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Inter-ocular transfer of the tilt illusion shows that monocular orientation mechanisms are colour selective

Jason D. Forte [a,*], Colin W.G. Clifford [b]

[a] *National Vision Research Institute, Department of Optometry and Vision Sciences, The University of Melbourne,*
Corner of Cardigan and Keppel Streets, Carlton, Vic. 3053, Australia
[b] *Colour, Form and Motion Laboratory, Visual perception Unit, School of Psychology, The University of Sydney, Sydney, NSW 2006, Australia*

Abstract

A vertical grating appears tilted when surrounded by a tilted inducer grating: the tilt illusion. We investigated the inter-ocular transfer of the tilt illusion for gratings modulated along parallel or orthogonal vectors in a $L - M$ and $L + M + S$ cone contrast space. We found that the monocular component of the tilt illusion is entirely colour selective and the binocular component shows only weak colour selectivity. These results suggest that colour and orientation processing interact at monocular stages of visual processing, whereas binocular visual mechanisms code for form in a manner that is largely insensitive to chromatic signature.
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1. Introduction

The tilt illusion and tilt aftereffect, both first documented by Gibson and Radner (1937), show interactions between colour and form processing in human vision. The tilt illusion occurs when a vertical grating appears rotated away from a surrounding grating that is oriented at 15° to the vertical. The tilt aftereffect shows a similar repulsion of a vertical test when it follows a period of adaptation to an oriented grating. Experiments have found the tilt aftereffect occurs for adapting and test stimuli that differ in colour and luminance (Held & Shattuck, 1971; Lovegrove & Over, 1973; although see Wade & Wenderoth, 1978; Clifford, Pearson, Forte, & Spehar, 2003). Similar results have been obtained for the tilt illusion (Lovegrove, 1977; Lovegrove & Over, 1973 although see Wade, 1980; Clifford, Spehar, Solomon, Martin, & Zaidi, 2003).

Large tilt aftereffects have been found for stimuli that vary in colour contrast without modulating luminance contrast—so called "isoluminant" stimuli that isolate chromatic processing (Clifford, Pearson et al., 2003; Flanagan, Cavanagh, & Favreau, 1990). Although the tilt illusion has been reported to disappear using isoluminant stimuli (Livingstone & Hubel, 1987), more recent work by Clifford, Spehar et al. (2003) showed that the tilt illusion is influenced both by chromatic and luminance mechanisms and that the loss of the tilt illusion at equiluminance reported by Livingstone and Hubel (1987) is not a general result. Clifford, Spehar et al. (2003) measured tilt illusions for stimuli defined according to DKL colour space (Derrington, Krauskopf, & Lennie, 1984). The three cardinal axes of DKL colour space correspond to modulation of the sum of L, M, and S cone responses (achromatic), the difference between L and M cone responses (red-green), and the S-cone response (blue-yellow). The tilt illusion was found to show some degree of colour selectivity, with maximum effects occurring when both test and

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inducer were modulated along the same direction in colour space. However, significant tilt illusions were also found when the test and inducer were modulated along orthogonal directions in colour space. This selectivity was observed regardless of whether or not the modulation was along a cardinal axis of DKL space. These results show that there is a colour selective component and a colour invariant (not selective for colour) component to the tilt illusion, suggesting that the tilt illusion may be mediated by more than one mechanism.

Further evidence of multiple mechanisms underlying the tilt illusion and tilt aftereffect comes from studies demonstrating inter-ocular transfer (IOT) when the test is presented in one eye and the inducer in the other (Paradiso, Shimojo, & Nakayama, 1989; Wade, 1980). Inter-ocular transfer implies that the tilt illusion involves binocular mechanisms. However, the IOT is not complete because the magnitude of the tilt illusion is less for the dichoptic stimulus than the monocular stimulus, suggesting that at least part of the effect is mediated by monocular neurones. As the previous studies used achromatic stimuli to measure inter-ocular transfer, it is not known whether the colour selective/colour invariant distinction is related to the monocular/binocular processes.

Studies of the McCollough effect suggest there are differences between monocular and binocular processing of colour and orientation (McCollough, 1965). The McCollough effect is an orientation contingent colour aftereffect, where adaptation to a horizontal orange-black grating causes a subsequently viewed black-white horizontal grating to appear bluish green-black (the perceived colour is a low saturation complement of the inducing colour). A vertically viewed black-white grating does not appear bluish green-black after adaptation to the same horizontal orange-black grating. It is possible to induce different colours for vertical and horizontal gratings by adapting to differently coloured vertical and horizontal gratings. Although studies of the McCollough effect do not show inter-ocular transfer, Vidyasagar (1976) showed that it is possible to obtain opposite monocular and binocular McCollough effects following different colour sequences for binocular and monocular adaptation. This suggests that there are separate monocular and binocular colour-tuned orientation-selective mechanisms.

Here, we studied the tilt illusion using dichoptic presentations of the test and inducer with various colour vectors in the achromatic/red-green plane of DKL colour space, and examined whether monocular and binocular mechanisms are related to colour selective and colour invariant mechanisms of the tilt illusion. We found that the tilt illusion shows complete IOT for orthogonal colour vectors, indicating that the colour invariant mechanism is completely binocular. The tilt illusion shows incomplete IOT for parallel colour vectors, showing that there is a monocular colour selective mechanism. We calculated the colour selectivity for monocular and binocular mechanisms, and found that the monocular mechanism is completely colour selective and that the binocular mechanism is largely unselective for colour. Our data support the notion that the tilt illusion is mediated by an early (monocular) colour selective orientation mechanism and a later (binocular) colour insensitive mechanism.

2. Methods

Two of the authors (CC and JF) and two experienced observers, who were naïve to the purposes of the study (ER and TW), served as subjects. All had normal or corrected-to-normal vision. Stimuli were generated using Matlab software to drive a VSG 2/5 graphics board (Cambridge Research Systems), and presented on a 21″ Sony Trinitron GM 520 monitor with a frame-rate of 120 Hz. The stimuli were modulated around a fixed white point (CIE-1931 chromaticity co-ordinates; $x = 0.28$, $y = 0.30$) with a luminance of 66.0 cdm^{-2}. Subjects viewed the screen from a distance of 57 cm. The testing cubicle was dark and its walls were covered with matt black material to reduce reflected light. A chin-rest was used to restrain head movements.

To make a dichoptic display, stimuli were placed at two separate locations on the monitor. Two 10 cm diameter 50 cm long cardboard tubes with non-reflective interior surfaces were positioned against the monitor at the stimulus locations so that only one stimulus was visible through each of the tubes. A mirror haploscope was used to fuse the two stimuli while maintaining appropriate eye vergence and accommodation for the 57 cm viewing distance. The tubes removed any visual cues for vertical or horizontal.

Stimulus contrasts were specified in a two dimensional cone space that allowed modulations along the achromatic axis and the L − M axis of the DKL colour space (Derrington et al., 1984). Conversion of DKL cone contrast to phosphor modulations were performed using the methods described by Brainard (1996) and Nakano (1996), with Smith and Pokorny (1975) cone fundamentals and the spectral output of the monitor phosphors measured using a PR-650 Spectroscan colourimeter (Photo Research).

Prior to the tilt illusion experiments, an isoluminant L − M axis was determined separately for each subject using a minimum motion technique (Anstis & Cavanagh, 1983) with a 9.0° sinusoidal grating with a spatial frequency of 1.0 cycle/deg. Detection thresholds were measured for the isoluminant L − M and achromatic cardinal directions of DKL colour space with stimulus contrast being specified in units of detection threshold for each observer.

For the tilt illusion experiments, the test stimuli consisted of a 1.0 cycle/deg diameter sinusoidal grating in a circular aperture with a diameter subtending 3.0 deg of visual angle. The surround stimuli (also 1.0 cycle/deg) were presented in an annulus with inner diameter of 3.0° and an outer diameter of 9.0°, and oriented at 15° and −15° (where the largest tilt effects occur; Over, Broerse, & Crassini, 1972).

Stimuli were ramped on with a 100 ms duration raised cosine temporal window, maintained at full contrast for 200 ms, and ramped off with a 100 ms duration raised cosine. Test and surround stimuli were presented at a contrast that was $1.5 \log_{10}$ units above detection threshold. The experiments followed a forced-choice procedure, where subjects used a response box to indicate whether the test stimulus appeared tilted clockwise or anti-clockwise from subjective vertical. The subjects' previous responses were used to determine the physical orientation of subsequent test stimuli according to an adaptive psychophysical procedure under computer control (Kontsevich & Tyler, 1999). Subjective vertical was based on 30 trials for each stimulus condition. To control for any biases in perceived vertical between the two eyes, a series of measurements were taken with only the test in each eye and used to correct subject vertical to screen vertical before each block of trials. These measurements ensured that surrounds were presented at 15° and −15°. During experimental trials, the magnitude of the tilt illusion was taken as half the difference in perceived vertical between interleaved trials in which the surround orientation was 15° and −15°. This served to remove any remaining bias in perceived vertical during the experiment and to avoid the build-up of adaptation to a particular surround orientation over a block of trials. In this way, the magnitude of the tilt illusion was determined in 60 trials for each subject for each stimulus configuration.

We initially measured the tilt illusion for four cardinal combinations of test and surround colour. Test and surround could each be modulated along either the achromatic (light–dark: "L") or the L − M (red–green: "R") cardinal axis of DKL colour space. Subjective magnitude of the tilt illusion was determined for tests and surround with parallel (the same) colour vectors (L/L and R/R), as well as tests and surround with orthogonal (different) colour vectors (L/R and R/L). In each block of trials one test-surround colour combination was tested, with test presented in both eyes and surrounds presented intra-ocularly (in the same eye) or inter-ocularly (in the opposite eye).

We then measured the magnitude of the tilt illusion for four non-cardinal axes. The non-cardinal axes were defined by rotating the cardinal axes by 45°. This is equivalent to averaging the cardinal colour vectors, to produce light red–dark green ("LR") or light green–dark red ("LG") axes of DKL colour space. Tilt magni-

tude was determined for tests and surround with parallel (the same) colour vectors (LR/LR and LG/LG), as well as tests and surround with orthogonal (different) colour vectors (LR/LG and LG/LR). As with testing along the cardinal axes, each block of trials consisted of one test-surround colour combination, with tests presented in both eyes and surrounds presented intra-ocularly (in the same eye) or inter-ocularly (in the opposite eye).

3. Results

The magnitude of the tilt illusion was averaged across the eye of test presentation as the data showed no systematic differences depending on which eye contained the test. The tilt illusion shows substantial inter-ocular transfer, demonstrating that it is mediated largely by binocular mechanisms (Wade, 1980). Fig. 1A shows the
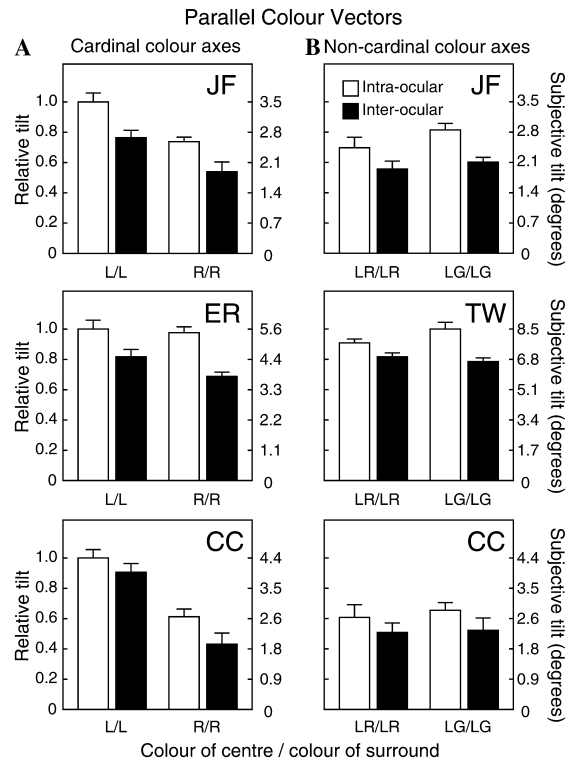

Fig. 1. (A) Tilt illusion magnitude for stimulus centre and surround colour vectors modulated along parallel (the same) cardinal colour axes. Centre/surround colour vectors where modulated in the light–dark direction (L/L) or red-green direction (R/R). Unfilled bars show tilts for centre and surround in the same eye (intra-ocular). Black bars show tilts for centre and surround stimuli in opposite eyes (inter-ocular). The right y-axis shows the raw tilt illusions in degrees. The left y-axis shows the tilt illusion normalized to the maximum tilt illusion for each observer across stimulus conditions. Error bars are standard errors of tilt illusions calculated for 3–5 separate measurements. (B) Tilt illusions for centre and surround vectors modulated along parallel (the same) non-cardinal colour axes, giving centre/surround combinations of light red–light red (LR/LR) and light green–light green (LG/LG).

magnitude of the tilt illusion for three observers for stimulus surrounds in the same eye (intra-ocular) or other eye (inter-ocular) as the test, with tests and surrounds modulated along parallel (the same) cardinal red-green (R) or light–dark (L) colour axes. The right *y*-axis shows the raw tilt illusions. The left *y*-axis shows the tilt illusion normalized to the maximum tilt illusion for each observer. Error bars are standard errors of tilt illusions calculated for 3–5 separate runs. The tilt illusion is greater for luminance contrast than colour contrast stimuli, but the normalized tilt illusion for the inter-ocular condition is less than the intra-ocular condition for both colour vectors. The relative magnitude of the tilt illusion for luminance and colour directions is different for the three observers, but the relative strength of the inter-ocular condition is similar. Fig. 1B shows the magnitude of the tilt illusion for tests and surrounds modulated along the same (parallel) light red–dark green (LR) or light green–dark red (LG) non-cardinal colour axes. As for stimuli modulated along the cardinal colours, the illusion for the inter-ocular condition is less than the intra-ocular condition for both colour vectors. The difference in magnitude of tilt illusions for same eye and inter-ocular surrounds suggests that performance in the same eye condition cannot be accounted for by a binocular mechanism, implying that there is a monocular tilt mechanism for test and surrounds with parallel colour axes.

The tilt illusion shows little difference between inter-ocular and intra-ocular presentation when the test and surround are modulated in orthogonal colour directions. Fig. 2A shows the tilt illusion when the centre is modulated in the RG direction and the surround is modulated in the LD direction, and vice versa. The labels on the *x*-axis of the graph indicate the colour direction of the test stimulus. The left *y*-axis shows the tilt illusion normalized to the maximum tilt illusion for each observer. As with the test and surrounds modulated along parallel colour axes, the greatest tilt illusion occurs when the test is modulated in the LD colour direction. Fig. 2B shows that the corresponding tilt illusions for non-cardinal orthogonal test and surrounds follow the same pattern as that found for cardinal directions. The equivalence in tilt illusion magnitude for intra and inter-ocular surrounds suggests that performance in the same eye condition is completely accounted for by a binocular mechanism.

We computed IOT by dividing the magnitude of the inter-ocular tilt illusion by the magnitude of the same eye tilt illusion. If the same eye tilt illusion is mediated by a purely binocular mechanism, then the inter-ocular tilt illusion should be of the same magnitude, and the IOT will be close to one. If there is only a monocular mechanism, then the inter-ocular tilt illusion should be zero, and the IOT will be zero.

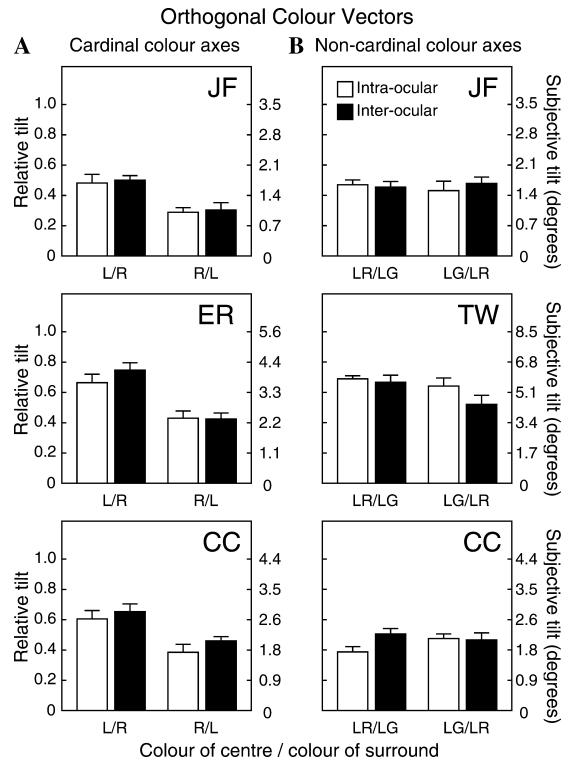Fig. 3A shows that the IOT for JF is close to one for orthogonal test and surround colour vectors along car-

Fig. 2. (A) Tilt illusion magnitude for stimulus centre and surround colour vectors modulated along orthogonal (different) cardinal colour axes. Centre/surround colour vectors where modulated in the light-dark/red-green (L/R) and red-green/light-dark direction (R/L). Unfilled bars show tilts for centre and surround in the same eye (intra-ocular). Black bars show tilts for centre and surround stimuli in opposite eyes (inter-ocular). Other details as per Fig. 1. (B) Tilt illusions for centre and surround vectors modulated along orthogonal (different) non-cardinal colour axes, giving centre/surround combinations of light red–dark green centre and light green–dark red surround (LR/LG), and light green–dark red centre and light red–dark green surround (LG/LR).

dinal colour axes. The IOT for parallel colour vectors are less than one, showing incomplete IOT, which suggests that there is a monocular mechanism that is colour selective. The complete IOT for orthogonal vectors suggests that there is a colour invariant mechanism that is purely binocular. Figs. 3C and E show corresponding data for CC and ER that are similar to the pattern displayed by JF.

Fig. 3B shows that the pattern of IOT for non-cardinal colour axes is no different to that found for cardinal axes for JF. The orthogonal colour vectors show complete IOT (values close to one), while the parallel vectors show IOT less than one. Thus, a colour invariant binocular mechanism and colour selective monocular mechanism exist for both cardinal and non-cardinal colour axes. Figs. 3D and F show corresponding data for CC and TW. There is some variability in the orthogonal data for CC and TW. However, the IOT for orthogonal vectors are generally close to or above 1, suggesting there is complete IOT for orthogonal colour vectors.
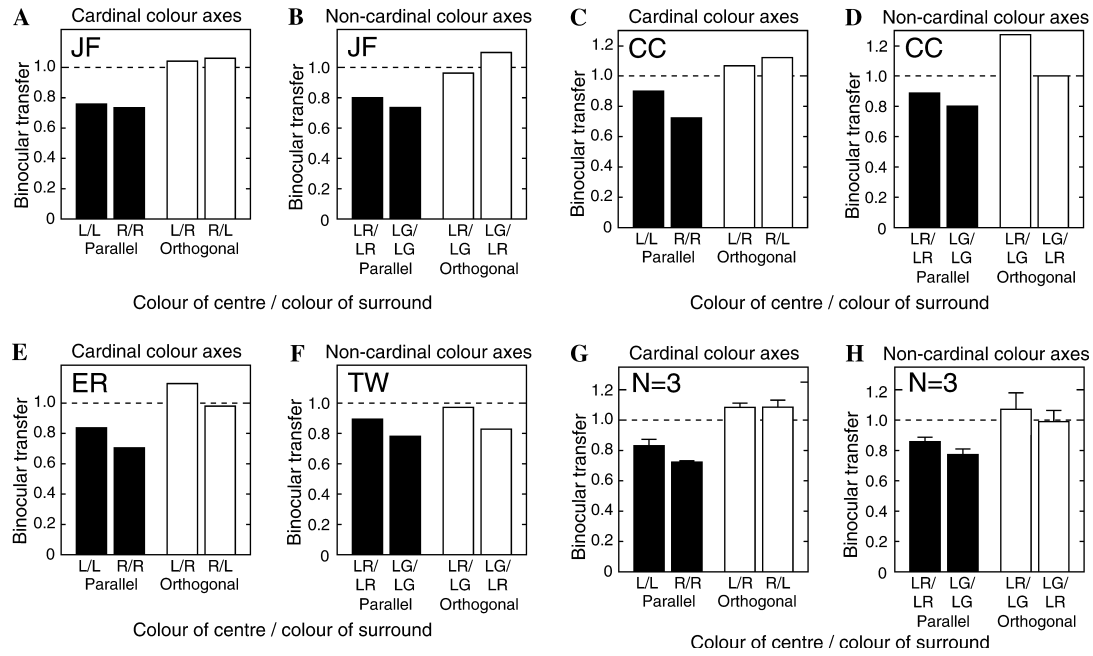
Fig. 3. (A) Inter-ocular transfer (IOT) of the tilt illusion for JF with centre and surround modulated along parallel (filled bars) and orthogonal (open bars) colour vectors in cardinal colour space. L/L corresponds to centre/surround colour vectors that are light-dark/light-dark. R/R corresponds to centre/surround colour vectors that are red-green/red-green. L/R corresponds to centre/surround colour vectors that are light-dark/red-green. R/L corresponds to centre/surround colour vectors that are red-green/light-dark. The dashed line corresponds to an IOT value of one, indicating complete inter-ocular transfer. (B) IOT of the tilt illusion for JF with centre and surround modulated along parallel (filled bars) and orthogonal (open bars) colour vectors in non-cardinal colour space. LR/LR corresponds to a centre and surround modulated along a light red–dark green vector. LG/LG corresponds to a centre and surround modulated along a light green–dark red vector. LR/LG corresponds to a centre modulated along a light red–dark green vector and a surround modulated along a light green–dark red vector. LG/LR corresponds to a centre modulated along a light green–dark red vector and a surround modulated along a light red–dark green vector. (C,D) Corresponding IOT for CC using stimuli modulated in cardinal and non-cardinal colour axes. (E) IOT for ER with stimuli modulated along cardinal colour axes. (F) IOT for TW with stimuli modulated along non-cardinal colour axes. (G) Average IOT for three subjects with stimuli modulated along cardinal colour axes. Error bars are standard errors based on three subjects' inter-ocular transfer. (H) Average IOT for three subjects with stimuli modulated along non-cardinal colour axes. Error bars are standard errors based on three subjects' inter-ocular transfer.

Figs. 3G and H show the average IOT across observers for cardinal and non-cardinal axes, respectively. There is only evidence of incomplete IOT for the parallel colour vectors.

The observed difference in IOT for parallel and orthogonal surrounds was confirmed by an analysis of variance (ANOVA) that was performed separately on the cardinal and non-cardinal tilt illusion data. For both cardinal and non-cardinal stimuli, the IOT for tests with orthogonal surrounds was significantly greater ($p < .05$) than the IOT for tests with parallel surrounds.

While the data show evidence for a monocular mechanism that is colour selective and a colour invariant mechanism that is purely binocular, we have not yet established if the binocular mechanism is purely colour invariant. To do so, we calculated the colour selectivity index for the binocular mechanism (CSI_{bin}) by dividing the difference in the inter-ocular tilt illusion for parallel (I_{para}) and orthogonal (I_{orth}) colour vectors by the sum of the same two values:

$$CSI_{bin} = \frac{I_{para} - I_{orth}}{I_{para} + I_{orth}}.$$

The inter-ocular tilt illusion can only be mediated by a binocular mechanism. If there is no colour selectivity then the tilt illusion for parallel and orthogonal colour vectors will be the same and the colour selectivity index will be 0. If there is complete colour selectivity then the tilt illusion for the orthogonal condition will be negligible and the colour selectivity index will be close to 1. The average colour selectivity across subjects is 0.12 ± 0.02 (standard error for three subjects), indicating that the binocular mechanism is weakly colour selective.

We also computed the colour selectivity index for the monocular mechanism (CSI_{mon}) using the difference between the same eye (S_{para} and S_{orth}) and inter-ocular tilt illusions to isolate the monocular component:

$$CSI_{mon} = \frac{(S_{para} - I_{para}) - (S_{orth} - I_{orth})}{(S_{para} - I_{para}) + (S_{orth} - I_{orth})}.$$

The average colour selectivity across subjects is 1.45 ± 0.26 (standard error for three subjects), indicating that the monocular mechanism is purely colour selective. The measure of monocular colour selectivity is considerably more variable than for binocular colour selectivity because we are taking ratios of small numbers

(the difference between the inter-ocular and intra-ocular conditions) in the monocular colour selectivity calculation.

4. Discussion

Our results confirm that the tilt illusion is mediated by both monocular and binocular orientation-selective mechanisms (Wade, 1980). The binocular mechanism is largely colour invariant while the monocular mechanism is completely colour selective. If both stages contribute to the tilt illusion when viewed binocularly, the tilt illusion should be broadly tuned for colour, as found by Clifford, Spehar et al. (2003).

Our evidence for the involvement of a largely colour invariant binocular mechanism in the tilt illusion is consistent with studies that show low levels of IOT for the McCollough effect (Coltheart, 1973; Lovegrove & Over, 1973; MacKay & MacKay, 1973). The McCollough effect occurs when adaptation to a high spatial frequency square-wave coloured grating causes a black-white grating of the same orientation to appear coloured with the complementary hue of the adaptor. This orientation contingent colour aftereffect has been attributed to adaptation of "double-duty" neurons selective for both colour and orientation (Vidyasagar, 1976). The effect does not occur if the adapting stimulus is presented to the opposite eye as the test grating. The lack of IOT has been cited as evidence that the McCollough effect does not involve binocular mechanisms (Coltheart, 1973; Lovegrove & Over, 1973; MacKay & MacKay, 1973). Our data show complete colour selectivity of monocular orientation processing mechanisms but only weak colour selectivity for binocular mechanisms underlying orientation processing. The weak colour selectivity of binocular orientation processing mechanisms would account for the lack of IOT of the McCollough effect.

How do the current results bear on the mechanisms that are believed to underlie the tilt illusion? Our results suggest the tilt illusion depends on more than one level of visual processing (Wenderoth & Johnstone, 1987). We consider the physiological evidence to address where these mechanisms might be located in the visual pathway.

Our data are not consistent with the monocular mechanism being mediated by subcortical neurones. Neurones in the primate LGN do not show strong orientation tuning (Smith, Chino, Ridder, Kitagawa, & Langston, 1990; Xu, Ichida, Shostak, Bonds, & Casagrande, 2002) and prefer stimuli modulated along the cardinal chromatic axes that correspond to the M–L and $S - (M + L)$ cone opponent post-receptoral mechanisms (Derrington et al., 1984). The colour selective monocular mechanism identified here is probably not mediated by such subcortical neurones because the tilt illusion shows sharp orientation dependence (Gibson & Radner, 1937) and the pattern of results is similar for cardinal and non-cardinal chromatic stimuli (Clifford, Pearson et al., 2003; Clifford, Spehar et al., 2003).

The colour selective monocular mechanism could be mediated by early cortical neurones. There is substantial evidence for neurones in primary visual cortex that respond to both colour and luminance and are tuned for orientation and spatial frequency (Johnson, Hawken, & Shapley, 2001; Lennie, Krauskopf, & Sclar, 1990; Thorell, De Valois, & Albrecht, 1984). The preferred colour of these cells is distributed over a broad range of colour space (Lennie et al., 1990), consistent with our data showing colour selective effects for both cardinal and non-cardinal colour axes. The colour selectivity of the monocular mechanisms underlying the tilt illusion implies there are interactions between monocular cells with the same colour preference. This would be an interesting prospect given that the orientation and spatial frequency tuning in cortex is believed to rely in part on cortico–cortico interactions (see review by Shapley, Hawken, & Ringach, 2003).

The largely colour invariant binocular mechanism presumably involves cortical mechanisms because subcortical neurones only receive excitatory input from one eye (Rodieck & Dreher, 1979). Cells in primary visual cortex often display a preference for stimulation in one eye over the other but most are excited by binocular stimulation (Schiller, Finlay, & Volman, 1976). If binocular interactions occur after monocular processing, then the binocular, largely colour invariant mechanism may involve higher stages of visual processing than the colour selective monocular mechanism. There is little physiological evidence on the binocular and colour tuning properties in early cortical visual pathway to confirm this. However, our evidence for a largely colour invariant binocular mechanism might indicate that the cortical connections of orientation tuned binocular neurones are not very selective for colour.

Acknowledgments

References

Anstis, S., & Cavanagh, P. (1983). A minimum motion technique for judging isoluminance. In J. Mollon & R. T. Sharpe (Eds.), *Colour vision: Physiology and psychophysics* (pp. 156–166). London: Academic Press.

Brainard, D. H. (1996). Part IV: Cone contrast and opponent modulation color spaces. In P. K. Kaiser & R. M. Boynton

(Eds.), *Human color vision* (pp. 563–579). Washington, DC: Optical Society of America.

Clifford, C. W., Pearson, J., Forte, J. D., & Spehar, B. (2003). Colour and luminance selectivity of spatial and temporal interactions in orientation perception. *Vision Research, 43*(27), 2885–2893.

Clifford, C. W., Spehar, B., Solomon, S. G., Martin, P. R., & Zaidi, Q. (2003). Interactions between color and luminance in the perception of orientation. *Journal of Vision, 3*(2), 106–115.

Coltheart, M. (1973). Letter: Colour-specificity and monocularity in the visual cortex. *Vision Research, 13*, 2595–2598.

Derrington, A. M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology, 357*, 241–265.

Flanagan, P., Cavanagh, P., & Favreau, O. E. (1990). Independent orientation-selective mechanisms for the cardinal directions of colour space. *Vision Research, 30*(5), 769–778.

Gibson, J. J., & Radner, M. (1937). Adaptation, after-effect, and contrast in the perception of tilted lines. I. Quantitative studies. *Journal of Experimental Psychology, 12*, 453–467.

Held, R., & Shattuck, S. R. (1971). Color- and edge-sensitive channels in the human visual system: tuning for orientation. *Science, 174*(6), 314–316.

Johnson, E. N., Hawken, M. J., & Shapley, R. (2001). The spatial transformation of color in the primary visual cortex of the macaque monkey. *Nature Neuroscience, 4*(4), 409–416.

Kontsevich, L. L., & Tyler, C. W. (1999). Bayesian adaptive estimation of psychometric slope and threshold. *Vision Research, 39*(16), 2729–2737.

Lennie, P., Krauskopf, J., & Sclar, G. (1990). Chromatic mechanisms in striate cortex of macaque. *Journal of Neuroscience, 10*(2), 649–669.

Livingstone, M. S., & Hubel, D. H. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *Journal of Neuroscience, 7*(11), 3416–3468.

Lovegrove, W. (1977). Inhibition between channels selective to contour orientation and wavelength in the human visual system. *Perception & Psychophysics, 22*(1), 49–53.

Lovegrove, W. J., & Over, R. (1973). Colour selectivity in orientation masking and aftereffect. *Vision Research, 13*(5), 895–902.

MacKay, D. M., & MacKay, V. (1973). Orientation-sensitive after-effects of dichoptically presented colour and form. *Nature, 242*, 477–479.

McCollough, C. (1965). Color adaptation of edge-detectors in the human visual system. *Science, 149*, 1115–1116.

Nakano, Y. (1996). Part III: Color vision mathematics: A tutorial. In P. K. Kaiser & R. M. Boynton (Eds.), *Human color vision* (pp. 544–562). Washington, DC: Optical Society of America.

Over, R., Broerse, J., & Crassini, B. (1972). Orientation illusion and masking in central and peripheral vision. *Journal of Experimental Psychology, 96*(1), 25–31.

Paradiso, M. A., Shimojo, S., & Nakayama, K. (1989). Subjective contours, tilt aftereffects, and visual cortical organization. *Vision Research, 29*(9), 1205–1213.

Rodieck, R. W., & Dreher, B. (1979). Visual suppression from nondominant eye in the lateral geniculate nucleus: A comparison of cat and monkey. *Experimental Brain Research, 35*(3), 465–477.

Schiller, P. H., Finlay, B. L., & Volman, S. F. (1976). Quantitative studies of single-cell properties in monkey striate cortex. II. Orientation specificity and ocular dominance. *Journal of Neurophysiology, 39*(6), 1320–1333.

Shapley, R., Hawken, M., & Ringach, D. L. (2003). Dynamics of orientation selectivity in the primary visual cortex and the importance of cortical inhibition. *Neuron, 38*(5), 689–699.

Smith, E. L., 3rd, Chino, Y. M., Ridder, W. H., 3rd, Kitagawa, K., & Langston, A. (1990). Orientation bias of neurons in the lateral geniculate nucleus of macaque monkeys. *Visual Neuroscience, 5*(6), 525–545.

Smith, V. C., & Pokorny, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Research, 15*(2), 161–171.

Thorell, L. G., De Valois, R. L., & Albrecht, D. G. (1984). Spatial mapping of monkey V1 cells with pure color and luminance stimuli. *Vision Research, 24*(7), 751–769.

Vidyasagar, T. R. (1976). Orientation specific colour adaptation at a binocular site. *Nature, 261*(5555), 39–40.

Wade, N. J. (1980). The influence of colour and contour rivalry on the magnitude of the tilt illusion. *Vision Research, 20*(3), 229–233.

Wade, N. J., & Wenderoth, P. (1978). The influence of colour and contour rivalry on the magnitude of the tilt after-effect. *Vision Research, 18*(7), 827–835.

Wenderoth, P., & Johnstone, S. (1987). Possible neural substrates for orientation analysis and perception. *Perception, 16*(6), 693–709.

Xu, X., Ichida, J., Shostak, Y., Bonds, A. B., & Casagrande, V. A. (2002). Are primate lateral geniculate nucleus (LGN) cells really sensitive to orientation or direction? *Visual Neuroscience, 19*(1), 97–108.