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Contingent aftereffects distinguish conscious and preconscious color processing

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The brain can process input without perception, but what distinguishes conscious from preconscious processing? Using aftereffects induced by quickly alternating images, we show that cortical mechanisms track color much faster than perception, responding well to color alternations that are too rapid to be perceptible. The more restricted frequency response of the conscious perception of color suggests that extra integrative steps give conscious color perception a time course substantially slower than that of early cortical mechanisms.

There are limits to what humans can see and how quickly they can perceive it. Some of these limits are set by the manner in which the brain processes incoming information, and it is of particular interest to distinguish the processing available to conscious perception from that hidden from awareness. Here we show that associations between color and orientation are formed and processed by the brain at speeds at which color itself (let alone the orientation-color conjunction) is imperceptible.

Humans consciously discern color alternations only up to approximately 15 Hz (33 ms per frame) with sensitivity plummeting to immeasurably low values when this frequency is exceeded[1,2] (although more recent findings suggest a slightly greater temporal resolution up to 18.8 Hz (ref. 3)). Although the conscious perception of color seems to be limited to such low frequencies, findings from electrophysiology suggest that cells in primate visual cortex can track color alternations at rates as high as 30 Hz (ref. 4). These findings suggest that color-sensitive cells in V1 can track color faster than conscious perception. However, there has been no direct comparison of the speed of conscious and preconscious color mechanisms, so although both neurons in monkey V1 (refs. 4,5) and human scalp potentials thought to be of cortical origin[5] can track flicker at frequencies as high as 60 Hz, the physiological origin of the slower processing of chromatic information has not been identified. We sought to find a dissociation between cortical color processing and conscious color perception using aftereffects in humans to infer the physiological origins of the decrease in the speed of color perception.

The McCollough effect[6] is an orientation-contingent color aftereffect. Subjects who have adapted, by prolonged exposure, to (for example) vertical green bars and horizontal red bars (**Fig. 1a**) will then see neutral vertical bars as reddish and neutral horizontal bars as greenish (**Fig. 1b**). A McCollough effect can be induced without attention and without awareness of the stimuli[7], but because the cortex is the origin of both orientation selectivity and color contrast adaptation[8,9], the effect must arise from cortical mechanisms[7]. Yet the effect does not transfer between the eyes[6]. This implicates processing early in primary visual cortex, where left and right inputs are not yet combined, although elaborations of this experiment have demonstrated an interplay between monocular and binocular representations[10]. These characteristics make the effect ideal for investigating the limits of color processing in the preconscious visual cortex, just as other aspects of preconscious vision have been probed with different aftereffects[11–14].

The basic logic of the present study was to compare the speed of color processing at the site of origin of the McCollough effect with the speed of processing that is reflected in direct subjective reports. As the duration of each frame in a series of alternating colored gratings (that induce a McCollough effect) falls much below 33 ms, conscious perception of color will fail, but what will happen to the aftereffect?

To induce the aftereffect, we used a four-frame sequence (**Fig. 1c**; C. Bodelon, M. Fallah & J.H. Reynolds, *J. Vis.* 5, 758a, 2005) in which color and orientation alternated from one frame to the next and the gratings were phase-shifted every other frame to ensure that the sum of

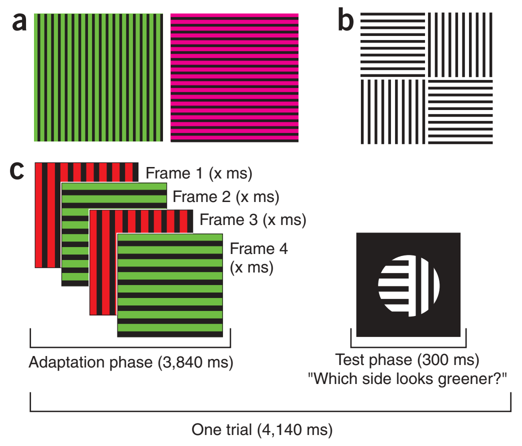

Figure 1 Demonstration and implementation of the McCollough effect. (**a**) Stimuli used to generate the McCollough effect. (**b**) After adapting to the stimuli in **a**, an orientation-contingent color aftereffect (McCollough effect) can be seen: the vertical bars appear redder and the horizontal bars appear greener. (**c**) We measured the strength of this aftereffect at different frame durations. The schematic of one trial is shown. Each trial consisted of 3.84 s of adaptation (to a four-frame stimulus cycle, repeating 3,840/($t \times 4$) times, where t = ms per frame), followed by a 300-ms-long test stimulus. Subjects were exposed to 100 trials of adaptation and 100 trials of counteradaptation in each block. Aftereffect strength was defined as the chromatic contrast between the two sides of the test stimulus necessary to null the aftereffect colors.

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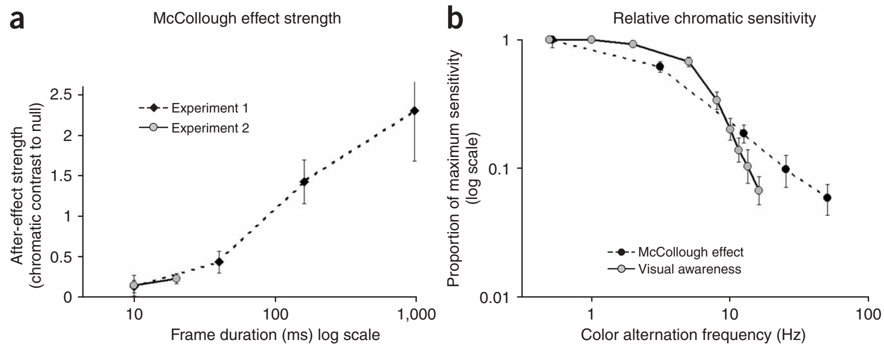

Figure 2 Frequency response of the McCollough effect. (**a**) McCollough effect strength (chromatic contrast necessary to null the aftereffect, ± 2 s.e.m. between subjects) as a function of frame duration (ms; log scale). A significant McCollough effect was induced at frame durations as short as 10 ms and 20 ms (color alternation rates of 50 Hz and 25 Hz; $t(9) = 2.273$, $P < 0.05$, and $t(9) = 7.48$, $P < 0.0001$, respectively; **Supplementary Methods**). This is much faster than the rate at which conscious color processing occurs. (**b**) Relative chromatic contrast sensitivity (proportion of effective contrast at the slowest alternation rate, ± 1 s.e.m. between subjects; log scale) as a function of color alternation rate (Hz; log scale) for visual awareness and McCollough effect mechanisms. The steeper slope of the frequency response function for conscious perception ($t(13) = 2.89$, $P < 0.05$; **Supplementary Methods**) suggests significant temporal integration between the cortical sites of the after effect and visual awareness.

all four frames was a uniform yellow field. This four-frame sequence was cycled at different frame durations (10, 20, 40, 160 and 960 ms per frame) in different runs in two different experiments. In each case, the strength of the induced aftereffect was measured as the amount of chromatic contrast (as indexed by L-cone contrast with luminance fixed) needed in the test stimulus to null the aftereffect colors (details in **Supplementary Methods** online).

An orientation-contingent color aftereffect was successfully induced with frame durations as short as 10 ms and 20 ms (**Fig. 2a**). This is far faster than the speed at which humans can consciously track color[1,2]. We concluded that the cortical conjunction-selective neurons responsible for the effect are not directly accessible to consciousness, and that these neurons can track their preferred conjunctions at extremely high speeds.

There are two plausible reasons why McCollough aftereffects can be induced at frame rates at which conscious perception fails. One possibility is that the direct perception of color has a higher chromatic contrast threshold than the McCollough aftereffect, but that the temporal responses at those two points in the visual system are identical. Alternatively, increasing the color alternation rate might cause a faster decline in the chromatic contrast available to conscious perception than that available at the McCollough effect site. This would suggest that the neural representation must go through additional processing and temporal integration before visual awareness is achieved.

The strength of the McCollough effect did decrease with frame duration (**Fig. 2a**). Owing to inevitable temporal integration, decreasing frame duration (and thus increasing the color alternation rate) is equivalent to a reduction in the contrast of the inducing stimulus. In a separate study, we determined that the strength of the aftereffect increases proportionately to the chromatic contrast of the inducing gratings (the chromatic contrast needed to null the aftereffect was about 7.5% of the contrast in the inducing stimuli). Using these relationships we computed the rate of loss of the effective chromatic contrast of the inducing stimuli operative in generating the McCollough effect, as a function of color alternation rate (**Fig. 2b** and **Supplementary Methods**).

Because the physical chromatic contrast of the inducing stimuli was constant for all color alternation frequencies, this measure of effective chromatic contrast indicates the extent to which temporal integration over the rapid stimulus cycle reduces chromatic contrast sensitivity at the site of origin of the McCollough effect. Likewise, in the case of conscious visual awareness, processing that occurs in the visual stream before awareness limits sensitivity to rapid color alternations and calls for a corresponding increase in the minimum physical contrast necessary to perceive the alternating colors (**Supplementary Methods**). By comparing this decline in visual contrast sensitivity with the decline in contrast sensitivity of the McCollough effect, we can compare the temporal frequency response of the visual system at the stage where the McCollough effect originates with that at the stage where the visual system culminates in conscious perception.

The normalized chromatic contrast sensitivity, as a function of increasing color alternation frequency, declined at a slower rate for the McCollough effect mechanism than for color sensitivity of visual awareness (**Fig. 2b**). The steeper slope of conscious perception suggests that more than a simple difference in sensitivity is involved: the McCollough effect survives at rapid, subjectively imperceptible alternation rates because the cortical representation involved in generating the aftereffect tracks rapid color fluctuations more swiftly than does visual perception.

These findings demonstrate that conjunctions of orientation and color are cortically represented at frame rates much faster (50 Hz) than those at which color conjunctions[3] and even color alone[1,2] can be consciously perceived (16 Hz). Evidently the rapidity of conscious perception of color is limited by cortical rather than precortical processes that integrate the visual input over time.

Note: Supplementary information is available on the Nature Neuroscience website.

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COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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Supplementary information

Separate experiments investigated how the rate of colour alternation influences (a) the effective chromatic contrast available to induce a McCollough effect and (b) visual awareness mechanisms. For (a), McCollough effect strength was measured first as a function of frame duration (Fig. 2a, Experiments 1 and 2), then as a function of chromatic contrast (not shown; Experiment 3: effect strength was nearly proportional to contrast). These two functions described how decreased frame duration (and thus increased colour alternation frequency) translates to decreased effective contrast in the stimulus inducing the after-effect (filled circles, Figure 2b). For (b), we measured the chromatic contrast required to directly perceive alternating colours at varying alternation rates (open circles, Figure 2b, Experiment 4). Figure 2b shows a steeper loss of sensitivity with increasing alternation frequency for conscious colour perception than for generation of the McCollough effect (Experiment 5 directly studies this difference in frequency response slopes).

Methods

Equipment and participants:

All experiments were conducted on University of California, San Diego undergraduates who provided written consent. Experiments were run on a Cambridge Research Systems VSG 2/5 board controlling a 21” IIyama Vision Master Pro 514 colour monitor. The monitor was set to a resolution of 1024x768 at a refresh rate of 100 Hz for Experiments 1-3, and to a resolution of 800x600 at a refresh rate of 160 Hz, for Experiments 4 and 5. The monitor was gamma corrected independently for each of these settings; phosphor persistence measurable with a photodiode lasted less than 4 msec.

Experiments 1 and 2

McCollough effect strength was measured with a nulling procedure. Subjects were exposed to 100 trials (about 6.33 min) of adaptation followed by 100 trials of counter-adaptation (where the colour-orientation pairings were switched). Each trial consisted of 3.8 s of a four-frame adaptation sequence (see Figure 1 c; gratings were roughly 1.82 cycles/degree filling the entire screen: roughly 36° in width, 27° in height; the CIE chromaticity coordinates for red and green were (0.6168, 0.3449) and (0.2696, 0.6130) respectively, their alternation yielding an L-cone modulation of 25% at a luminance of 16 cd/m^2) followed by a 300 ms presentation of the test field (Figure 1 b; about 15 degrees wide, presented on a black background). Subjects were asked to indicate which side of the test field "looked greener". Based on the subject's response, the chromaticity of the "whites" of the test stimulus was adjusted for the next trial to null the indicated after-effect colours while maintaining isoluminance at 45 cd/m^2. After about 50 trials, or about 3 minutes of adaptation, after-effect strength reached an asymptotic value.

For any given trial, the chromatic contrast (percent L-cone contrast) between the red-adapted and green-adapted sides of the test field was the measure of the momentary after-effect strength. The overall after-effect strength for a given frame duration was defined for each subject as the average momentary after-effect strength during the last 50 trials of the adaptation and counter-adaptation periods.

Experiment 1 used four different frame durations (10, 40, 160, and 960 ms; corresponding to colour alternation rates of 50, 12.5, 3.125, and 0.52 Hz) at maximum chromatic contrast of the adapting gratings. McCollough effect strengths were significantly greater than zero for all alternation rates (50 Hz: $t(9)=3.2$, $p<0.05$; 12.5 Hz: $t(9)=6.3$, $p<0.001$; 3.125 Hz: $t(9)=9.5$, $p<0.0001$; $t(9)=7.7$, $p<0.0001$).

Experiment 2 was conducted on 5 of the 10 subjects from Experiment 1 to verify the finding of a significant McCollough effect at 50 Hz colour alternation. We independently measured McCollough effect strength for frame durations of 10 and 20 ms (colour alternation rates of 50 and 25 Hz) twice for each subject. Again, the after-effect was significant at both frame rates (50 Hz: $t(9)=2.3$, $p<0.05$; 25 Hz: $t(9)=7.5$, $p<0.0001$).

Experiment 3

To find the strength of the McCollough effect as a function of chromatic contrast in the inducing gratings, Experiment 3 manipulated chromatic contrasts of the inducing stimuli to be one of four values: 3.17%, 6.34%, 12.68%, and 25.36% (L-cone contrast) all presented at 960 ms per frame. After-effect strength was roughly proportional with inducing contrasts (for our stimuli, mean after-effect strengths were 0.24, 0.65, 1.06, and 1.79% L-cone contrast, respectively; that is, about 7.5% of inducing L-cone contrast).

Experiment 4

To measure the degree to which increasing frequency of colour alternation decreased the effective chromatic contrast available to visual awareness, we used a standard Yes/No detection staircase on isoluminant chromatic flicker. The red-green isoluminance ratio was set for each subject using a minimum motion procedure[17]. Using this ratio, we could manipulate L-cone modulation without altering the luminance. Eight frame durations were used (25, 31.25, 37.5, 43.75, 50, 62.5, 100, 250, and 500 ms, a range suggested by previous research[11, 12], corresponding to colour alternation rates of 16, 13.3, 11.43, 10, 8, 5, 2, 1, and 0.5 Hz).

Subjects were presented with a flickering two frame sequence and indicated whether or not they could “see both red and green”. If the colours were seen, the chromatic contrast for the next trial at that frame duration was decreased, if the colours were not seen, the chromatic contrast was increased. Frequency of seeing curves were fit to the response patterns of each subject at each alternation frequency, and 50% thresholds were estimated. Relative sensitivity (1/threshold) from this experiment is plotted in Figure 2 b. While only the uniform field flicker results are reported here, we also measured chromatic sensitivity to a flickering field with uniform black bars (simulating McCollough effect conditions); the bars simply made the detection task uniformly more difficult, increasing the threshold contrast by approximately 30%.

Experiment 5

The purpose of Experiment 5 was to quantitatively demonstrate the difference in slopes observed in the previous experiments. We measured chromatic modulation sensitivity (as in Experiment 4) and McCollough effect strength (as in Experiments 1-3), in 14 subjects at color alternation rates of 6.7 and 13.3 Hz. The slope for each of the perception tasks was defined as either the proportion of color contrast sensitivity or proportion of McCollough effect strength at 6.7 Hz, that was measured at 13.3 Hz. The difference in slopes was indeed significant ($t(13)=2.89$; $p<0.05$), with color contrast sensitivity at 13.3 Hz equal to 0.45 of the sensitivity at 6.7 Hz, and McCollough effect strength only being reduced to 0.65 of the 6.7 Hz strength.