Rapid Communication

Common mechanisms for 2D tilt and 3D slant after-effects

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Abstract

By presenting oriented Gabor patches either monocularly or binocularly, we dissociated retinal orientation from perceived tilt and perceived slant. After adapting to binocular patches, with zero apparent tilt and non-zero slant, small tilt after-effects (TAEs) and large slant after-effects (SAE) were measured. Adapting to monocular patches with non-zero tilt and zero slant produced large TAEs and smaller SAEs. This pattern of results suggests that a common, low-level adaptation to monocular orientation is involved in slant and tilt after-effects. However, the *incomplete* transfer between slant and tilt makes it clear that higher-level adaptation is also involved, perhaps at the level of surface representation.
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1. Introduction

Visual after-effects have proven to be a useful tool for examining the computational mechanisms involved in perception (e.g. McCollough, 1965). Adaptation experiments not only inform us about the plasticity of the visual system, but perceptual after-effects can also shed light on the hierarchy and structure of normal visual processing. Specifically, by manipulating the attributes of adaptation stimuli and monitoring the resultant after-effects, we can probe the individual steps involved in recovering three-dimensional (3D) shape. Here we use an adaptation paradigm to examine tilt and slant perception and their dependence on common mechanisms. Tilt refers to the orientation of visual features within the fronto-parallel plane and is independent of the 3D orientation of the surface on which the features lie. Slant describes the orientation of the surface in depth; specifically, in this paper, the angle of rotation about a horizontal axis.

Many studies (e.g. Gibson, 1937) have investigated the tilt after-effect (TAE). Looking at a tilted patch for an extended period of time causes a subsequently viewed vertical patch to appear tilted in the opposite direction. Similarly, adapting to a surface slanted in depth causes a subsequently viewed fronto-parallel test surface to appear slanted in depth in the opposite direction (e.g. DeValois, von der Heydt, Adorjani & DeValois, 1975; Köhler & Emery, 1947).

Recent studies have found that in the case of stereo-depth after-effects, adaptation occurs predominantly at the level of surface or shape representation (Domini, Adams & Banks, 2001; Poom & Borjesson, 1999). However, there is also some evidence of adaptation to binocular disparity per se (Berends & Erkelens, 2001). Similarly, partial inter-ocular transfer of the TAE suggests that tilt adaptation occurs at both higher-level and lower-level sites (hence incomplete transfer).

Here we investigate whether (a) monocular adaptation to a tilted patch leads to binocular slant after-effects (SAEs), or (b) binocular adaptation to a slanted surface produces monocular TAEs.

Let us consider (a) first. It is not at all obvious whether monocular tilt adaptation would produce a 3D SAE. 3D after-effects are commonly accounted for by disparity adaptation, or adaptation at the level of surface slant representation. However, during monocular adaptation there is no disparity input and the surface appears fronto-parallel. Therefore, neither of these explanations is plausible. Stereoscopic slant perception relies on inter-ocular differences in the position and possibly also the orientation (e.g. Blakemore, Fiorentini & Maffei, 1972) of monocular features. Monocular adaptation could lead to a SAE by altering the input to

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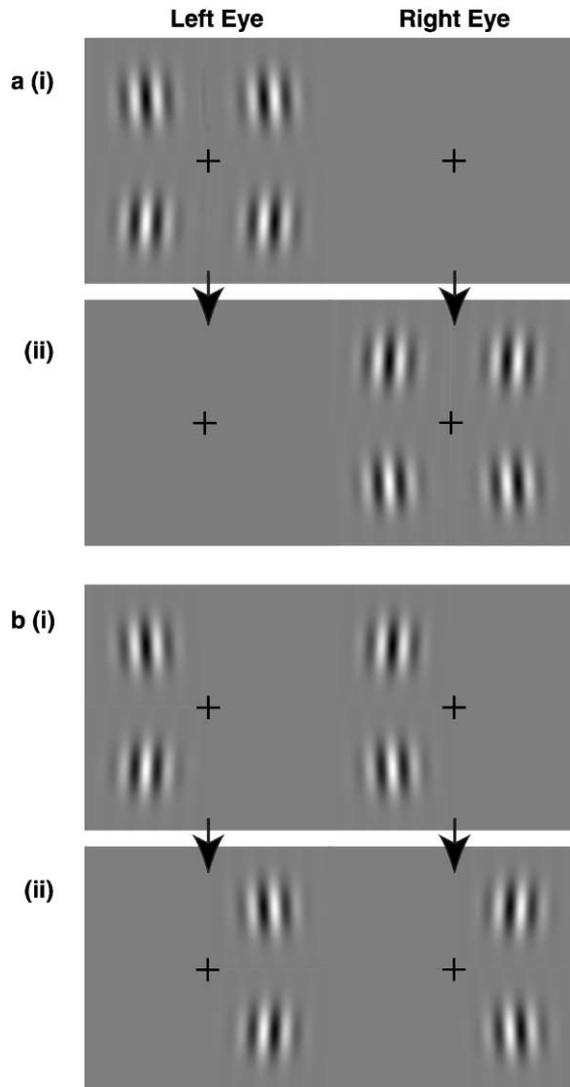*E-mail address:* wendy@psy.gla.ac.uk (W.J. Adams).

Fig. 1. Adaptation stimuli. Monocular adaptation stimuli are shown in a(i) and a(ii). The left eye a(i) and then the right eye's stimulus a(ii) were shown alternately for 3 s each. During the 3 s, 4 different phases were presented (not represented here). Binocular adaptation stimuli are shown in b(i) and b(ii). Binocular stimuli were displayed for 3 s in the left visual field b(i) and then in the right visual field b(ii). Again, four different phases were used (not shown here) and the stimuli alternated between (i) and (ii) for a total of 6 min. Cross-fusion will give an impression of the stimuli.

binocular mechanisms which compute slant. In other words, if position or orientation coding of features was altered, and this altered representation was then used as an input to compute slant, then misperceptions of slant would follow. In the current study, position is not adapted, but orientation of features (tilt) is. We are aware of only one study that has tested whether monocular tilt adaptation can lead to binocular SAEs. In a similar experiment to the present one, Köhler and Emery (1947) presented oppositely oriented lines alternately to the two eyes. They then looked for changes in perceived slant when binocular, vertical line stimuli were

viewed, but failed to find the depth after-effects predicted by low-level, monocular adaptation mechanisms.

Secondly, let us consider the transfer (b) from binocular adaptation to a monocular TAE. Consider the stimuli shown in Fig. 1b. The oriented monocular image features are tilted. However, when the images are fused, no perceived tilt is present. Such stimuli could therefore only produce a TAE via some low-level tilt adaptation to the monocular features. Looking at the transfer of after-effects in this way can shed light on the mechanisms underlying tilt and slant perception.

2. Methods

Three observers (1 author, 2 naïve) took part in the experiment. Stimuli were viewed in a split-screen modified Wheatstone stereoscope with all cues consistent with the viewing distance of 80 cm. Stimuli were Gabor patches, each subtending 4°. The patches had a spatial frequency of 1 cycle/deg and 100% contrast. The stimuli were pre-generated and displayed using Matlab. There were two different adaptation conditions (monocular and binocular) and two separate sessions for each condition were conducted at least one day apart. Three additional test sessions were conducted without any adaptation, to establish baseline values.

The monocular adaptation condition is represented in Fig. 1a. The two sets (a(i) and a(ii)) were shown alternately for 3 s each for a total of 6 min. In adaptation set a(i), the left eye viewed Gabors tilted by $-3°$ from vertical in the top-left and top-right quadrants, and Gabors with $+3°$ orientation in the bottom quadrants. The right eye was presented with a uniform grey field. During the 3 s the patches switched randomly between four possible phases for 120 ms each. This phase shifting eliminated the problem of luminance after-effects. In set a(ii) the right eye viewed $+3°$ Gabors in the top two quadrants and $-3°$ Gabors in the bottom, while the left eye viewed a uniform grey field. The percept during this adaptation was of fronto-parallel gratings, tilted away from vertical, although this perceived tilt reduced during adaptation.

The binocular adaptation condition is represented in Fig. 1b. The two sets (b(i) and b(ii)) were shown alternately for 3 s each for a total of 6 min. In adaptation set b(i) the left eye viewed a $-3°$ patch in the top-left and a $+3°$ patch in the bottom-left quadrant, while the right eye viewed a $+3°$ patch in the top-left and a $-3°$ patch in the bottom-left quadrant. In set b(ii), the left eye viewed a $-3°$ patch in the top-right and a $+3°$ patch in the bottom-right quadrant, while the right eye viewed a $+3°$ patch in the top-right and a $-3°$ patch in the bottom-right quadrant. Again, during each 3 s presentation, four different phases were shown in random order. The phase of the left and right eyes' stimulus was paired

(the stimulus did not jump back and forth in depth). The perception during the binocular adaptation was of vertically oriented gratings, slanted top away for the upper visual field and bottom away in the lower visual field. Having differently oriented gratings in the upper and lower visual field in all presentations eliminated torsional eye movements.

It is important to note that in each type of adaptation, the individual retinal images were identical in orientation and duration of presentation. However, the presence or absence of binocular pairing in time produced either slant or tilt perception. Testing followed.

On each trial, a top-up of the adaptation stimuli was shown (except in the baseline condition), lasting 6 s in total. Then either a monocular or binocular test stimulus was shown for 1 s (see Fig. 2). Monocular stimuli con-

sisted of two patches such as the right eye's half of Fig. 1b(i). A diagonal fixation cross indicated that a tilt judgement was to be made. Specifically, observers judged whether the top patch tilted right and the bottom patch left, or vice versa, i.e. middle left or middle right.

A horizontal–vertical fixation cross indicated that a slant judgement should be made to a binocular test stimulus such as both eye's sections of Fig. 1b(i). Observers judged whether the top patch was slanted top away and the bottom patch slanted top forward, or vice versa, in other words, whether the middle of the stimulus pointing forward or backwards. The orientation of the test patches varied within the range −3° to 3°. The upper and lower patches always had equal and opposite orientation angles and opposite phase (chosen randomly).

All combinations of test location (left or right visual field) and test eye (left eye or right eye) gave four sets of tilt judgements. There were also two types of slant judgements (binocular, left or right visual field). For each of these six judgement conditions, each observer completed ten trials at nine different test orientations. This was completed before adaptation to get a baseline measure and after both types of adaptation, in a total of six sessions. Using this method, the magnitude of the tilt and SAEs was measured after both monocular and binocular adaptation.

3. Results

After-effects were calculated in the following way: For each type of test judgement, (e.g. monocular tilt judgements, left eye, left visual field, following binocular adaptation) a cumulative Gaussian was fitted to the data. A confidence limit of ±1 standard deviation was obtained for the 50% threshold (the point where the test stimulus appeared vertical) using the Psychofit Matlab toolbox (Wichmann & Hill, 2001). Similarly, a cumulative Gaussian was fitted to the baseline data for the same condition (tilt judgments, left eye, left visual field). The magnitude of the after-effect, in this case the TAE, was calculated as the difference between the means of the fitted distributions.

After-effects were calculated in this way for all adaptation and test conditions. Data was then averaged over field location and eyes (tilt judgements only) within observers to give overall values for the tilt and SAEs following monocular and binocular adaptation. There were no systematic differences between left and right eyes or visual fields. This averaged data is shown in Fig. 3, as a percentage of complete adaptation (i.e. the angle as a fraction of 3° of adaptation). The error bars give confidence limits of ±1 standard deviation of the magnitude of the after-effects (the mean difference between pre- and post-adaptation 50% thresholds). Clear slant
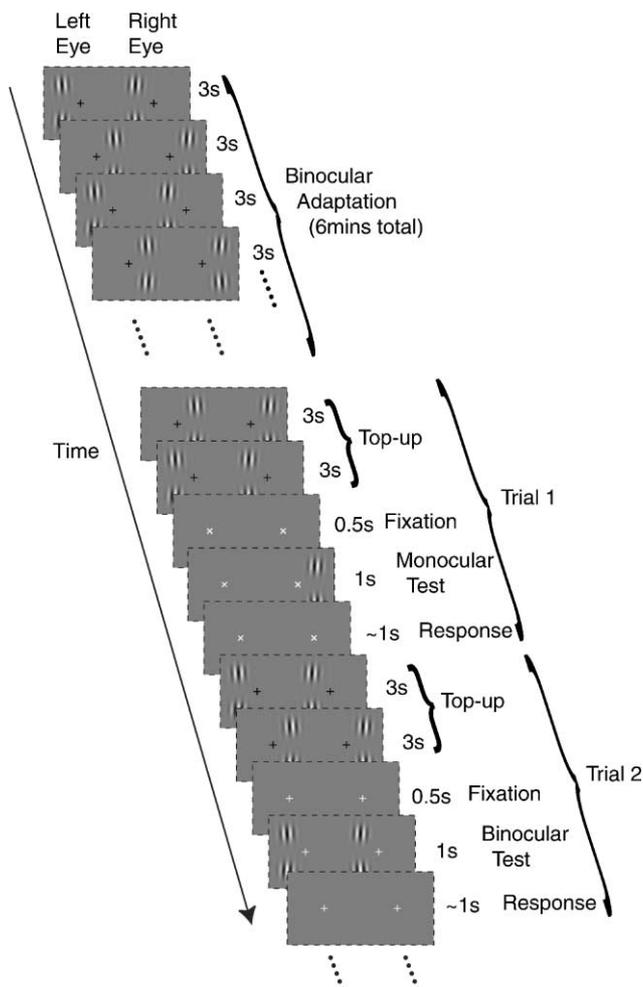

Fig. 2. Time course of experiment. After 6 min of adaptation, the testing trials began. On each trial, 6 s of top-up were shown, in which the phase of the stimuli was randomized as in the adaptation period. Also the order of presentation (left eye/right eye, or left side/right side) was chosen randomly. A fixation cross on an otherwise grey field was displayed for 0.5 s, followed by a 1 s test stimulus whose type (monocular or binocular) and orientation were chosen pseudo-randomly. The observer's response triggered a new trial.
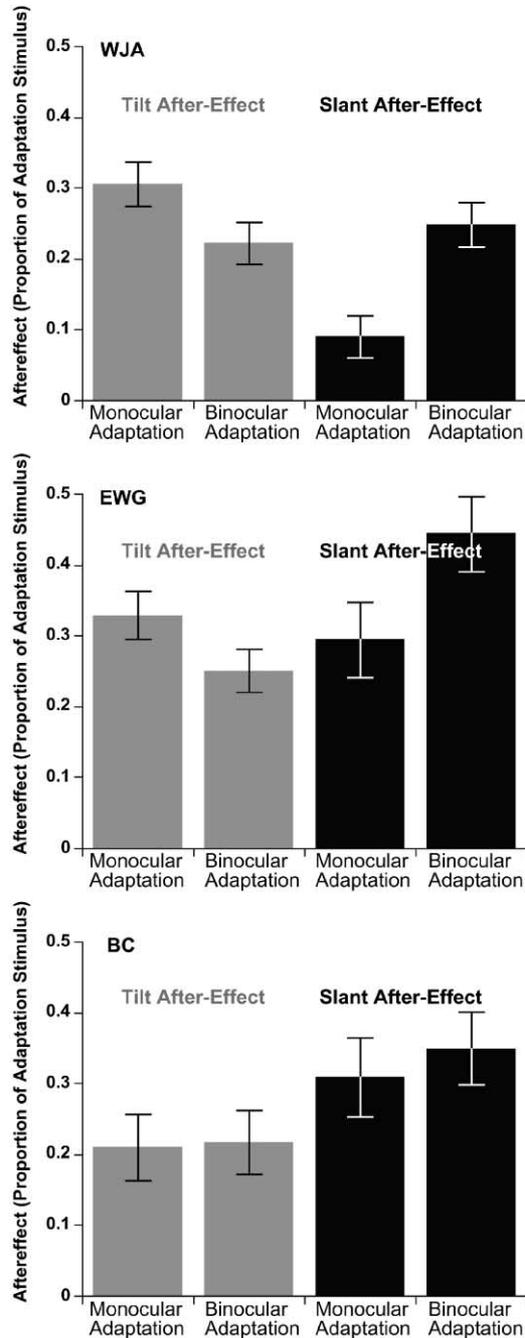
Fig. 3. Results summary. The magnitude of the TAE (grey bars) and SAEs (black bars) following both types of adaptation (horizontal axes). The after-effects are shown as a proportion of the adaptation stimulus, i.e. the orientation that appeared vertical (or fronto-parallel) divided by 3°. Error bars show ±1 standard deviation of the after-effect.

and tilt after-effects were observed for all three participants after both monocular and binocular adaptation. These after-effects were all significantly different from zero at the 95% confidence limit (Rice, 1988). As expected, monocular adaptation produced a large TAE (28% on average) and binocular adaptation produced a large SAE (35% on average). More interestingly, we observed cross-overs between monocular and binocular conditions. Monocular adaptation produced a significant SAE (23%) and reversely, binocular adaptation produced a significant TAE (23%).

4. Discussion

Our first finding is that for all observers, monocular adaptation produced a large TAE (Fig. 3, column 1). However, inter-ocular transfer of the TAE (Gibson, 1937) will have reduced the size of all TAEs measured here, as the left and right eyes saw oppositely tilted stimuli during adaptation.

Our second finding is that, following *binocular* adaptation, all observers showed a TAE (Fig. 3, column 2), despite the adaptation stimulus giving rise to a percept of zero tilt. This demonstrates that low level, monocular adaptation to retinal orientation affected subsequent tilt judgements.

For two of the three observers, monocular adaptation produced larger TAEs than binocular adaptation. In other words, when the adaptation stimulus was perceived as tilted, it produced a larger TAE than when the same retinal orientations were presented binocularly and thus perceived as having zero tilt. For the third observer, monocular and binocular adaptation produced similarly sized TAEs. This difference between monocular and binocular adaptation cannot easily be explained by different levels of adaptation of monocular and binocular cells in the two conditions. Two types of cells are relevant here, monocular cells which respond only to inputs from one eye, and 'OR' cells which respond equally to inputs from either eye or both eyes, (e.g. Howard & Rogers, 1995). In fact, these cells probably form part of a continuous 'ocular-dominance scale' as proposed by Hubel and Wiesel (1962) after studies in the cat visual cortex. Schiller, Finlay and Volman (1976) also categorised these cells in monkey V1. Inter-ocular transfer of the TAE can be attributed to adaptation of OR cells (e.g. Moulden, 1980).

In the current study, during *monocular* adaptation, monocular 'left eye' cells are exposed to one sign of orientation, and monocular 'right eye' cells to the other. Binocular OR cells are alternately exposed to positive and negative orientations. During *binocular* adaptation, the situation is identical, except that binocular OR cells are simultaneously, rather than alternately, exposed to positive and negative orientations. It seems unlikely that these OR cells would contribute to a TAE following either type of adaptation. Rather, the lack of a net adaptation within OR cells will have reduced the measured TAE. Furthermore, whatever the role of the OR cells during adaptation, it is difficult to see why the contribution would be different in the two adaptation conditions. (Cells which respond only to input from both

eyes, 'AND' cells, do have different excitatory inputs during monocular and binocular adaptation conditions, but are not involved during monocular testing.)

As mentioned above, one difference between the two adaptation conditions is that during monocular adaptation the stimuli have non-zero apparent tilt. However, during binocular adaptation the stimuli have zero apparent tilt. The difference in the resultant TAEs might be explained by adaptation at a higher-level site, such as surface representation (Domini et al., 2001). Our data provide some evidence that TAE's are a result of two components; the (low-level) adaptation to retinal orientation demonstrated in the binocular adaptation condition, as well as a higher-level adaptation that is a function of perceived orientation.

Our third finding is that following monocular adaptation to a perceptually fronto-parallel surface with tilted features, a SAE was measured for all three observers using binocular stimuli (Fig. 3, column 3). In contrast to Köhler and Emery's (1947) finding, tilt adaptation can affect subsequent slant judgements. It is interesting to consider the mechanism by which our SAE was generated, following monocular adaptation. As mentioned above, stereoscopic depth perception uses the differences (disparities) between monocular features to recover 3D structure. In theory, our SAE could be caused by manipulating stereoscopic depth perception in two ways: (1) by changing the mapping between disparity and perceived slant, or (2) by altering the input (position disparity or orientation disparity) used by mechanisms that compute slant.

Let us consider option (1). There is evidence that the mapping between retinal disparity and perceived slant can be affected by long-term adaptation (Adams, Banks & van Ee, 2001). However, during our monocular adaptation condition there is no binocular stimulation. Therefore it is unlikely that the input–output function of binocular mechanisms would be affected in this case. This leaves option (2); that the depth after-effect is mediated via the alteration of the monocular inputs to binocular mechanisms that compute slant. These inputs could be position or orientation of features. In our set-up, it is orientation rather than position adaptation that is occurring; different phase stimuli are used, the absolute position of features varies, but their orientation is constant. Our data therefore provide strong evidence that differences between the orientations of monocular features (orientation disparities) are used to recover depth.

Whether or not orientation disparities per se give rise to depth perception is a contentious issue. It is difficult to establish an independent role of orientation disparity because differently oriented features also give rise to a vertical gradient of horizontal position disparities. Psychophysical experiments on humans have attempted to differentiate the two by putting position and orientation disparities into conflict (Ninio, 1985; von der Heydt, Adorjani, Hänny & Baumgartner, 1978) or by making one or other of the cues more reliable (Cagenello & Rogers, 1993; DeValois et al., 1975). These studies have not led to any clear consensus on a role for orientation disparity.

Neurophysiologcial studies in the cat (Blakemore et al., 1972; Nelson, Kato & Bishop, 1977) and the macaque (Bridge & Cumming, 2001) have led to similar conclusions; although cells have been found which are sensitive to inter-ocular orientation differences, this cannot be disentangled from sensitivity to position disparity.

By dissociating position and orientation with phase shifted stimuli, we have provided strong evidence to suggest that orientation disparity information is exploited by the visual system. In contrast, Köhler and Emery (1947) found the opposite result. They give sparse experimental details, only that they presented differently tilted lines alternately to the two eyes using a mirror stereoscope. It is therefore difficult to determine why we found a SAE and they did not. Possibilities include insufficient adaptation time and stimulus differences—they used single line stimuli. They may have used adaptation stimuli with different orientations from ours. Also, their test procedure may have been too insensitive to measure the after-effect. They only state that they "never obtained the faintest indication of such effects" when viewing vertical test lines.

It should be noted that for one observer, BC, the SAE produced by monocular adaptation was larger than the TAE. This may seem initially surprising, but is probably a result of inter-ocular transfer of the TAE, which can produce an after-effect in the un-adapted eye as large as 40%–100% of the effect measured in the adapted eye (Campbell & Maffei, 1971; Gibson, 1937).

The fourth, perhaps less surprising observation is that binocular adaptation produced a large SAE (Fig. 3, column 4). For all three observers, binocular adaptation (which was accompanied by perceived slant) produced a larger SAE than monocular adaptation (perceived as fronto-parallel). It is possible that the mapping between retinal disparity and slant was adapted directly (Adams et al., 2001) or that adaptation at the level of surface representation occurred (Domini et al., 2001; Poom & Borjesson, 1999).

In summary, our data show that tilt and SAEs are inter-related, and are the result of adaptation at multiple stages of representation. In particular, low-level tilt adaptation contributes to both tilt and SAEs. Our data also suggest that a number of stages are involved in tilt and slant perception. We provide strong evidence that orientation disparities provide a source of information in addition to position disparities for recovering 3D scene structure.

Acknowledgements

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