Research Report

PERCEPTION OF THE MCCOLLOUGH EFFECT CORRELATES WITH ACTIVITY IN EXTRASTRIATE CORTEX: A Functional Magnetic Resonance Imaging Study

G. Keith Humphrey,[1] Thomas W. James,[1] Joseph S. Gati,[2] Ravi S. Menon,[2] and Melvyn A. Goodale[1]

[1]University of Western Ontario, London, Canada, and [2]Advanced Imaging Labs, London, Canada

Abstract—*The McCollough effect is a striking color aftereffect that is linked to the orientation of the patterns used to induce it. To produce the McCollough effect, two differently oriented grating patterns, such as a red-and-black vertical grating and a green-and-black horizontal grating, are viewed alternately for a few minutes. After such colored gratings are viewed, the white sections of a vertical black-and-white test grating appear to be tinged with green, and the white sections of a horizontal grating appear to be tinged with pink. We present evidence from a functional magnetic resonance imaging study that the perception of the McCollough effect correlates with increased activation in the lingual and fusiform gyri—extrastriate visual areas that have been implicated in color perception in humans.*

The McCollough effect (McCollough, 1965) is a visual aftereffect that is believed to reflect an adaptation of color- and orientation-coding mechanisms. It is one of a family of contingent aftereffects in which mechanisms that normally code for separate dimensions become associated following exposure to stimuli in which particular values on these dimensions are reliably paired (for review, see Durgin, 1996). These aftereffects may reveal dynamic and adaptive ways in which the visual system recalibrates as a result of an odd "diet" of perceptual input (for differing views on such recalibration, see Bedford, 1995; Dodwell & Humphrey, 1990; Durgin & Profitt, 1996; Humphrey, 1998).

Several aspects of the McCollough effect suggest that it involves mechanisms at an early stage of visual processing (for review, see Humphrey, 1998; Skowbo, Timney, Gentry, & Morant, 1975; Stromeyer, 1978). After induction of the aftereffect in one eye, the effect does not transfer to the other eye (e.g., McCollough, 1965; Murch, 1972). The aftereffect is also quite specific to the retinal area that was exposed to the inducing stimuli (Stromeyer, 1972). Moreover, for the best effect, the orientation and size of the test stimulus must match those of the inducing stimulus in retinotopic coordinates (Bedford & Reinke, 1993; McCollough, 1965). Wavelength, and not the perceived color, determines the aftereffect hue (Thompson & Latchford, 1986). All these results support a suggestion, originally made by McCollough (1965), that the aftereffect reflects changes occurring early in the cortical visual pathway, perhaps as early as area 17 or V1. Studies of neurological patients with damage to the occipitotemporal pathway suggest that V1 must be relatively intact for the McCollough effect to work (Humphrey, 1998; Humphrey, Goodale, Corbetta, & Aglioti, 1995; Humphrey, Goodale, & Gurnsey, 1991). Finally, a recent study has demonstrated that single neurons in area V1 of the macaque monkey adapt to the joint presentation of two patterned stimuli (Carandini, Barlow, O'Keefe, Poirson, & Movshon, 1997). This result provides neurophysiological evidence that cells in V1 have the requisite properties for mediating a contingent aftereffect.

Although there is evidence consistent with the proposal that orientation-contingent color aftereffects are mediated by mechanisms in V1, the perception of color in humans has been associated with activity in extrastriate areas. Both neuropsychological studies (reviewed in Zeki, 1990) and neuroimaging studies (Hadjikhani, Liu, Dale, Cavanagh, & Tootell, 1998; Howard et al., 1998; Kleinschmidt, Lee, Requardt, & Frahm, 1996; McKeefry & Zeki, 1997; Sakai et al., 1995; Wandell, Baseler, Poirson, Boynton, & Engel, 1999; Zeki et al., 1991) have suggested that neural circuitry in the lingual and fusiform gyri in the ventromedial occipital area is involved in the human perception of color. In addition, recent functional magnetic resonance imaging (fMRI) studies have shown that the perception of simple colored afterimages (in which no contingencies are involved) is associated with activation of the posterior fusiform gyrus (Hadjikhani et al., 1998; Sakai et al., 1995). Another study has shown that direct stimulation of regions of the lingual and fusiform gyri can elicit color sensations (Allison et al., 1993). One recent study has shown that imagining colors activates extrastriate cortex, including parts of the fusiform gyrus, but the network of regions activated by color imagery was different from that activated by color perception (Howard et al., 1998). Although regions of extrastriate cortex are reliably activated by colored stimuli, some studies have shown that early visual areas, such as V1/V2, are also activated by colored stimuli (Howard et al., 1998; Kleinschmidt et al., 1996; McKeefry & Zeki, 1997; Wandell et al., 1999).

In the present study, we sought to determine whether or not an orientation-contingent color aftereffect is correlated with neural activity in area V1 or in the lingual and fusiform gyri. Such an investigation could reveal which early visual areas mediate the plastic (and presumably adaptive) changes that take place in the visual system as a result of aftereffect induction. To examine the relationship between the perception of the McCollough effect and cortical activity, we used high-resolution fMRI to measure the blood-oxygen-level-dependent, or BOLD, response (Ogawa et al., 1992) before and after McCollough adaptation. To set up our experimental and control conditions, we took advantage of the fact that the McCollough effect is tuned to the orientation of the inducing stimuli, so that test stimuli oriented 45° from the inducing stimuli do not evoke the aftereffect (e.g., McCollough, 1965). Thus, in various conditions, subjects were presented with *congruent* test patterns that had the same orientations as the inducing stimuli and with *noncongruent* test patterns that were oriented 45° from the inducing stimuli (see Fig. 1).

Address correspondence to G. Keith Humphrey, Department of Psychology, University of Western Ontario, London, Ontario, Canada N6A 5C2; e-mail: keith@julian.uwo.ca.

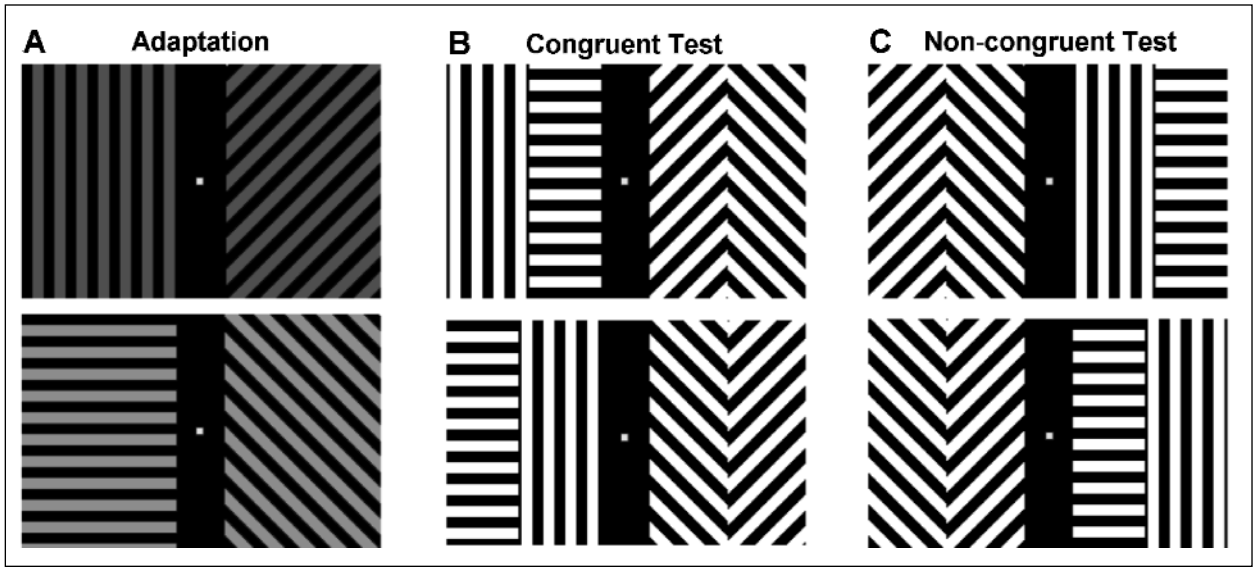


Fig. 1. Examples (not to scale) of the type of stimulus displays used to induce the McCollough effect (a) and of the test patterns (b and c). During McCollough adaptation, subjects fixated on the dot in the center of the display and viewed, for example, the stimulus illustrated in the top of (a) alternating with the stimulus illustrated below. The test patterns were composite vertical-horizontal patterns and left-oblique/right-oblique patterns. During the test phase, the test gratings were either congruent or noncongruent with the adaptation orientations. If, as in the present example, a subject was adapted to vertical-horizontal gratings on the left and oblique gratings on the right, then the congruent test would be composite vertical-horizontal patterns on the left and composite oblique patterns on the right, as in (b). The two versions of the congruent test, shown in the top and bottom of (b), were alternated. The noncongruent test for this subject would be oblique test patterns on the left and vertical-horizontal test patterns on the right, as in (c). The two versions of the noncongruent test were also alternated. The same test patterns used for the post-McCollough-adaptation test were used for the pre- and post-contrast-adaptation tests.

METHOD

Participants

Four female and 2 male subjects ranging in age from 25 years to 30 years participated in the experiment. The subjects had no known color vision deficiencies. None had experienced the McCollough effect prior to the experiment. The subjects were in supine position, and tightly packed foam padding was used to immobilize their heads.

Stimuli

Square-wave gratings with a spatial frequency of 2.4 cycles per degree were used for both adaptation and testing (see Fig. 1). The stimuli were rear-projected onto a translucent screen mounted normal to the bed of the scanner just above the subject's abdomen. The test and adaptation stimuli subtended a total of 20º of visual angle horizontally and 15º of visual angle vertically. The stimuli were viewed through a mirror attached to the inside of the RF head coil. The colors and luminance of the adaptation grating bars were as follows (the first two numbers are the *x* and *y* CIE [Commission Internationale de l'Eclairage] coordinates, and the third number is the luminance in cd m^{-2}): green (.318, .631, 70), red (.402, .233, 70), gray (.357, .419, 70), and black (.361, .419, 17.8). Thus, the green, red, and gray bars in the adaptation gratings were equiluminant. The colors and luminance of the test grating bars were as follows: white (.362, .414, 56) and black (.361, .419, 4.8). In addition to the gratings, subjects were presented with a gray test pattern that was a homogeneous gray field.

During adaptation and testing, subjects were instructed to fixate on a small fixation dot in the center of the display. The adapting patterns alternated every 3 s for a total of 6 min. The phase of each of the patterns was also alternated, so that every second time a pattern was presented, it was 180º out of phase with the previous presentation of the pattern.

Procedure

There were three test periods in which the subjects were scanned. The first test period occurred before any adaptation (pretest). Because the two test patterns should not produce different activation prior to adaptation, we expected no differences between them on the pretest. After the pretest, subjects were adapted to vertical and horizontal black-and-gray gratings in one visual field and to left-oblique and right-oblique black-and-gray gratings in the other visual field (contrast adaptation), and then we repeated the same test as used in the pretest. The contrast adaptation was an important control for the interpretation of any differences in activation that might occur as a result of McCollough adaptation. For example, if the same changes in activation occurred after adaptation to the black-and-gray patterns as after McCollough adaptation, then it could not be concluded that any differences in activation we observed in the third test period were

necessarily related to the McCollough effect. The adaptation with the black-and-gray patterns was for 6 min and was followed by a 5-min waiting period in the dark. No functional imaging was done during the adaptation or the waiting period. After the waiting period, subjects were scanned while they viewed test patterns that were congruent and noncongruent with the black-and-gray adaptation patterns.

After the post-contrast-adaptation test period, subjects were adapted for 6 min with alternating red-and-black and green-and-black gratings (McCollough adaptation). The left-right position of the adaptation gratings was switched relative to the position used during the black-and-gray adaptation. If, for example, a subject had been adapted to vertical and horizontal black-and-gray gratings in the right visual field and to the oblique black-and-gray gratings in the left visual field, the subject was now adapted to red-and-black vertical and green-and-black horizontal gratings in the left visual field and right-oblique red-and-black and left-oblique green-and-black gratings in the right visual field (see Fig. 1).[1] After this 6 min of McCollough adaptation, subjects waited 5 min in the dark. The final test was begun after the 5-min waiting period (post-McCollough-adaptation test).

The three different test patterns (congruent, noncongruent, and gray) were presented to each subject in three separate blocks during each of the test periods. The order of presentation of the three test patterns was varied randomly within each block and across subjects. There were two versions of the congruent and noncongruent test patterns (see Fig. 1) that alternated every 2 s for a total of 23.5 s for each pattern in each block. The homogeneous gray field was also presented for 23.5 s during each block of test trials.

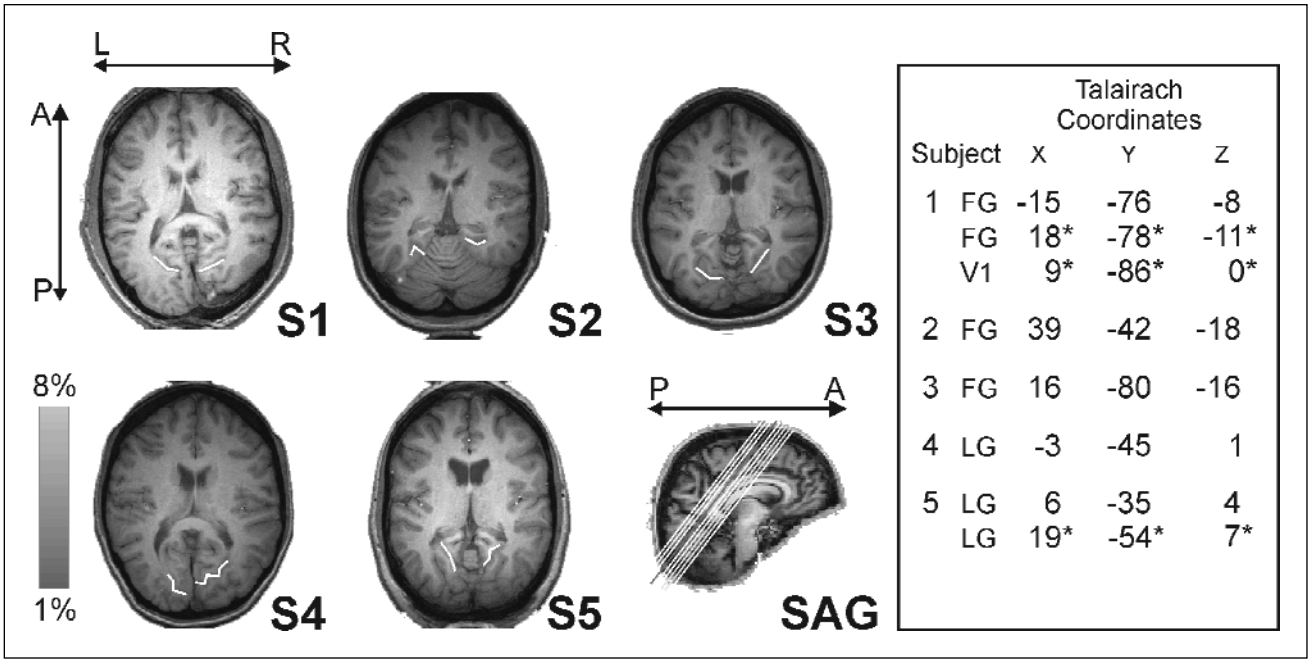
fMRI Data Collection Procedure

All imaging was done with a 4-T whole-body MRI system (Varian, Palo Alto, Calif.; Siemens, Erlangen, Germany) with a head coil. Scan planes were oriented parallel to the calcarine sulcus with the middle slice centered on the sulcus. The field of view was 19.2 × 19.2 cm (64 × 64 matrix), giving an in-plane resolution of 3.0 × 3.0 mm. Nine contiguous 6-mm slices were collected using T2*-weighted segmented echo-planar-imaging acquisition (echo time = 15 ms, repetition time = 65 ms, flip angle = 15°, 4 segments/plane, navigator-corrected) for BOLD-based imaging. A single stimulus state lasted for 23.5 s (10 imaged volumes at 2.35 s each). The three stimulus states were repeated three times in random order for a total of 90 image volumes per test scan. Functional activation data were superimposed onto high-resolution T1-weighted anatomical images that were collected during the same session (three-dimensional magnetization-prepared turbo FLASH acquisition using an inversion time of 500 ms, echo time of 6 ms, repetition time of 11 ms, and 11° flip angle).

RESULTS

The data from the pretest, post-contrast-adaptation test, and post-McCollough-adaptation test were analyzed independently.[2] Data sets were first filtered with a high-pass Fermi filter to eliminate low-order drift. To locate voxels (volume elements) that responded differentially when subjects viewed the test patterns during the three tests, we calculated activation maps that compared the congruent state with a homogeneous-gray state, and the noncongruent state with a homogeneous-gray state. This was done by using voxel-by-voxel t tests ($p < .01$) and produced a congruent map and a noncongruent map. Differences between the congruent and noncongruent maps were then analyzed and were considered indicative of differences between the congruent and noncongruent test states.

The pretest results were used to calculate a unique criterion for each subject that could be used to determine the significance of voxels in suc-



Subject		Talairach Coordinates X	Y	Z
1	FG	-15	-76	-8
	FG	18*	-78*	-11*
	V1	9*	-86*	0*
2	FG	39	-42	-18
3	FG	16	-80	-16
4	LG	-3	-45	1
5	LG	6	-35	4
	LG	19*	-54*	7*

Fig. 2. Areas of brain activation associated with perception of the McCollough effect. Slice orientation is indicated on the sagittal ("SAG") image in the bottom right. All slices were taken parallel to the calcarine sulcus. The blue line indicates a slice through the calcarine sulcus. The yellow lines indicate the two slices where most of the active loci were found after McCollough adaptation. The five axial-oblique images depict one of these slices in 5 different subjects. The white lines indicate the collateral sulcus, with the lingual gyrus being medial and anterior and the fusiform gyrus being lateral and posterior. Active voxels are shown in yellow through orange. These are voxels that passed a t test ($p < .01$) and met a contiguity-filter criterion derived from the pretest data. Subjects 1 through 3 showed active voxels in the fusiform gyrus (FG) after McCollough adaptation, and Subjects 4 and 5 showed active voxels in the lingual gyrus (LG). Talairach coordinates are given in the table on the right and were found by morphing each subject's high-resolution anatomical volume into Talairach space using the Stimulate analysis package (Center for Magnetic Resonance Research, University of Minnesota, Minneapolis). Asterisks indicate coordinates for active loci that are not shown in this figure. Subject 1 produced active voxels in primary visual cortex (V1), in addition to the active voxels in the FG. L = left, R = right, A = anterior, P = posterior.

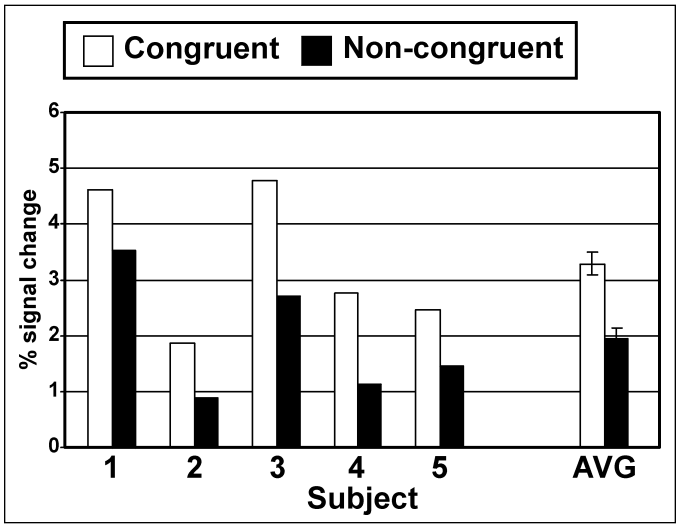


Fig. 3. Average percentage of signal change for individual subjects for the congruent and the noncongruent states in the post-McCollough-adaptation test. The average signal change across the 5 subjects is also shown (AVG; the error bars indicate the standard error used in paired t tests).

subject, but did not overlap at all in the other subject. In all 3 subjects who showed activation, an analysis of the time series of these active voxels showed that signal intensity was significantly lower when subjects viewed the congruent as opposed to the noncongruent test pattern. Such a decrease in activity could be due to a reduction in sensitivity as a result of "fatigue" of mechanisms coding for the orientations presented during contrast adaptation (Tootell et al., 1998).

DISCUSSION

This is the first study to map those areas in the human brain that are associated with the perception of a contingent aftereffect. The results show that brain activation associated with the experience of the McCollough effect, an orientation-contingent color aftereffect, can be seen in the lingual and fusiform gyri. These are the same areas that both neuropsychological and neuroimaging studies have implicated in the perception of "real" color in humans. It is not clear, however, whether the activity in these extrastriate regions reflects plastic changes that have occurred because of the McCollough effect induction, or whether the activity reflects only color perception. In other words, the activity we observed may reflect color perception but not the adaptation process itself. Given the mass of evidence for the involvement of early visual areas such as V1 in the McCollough effect, it may be that V1 is the locus for the changes that are actually taking

place during induction of the effect. The perceptual "readout" of such changes, however, may depend on mechanisms further downstream in various regions of extrastriate cortex (see Bartels & Zeki, 1998), such as the lingual and fusiform gyri. Our results parallel previous findings that the fMRI signal in extrastriate cortex correlates with the perception of another visual aftereffect, the motion aftereffect. In these experiments, perception of motion aftereffects was correlated with activity in the V5/MT complex, an extrastriate area that has been implicated in the perception of motion (Culham et al., 1999; He, Cohen, & Hu, 1998; Tootell et al., 1995). Although there is evidence for the involvement of early visual areas, such as V1, in some motion aftereffects (for review, see Niedeggen & Wist, 1998), the neuroimaging results, like the results of our research, have revealed activity in extrastriate regions only.

Although the absence of reliable activation in early visual areas was surprising, there are a number of possible reasons for such a result. There is some evidence that colored stimuli that produce weak signals in V1 may produce a somewhat larger signal in extrastriate cortex (Wandell et al., 1999). It may be that the signal differences produced by the McCollough effect are too weak to be detected in V1, but are still detectable in extrastriate cortex. We should note, however, that even when a more liberal criterion was used in setting our contiguity filter, we still did not detect activity in area V1, except in the single subject who already showed such activity. It could also be that the mechanisms in early visual areas that are crucial for producing the McCollough effect operate on a spatial scale that is not well measured under the imaging conditions that we used. All the stimuli in our study, both the congruent and the noncongruent, were oriented gratings—patterns that were, relative to baseline (i.e., homogeneous gray), powerful stimuli for driving activity in V1. Thus, any activation due to the McCollough effect would have to have been superimposed on what were already high levels of activation caused by the oriented gratings. Another possibility that should be considered is that the adaptation that leads to the perception of the aftereffect may involve neural mechanisms that are not likely to produce differences in blood flow—which of course is what is being measured indirectly by fMRI. It is possible that the process of adaptation produces only subtle changes in the profile of the activity of the neural elements coding color and orientation.

In summary, the results show that brain activation associated with the experience of the McCollough effect is seen in the same extrastriate areas that other research has implicated in human color perception. It is unlikely, however, that this activity directly reflects the plastic changes underlying the adaptation process itself. Further research is needed to determine the neural correlates of such plasticity.

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