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Colour and luminance selectivity of spatial and temporal interactions in orientation perception

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Abstract

Previous studies have commented upon the similar phenomenology of simultaneous and successive interactions in the perception of orientation. These similarities have been taken as evidence of common mechanisms underlying the simultaneous tilt illusion (TI) and the successive tilt aftereffect (TAE). We measured the TI and TAE for four subjects for combinations of test and inducing stimuli modulated along either the same or orthogonal axes of colour space within the $L + M + S$, $L - M$ colour–luminance plane. The largest TI and TAE were found when test and inducer were modulated along the same axis of colour space. The TI consistently showed greater selectivity for colour/luminance than the TAE. The results are discussed in relation to the known chromatic properties of the primate visual pathways. Specifically, we suggest that both the TI and TAE involve colour- and luminance-specific neurons in primary visual cortex as well as cue-invariant mechanisms in extrastriate cortex.

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1. Introduction

At the early stages of visual processing in humans and other primates, chromatic signals are carried to primary visual cortex (V1) via two chromatic channels and a third, achromatic (luminance) channel (Derrington, Krauskopf, & Lennie, 1984; DeValois, Abramov, & Jacobs, 1966; DeValois, Cottaris, Elfar, Mahon, & Wilson, 2000; Hendry & Yoshioka, 1994; Martin, White, Goodchild, Wilder, & Sefton, 1997; Wiesel & Hubel, 1966). Psychophysical evidence for the existence of separable post-receptoral mechanisms for the processing of colour and luminance comes from studies using adaptation (Bradley, Switkes, & DeValois, 1988; Krauskopf & Gegenfurtner, 1992; Krauskopf, Williams, & Heeley, 1982), masking (Gegenfurtner & Kiper, 1992; Li & Lennie, 1997; Mullen & Losada, 1994; Sankerelli & Mullen, 1997) and subthreshold summation (Gunther & Dobkins, 2003; Mullen, Cropper, & Losada, 1997;

Mullen & Sankerelli, 1999). It has been suggested that the cortical pathways for colour and form perception maintain this early segregation with the luminance channel dominating form perception and the chromatic channels driving colour perception (Livingstone & Hubel, 1984, 1987, 1988).

Numerous psychophysical experiments have sought to investigate interactions between colour and form processing in human vision by making use of visual illusions such as the tilt illusion (TI) and tilt aftereffect (TAE), both first documented by Gibson and Radner (1937). When surrounded by a grating oriented at around 15° to the vertical, a vertical grating appears repelled in orientation away from the orientation of the surround: the TI (Fig. 1). TAE is the temporal analogue of the TI, whereby adaptation to a 15° grating causes a subsequently viewed vertical test grating to be repelled in orientation away from that of the adapter. Some early experiments found evidence for chromatic selectivity in the TAE (Held & Schattuck, 1971; Lovegrove & Over, 1973) and TI (Lovegrove, 1977; Lovegrove & Badcock, 1981; Lovegrove & Over, 1973); others did not (TAE: Wade & Wenderoth, 1978; TI: Wade, 1980).

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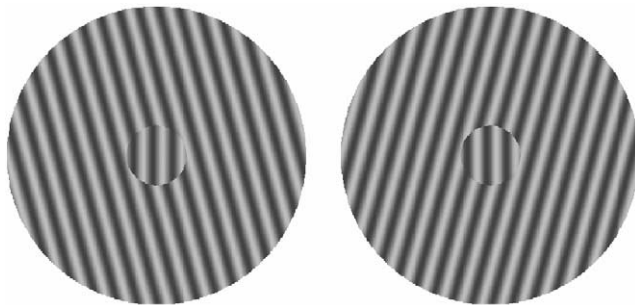


Fig. 1. The tilt illusion (TI). A vertical test patch appears repelled in orientation away from a surround oriented at 15° . The magnitude of the TI is taken as half the difference between the orientation of subjective vertical for $\pm 15^\circ$ surrounds.

While previous experiments had used stimuli defined by luminance or combinations of colour and luminance, Livingstone and Hubel (1987) studied orientation illusions using equiluminant stimuli (stimuli defined by modulations in chromaticity in the absence of luminance modulation). They reported that the TI disappeared when they made either the test stripes, or the inducing stripes, or both, equiluminant red and green. On this basis, they concluded that only the luminance channel has inhibitory interactions between different orientations.

We recently showed that the TI is influenced both by chromatic and luminance mechanisms (Clifford, Spehar, Solomon, Martin, & Zaidi, 2003), and that the loss of the TI at equiluminance reported by Livingstone and Hubel (1987) is not a general result. That study used stimuli defined according to DKL colour space (Derrington et al., 1984). The three cardinal axes of DKL colour space, illustrated in Fig. 2A, correspond to modulation of (1) only the *S*-cone response, (2) only the difference between *L*- and *M*-cone responses, or (3) the sum of the three cone responses (luminance), respectively. We found that the TI shows a degree of selectivity such that the effect is largest when both test and inducer are modulated along the same axis of colour space. This was found to be the case regardless of whether or not the modulation is along a cardinal axis of DKL space. The results of that study show that colour and orientation are intimately coupled in visual processing. Further, they suggest that the cardinal chromatic axes have no special status at the level(s) of visual cortex at which the TI is mediated.

It is interesting to compare the colour/luminance selectivity of the TI found by Clifford, Spehar, et al. (2003) to that reported in an earlier study of the TAE (Flanagan, Cavanagh, & Favreau, 1990). Flanagan et al. (1990) found that, for an adapting stimulus modulated along a cardinal axis of DKL colour space, the TAE is maximal when the test is modulated along the same chromatic axis and is near minimum when the test is modulated along an orthogonal axis. They also found

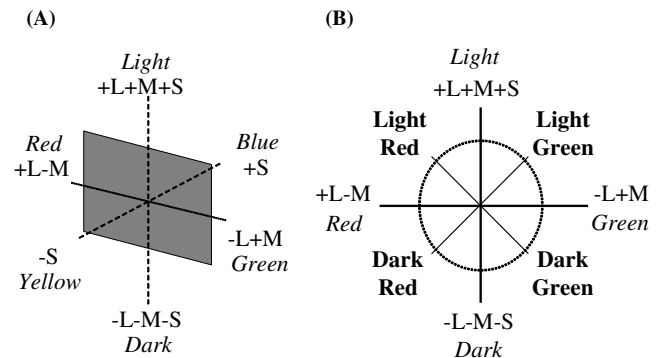


Fig. 2. (A) Chromatic sensitivities of the channels defining DKL colour space (Derrington et al., 1984). The shaded plane, containing all of the stimuli used in the experiments described here, is shown in detail in (B). (B) The stimuli in Experiments 1 and 3 consisted of sinusoidal spatial modulations along the cardinal luminance and *L-M* axes. The stimuli in Experiments 2 and 4 consisted of modulations along the intermediate non-cardinal axes: light red–dark green and light green–dark red. For each subject, the contrast of all stimuli was equated in terms of increments of detection threshold such that it lay at the same distance from the white point in DKL space (···).

that the TAE is smaller for non-cardinal than cardinal adapting colours and that, for non-cardinal stimuli, the maximum TAE does not always occur when the test is the same colour as the adapter. On this basis, they suggested that the colour preferences of orientation-selective mechanisms in human vision can be characterised principally by the three cardinal axes of DKL colour space (Derrington et al., 1984). In the context of the TI, Clifford, Spehar, et al. (2003) found no such evidence for primacy of the cardinal axes of DKL colour space.

This apparent difference in the colour/luminance selectivity of the TAE and TI is surprising, given that the two effects have long been widely held to be mediated by a common mechanism (Clifford, Wenderoth, & Spehar, 2000; Harris & Calvert, 1989; Magnussen & Kurtenbach, 1980; O'Toole & Wenderoth, 1977; Sekuler, 1974; Tolhurst & Thompson, 1975; Wenderoth & Johnstone, 1987) because they show similar dependence on spatial frequency and orientation. Both the TAE and the TI are strongest when inducer and test are similar in spatial frequency (TAE: Ware & Mitchell, 1974; TI: Georgeson, 1973). For both effects, a vertical test appears repelled away from an inducer oriented at between 0° and 50° and attracted to an inducer oriented between 50° and 90° , with the largest effects occurring at around 15° and 75° (TAE: Gibson & Radner, 1937; TI: Over, Broerse, & Crassini, 1972). When the test stimulus is obliquely oriented, both effects show a similar dependence on the relative orientation of inducer and test (TAE: Mitchell & Muir, 1976; TI: O'Toole & Wenderoth, 1977).

Given widespread acceptance that the TAE and TI share a common mechanism, we thought it worthwhile to establish whether the apparent difference in colour/luminance selectivity reflects a genuine difference be-

tween the two effects and is not simply a consequence of differences in stimuli, methodology or observers between the two studies. Consequently, we decided to compare the selectivity for colour of the TAE and TI for a single set of subjects using, as far as possible, the same stimuli and methods.

2. Methods

Three of the authors (CC, JP and BS) and one experienced observer naïve to the purposes of the study (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, Rochester, Kent, UK) and presented on a 21" Sony Trinitron GM 520 monitor. The background and white point for colour space calculations was set at CIE chromaticity coordinates of (0.280, 0.303) and a luminance of 66.0 cd m⁻². The screen was viewed from a distance of 55 cm. The testing cubicle was dark, and its walls were covered with matt black material to remove any external references to vertical. A sheet of black cardboard containing a circular aperture was used to obscure the screen's edges. A chin-rest was used to minimize head movements.

Prior to Experiment 1, an isoluminant *L–M* isolating axis was determined separately for each subject using a minimum motion technique (Anstis & Cavanagh, 1983). Stimuli were vertical 1.0 cycle/deg sinusoidal gratings presented in a circular aperture with a diameter subtending 15.0° of visual angle. The apparent motion stimulus continually cycled through four spatial phases lasting 200 ms each until the subject indicated the perceived direction of motion with a button press. Detection thresholds were measured in the luminance and *L–M* directions of DKL colour space (Derrington et al., 1984) using a vertical 1.0 cycle/deg sinusoidal grating in a circular aperture with a diameter subtending 15.0° of visual angle.

Experiment 1 measured the TI for four cardinal combinations of test and surround colour. Test and surround could each be modulated along either the luminance or the *L–M* cardinal axis of DKL colour space. Test and surround stimuli were presented at the same multiple of detection threshold (40× detection threshold for subjects CC, JP and BS and 30× detection threshold for subject TW). Each test stimulus consisted of a 1.0 cycle/deg sinusoidal grating in a circular aperture with a diameter subtending 3.0° of visual angle. The surround stimulus, also a 1.0 cycle/deg grating, was presented in an annulus with inner and outer diameters of 3.0° and 15.0°, respectively, concentric with the test stimulus. Stimuli were presented at their maximal contrast for 200 ms. Contrast was ramped on and off for 100 ms each according to a raised cosine function.

Measurement of the TI followed a forced-choice procedure. Subjects were required to report via a response box whether the test stimulus appeared tilted clockwise or anti-clockwise from subjective vertical. The subject's 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). In this way, the orientation of subjective verticality was determined in 60 trials for each subject for each stimulus configuration. To control for any biases in perceived vertical that a subject may have, the magnitude of the TI was taken as one half the difference in perceived vertical between interleaved trials in which the surround orientation was 15° and –15°. Two such estimates of the magnitude of the TI were made for each subject for each stimulus condition and their average taken, such that each data point in Figs. 3 and 4 is based upon a total of 120 trials.

Experiment 2 measured the TI for four non-cardinal combinations of test and surround colour. Each non-cardinal stimulus was formed by combining luminance and *L–M* modulations in equal multiples of threshold contrast (Fig. 2B). This produced perceptually different stimuli depending on the relative spatial phase of the two modulations. If the light part of the luminance modulation was in phase with the red part of the *L–M* grating then the resulting stimulus modulated between light red and dark green. If the light part of the luminance modulation was in phase with the green part of the *L–M* grating then the resulting stimulus modulated between light green and dark red. The projections onto the luminance axis of DKL colour space were the same

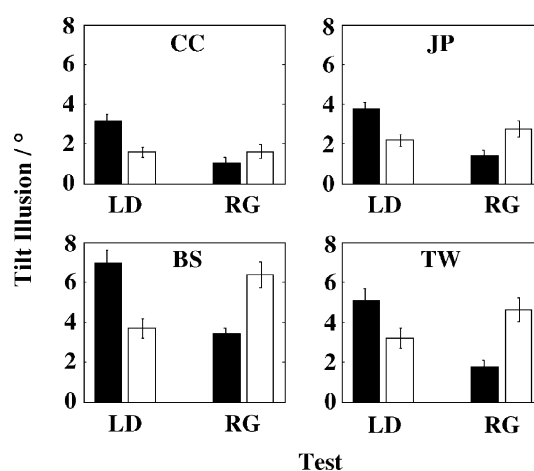


Fig. 3. Tilt illusion for cardinal stimuli. Illusion magnitude in degrees for each of four subjects. Test stimuli are labelled on the abscissa as LD (light–dark) or RG (red–green). Filled bars denote LD inducers; hollow bars denote RG inducers. In all figures, error bars correspond to ± 1 standard error of the mean, calculated from combinations of the standard error estimates obtained from the psychophysical procedure (Kontsevich & Tyler, 1999).

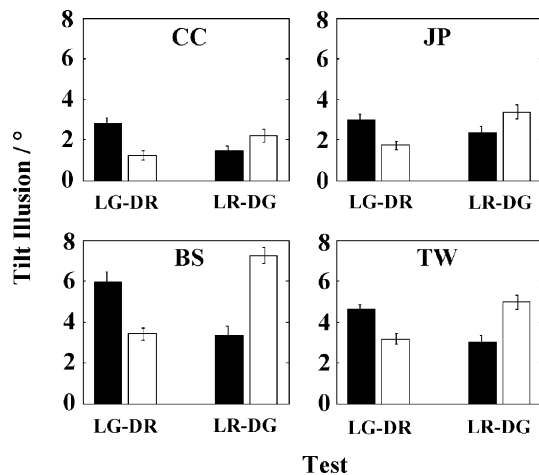


Fig. 4. Tilt illusion for non-cardinal stimuli. Illusion magnitude in degrees for each of three subjects. Test stimuli are labelled on the abscissa as LG-DR (light green–dark red) or LR-DG (light red–dark green). Filled bars denote LG-DR inducers; hollow bars denote LR-DG inducers.

for the two resulting non-cardinal modulations, as were the projections onto the cardinal chromatic $L-M$ axis. The contrast of each cardinal component was set to $1/\sqrt{2}$ of that of the cardinal stimuli in Experiment 1. In all other details Experiment 2 was the same as Experiment 1.

Experiment 3 measured the TAE for the four cardinal combinations of test and inducing colour used in Experiment 1. The test stimulus was a 1.0 cycle/deg sinusoidal grating in a circular aperture with a diameter subtending 3.0° of visual angle. The adapting stimulus (also 1.0 cycle/deg) counterphased at 1 Hz and was presented in a 15.0° circular aperture concentric with the test stimulus. The duration of the initial phase of adaptation was 60 s, with 5 s of top-up adaptation following each presentation of a test stimulus. As in Experiments 1 and 2, test stimuli were presented in a raised cosine temporal window, such that the stimulus was present at full contrast for 200 ms and ramping on and off took 100 ms each.

Measurement of the TAE was in all senses analogous to measurement of the TI in Experiments 1 and 2, except that it was not possible to interleave trials between 15° and -15° inducers as the effects of adaptation to those two orientations would tend to cancel out. Instead, the magnitude of the TAE was taken as one half the difference in perceived vertical between separate trials in which the surround orientation was 15° and -15° . Two such estimates of the magnitude of the TAE were made for each subject for each stimulus condition and their average taken, such that each data point in Figs. 6 and 7 is based upon a total of 120 trials.

Experiment 4 measured the TAE for the four non-cardinal combinations of test and inducing colour used

in Experiment 2. In all other details Experiment 4 was the same as Experiment 3.

3. Results

3.1. Experiments 1&2: tilt illusion

We measured the effect of a surround grating oriented at 15° to the vertical on the perceived orientation of a central test grating. In Experiment 1, centre and surround gratings were modulated either in luminance (LD) or along the $L-M$ isoluminant axis (RG). Fig. 3 shows the magnitude of the TI in degrees for four subjects. By convention, positive sign corresponds to a repulsive TI. Test stimuli are labelled on the abscissa. Filled bars denote light–dark inducers; hollow bars denote red–green inducers. For all four subjects there is a tendency for the TI to have a greater magnitude when test and surround are modulated along the same axis of colour space than orthogonal axes. This is evident in Fig. 3 from the fact that for LD test stimuli the TI is consistently larger for LD than RG surround stimuli while for RG test stimuli the TI is consistently larger for an RG surround.

In Experiment 2, centre and surround gratings were modulated along non-cardinal axes of colour space intermediate between the luminance and $L-M$ isoluminant axes. Fig. 4 shows that the pattern of chromatic selectivity for non-cardinal is the same as for the cardinal stimuli in Experiment 1. Specifically, the TI for LD–RG test stimuli is consistently larger for an LD–RG surround while the TI for LR–DG stimuli is consistently larger for an LR–DG surround.

The following analysis was carried out to quantify the degree of selectivity for colour/luminance evident from the data of Experiments 1 and 2. For each subject in each experiment, we calculated the difference between the sum of the TIs in the two “same” test-inducer conditions and the sum in the two “different” conditions. This total was then divided by the sum of the TIs across all four conditions and multiplied by 100 to give selectivity as a percentage. A value of 100% would correspond to complete colour/luminance selectivity, such that there was a non-zero TI only when test and inducer were modulated along the same axis of colour space. A value of 0% would correspond to no selectivity, such that the sum of the tilt illusions in the “same” and “different” conditions was the same. Negative values of selectivity correspond to cases in which the tilt illusion is larger for the “different” than the “same” conditions.

Fig. 5 shows the colour/luminance selectivity calculated from the data of Experiments 1 and 2 for each of the four subjects. Selectivity averaged across subjects was 28% for cardinal (filled bars) and 27% for non-cardinal stimuli (hollow bars). Planned contrasts show

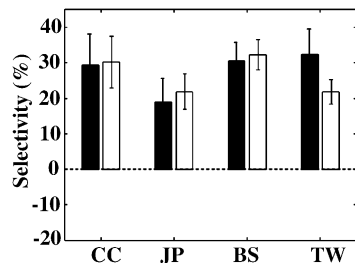


Fig. 5. Selectivity of the tilt illusion. Data are shown for each of four subjects as a percentage of overall illusion strength. Filled bars denote the results of Experiment 1 using cardinal test and surround stimuli. Hollow bars denote the results of Experiment 2 using non-cardinal test and surround stimuli.

that the selectivity of the non-cardinal TI is significantly greater than zero ($t_3 = 9.61$; $p < 0.01$ one-tailed with Bonferroni correction) but that there is no significant difference between cardinal and non-cardinal selectivities ($t_3 = 0.41$; $p > 0.1$).

3.2. Experiments 3&4: tilt aftereffect

In Experiments 3 and 4, we measured the effect of adaptation to a grating oriented at 15° to the vertical on the perceived orientation of a subsequent test grating. In Experiment 3, adapting and test gratings were modulated either in luminance (LD) or along the $L-M$ isoluminant axis (RG). Fig. 6 shows the magnitude of the TAE in degrees for three subjects. There is a tendency, albeit a weaker one than for the TI (Fig. 3), for the TAE to have a greater magnitude when test and inducer are modulated along the same axis of colour space than orthogonal axes.

In Experiment 4, adapting and test gratings were modulated along non-cardinal axes of colour space. Fig.

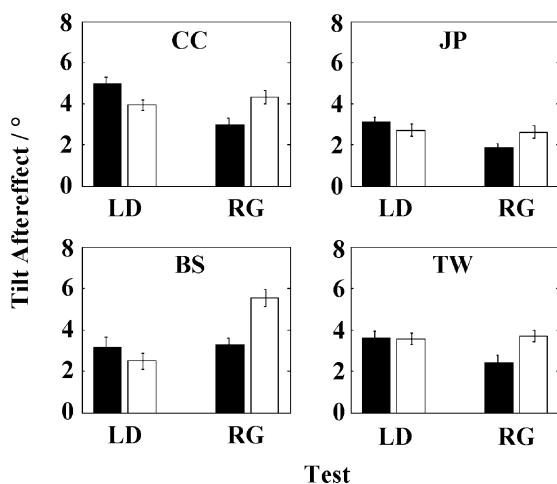


Fig. 6. Tilt aftereffect for cardinal stimuli. Aftereffect magnitude in degrees for each of four subjects. Test stimuli are labelled on the abscissa as LD (light–dark) or RG (red–green). Filled bars denote LD inducers; hollow bars denote RG inducers.

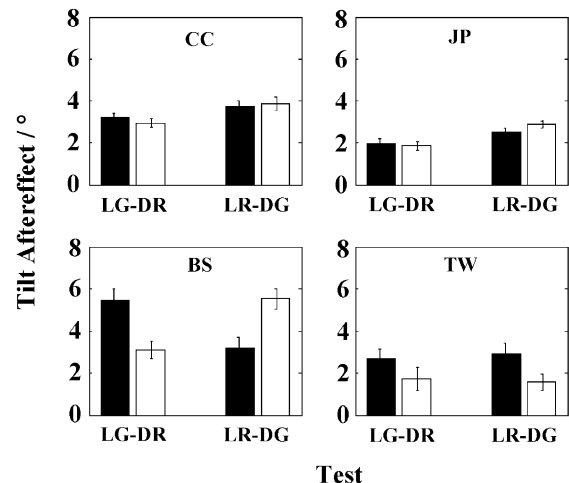


Fig. 7. Tilt aftereffect for non-cardinal stimuli. Aftereffect magnitude in degrees for each of four subjects. Test stimuli are labelled on the abscissa as LG–DR (light green–dark red) or LR–DG (light red–dark green). Filled bars denote LG–DR inducers; hollow bars denote LR–DG inducers.

7 shows that the results were quite variable between observers, with only subject BS showing a consistent difference in the magnitude of the TAE for “same” and “opposite” conditions.

Fig. 8 shows the colour/luminance selectivity of the TAE calculated from the data of Experiments 3 and 4 for each of the four subjects. Selectivity averaged across subjects was 14% for cardinal (filled bars) and 8% for non-cardinal stimuli (hollow bars). Planned contrasts show that the selectivity of the non-cardinal TAE is not significantly greater than zero ($t_3 = 1.15$; $p > 0.1$) and that there is no significant difference between cardinal and non-cardinal selectivities ($t_3 = 1.31$; $p > 0.1$).

Fig. 9 shows selectivity of the TI (top row) and TAE (bottom row) for the three planes defined by pairs of cardinal axes in DKL colour space: luminance, $L-M$ (left); luminance, $S - (L + M)$ (middle); the equiluminant plane (right). Data are shown for two subjects, CC and JP, as a percentage of overall illusion/aftereffect strength. Filled and hollow bars denote cardinal and

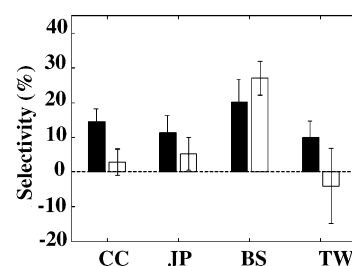


Fig. 8. Selectivity of the tilt aftereffect. Data are shown for each of four subjects as a percentage of overall illusion strength. Filled bars denote the results of Experiment 3 using cardinal test and surround stimuli. Hollow bars denote the results of Experiment 4 using non-cardinal test and surround stimuli.

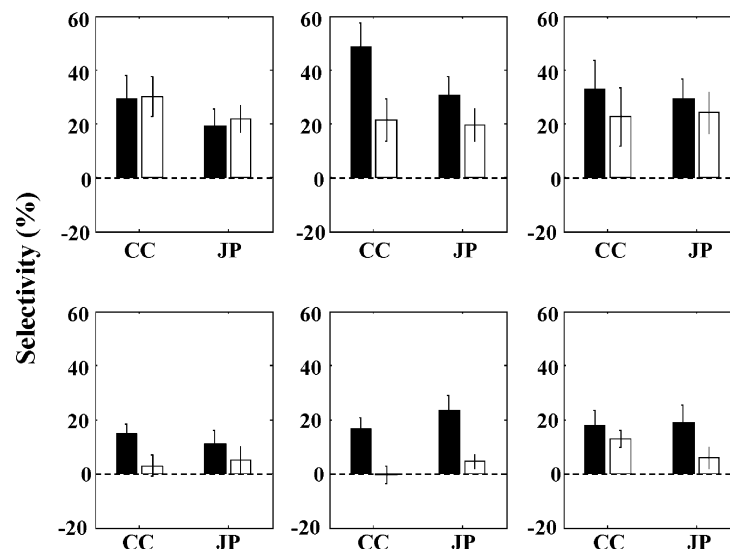


Fig. 9. Selectivity of the tilt illusion (top row) and tilt aftereffect (bottom row) for the three planes defined by pairs of cardinal axes in DKL colour space: luminance, $L-M$ (left); luminance, $S-(L+M)$ (middle); the equiluminant plane (right). Data are shown for two subjects, CC and JP, as a percentage of overall illusion/aftereffect strength. Filled and hollow bars denote cardinal and non-cardinal stimuli, respectively.

non-cardinal stimuli, respectively. The pattern of results is similar in all cases, with each TI larger than the corresponding TAE and effects for cardinal stimuli generally larger than for the corresponding non-cardinal stimuli.

4. Discussion

Experiments 1 and 2 show colour/luminance selectivity of the TI in the range 19–32% (mean 28%) for cardinal test and inducing stimuli and 22–32% (mean 27%) for non-cardinal. These results support the conclusion of Clifford, Spehar, et al. (2003) that the cardinal chromatic axes have no special status for orientation processing at the level(s) of visual cortex at which the TI is mediated. For the TAE, Experiments 3 and 4 show selectivity in the range 10–20% (mean 14%) for cardinal stimuli and –4% to +27% (mean 8%) for non-cardinal. A comparison of corresponding conditions (Fig. 10) shows that in all 16 cases the TI showed a higher degree of selectivity than the TAE. As can be seen in Fig. 11, there is some suggestion in our data of a higher degree of colour/luminance selectivity for cardinal than non-cardinal TAEs, as reported by Flanagan et al. (1990). However, variability between subjects, particularly for the colour/luminance selectivity of non-cardinal TAEs (Figs. 7 and 8), meant that the difference in selectivity between cardinal and non-cardinal TAEs failed to reach significance. Thus, it is not safe to conclude that there is any consistent difference between the TI and TAE in terms of their relative selectivity for cardinal and non-cardinal stimuli.

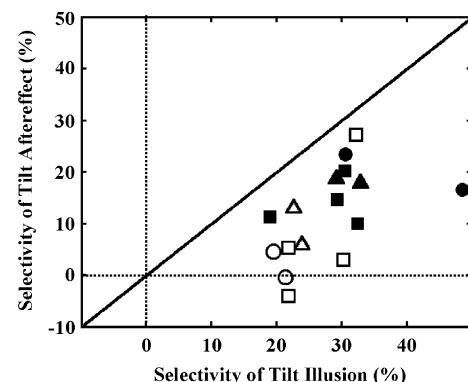


Fig. 10. Direct comparison of the selectivity of the tilt aftereffect and tilt illusion for corresponding subjects and stimulus conditions for the three planes defined by pairs of cardinal axes in DKL colour space: luminance, $L-M$ (squares); luminance, $S-(L+M)$ (circles); the equiluminant plane (triangles). Filled symbols denote cardinal stimuli; hollow symbols non-cardinal. Points lying below the diagonal line indicate that selectivity is greater for the tilt illusion than for the tilt aftereffect.

The TI and TAE are widely held to share common mechanisms, the most likely candidate being inhibitory interactions between orientation-selective mechanisms within primary and/or extrastriate visual cortex (Blakemore, Carpenter, & Georgeson, 1970; Blakemore & Tobin, 1972; Carpenter & Blakemore, 1973; Magnussen & Kurtenbach, 1980; Morrone, Burr, & Maffei, 1982; O'Toole & Wenderoth, 1977; Wenderoth & Johnstone, 1987). Colour/luminance selectivity would then be expected to reflect the diversity of chromatic tuning found in those areas, with no special status accorded to the cardinal axes of DKL colour space (V1:

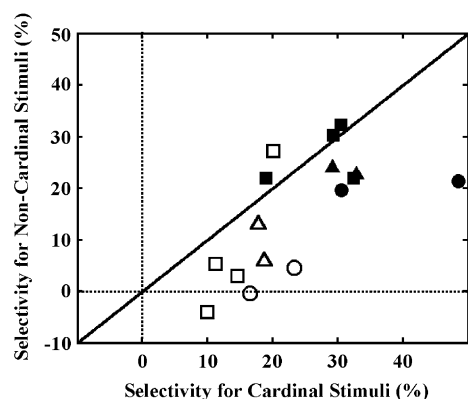


Fig. 11. Direct comparison of selectivity for cardinal and non-cardinal stimuli for corresponding subjects and stimulus conditions for the three planes defined by pairs of cardinal axes in DKL colour space: luminance, $L-M$ (squares); luminance, $S-(L+M)$ (circles); the equiluminant plane triangles. Filled circles denote the tilt illusion; hollow, the tilt aftereffect. Points lying below the diagonal line indicate cases where selectivity was greater for cardinal than non-cardinal stimuli.

DeValois et al., 2000; Hanazawa, Komatsu, & Murakami, 2000; Johnson, Hawken, & Shapley, 2001; Lennie, Krauskopf, & Sclar, 1990; Leventhal, Thompson, Liu, Zhou, & Ault, 1995; Thorell, DeValois, & Albrecht, 1984; Wachtler, Sejnowski, & Albright, 2003; V2: Kiper, Fenstemaker, & Gegenfurtner, 1997; Roe & Ts'o, 1999; Xiao, Wang, & Felleman, 2003; V3: Gegenfurtner, Kiper, & Levitt, 1997; V4: Yoshioka, Dow, & Vautin, 1996; IT: Komatsu, Ideura, Kaji, & Yamane, 1992).

In the present study, as in previous ones (Clifford, Spehar, et al., 2003; Flanagan et al., 1990), significant TIs and TAEs were consistently obtained for inducing stimuli modulated along chromatic axes orthogonal in DKL space to that of the test. This shows that substantial colour-insensitive interactions underlie the two effects in addition to their colour-specific component. This colour-insensitive component may reflect the operation of higher-level visual mechanisms that code for form in a cue-invariant manner (Clifford, Spehar, et al., 2003; Hardy & DeValois, 2002). While processing of information about orientation and colour appears to be closely coupled at the early stages of the visual hierarchy (Clifford, Arnold, & Pearson, 2003; Holcombe & Cavanagh, 2001; Lennie, 1998; McClurkin, Optican, Richmond, & Gawne, 1991), there may be low preservation of colour specificity with successive stages of form processing.

The greater colour/luminance selectivity of the TI than the TAE suggests that the TAE might engage cue-invariant mechanisms more strongly than does the TI. Interestingly, the TAE data from the study of Flanagan et al. (1990) show weaker overall TAE magnitudes than those reported here ($\sim 2^\circ$) but a higher degree of selectivity ($\sim 25\%$). One possible explanation for this dis-

crepancy between the results of that study and those presented here could be stimulus differences. There is reason to expect the experimental procedure employed by Flanagan et al. (1990) to produce less adaptation of high-level cue-invariant mechanisms than ours because, unlike their study, we used an adapting stimulus considerably larger than the test grating and because extraneous cues to orientation such as the edge of the screen were eliminated. Thus, our procedure would be more effective in adapting the response properties of neurons at the same retinotopic location with large receptive fields. Such neurons are found at the higher levels of the visual hierarchy and typically code for form in a cue-invariant manner. Consequently, our stimuli would generate more adaptation of cue-invariant mechanisms and thus less selectivity as a proportion of the overall aftereffect magnitude.

When the absolute selectivity of the TAE in our study is calculated in terms of degrees of orientation then the average comes to 0.4° , which is similar to that evident from the data of Flanagan et al. (1990) in their Fig. 6. The difference between the selectivities observed in the two studies emerges only when selectivity is expressed as a percentage of the total aftereffect, since the data of Flanagan et al. (1990) show weaker overall TAE magnitudes. This suggests that the difference between the selectivities observed in the two studies results from a difference in the degree to which high-level cue-invariant mechanisms were adapted. Given that the experimental procedures used in the current study to measure the TI and TAE were matched as closely as possible and involved a single set of subjects, we maintain that the comparison of colour/luminance selectivity between TI and TAE carried out here is a meaningful one notwithstanding the fact that other experimental procedures might produce quantitatively different estimates of selectivity.

Recent physiological data shows that the colour and luminance selectivity of the suppressive surround of neurons in macaque visual cortex actually increases from V1 to V2 (Solomon, Peirce, Krauskopf, & Lennie, 2003). Thus, it may emerge that there is not as simple a progression from selectivity to cue-invariance along the visual hierarchy as is generally believed. Future work will use interocular transfer of the TI to investigate how the proposed distinction between low-level colour-specific mechanisms and higher-level cue-invariant mechanisms maps onto monocular and binocular mechanisms in the visual system.

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References

- Anstis, S. M., & Cavanagh, P. (1983). A minimum motion technique for judging equiluminance. In J. Mollon, & R. T. Sharpe (Eds.), *Colour vision: Physiology and psychophysics* (pp. 156–166). London: Academic Press.
- Blakemore, C., Carpenter, R. H., & Georgeson, M. A. (1970). Lateral inhibition between orientation detectors in the human visual system. *Nature*, 228, 37–39.
- Blakemore, C., & Tobin, E. A. (1972). Lateral inhibition between orientation detectors in the cat's visual cortex. *Experimental Brain Research*, 15, 439–440.
- Bradley, A., Switkes, E., & DeValois, K. (1988). Orientation and spatial frequency selectivity of adaptation to color and luminance gratings. *Vision Research*, 28, 841–856.
- Carpenter, R. H., & Blakemore, C. (1973). Interactions between orientations in human vision. *Experimental Brain Research*, 18, 287–303.
- Clifford, C. W. G., Arnold, D. H., & Pearson, J. (2003). A paradox of temporal perception revealed by a stimulus oscillating in colour and orientation. *Vision Research*, 43, 2245–2253.
- Clifford, C. W. G., Spehar, B., Solomon, S. G., Martin, P. R., & Zaidi, Q. (2003). Interactions between colour and luminance in the perception of orientation. *Journal of Vision*, 3, 106–115.
- Clifford, C. W. G., Wenderoth, P., & Spehar, B. (2000). A functional angle on some aftereffects in cortical vision. *Proceedings of the Royal Society of London Series B*, 267, 1705–1710.
- Derrington, A. M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology (London)*, 357, 241–265.
- DeValois, R. L., Abramov, I., & Jacobs, G. H. (1966). Analysis of response patterns of LGN cells. *Journal of the Optical Society of America*, 56, 966–977.
- DeValois, R. L., Cottaris, N. P., Elfar, S. D., Mahon, L. E., & Wilson, J. A. (2000). Some transformations of color information from geniculate nucleus to striate cortex. *PNAS*, 97, 4997–5002.
- Flanagan, P., Cavanagh, P., & Favreau, O. E. (1990). Independent orientation-selective mechanisms for the cardinal directions of colour space. *Vision Research*, 30, 769–778.
- Gegenfurtner, K. R., & Kiper, D. C. (1992). Contrast detection in luminance and chromatic noise. *Journal of the Optical Society of America A*, 9, 1880–1888.
- Gegenfurtner, K. R., Kiper, D. C., & Levitt, J. B. (1997). Functional properties of neurons in macaque area V3. *Journal of Neurophysiology*, 77, 1906–1923.
- Georgeson, M. A. (1973). Spatial frequency selectivity of a visual tilt illusion. *Nature*, 245, 43–45.
- Gibson, J. J., & Radner, M. (1937). Adaptation, after-effect, and contrast in the perception of tilted lines. I. Quantitative studies. *Journal of Experimental Psychology*, 20, 453–467.
- Gunther, K. L., & Dobkins, K. R. (2003). Independence of mechanisms tuned along cardinal and non-cardinal axes of color space: evidence from factor analysis. *Vision Research*, 43, 683–696.
- Hanazawa, A., Komatsu, H., & Murakami, I. (2000). Neural selectivity for hue and saturation of colour in the primary visual cortex of the monkey. *European Journal of Neuroscience*, 12, 1753–1763.
- Hardy, J. L., & DeValois, K. K. (2002). Color-selective analysis of luminance-varying stimuli. *Vision Research*, 42, 1941–1951.
- Harris, J. P., & Calvert, J. E. (1989). Contrast, spatial frequency and test duration effects on the tilt aftereffect: implications for underlying mechanisms. *Vision Research*, 29, 29–35.
- Held, R., & Schattuck, S. R. (1971). Colour and edge sensitive channels in the human visual system: tuning for orientation. *Science*, 174, 314–316.
- Hendry, S. H., & Yoshioka, T. (1994). A neurochemically distinct third channel in the macaque dorsal lateral geniculate nucleus. *Science*, 264, 575–577.
- Holcombe, A. O., & Cavanagh, P. (2001). Early binding of feature pairs for visual perception. *Nature Neuroscience*, 4, 127–128.
- 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, 409–416.
- Kiper, D. C., Fenstemaker, S. B., & Gegenfurtner, K. R. (1997). Chromatic properties of neurons in macaque area V2. *Visual Neuroscience*, 14, 1061–1072.
- Komatsu, H., Ideura, Y., Kaji, S., & Yamane, S. (1992). Color selectivity of neurons in the inferior temporal cortex of the awake macaque monkey. *Journal of Neuroscience*, 12, 408–424.
- Kontsevich, L. L., & Tyler, C. W. (1999). Bayesian adaptive estimation of psychometric slope and threshold. *Vision Research*, 39, 2729–2737.
- Krauskopf, J., & Gegenfurtner, K. (1992). Color discrimination and adaptation. *Vision Research*, 32, 2165–2175.
- Krauskopf, J., Williams, D. R., & Heeley, D. W. (1982). Cardinal directions of color space. *Vision Research*, 22, 1123–1131.
- Lennie, P. (1998). Single units and visual cortical organization. *Perception*, 27, 889–935.
- Lennie, P., Krauskopf, J., & Sclar, G. (1990). Chromatic mechanisms in striate cortex of macaque. *Journal of Neuroscience*, 10, 649–669.
- Leventhal, A. G., Thompson, K. G., Liu, D., Zhou, Y., & Ault, S. J. (1995). Concomitant sensitivity to orientation, direction, and color of cells in layers 2, 3, and 4 of monkey striate cortex. *Journal of Neuroscience*, 15, 1808–1818.
- Li, A., & Lennie, P. (1997). Mechanisms underlying segmentation of colored textures. *Vision Research*, 37, 83–97.
- Livingstone, M. S., & Hubel, D. H. (1984). Anatomy and physiology of a color system in primate primary visual cortex. *Journal of Neuroscience*, 4, 309–356.
- 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, 3416–3468.
- Livingstone, M. S., & Hubel, D. H. (1988). Segregation of form, color, movement and depth: anatomy, physiology and perception. *Science*, 240, 740–749.
- Lovegrove, W. (1977). Inhibition between channels selective to contour orientation and wavelength in the human visual system. *Perception & Psychophysics*, 22, 49–53.
- Lovegrove, W., & Badcock, D. (1981). The effect of spatial frequency on colour selectivity in the tilt illusion. *Vision Research*, 21, 1235–1237.
- Lovegrove, W. J., & Over, R. (1973). Colour selectivity in orientation masking and aftereffect. *Vision Research*, 13, 895–902.
- Magnussen, S., & Kurtenbach, W. (1980). Linear summation of tilt illusion and tilt aftereffect. *Vision Research*, 20, 39–42.
- Martin, P. R., White, A. J. R., Goodchild, A. K., Wilder, H. D., & Sefton, A. E. (1997). Evidence that blue-on cells are part of the third geniculocortical pathway in primates. *European Journal of Neuroscience*, 9, 1536–1541.
- McClurkin, J. W., Optican, L. M., Richmond, B. J., & Gawne, T. J. (1991). Concurrent processing and complexity of temporally encoded neuronal messages in visual perception. *Science*, 253, 675–677.
- Mitchell, D. E., & Muir, D. W. (1976). Does the tilt after-effect occur in the oblique meridian? *Vision Research*, 16, 609–613.
- Morrone, M. C., Burr, D. C., & Maffei, L. (1982). Functional implications of cross-orientation inhibition of cortical visual cells. I. Neurophysiological evidence. *Proceedings of the Royal Society of London, Series B: Biological Science*, 216, 335–354.

- Mullen, K. T., Cropper, S. J., & Losada, M. A. (1997). Absence of linear subthreshold summation between red–green and luminance mechanisms over a wide range of spatio-temporal conditions. *Vision Research*, 37, 1157–1165.
- Mullen, K. T., & Losada, M. A. (1994). Evidence for separate pathways for color and luminance detection mechanisms. *Journal of the Optical Society of America A*, 11, 3136–3151.
- Mullen, K. T., & Sankerelli, M. J. (1999). Evidence for the stochastic independence of the blue–yellow, red–green and luminance detection mechanisms revealed by subthreshold summation. *Vision Research*, 39, 733–745.
- O’Toole, B., & Wenderoth, P. (1977). The tilt illusion: repulsion and attraction effects in the oblique meridian. *Vision Research*, 17, 367–374.
- Over, R., Broerse, J., & Crassini, B. (1972). Orientation illusion and masking in central and peripheral vision. *Journal of Experimental Psychology*, 96, 25–31.
- Roe, A. W., & Ts’o, D. Y. (1999). Specificity of colour connectivity between primate V1 and V2. *Journal of Neurophysiology*, 82, 2719–2730.
- Sankerelli, M. J., & Mullen, K. T. (1997). Postreceptoral chromatic detection mechanisms revealed by noise masking in three-dimensional cone contrast space. *Journal of the Optical Society of America A*, 14, 2633–2646.
- Sekuler, R. (1974). Spatial vision. *Annual Review of Psychology*, 25, 195–232.
- Solomon, S. G., Peirce, J. W., Krauskopf, J., & Lennie, P. (2003). Chromatic sensitivity of surround suppression in macaque V1 and V2. *Journal of Vision*, 3, TA140.
- Thorell, L. G., DeValois, R. L., & Albrecht, D. G. (1984). Spatial mapping of monkey V1 cells with pure color and luminance stimuli. *Vision Research*, 24, 751–769.
- Tolhurst, D. J., & Thompson, P. G. (1975). Orientation illusions and after-effects: inhibition between channels. *Vision Research*, 15, 967–972.
- Wachtler, T., Sejnowski, T. J., & Albright, T. D. (2003). Representation of color stimuli in awake macaque primary visual cortex. *Neuron*, 37, 681–691.
- Wade, J. N. (1980). The influence of colour and contour rivalry on the magnitude of the tilt illusion. *Vision Research*, 20, 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, 827–835.
- Ware, C., & Mitchell, D. E. (1974). The spatial selectivity of the tilt aftereffect. *Vision Research*, 14, 735–737.
- Wenderoth, P., & Johnstone, S. (1987). Possible neural substrates for orientation analysis and perception. *Perception*, 16, 693–709.
- Wiesel, T. N., & Hubel, D. H. (1966). Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey. *Journal of Neurophysiology*, 29, 1115–1156.
- Xiao, Y., Wang, Y., & Felleman, D. J. (2003). A spatially organized representation of colour in macaque cortical area V2. *Nature*, 30, 535–539.
- Yoshioka, T., Dow, B. M., & Vautin, R. G. (1996). Neuronal mechanisms of color categorization in areas V1, V2 and V4 of macaque monkey visual cortex. *Behavioural Brain Research*, 76, 51–70.