Perception, 2010, volume 39, pages 620 – 626

doi:10.1068/p6529

Adaptation to combinations of form, colour, and movement

Alex Burmester, Jack Broerse
Department of Psychology, University of Queensland, St Lucia, QLD 4072, Australia;
e-mail: alexburm@gmail.com
Received 27 July 2009; in revised form 15 February 2010; published online 26 April 2010

Abstract. Observers typically report illusory colour on achromatic gratings after being adapted to orthogonally oriented gratings presented in complementary colours, where the colour apparent on each grating is complementary to the one that had been presented with that grating during adaptation (McCollough, 1965 *Science* **149** 1115 – 1116). We used this procedure, but presented homogenous fields at test instead of achromatic gratings. When adaptation stimuli moved in directions locally orthogonal to their orientation, we found that, for up to 7 – 8 min after adaptation, a flower-like illusory pattern was evident on both homogenous fields; after this time illusory radial lines and concentric circles were evident and were colour-contingent (eg for adaptation with green concentric circles and magenta radial lines, concentric circles were apparent on a magenta test field and radial lines were apparent on a green test field). When stimuli were stationary during induction, colour-contingent illusory forms were also apparent at test. The results demonstrate that an aftereffect, reciprocal to the McCollough effect, can be produced under appropriate induction conditions, and that this effect is not due to retinal afterimages.

1 Introduction

1.1 *Simple and contingent aftereffects and the McCollough effect*

When an observer is presented with a grating moving in one direction for several seconds and is subsequently presented with a stationary grating, the stationary grating appears to move slowly in the opposite direction (ie a motion aftereffect or MAE). The MAE is referred to as a simple aftereffect because it can be induced with any moving stimulus and can be viewed on almost any test stimulus. Simple aftereffects such as the MAE are often contrasted with contingent aftereffects such as the McCollough effect (ME). The ME was first reported when, after inspecting vertical lines on an orange background for several minutes and then horizontal lines on a blue background for several minutes, observers reported illusory colour on an achromatic vertical and horizontal grating (McCollough 1965). The illusory colour on the achromatic vertical lines was complementary to the colour that had been paired with the vertical lines during induction and, likewise, the illusory colour that appeared on the achromatic horizontal lines was complementary to the colour that had been paired with the horizontal lines during induction (ie orange appeared on the achromatic horizontal lines and blue appeared on the achromatic vertical lines). The ME is known as a contingent aftereffect because the illusory colour is contingent on the orientation of lines in the test pattern.

1.2 *Colour-contingent pattern aftereffects*

Dawson and Stromeyer (1978) found that, after observers viewed two vertical low-frequency square-wave stimuli, each in counterphase to the other (so that light bars on one corresponded to dark bars on the other) and each in a complementary colour, homogenously coloured fields elicited illusory gratings that were colour contingent. On each homogenously coloured test field, the illusory grating that appeared was in spatial counterphase to the grating that had been presented with that colour during adaptation. For instance, if an observer was adapted to a magenta grating with a dark bar just to the left of fixation and a green grating with a dark bar just to the right of fixation, she/he would perceive an illusory grating with a dark bar to the left of fixation on a green field and an illusory grating with a dark bar on the right of fixation on a magenta field. This illusory form was most prominent when the homogenous test fields were switched and would then fade rapidly. The fact that these illusory gratings were colour-contingent (with the contingencies reversed from adaptation to test) and faded after the switch between fields suggested they were not simple retinal afterimages. They also persisted after bleaching of the retina by exposure to a strong light source, which is further evidence against them being retinal afterimages.

In another experiment, Humphrey et al (1994) induced observers with the same stimulus sequence as that used for ME induction—specifically, they showed observers a magenta (green) set of radial lines and a green (magenta) set of concentric circles, alternating for 20 min or so. They found that, afterwards, homogenous coloured fields elicited illusory forms contingent on colour, so that, for instance, after observers were presented with green concentric circles and magenta radial lines during adaptation, a green test field elicited illusory radial lines and a magenta test field elicited illusory concentric circles.

As in the Dawson and Stromeyer (1978) study, the illusions produced in the Humphrey et al (1994) study had their colour-form contingencies reversed from adaptation to test. Also, they were present even after retinal bleaching with a bright light source. These observations suggest they were not retinal afterimages. However, as in the Dawson and Stromeyer (1978) study, the illusions produced in the Humphrey et al (1994) study were contrast-defined. It is necessary to further differentiate these illusions from retinal afterimages, given that afterimages are also contrast-defined and have a comparable retention time to the ME when induced under similar conditions (Hansel and Mahmud 1978).

Because the illusions found by Humphrey et al (1994) followed the same reversal of orientation/pattern colour contingencies as the ME, they were presumed to be a colour-contingent pattern aftereffect (CCPA)—an aftereffect that is reciprocal to the ME (ie same induction, opposite test) and so involves the perception of an illusory form/pattern that is colour-contingent, rather than illusory colour that is form/pattern-contingent. Reciprocal aftereffects have been demonstrated before. For example, Favreau et al (1972) demonstrated that, with the same induction procedure, both direction of motion-contingent colour aftereffects as well as colour-contingent MAEs could be produced, depending on what test stimulus was used. Direction of motion-contingent colour aftereffects was also reported by Hepler (1968) and colour-contingent motion aftereffects were also reported by Mayhew and Anstis (1972).

1.3 *Induction with moving stimuli*

Recently, McCollough (2000) demonstrated that the ME could be elicited on stationary achromatic patterns after adaptation with slowly moving coloured patterns. Therefore, if the CCPA produced by Humphrey et al (1994) is truly reciprocal to the ME, it should be possible to induce stationary CCPAs after induction to moving coloured patterns. Attempting to induce CCPAs with moving patterns would add another control against retinal afterimages, as stimuli moving at an appropriate speed do not produce contrast-defined contours in a retinal afterimage. Therefore, in the current study, observers were adapted to radial lines and concentric circles presented in complementary colours with each pattern moving equally in opposite directions locally orthogonal to the orientation of that pattern, in an attempt to produce CCPAs while controlling for retinal afterimages. In a second condition stationary stimuli were used to replicate the results of Humphrey et al (1994).

2 Method

2.1 *Participants*

Twenty-four participants took part in the study. Twenty participants were first year Psychology students at the University of Queensland, and earned course credit by taking part in the study. Four participants were volunteers recruited directly by the experimenter. Only one of the participants was familiar with the expected outcomes of the experiments.

2.2 *Equipment*

A custom software package, VSG Visual Objects 3.0 (Paul Jackson), was used to control the display of stimuli. The program was running on a Dell IBM compatible computer with a Pentium (model II, 300 MHz) processor. Stimuli were displayed on a Hitachi 20 inch monitor running at a resolution of 1024×780 pixels with a refresh rate of 70 Hz. This monitor was connected to a VSG 3.0 Stimulus Generator Video Card (Cambridge Research Laboratories).

2.3 *Stimuli*

A radial-line stimulus with an angular frequency of 1 cycle per 24°—16 black and 16 coloured sectors, and a concentric-circle pattern with 8 cycles visible on the disk at any one time—was used. The circles in the concentric-circle pattern were all of equal width on the screen. Both patterns subtended a visual angle of 18.81 deg when the observer was seated 80 cm from the screen and had a diameter of 26.5 cm on the screen. The patterns were constructed by using sine-wave luminance profiles, such that the luminance varied in correspondence to a sine-wave across the pattern. For each participant, one of the patterns was black (CIE $Y = 2.3$, $x = 0.308$, $y = 0.340$) and magenta (CIE_{Yxy} $Y = 27.9$, $x = 0.362$, $y = 0.208$) and the other pattern was black and green (CIE_{Yxy} $Y = 27.5$, $x = 0.299$, $y = 0.569$). Between the presentations of each coloured pattern, a grey (CIE_{Yxy} $Y = 15$, $x = 0.311$, $y = 0.385$) homogenous field was presented. For the pre-tests and post-tests, magenta (CIE_{Yxy} $Y = 15.0$, $x = 0.366$, $y = 0.222$) and green (CIE_{Yxy} $Y = 14.6$, $x = 0.300$, $y = 0.533$) homogenous fields were used. The colours used with the radial line and concentric-circle patterns were of approximately equal luminance and the homogenous coloured fields were equal to the average luminance of the coloured patterns. In the moving-stimulus conditions, movement of the patterns occurred at a rate of 0.2 Hz and occurred for 7.5 s in each direction, orthogonal to the local orientation of the pattern (ie concentric circles expanded and contracted, while radial lines rotated clockwise and counterclockwise).

2.4 *Design*

A 2×2 factorial mixed design was used. The within-subjects factor was testing condition, with the levels being pre-test and post-test. The between subjects factor was movement condition, with the levels being stationary and moving. The colour-pattern pairings were counterbalanced across participants, so that half saw black and magenta radial lines and black-and-green concentric circles and the other half saw the opposite colour-pattern combinations. Half of the participants saw moving patterns and half saw stationary patterns for the entire induction period. An equal number of participants saw moving and stationary patterns for each of the colour–pattern pairings. Table 1 summarises this design.

2.5 *Procedure*

Each experiment was conducted in the following sequence: pre-test, induction, post-test. For the pre-test and post-test, which were exactly the same, participants were presented with green and magenta homogenous fields. Each field was presented for 3 s and the two fields alternated for a total of 1 min, so each field was presented 10 times. The homogenous fields were presented on the same screen as the stimuli used during adaptation,

Table 1. Design of the experiment.

Induction condition	Green radials, Magenta circles	Magenta radials, Green circles
Moving pattern	$N = 6$	$N = 6$
Stationary pattern	$N = 6$	$N = 6$

and were the same size as those stimuli. During the pre-test and post-test, the participant was seated 80 cm from the screen. Therefore, the homogenous fields subtended the same visual angle (18.8 deg) as the inducing stimuli. The post-test took place 10 min after induction. During the intervening time, the lights in the room were kept on and the participant was instructed to look around and to look at the lights, in order to assist with the dissipation of retinal afterimages.

Before both the pre-test and post-test, the participants were each given identical verbal instructions telling them to fixate on the centre of the screen and report any illusory form that consistently appeared with either the green or magenta fields, or both. They were required to report the nature of the illusory form on a forced-choice questionnaire (choices included: radial lines, concentric circles, random texture/noise, squiggles, nothing/blank) and were required to give a magnitude estimate on a scale of 0 – 10, comparing the illusory form to the form veridically perceived during induction. During induction, one pattern was presented for 15 s followed by a blank grey green for 2 s. The other pattern was then presented for 15 s, followed by another blank grey screen for 2 s. This cycle was repeated 40 times for each participant, so that induction took 22 min 40 s.

3 Results

3.1 *Number of appropriate reports*

Because there were 2 tests (a green homogenous field and a magenta homogenous field) and twelve subjects in each induction condition, there was a total of 24 possible appropriate reports. An 'appropriate' report, as used here, means that the colour – orientation contingencies were reversed from adaptation to test. For instance, if adapted to a magenta radial line grating and a green grating of concentric circles, the observer would perceive illusory circles on a magenta test field and illusory radial lines on a green test field. There were 17 appropriate reports in the stationary condition and 18 in the moving condition. Most of the 'inappropriate' reports were that nothing was seen. Other inappropriate reports were that other patterns were seen or patterns were seen that did not correspond to the induced colour – pattern contingencies.

3.2 *Magnitude estimation*

A repeated-measures t-test revealed that, for the pre-test condition, there was no significant difference between magnitude estimates on the magenta homogenous field ($M = 2.62$, $\mathrm{SD} = 12.84$) and magnitude estimates on the green homogenous field ($M = 1.39$, $\mathrm{SD} = 4.75$), $t = -0.432$, ns. Another repeated-measures t-test revealed that, for the post-test condition, there was no significant difference between magnitude estimates on the magenta homogenous field ($M = 45.58$, $\mathrm{SD} = 26.78$) and magnitude estimates on the green homogenous field ($M = 40.25$, $\mathrm{SD} = 29.79$), $t = -1.31$, ns. Therefore for each participant a pre-test and post-test score was produced that was the mean of the two magnitude estimates on the two different test patterns. These scores were used for further analyses. Pre-test scores were subtracted from post-test scores to give a difference score for each subject's magnitude estimation. A between-subjects ANOVA (see table 2) conducted on these scores revealed there was no significant difference between the condition where

Table 2. A summary of the ANOVA analysis conducted on magnitude-estimate scores.

Source	Sum of squares	Degrees of freedom	Mean square	F	Significance
Colour–pattern Pairing	127.43	1	127.43	0.31	0.584
Movement Condition	4566.71	1	4566.71	11.083	0.003*
Colour Movement	× 278.926	1	278.926	0.677	0.420
Error	8241.17	20	412.06		
Total	13215.25	23			

* $p < 0.05$, $N = 24$.

radial lines were presented in magenta (and concentric circles in green) ($M = 43.21$, SD $= 27.25$) and the condition where concentric circles were presented in green (and radial lines in magenta) ($M = 38.60$, SD $= 21.14$), $F = 1.57$, ns. However, it did show that magnitude estimates made by subjects in the moving-stimuli condition ($M = 27.11$, SD $= 19.00$) were significantly lower than those made by subjects in the stationary-stimuli condition ($M = 54.70$, SD $= 20.62$), $F = 11.62$, $p = 0.003$.

4 Discussion

The results of this study demonstrate that observers consistently perceived colour-contingent illusory radial lines and concentric circles on homogenous coloured test fields after being adapted to coloured radial lines and concentric circles. The colour–orientation contingencies were reversed from induction to test, such that an observer would perceive (for example) illusory radial lines on a magenta test field and illusory concentric circles on a green test field after being adapted to a green-radial-line grating and a magenta concentric-circle grating. The experiment included a condition in which the induction stimuli each moved in equal and opposite directions locally orthogonal to the orientation of the pattern as well as a condition where they were stationary. The colour-contingent aftereffects were reported in both conditions.

For the conditions where stimuli were moving during induction, pilot studies indicated that if observers were shown the homogenous test field up to 7–8 min after induction, no CCPA was evident. Instead, a flower-like pattern was evident on both coloured fields. After the 7–8 min delay, however, illusory patterns appeared that showed the orientation–colour contingencies appropriate for a CCPA [ie illusory radial lines on a green (magenta) test field and illusory concentric circles on a magenta (green) test field after induction to magenta (green) radial lines and green (magenta) concentric circles]. These observations can be explained by properties of motion processors in the visual system.

4.1 *Dual-channel motion processing*

It has been observed that after adaptation the strength of a MAE decays first quickly and then slowly (Masland 1969). Approximately concurrent with these two phases of decay is a change in the nature of the stimulus that will elicit the MAE—during the first stage, a MAE will be perceived on almost any patterned stimulus and during the second stage, the MAE becomes selective in the inducing pattern, such that only a stationary version of it will elicit a MAE (Favreau 1981). The first phase of the MAE therefore appears contour-insensitive, while the second is contour-sensitive.

A similar biphasic characteristic is apparent in the colour-contingent MAE, which is observed after adaptation to contours (of the same orientation) moving in opposite directions presented in complementary colours. Immediately after adaptation, the colour-contingent MAE cannot be obtained on stationary coloured gratings, but does appear 7 min later (Favreau 1976). Therefore, the first phase of the colour-contingent MAE appears to be colour-insensitive, while the second phase is colour-sensitive. Because the orientation of contours used in both stimuli during induction of the colour-contingent MAE are the same, and are moved equally in opposite directions, a 'colour-blind' motion-sensitive channel would produce no MAE for this induction procedure. Indeed, Favreau (1981) suggests that the biphasic characteristics of the MAE and the colour-contingent MAE can be explained by the adaptation of two channels in the visual system—one that recovers quickly from adaptation, is colour-blind, and contour insensitive, and one that recovers slowly from adaptation, is colour-sensitive, and contour sensitive. Favreau (1981) suggests further that the first channel interferes with the second channel while the first is recovering from adaptation. Given that this recovery is much quicker for the first channel than the second, the interference stops at a certain time after induction (presumably depending on the length of adaptation).

We suggest that the colour-insensitive and colour-sensitive channels described by Favreau (1976) can explain the illusions produced in the condition of the current study where stimuli were moving during adaptation. The first, non-contingent illusion that was present during the first 7–8 min following adaptation represents the activity of the contour-insensitive and colour-insensitive channel and, likewise, the contingent illusion present after this time represents the activity of the contour-sensitive and colour-sensitive channel.

4.2 *Induction with stationary stimuli*

When stimuli were not moving during induction, a colour-contingent pattern aftereffect was still found. However, in this condition, no flower-like pattern is evident in the minutes following induction. Instead, strong afterimages of both induction stimuli are evident. Because of the presence of these afterimages, it is difficult to see whether this flower-like pattern or any other pattern is present immediately after induction. However, once the afterimages dissipate, it is still clear that a colour-contingent aftereffect is produced in this condition. The aftereffect in this condition can be explained as a shift in the colour-sensitivity of two different pattern channels, without the need for the involvement of motion-sensitive channels. This account represents the standard explanation of the McCollough effect (McCollough 1965), whereby mechanisms conjointly sensitive to orientation and colour become adapted and so have their sensitivity distributions shifted. We would suggest that the aftereffect in the stationary-induction condition is present immediately after test but is not visible, owing to the presence of the strong afterimages of inducing stimuli. We further suggest that the non-contingent flower-like pattern would not be visible because motion-sensitive mechanisms are not involved in the aftereffect under stationary-induction conditions.

4.3 *The role of eye movements*

A greater number of reports and a greater mean magnitude estimate for the illusory contours were given for induction with stationary patterns than for induction with moving patterns. Humphrey et al (1994) found that the CCPA was very sensitive to the eye movements of participants during induction. When participants did not fixate on the centre of the induction patterns throughout the induction period, the magnitude estimates and number of reports decreased significantly. A moving induction stimulus is more likely than a stationary induction stimulus to elicit eye movements, as participants may tend to follow the moving contours with their eyes. Because these eye movements would de-centre the adapting patterns and so create an inconsistent mapping between colour and orientation, they would reduce the effectiveness of the moving induction condition and so reduce the mean magnitude estimates for the effects, as well as the frequency of reports of the illusion.

5 Conclusion

In conclusion, in this study we used the induction procedure typically used for the McCollough effect, but this time we used homogenous coloured fields at the test stage and found that colour-contingent illusory, shimmering forms were produced. We suggest that under conditions where stimuli are moving, these patterns are the result of a release from inhibition of pattern channels tuned to orthogonal directions of motion, within separate colour channels. We suggest that under conditions where stimuli are stationary, these aftereffects are due to interactions between orientation-coding mechanisms and colour-coding mechanisms, without the involvement of motion-sensitive mechanisms.

References

Dawson B M, Stromeyer C F III, 1978 "Form aftereffect contingent upon a colour shift" *Perception* **7** 417 – 421

Favreau O E, Emerson V F, Corballis M C, 1972 "Motion perception: a color-contingent aftereffect" *Science* **176** 78 – 79

Favreau O E, 1976 "Interference in colour-contingent motion aftereffects" *Quarterly Journal of Experimental Psychology* **28** 553 – 560

Favreau O E, 1981 "Evidence for parallel processing in motion perception" *Acta Psychologica* **48** 25 – 34

Hansel C E, Mahmud S H, 1978 "Comparable retention times for the negative color afterimage and the McCollough Effect" *Vision Research* **18** 1601 – 1605

Hepler N, 1968 "Color: a motion-contingent aftereffect" *Science* **162** 376 – 377

Humphrey G K, Gurnsey R, Bryden P J, 1994 "An examination of colour-contingent pattern aftereffects" *Spatial Vision* **8** 95 – 117

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

McCollough C, 2000 "Do McCollough effects provide evidence for global pattern processing?" *Perception & Psychophysics* **62** 350 – 362

Masland R H, 1969 "Visual *motion* perception: Experimental modification" *Science* **165** 819 – 821

Mayhew J E W, Anstis S M, 1972 "Movement aftereffects contingent on color, intensity, and pattern" *Perception & Psychophysics* **12** 77 – 85

ISSN 0301-0066 (print) ISSN 1468-4233 (electronic)

PERCEPTION

VOLUME 39 2010

www.perceptionweb.com