

SUBJECTIVE CONTOURS, TILT AFTEREFFECTS, AND VISUAL CORTICAL ORGANIZATION

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Abstract—The tilt aftereffect (TAE) was used to study interactions between real and subjective contours. Subjects adapted to either real or illusory lines and were then shown test stimuli containing real or illusory lines. In our first experiment, we found that there is a marked asymmetry in the interactions between real and subjective stimuli. Adaptation to real lines produces comparable TAEs with real and subjective test lines. With either type of test stimulus the maximum effect occurs with a 10–20 deg difference between the orientations of the adaptation and test stimuli. Also, there is a strong TAE when the adaptation and test stimuli contain only subjective lines. However, there is a significantly weaker TAE when the adaptation stimulus is subjective and the test stimulus is real. In a second experiment we find that interocular transfer of tilt aftereffects is greater when the test stimulus is subjective than when it is real. These results are consistent with physiological reports that a subset of orientation selective cells in visual cortex is responsive to subjective contours and that these cells are more binocular, on average, than those responsive only to real contours. Our findings also suggest that the perception of subjective contours is based on the activation of neurons with properties, such as orientation selectivity, which are characteristic of early visual cortical areas.

Subjective contour Illusory contour Tilt aftereffect Interocular transfer

INTRODUCTION

Subjective or illusory contours are lines or edges perceived where there is no luminance or color discontinuity. Although they have been studied extensively, fundamental issues remain unresolved (for a review see Petry & Meyer, 1987). One of the most basic points which remains unsettled is the neural mechanism(s) responsible for the perception of the illusory contours. A broad spectrum of explanations has been proposed which ranges from simple neural connectivity models to cognitive interpretation schemes. For instance, Grossberg and Mingolla (1985) have shown theoretically that under some conditions interactions between orientation-selective neurons can lead to the generation of a neural response associated with an illusory line. A strikingly different approach to explain the perception of subjective contours is epitomized by the work of Gregory (1972) and Rock and Anson (1979), among others. To use an example, these authors suggest that an illusory triangle is seen in the "Kanizsa triangle" figure because a triangle occluding three disks is the most concise interpretation of the stimulus or simply the interpretation most consistent with everyday visual experience.

Into this unsettled situation have come very interesting physiological results which show that some cells in the visual cortex of macaque monkeys can be activated by subjective contours (Peterhans, von der Heydt & Baumgartner, 1986; von der Heydt, Peterhans & Baumgartner, 1984). Von der Heydt and coworkers found that cells in cortical area V1 respond only to real contours whereas 40% of the cells in V2 respond to subjective contours. All cells in V2 respond to real contours as well. The distribution of receptive field types is schematized in Fig. 1. Assuming that the human visual cortex is similar to macaque cortex, these findings suggest that the perception of subjective contours may be determined to some significant degree by the response of cells in early visual cortical areas. Responses to subjective contours have also been found in cat visual cortex (Redies, Crook & Creutzfeldt, 1986), and there is behavioural evidence that cats perceive subjective contours (Bravo, Blake & Morrison, 1988).

Our goal in the present paper is to determine whether the perception of subjective contours is consistent with the properties of V2 neurons, as suggested by the physiological results of von der Heydt et al. Specifically, cells in this cortical

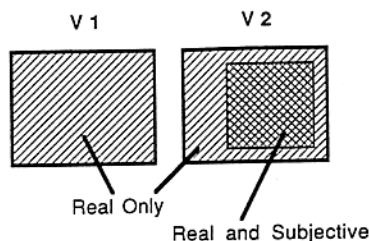


Fig. 1. Schematic representation of the distribution of cells in V1 and V2 based on von der Heydt et al.'s (1984) results. The large box on the left represents cortical area V1 in which cells respond only to real lines and edges. The large box on the right represents V2. The cells in this area also respond to real stimuli and about 40% (small box) can be activated by subjective contours as well.

area are known to be orientation selective and highly binocular (Baizer, Robinson & Dow, 1977; Livingstone & Hubel, 1987; Zeki, 1978). To assess the possibility of orientation selective cells responding to subjective contours we employed the tilt aftereffect (TAE). This effect occurs, for example, if you adapt for a few seconds by looking at lines tilted counterclockwise from vertical and then look at a test stimulus composed of vertical lines. The vertical lines appear to be tilted clockwise, away from the adapting orientation.

Since Gibson first reported this phenomenon (Gibson, 1933; Gibson & Radner, 1937), several explanations have been offered. One simple explanation is that the adaptation stimulus fatigues cortical neurons (Kohler & Wallach, 1944; Osgood & Heyer, 1952). When the adapting pattern is presented, it causes cells to fire most that prefer its orientation. Likewise, when the test pattern is shown, the pattern of activity is centred around cells preferring its orientation. However, those cells that were stimulated by the adaptation pattern may respond less than they otherwise would because of fatigue. Thus, the pattern of neural activity is shifted away from the adaptation orientation and a tilt aftereffect results. As in other explanations of the TAE, such as those based on lateral inhibition (Deutsch, 1964; Ganz, 1966; Tolhurst & Thompson, 1975), the aftereffect results from the orientation selectivity of visual neurons.

Our approach in this paper is to see whether adaptation to subjective contours produces after-effects comparable to those obtained after adapting to a real line, thus supporting the hypothesis that the cells activated by subjective contours are orientation selective, as are those in V2. There was one previous study of tilt aftereffects with subjective contours (Smith &

Over, 1975) but we avoided the complexity of interpretation caused by their particular stimulus configuration (see Discussion). To test the binocularity of the cells responding to real and subjective contours we have also measured interocular transfer of the TAEs obtained with real and subjective lines.

EXPERIMENT 1: TILT AFTEREFFECTS WITH REAL AND SUBJECTIVE LINES

Methods

Two of the authors and three naive observers served as subjects in these experiments. Subjects sat at a viewing distance of 57 cm, facing a vector oscilloscope (Hewlett-Packard 1345A) used to display visual stimuli. This display monitor has a fast phosphor (P4; decay to 1% in 0.47 msec) allowing brief stimulus presentations, and 2048×2048 pixel resolution on a screen measuring 8.5×11.5 cm. Lines in the stimuli had a luminance of 56 cd/m^2 on a background luminance of 11 cd/m^2 . The stimuli were composed of offset arcs of circles arranged to give two straight subjective contours (Fig. 2). Two-dimensional Fourier analysis of this type of pattern confirms that no energy at the orien-

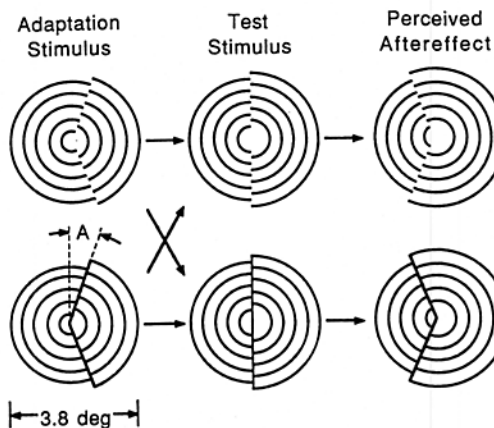


Fig. 2. Paradigm for exp. 1. The stimuli were composed of offset segments of circles. Subjects adapted to either real or subjective contours (left) and following a 100 msec delay they saw a test stimulus containing real or subjective contours flashed on for 50 msec (center). They indicated whether the straight lines in the test stimulus appeared tilted to the left or right of vertical. In each experimental session the type of adaptation (real or subjective) was fixed and the real and subjective test stimuli were randomly interleaved. The TAE is illustrated on the right; a vertical test stimulus appears tilted away from the lines in the adaptation pattern. For the purpose of illustration, the magnitude of the TAE is exaggerated.

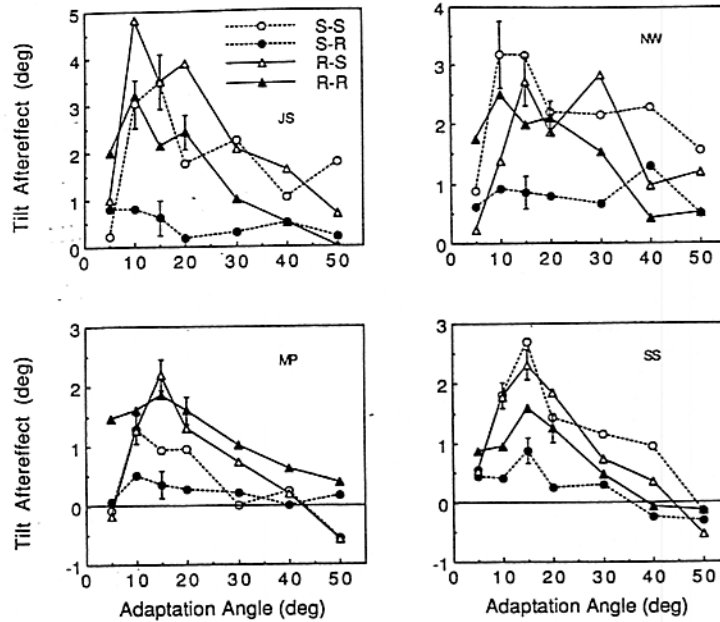


Fig. 3. Tilt aftereffect as a function of adaptation angle. For each of the 4 subjects there are 4 curves representing the conditions in which the adaptation and test stimuli were real or subjective (R = real, S = subjective). Consistently strong aftereffects were obtained except when the adaptation stimulus was subjective and the test stimulus was real (●—●). Error bars indicate the standard error averaged across adaptation angle for each curve.

tation of the subjective contours stands out in the spectral distribution (Vogels & Orban, 1987). A fixation spot 9 arc min in diameter was always visible at the location of the center of the stimulus. To obtain a comparable condition with real contours, real lines were added at the locations of the subjective contours. Tilt aftereffects were measured in the four conditions in which the adaptation and test stimuli were real or subjective contours (Fig. 2). In a given experimental session a subject adapted for 1.5 sec to either a real or subjective stimulus and following a 100 msec delay a test stimulus was flashed on for 50 msec. Subjects pressed a button to indicate whether the real or subjective lines in the test stimulus appeared tilted to the left or right of vertical. One second after their response the adaptation pattern was again displayed for 1.5 sec. In each experimental session the angle from vertical of the straight lines in the adaptation pattern was fixed (the adaptation angle A in Fig. 2). The type of adaptation pattern (real or subjective) was also fixed. The method of constant stimuli was used with the angle of the lines in the test pattern typically covering a range of 8 deg in 1 deg steps. Test patterns with real or subjective lines were randomly interleaved.

Probit analysis (Finney, 1971) was used to fit psychometric functions to the data. Each psychometric curve was typically based on 64

responses. The apparent vertical, following adaptation, was calculated as the angle of the lines in the test pattern to which the subject would respond tilted-left and tilted-right 50% of the time. Prior to each adaptation run, subjects viewed the same set of test patterns and they indicated whether the real or subjective lines appeared tilted clockwise or counterclockwise. Probit analysis was used to determine the angle of apparent vertical prior to adaptation. The tilt aftereffects we report are the measurements of apparent vertical following adaptation minus the baseline perception of vertical obtained prior to adaptation. We found that this procedure of subtracting the baseline reading was beneficial because some subjects consistently perceived the lines to be straight and vertical when they were slightly tilted. Because tilt aftereffects are known to be long-lasting (Wolfe & O'Connell, 1986), we required subjects to have an interval of at least 1-2 hours between experimental sessions. We found that this long inter-run delay considerably decreased variability in the TAEs measured.

Results

Tilt aftereffects for four subjects are shown in Fig. 3. For each subject there are four curves representing the conditions in which the adaptation and test stimuli were real or subjective. The

filled triangles joined by solid lines show the conventional TAE when both adaptation and test stimuli are real. Consistent with previous studies, this TAE is largest when the adaptation angle is 10–20 deg. The maximal effect for the different subjects ranged from 1.6 to 3.2 deg. When the subjects adapted to real lines there were also strong tilt aftereffects when the test stimulus was subjective (open triangles joined by solid lines). The magnitudes of the TAEs with subjective test lines were comparable or slightly larger than those obtained with real test lines. The adaptation angles that gave the largest TAEs were also similar (i.e. 10–20 deg).

Strikingly different effects were obtained when the adaptation stimulus consisted of subjective contours. With a subjective test stimulus we generally find quite strong TAEs. For two of the subjects (NW and SS) these effects are stronger than those obtained in any of the other conditions. For all the subjects the aftereffects are comparable in magnitude to those obtained with an adaptation pattern containing real lines. In contrast, this is not at all the case when the adaptation stimulus is subjective and the test stimulus is real. The TAEs obtained in this condition are markedly smaller than those obtained in any of the other conditions, although they are non-zero (solid circles joined by dashed lines). Clearly, adapting to subjective lines does not strongly bias the perception of the orientation of subsequently-viewed real lines. Also, there is not a clear relationship between the magnitude of the TAE and the adaptation angle, as there is in the other experimental conditions.

Discussion

We have found that adapting to subjective contours produces strong tilt aftereffects when the test stimulus also contains subjective contours, suggesting that there are neurons which respond selectively to the orientation of illusory lines. This inference however hinges on the mechanism underlying tilt aftereffects, which has not been firmly established. Nonetheless, the two most common explanations—that the TAE is based on fatigue of cells responding to the orientation of the adaptation lines (Kohler & Wallach, 1944; Osgood & Heyer, 1952) or that it results from prolonged inhibition from orientation-selective cells activated by the adaptation lines (Deutsch, 1964; Ganz, 1966; Tolhurst & Thompson, 1975)—are founded on the assumption that the cells adapted are selec-

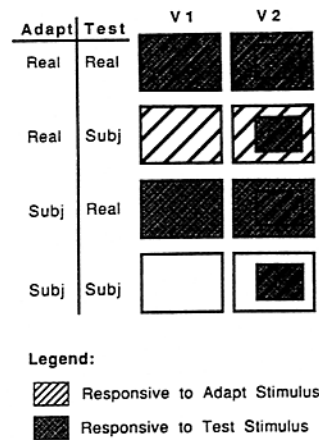


Fig. 4. Explanation of the asymmetrical interaction between real and subjective contours based on von der Heydt et al.'s (1984), physiological results. As in Fig. 1, the boxes on the left represent cortical area V1 and the boxes on the right represent area V2. The small box on the right represents the cells in V2 which are responsive to subjective contours. For each experimental condition the broad diagonal lines indicate cells presumably affected by the adaptation stimulus and the shaded areas indicate cells responsive to the test stimulus. Only in the third row, where the adaptation stimulus is subjective and the test stimulus is real, are there unadapted cells that respond to the test stimulus.

tive for the orientation of the adaptation stimulus. Our data suggest that subjective contours activate orientation selective cells as do real lines. This similarity is underscored by the results showing that real and subjective TAEs have similar dependences on the orientation of the lines in the adaptation patterns.

We suggest that the asymmetry in the interactions between real and subjective contours may be a reflection of a corresponding asymmetry in the distribution of receptive field types in visual cortex (Peterhans et al., 1986; von der Heydt et al., 1984). This hypothesis is schematized in Fig. 4. The left box represents cells in cortical area V1 which only respond to real lines. The right box represents area V2 in which almost all cells respond to real lines and somewhat less than half also respond to subjective contours (small box within V2). In each of the four experimental conditions those cells which are responsive and thus affected by the adaptation stimulus are hatched with diagonal lines. In the top two conditions, subjects adapted to real lines and orientation selective cells in both V1 and V2 are presumably adapted (thus both cortical areas are hatched). In the other two conditions subjects adapted to subjective contours. Only the small box in V2 is hatched because it is only these cells that are activated by subjective contours.

Cortical areas in which cells respond to the test stimulus are shaded. In the top condition in Fig. 4 the adaptation and test stimuli are both real so areas V1 and V2 are both shaded. All the cells responding to the test stimulus were previously adapted, so it is reasonable to expect a strong aftereffect. This is also true when the adaptation is real and the test is subjective (second row). The only cells responding to the subjective test stimulus are in the small box in V2 and they were adapted by the real lines. At the bottom of the figure is the condition in which both adaptation and test stimuli are subjective. As in the other conditions the cells responding to the subjective test stimulus (the small box in V2) were all previously adapted and we therefore expect a strong aftereffect. The one condition distinct from the others is in the third row. Adaptation to the subjective lines only affects the cells in the small box in V2. However all the cells in the shaded areas in V1 and V2 outside the small box respond to the real stimulus. Because all of these unadapted cells respond to the test stimulus, we might not expect as large a TAE. We suggest that this may account for the very weak effect we obtained in this experimental condition. In summary, it appears that the TAE results with real and subjective contours are quite consistent with the distribution of receptive field types in the macaque reported by von der Heydt et al. (1984).

EXPERIMENT 2: INTEROCULAR TRANSFER

We performed a second experiment using interocular transfer to determine if there is any psychophysical evidence that the cells responding to subjective contours are highly binocular. Underlying this experiment is the observation that cells in cortical area V2 are virtually all binocular (Zeki, 1978; Burkhalter & Van Essen, 1986; Hubel & Livingstone, 1987) whereas there are a significant number of monocular cells and cells dominated by one eye in V1 (Hubel & Wiesel, 1968). We assume, as others have, that interocular transfer of aftereffects relies on the binocularity of the cortical cells activated by the adaptation and test stimuli.* If this assumption is valid and if subjective contours only activate

the highly binocular neurons in V2, we can make two predictions about the relative strengths of interocular transfer with the four different adaptation and test conditions. First, when a subject adapts to real lines there should be greater interocular transfer if the test stimulus is subjective than if it is real. This is expected because the real test stimulus will activate many monocular and monocularly-dominated cells not adapted by the presentation of the real adaptation stimulus to the other eye. On the other hand, the subjective test stimulus presumably only activates highly binocular cells in V2 which will have been adapted. The second prediction is that transfer should be greater if both adaptation and test stimuli are subjective than if they are both real. As with the first prediction this is expected because the degree of transfer should be higher if the only cells activated by the test pattern are highly binocular.

Methods

Interocular transfer of the TAEs was measured using a procedure similar to that used in exp. 1. In order that the lines in the adaptation and test patterns were "viewed" by both and not just one cortical hemisphere, the TAEs were measured near horizontal instead of near vertical. The adaptation lines were tilted ± 75 deg from vertical (i.e. the adaptation angle was 15 deg since we measured the TAE near horizontal). The primary difference from the experiment already described was that a haploscope was used so that subjects viewed the adaptation pattern with the right eye and the test stimulus was shown to either eye, in a random fashion. Circular fixation targets with a radius of 0.29 deg were always visible to both eyes so that fusion could be maintained. The adaptation stimulus was fixed as real or subjective during each experimental session but real and subjective test stimuli were randomly interleaved. Because the TAE can last for hours (Wolfe & O'Connell, 1986), only one eye was adapted in each experimental session to avoid confounding intraocular and interocular TAEs. We interleaved test conditions for both eyes, and calculated the degree of interocular transfer as the ratio of the intraocular and interocular TAEs obtained in the same experimental session. This made the experiments "blind" because subjects never knew which eye was seeing the test pattern (because utrocular identification is quite poor—Ono & Barbeito, 1985). To control for the possibility that there might be absolute

*It should be noted that there are a variety of models of interocular transfer and that incomplete transfer does not require the existence of strictly-monocular cells (Cogan, 1987; Lehky, 1988).

Table 1. Tilt aftereffects measured near horizontal for three subjects (MP, AR, SS). The entries in the table are the magnitudes of the TAEs in deg and the associated standard errors. The adaptation lines were at tilts of ± 75 deg from vertical. In all cases the right eye was shown the adaptation stimulus. The test stimulus was shown to either the right ("Same") eye or the left ("Diff") eye. A comparison is made between the effects for three different conditions in which the adaptation and test stimuli were real or subjective contours

Subject	S/S		Adaptation/test lines R/S		R/R	
	Same	Diff	Test eye		Same	Diff
			Same	Diff		
MP	2.03 \pm 0.40	1.97 \pm 0.31	2.32 \pm 0.35	2.25 \pm 0.24	1.18 \pm 0.09	0.97 \pm 0.12
AR	1.89 \pm 0.41	2.00 \pm 0.38	1.96 \pm 0.47	1.72 \pm 0.35	1.37 \pm 0.46	0.44 \pm 0.19
SS	3.56 \pm 0.47	2.58 \pm 0.49	4.18 \pm 0.25	3.80 \pm 0.46	0.70 \pm 0.19	0.16 \pm 0.23

differences in orientation judgements between the two eyes, separate baseline measurements for each eye were made prior to adaptation and subtracted from the data. As in exp. 1 the method of constant stimuli was used with the orientation of the lines in the test patterns covering a range of 8 deg in 1 deg steps near horizontal. Subjects indicated whether the lines in the test pattern appeared tilted above or below horizontal. Each TAE measurement was based on psychometric curves fit to the data from at least 192 responses. Probit analysis was used and the TAE was calculated as the orientation perceived as horizontal following adaptation minus the orientation perceived as horizontal prior to adaptation.

Results

The magnitudes of the tilt aftereffects measured near horizontal (Table 1) are comparable to those measured near vertical (exp. 1). The degree of interocular transfer of the TAE is shown in Fig. 5. The ordinate gives the interocular transfer calculated as the interocular TAE divided by the intraocular TAE. The error bars show the standard deviation of the quotient. The top half of the figure gives a

comparison of the extent of transfer with real and subjective test stimuli when the adaptation stimulus was real. The percentage of transfer varies between subjects but we consistently find that transfer is greater when the test stimulus is subjective rather than real (92% vs 46%, on average).* This difference is significant at the 0.05 level (Wilcoxon-Mann-Whitney *U*-test).

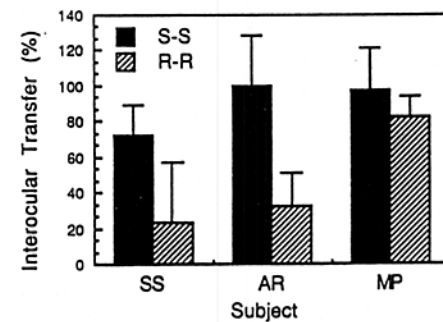
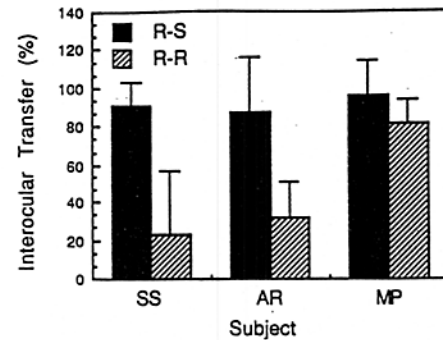


Fig. 5. Interocular transfer of the tilt aftereffect. The degree of transfer is the interocular TAE divided by the intraocular TAE and expressed as a percentage. The top panel compares the amount of transfer when the adaptation stimulus is real and the test stimulus is real or subjective (R = real, S = subjective). The bottom panel compares transfer when both adaptation and test stimuli are real or subjective. In both cases significantly greater transfer occurs when the test stimulus is subjective.

*The degree of interocular transfer in the conventional real-real tilt aftereffect is 46%, on average. Other investigators have reported somewhat greater transfer ranging from about 40-100% (Campbell & Maffei, 1971; Movshon et al., 1972). The lesser transfer we obtained is probably, in part, a result of the significantly shorter adaptation time (1.5 sec in our study; 20 sec by Campbell & Maffei, 1971; 2.5 min by Movshon et al., 1972) and other differences in timing between our experiment and the others. Additionally, Movshon et al. (1972) found that interocular transfer is significantly greater when a subject adapts his dominant eye and tests with the nondominant eye rather than vice versa. This may account for our inter-subject differences in the degree of transfer because the subject with the greatest real-real transfer (MP) has a strongly dominant right eye.

The lower half of Fig. 5 compares interocular transfer between conditions in which both adaptation and test stimuli were real or subjective. As before the transfer is greater when the test stimulus is subjective (subjective transfer = 92%, real transfer = 46%, on average). This difference is significant at the 0.05 level (U-test).

Discussion

The data demonstrate that interocular transfer is greater when the test stimulus is subjective than when it is real. This confirms the two predictions that we sought to test. If one accepts the assumption that cortical binocularity underlies interocular transfer, then the data imply that neurons activated by subjective contours are more binocular, on average, than those activated by real lines. This implication is consistent with the physiological results of von der Heydt et al. (1984) because they found cells responding to subjective contours only in cortical area V2 which is known to be more binocular than V1. It should be noted however, that other extrastriate areas are highly binocular (Zeki, 1978) and the cells responding to subjective contours cannot be placed conclusively in V2 on the basis of the psychophysical results.

GENERAL DISCUSSION

Subjective contours and response properties of cortical neurons

The key elements of our experimental findings can be readily explained using a model of visual processing based on physiological data from macaque monkeys. As already mentioned, the existence of a tilt aftereffect with subjective contours and its dependence on adaptation angle are consistent with the presence of orientation selective neurons responsive to subjective contours. The most interesting of our findings is the asymmetry in the interactions between real and subjective contours. As discussed following exp. 1, this asymmetry is consistent with physiological results showing that the cells activated by subjective contours are a subset of the cells in V2 which can be activated by real lines (von der Heydt et al., 1984; Peterhans et al., 1986). Our results also suggest that subjective contours are not simply weak stimuli for cells tuned to contours. First, strong TAEs are obtained when both the adaptation and test stimuli are subjective. This suggests that a certain group of cells is strongly adapted by the subjective contours.

Second, if real and subjective contours activate exactly the same populations of cells one wouldn't expect greater interocular transfer with subjective contours, as we observed.

In addition to our own results there is other psychophysical evidence for an asymmetry. First, in the Bourdon illusion it has been reported that real contours attract subjective contours more than subjective contours attract real contours (Walker & Shank, 1988). The direction of this asymmetry is consistent with the asymmetry we report in that real contours have a stronger influence on subjective contours than vice versa. A second type of asymmetry is found in a study of practice effects in orientation discrimination (Vogels & Orban, 1987). It was found that practice with discriminations of subjective contour orientation transferred to discrimination with real line orientation but there was little transfer in the opposite direction. It is not clear why the direction of this asymmetry (i.e. subjective contours affecting real lines more than the reverse) is opposite to that found with the tilt aftereffect and Bourdon illusion.

There was one previous study of tilt aftereffects with subjective contours which also reported strong TAEs, but in this study there was no asymmetry in the interactions of subjective contours with real contours (Smith & Over, 1975). The configuration of the stimulus used to produce subjective contours is shown in Fig. 6. We cannot give a definitive explanation for the difference between our data and theirs. However, a possible cause of the discrepancy is that the stimulus used by Smith and Over used real oriented edges to define the subjective contours (which appear to fill in the gap between the real contours) whereas ours did not. In fact, two-dimensional Fourier transforms of patterns similar to ours show no significant spectral energy at the orientation of the subjective contours (Vogels & Orban, 1987) whereas such energy is probably present in Smith and Over's stimuli. We can only speculate that Smith and Over's effects with real and subjective contours were more similar than ours because the subjective contour figures always contained real contours with the same orientation.



Fig. 6. Stimulus used to create subjective contours in Smith and Over's (1975) study of the tilt aftereffect.

In addition to the asymmetric relationship between real and subjective contours, our data are consistent with the physiological studies because subjective contours appear to activate cells which are more binocular, on average, than real contours. This implication arises from our finding that there is greater interocular transfer of the TAE when the test stimulus is subjective than when it is real. Physiologically it is found that real contours activate cells in V2 and also in V1 where many cells are monocular or dominated strongly by one eye. In contrast subjective contours only activate cells in V2 (Peterhans *et al.*, 1986; von der Heydt *et al.*, 1984) which are considerably more binocular than those in V1 (Burkhalter & Van Essen, 1986; Hubel & Livingstone, 1987; Zeki, 1978). As already mentioned, however, the psychophysical results cannot isolate the response to subjective contours in V2 because extrastriate cortex is in general highly binocular (Zeki, 1978).

Subjective contours, early visual processing, and cognitive inference

One of the fundamental questions regarding subjective contours is the level of visual processing at which they are manifest. It is possible that interactions between neurons in striate or prestriate cortex give rise to a neuronal response pattern to subjective contours that is indistinguishable from the response to a real line. On the other hand, it is conceivable that the subjective contours result from an unconscious thought process seeking to find a parsimonious interpretation of cleverly arranged visual patterns. There are now several different lines of evidence suggesting that subjective contours are not simply the result of "top-down" or "thought" processes. First, the physiological data demonstrate that neurons in V2 respond to subjective contours (Peterhans *et al.*, 1986; von der Heydt *et al.*, 1984). Second, our psychophysical data show that the perception of subjective contours reflects a property, orientation selectivity, which is characteristic of neurons in early visual cortical areas. One wouldn't expect thought processes to be orientation specific. Third, subjective contours such as those in the Kanizsa triangle disappear if they are constructed using equally luminant red and green (Brigner & Gallagher, 1974; Brussell, Stober & Bodinger, 1977; Frisby & Clatworthy, 1975; Gregory, 1977; Livingstone & Hubel, 1987). This finding appears inconsistent with models of the perception of subjective contours in which

they are the result of an interpretation of the spatial arrangement of the stimuli (Gregory, 1972; Rock & Anson, 1979). After all, even at isoluminance the perception of the spatial arrangement is intact.

Perhaps equiluminant patterns are simply weak stimuli for the cells which respond to subjective contours. Some recent data suggest this conclusion. Peterhans and von der Heydt (1988) find that cells responsive to subjective contours are common in the thick cytochrome oxidase rich stripes and the pale stripes of V2 but rare in the thin cytochrome oxidase stripes. Other studies have shown that the responses of neurons in the thin stripes are most dependent on color whereas the cells in the thick stripes respond to luminance discontinuities but are relatively unselective for color (Hubel & Livingstone, 1987). These findings taken together suggest that the equiluminant patterns may stimulate neurons predominantly in the thin cytochrome oxidase stripes which generally do not respond to subjective contours.

While we feel that our data combined with the physiological results (Peterhans *et al.*, 1986; von der Heydt *et al.*, 1984) clearly demonstrate an early neural process contributing to the perception of subjective contours, this conclusion does not nullify the possibility that something "inferential" is involved in their perception. Knowledge about the visual world may, through learning, be incorporated into the organization of the visual system. When line terminators are aligned in the real world they commonly indicate the presence of a real edge. It is possible that the high correlation between terminators and contours in the environment has led to the establishment of connections between end-stopped cells, such that aligned line ends, as in our stimuli, signal the presence of an edge even when one isn't present. In this sense the neuronal response to a subjective contour can be thought of as an "inference" even though it is made at a very early stage of visual processing. As such, the neuronal interconnections in prestriate cortex may embody an early component of what is commonly considered cognition.

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