 arc min) so that they appeared exactly horizontal or vertical. The program only allowed combinations of adaptor and test angle resulting in the following changes in angle: 5, 10, 20, 38, 56, 74. This means that if the test was vertical, adapting gratings could be 5, 10, 20, 38, 56, 74 and if the test was horizontal the adapting gratings were 85, 80, 70, 52, 34, 16. Whether the adaptor was oriented left or right to vertical (arbitrarily designated as $\theta = 0$) was determined randomly. There were 60 trials for each angle difference between adaptor and test, 360 trials in total for each observer.

5. Results

Figure 4 shows estimates of the size of the tilt aftereffect of the stimulus used in Experiments 1 and 2, by plotting by how much a vertical or horizontal test Gabor needed to be adjusted in tilt to appear either vertical or horizontal. The measured size of the direct tilt aftereffect was approximately 2–3.5°, peaking at an angle of 10–20° between adaptor and test. The indirect effect (mainly seen in the results here for a 74° difference between adaptor pattern and test) was $-1°$ on average.

This result accords fairly well with other estimates of the size of the tilt aftereffect. Gibson and Radner (1937) found aftereffects of 1–2.5° following adaptation to lines and Wolfe and O’Connell (1986) found effects of 2–5° with comparable stimuli. For circular gratings, estimates range from 2–4° (Clifford *et al.*, 2001) to 5–7° (Wenderoth and van der Zwan, 1989) to take some examples.

Overall, Experiments 2 and 3 show that standard tilt aftereffects are seen following adaptation to the stimulus used in Experiment 1. The two experiments also help to alleviate any worry that memory representations can account for the sensitivity changes following adaptation observed here, since it is unlikely that memory rep-

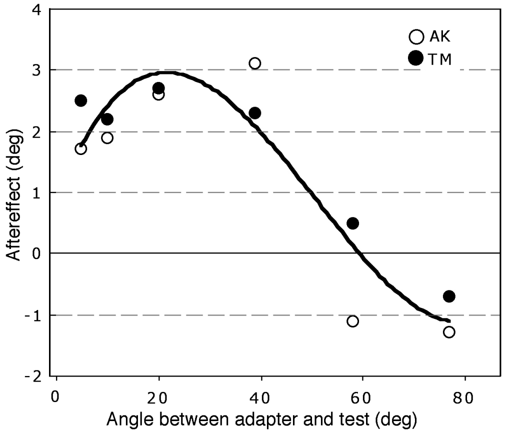


Figure 4. The results from Experiment 3. The graph shows the aftereffect measured by the adjustment of the orientation of a vertical or horizontal test following adaptation to various test orientations. The aftereffect is indicated by the average angle adjustment needed for perceived horizontal or vertical (pooled) as a function of differences in angle between adaptor and test. The black line shows a fit of a cubic polynomial to the average aftereffect to highlight the trends in the results.

resentations can lead to illusory perceptions in the opposite direction to what has been viewed.

6. General Discussion

The variation in environmental stimuli may be more important for visual perception than the absolute levels of stimulation. For a useful representation of the world it is less important to maintain an accurate representation of absolute stimulation levels, than signaling changes in the environment (Attneave, 1954; Cornsweet, 1970; Kingdom and Moulden, 1988; Land, 1974). Attneave, for example, argued that regions in the image which convey changes, such as changes in orientation, are the most important for object recognition (see also Hoffman and Richards, 1984; Hoffman and Singh, 1997; Kristjánsson and Tse, 2001). A more general version of a similar argument is that the response properties of neurons are adapted to the statistics of the input that we have been exposed to during the evolution of sensory systems (Simoncelli and Olshausen, 2001). Despite a whiff of circularity, this argument has some attractive features, and corresponds rather well with what is known about the operating characteristics of sensory systems.

The current results show that this general scenario applies to sensitivity to tilt. Even discrimination of properties of the adapting stimulus itself are improved with increased adaptation time, in this case the orientation of a Gabor patch. A likely possibility is that this effect of adaptation reflects the operation of a gain-control mechanism that adjusts the responses of the system to fit the characteristics of the input. Regan and Beverley (1985; see also Clifford *et al.*, 2001) previously found that adaptation to a high contrast circular grating resulted in better orientation judgments of two test Gabors (judgment of which one was oriented more clockwise), but importantly here, this is shown to apply to judgments of the tilt of the adapting stimulus itself, and this benefit becomes larger the longer the adaptation time, as had previously been shown to occur for adaptation to luminance defined motion (Bex *et al.*, 1999; Kristjánsson, 2001). The dynamic Gabor used here, which varied both in contrast and phase, ensures that local luminance changes cannot be used as a cue.

Adaptation reflects a process of fitting the operating characteristics of the system to the input characteristics (Clifford *et al.*, 2007). An important early theoretical development can be found in the adaptation-level theory of Helson (1964b; 1948). Helson argued that in establishing characteristics of perceptual performance the preceding stimulus level must be taken into account, noting that 'any momentary state of the system [represents] a quasi-stationary process in dynamic equilibrium' (Helson, 1948, p. 298). The state of the observer provides a frame of reference according to Helson: '[f]or every excitation-response configuration there is assumed a stimulus which represents the pooled effect of all the stimuli and to which the organism may be said to be tuned or adapted' (Helson, 1947, p. 2). Helson's work was pioneering in showing that judgments are made relative to flexible anchors.

The findings on tilt adaptation differ, on the surface, from contrast adaptation effects. Regan and Beverley (1985) found that adaptation to a high contrast grating also led to decreases in contrast sensitivity, as seen for example by Blakemore and Campbell (1969) and Pantle and Sekuler (1968) previously (see also Hammett *et al.*, 1994). But this leaves open the possibility that sensitivity to changes in spatial frequency might concurrently increase, even though detection is harmed. This could be analogous to perceived changes in speed (decreases in fact) found during motion adaptation (Bex *et al.*, 1999; Ledgeway and Smith, 1997; Thompson, 1981). Blakemore *et al.* (1973) observed that adaptation of a high contrast grating led to lowered perceived contrast of the adapting grating, as well as of the apparent contrast of a subsequently presented one. Abbonizio *et al.* (2002), have indeed suggested that such contrast adaptation may enhance contrast discrimination, but this may vary depending upon contrast levels. Greenlee and Heitger (1988), observed threshold increases from adaptation at low contrast levels, but a decrease at higher contrast levels. This does not, however, alter the importance of the finding that contrast adaptation can enhance contrast discrimination, at least under some circumstances. Contrast adaptation has been shown to be strongly orientation selective (Blakemore and Campbell, 1969; Bradley *et al.*, 1988; Pantle and Sekuler, 1968), and Ware and Mitchell (1974) found that adaptation effects of orientation are strongly selective for spatial frequency, so the increased sensitivity to changes in tilt found here may not necessarily be so surprising and, importantly, Regan and Beverley (1985) found that orientation discrimination improves with adaptation, while grating detection is concurrently degraded.

6.1. Some Caveats

Clifford *et al.* (2001) have shown benefits from adaptation also occur for the indirect tilt aftereffect (they found that adaptation to an orthogonal grating improved subsequent orientation discrimination). This was also observed by Dragoi *et al.* (2002) for very brief (400 ms) adapting gratings. Dragoi *et al.* also observed an increase in discrimination thresholds for iso-oriented gratings, in seeming contrast to what was observed here, but note that again the adapting gratings were only presented for 400 ms and some masking specific to iso-oriented gratings may occur with brief stimuli of this sort.

It should also be noted that the role of memory representations in mediating the increased sensitivity (see, e.g., Nachmias, 2006) is still unclear. While it is not obvious how such a memory representation would lead to aftereffects in the other direction to the adapted stimulus, it is hard to rule out such effects here, nor in other studies showing increased sensitivity from adaptation such as Bex *et al.* (1999), Kristjánsson (2001) or Regan and Beverley (1985). It is in fact quite possible that memory representations play a role in adaptation effects. Further research is necessary for conclusive answers.

Note also, that under no circumstances do our results reflect discrimination thresholds in the hyperacuity range, as have been seen in other circumstances. Orientation discrimination thresholds are typically in the range of 18 to 30 arc min (Regan, 2000; Westheimer, 1977). This has been explained by assuming that discrimination performance reflects a population response, rather than cone density. But this is typically seen for relatively high contrast stimuli. The contrast varying phase shifting Gabor patch used here may simply not lend itself very well to high acuity orientation discrimination.

7. Summary and Conclusions

Adaptation to tilt angle results in increased sensitivity to small deviations in tilt of the adapting stimulus itself. The dynamic nature of the stimulus used as adaptor and test, which varied temporally in phase and in contrast shows that this does not reflect adaptation to local luminance levels. This fits well with other findings from the literature on visual perception. There is, for example, evidence from the field of visual attention that attentional networks are sensitized to recent input features (Geng *et al.*, 2006; Kristjánsson *et al.*, 2007; Sigurdardottir *et al.*, 2008; see Kristjánsson, 2008, for review), which is entirely consistent with the ideas under discussion here. Such adaptive coding makes sense, of course, given the limited processing capacity of the nervous system. We choose to attend to things of relevance (Kristjánsson and Campana, 2010) and it is reasonable to expect that the response properties of our visual system might be adjusted to fit the incoming stimulus characteristics at a given point in time or space.

Notes

1. $P(CW) = 1/(1 + \mathrm{e}^{-(b_0+b_1)\Delta\theta})$, where b_0 and b_1 are regression coefficients and $\Delta\theta$ denotes the change in tilt angle.

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