

The McCollough effect reflects permanent and transient adaptation in early visual cortex

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The brain encounters input varying with many different time courses. Given such temporal variability, it would seem practical for adaptation to operate at multiple timescales. Indeed, to account for peculiar effects such as spacing, savings, and spontaneous recovery, many recent models of learning and adaptation have postulated multiple mechanisms operating at different timescales. However, despite this assumption, and compelling modelling results, different timescales of cortical adaptation and learning are rarely isolated in behaving animals. Here we demonstrate in a series of experiments that early visual cortex adapts at two distinct and separable timescales: fast (saturating with a time constant of roughly 30 seconds) and infinite (a perfect integrator: exhibiting no signs of decay or diminishing returns within the range of intervals tested). We further demonstrate that these two timescales sum linearly and appear to be operating independently and in parallel.

Keywords: McCollough effect, adaptation, aftereffects, associative learning

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Introduction

Some recent models of learning and adaptation invoke multiple processes with different timescales. These theories postulate that learning occurs at more than one timescale concurrently, and the final product of the learning—that which is measured in most experiments—is a combination of these processes. Such models have been introduced for saccade gain control (Kording, Tenenbaum, & Shadmehr, 2007), motor adaptation (Smith, Ghazizadeh, & Shadmehr, 2006), dark adaptation (Lamb, 1981), and habituation (Staddon & Higa, 1996), to name a few, and can explain a number of peculiar phenomena in learning, including savings, spontaneous recovery, and spacing effects. Furthermore, adaptation in cortical neurons reflects multiple timescales (from 30 msec to several minutes; Kohn, 2007; Wark, Lundstrom, & Fairhall, 2007). While a number of results suggest that models with multiple timescales of learning provide a better fit to physiology and behavior, as of yet, no results have isolated individual timescales of concurrent cortical learning. We investigated the time course of adaptation in the visual domain using the McCollough effect (McCollough, 1965) as a test case and psychophysically isolated two distinct timescales of learning.

The McCollough effect (McCollough, 1965, 2000) is an orientation contingent color aftereffect—adaptation to, e.g., red vertical and green horizontal gratings makes

subsequent neutral vertical and horizontal gratings appear greenish and reddish, respectively (Figure 1). The site of the McCollough effect has been disputed: some have placed it in V1 due to the independent monocular and binocular components and orientation selectivity (McCollough, 1965), others have argued for a pre-cortical locus (Harris, 1969), and some have suggested a locus much later than V1 (Humphrey, James, Gati, Menon, & Goodale, 1999). However, recent evidence suggests that the early visual cortex is the most likely locus: the aftereffect has been shown to be sensitive to color alternations as high as 50 Hz (Vul & MacLeod, 2006), well above the limits of conscious perception. Moreover, only early visual cortex is sensitive to such high frequency color alternations (Jiang, Zhou, & He, 2007). Thus, only areas V1–V4 have the chromatic temporal sensitivity to be consistent with the McCollough effect; of those, V1 seems most likely due to the independence of monocular and binocular adaptation (McCollough, 1965).

Like other forms of adaptation contingent on rare stimuli, the McCollough effect is peculiarly long lasting with storage of the aftereffect documented to last days (Jones & Holding, 1975) and informally reported to last weeks and months. Such long-lasting aftereffects, although at face value dramatically different from more common forms of adaptation, may not be an exception to the norm: it may simply be the case that they take longer to de-adapt in our natural environment because of the rarity of the stimuli on which they are contingent

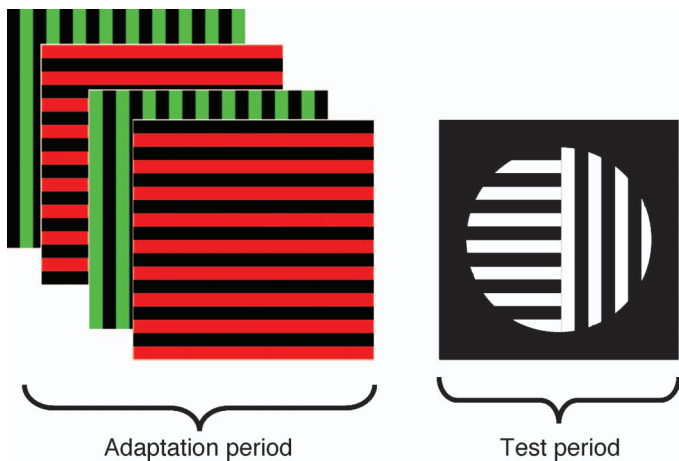


Figure 1. A typical “adaptation trial.” Subjects adapt to several seconds of a particular orientation-color pairing (see Methods for specific details for each experiment), then a test patch appears. Subjects indicate which side appears redder, and the whites of the test patch are adjusted according to the response to null the aftereffect.

(a scenario consistent with some simple gain-control models of adaptation; van de Grind, van der Smagt, & Verstraten, 2004). Long-lasting effects such as these have been reported for spiral motion aftereffects (Masland, 1969), motion contingent color aftereffects (Hepler, 1968), and attentional selection (Tseng, Gobell, & Sperling, 2004).

Nevertheless, because the McCollough effect seems to decay so slowly and may be built up quite quickly, some have postulated that it is a form of associative learning rather than “adaptation” (Allan & Siegel, 1991; Siegel & Allan, 1987), although it should be noted that the distinction between the two is rather difficult to pinpoint.

In our own laboratory, we have observed that when one adapts to a particular color-orientation pairing, then immediately adapts to the opposite pairing for an equal duration, the apparent asymptotic aftereffect strength is substantially greater in the initial adaptation period (Figure 2). Observations such as these suggest that the time course of McCollough effect build-up and decay may be the result of multiple timescales of adaptation. Such an underlying mechanism could produce adaptation that appears to be gained quickly (supported by a fast timescale) and forgotten slowly (supported by the slow timescale). Similarly, the existence of a fast and slow timescale of adaptation could produce the shifted asymptote suggested by the data in Figure 2: while the short timescale saturates in both cases, a longer timescale integrates both the positive and negative adaptation blocks, thus producing a greater net aftereffect in the first adaptation block than the second.

We explored the possibility that two or more timescales of adaptation underlie the McCollough effect, and can provide a general explanation of its growth and decay, in a series of experiments designed to isolate multiple timescales. In Experiment 1 we measure the decay of the McCollough effect immediately after adaptation and find that a portion of the aftereffect decays fairly quickly (fast timescale) to an apparently shifted baseline (slow or infinite timescale). In Experiment 2 we further measure the permanence of the baseline shift and its susceptibility to interference from un-adapted orientations: at these longer durations, we still find no evidence of decay of the aftereffect when other gratings intervene. In Experiment 3 we test whether the two timescales of orientation-contingent color adaptation operate in serial or in parallel (that is, whether adaptation at the fast timescale attenuates permanent adaptation), and find no evidence of such attenuation, suggesting that the two timescales sum

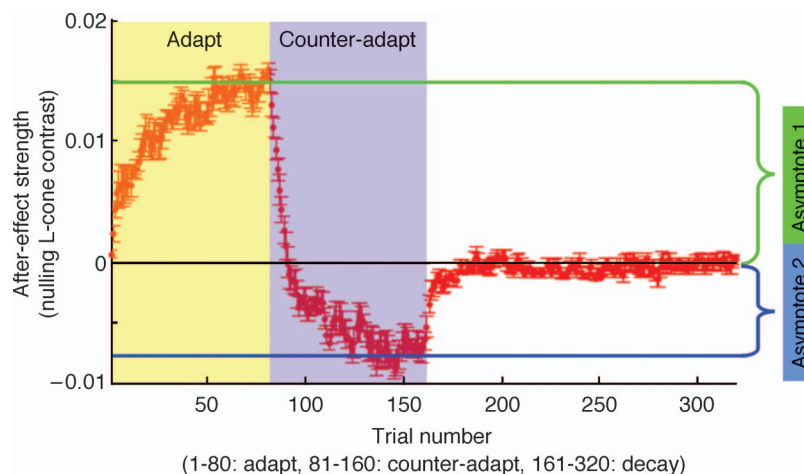


Figure 2. The build-up of adaptation of the McCollough effect (chromatic contrast necessary to null the aftereffect, ± 1 SEM across subjects) during adaptation (yellow), counter-adaptation (blue), and recovery (white). The asymptotes reached in adaptation and counter-adaptation differ, suggesting that multiple timescales of learning underlie the effect.

linearly and operate independently and in parallel. We then describe a simple linear model that provides a good fit to our data.

General methods

Equipment and participants

All experiments were conducted on University of California San Diego undergraduates. Each subject ran only once in any one experiment (but multiple subjects participated in two or more experiments). Experiments were run on a Cambridge Research Systems VSG 2/5 board controlling a 21-in. Iiyama Vision Master Pro 514 color monitor. The monitor was gamma corrected and set to a resolution of 1024×768 at a refresh rate of 100 Hz for all experiments.

Testing procedure

McCullough effect strength was measured with a nulling procedure during periods of adaptation and recovery. During the adaptation periods, an adaptation stimulus sequence lasting 3.8 seconds was followed by a 300-msec test trial stimulus. This adaptation/test trial cycle was repeated for the total duration of the adaptation period. The adaptation sequence consisted of four frames (each frame appearing for 960 msec) in which observers viewed gratings with a particular pairing of color and orientation (e.g., red vertical gratings) alternating with the orthogonal orientation and complementary color (e.g., green horizontal gratings; see [Figure 1](#)). The grating orientation set could be cardinal (horizontal and vertical) or oblique (45° and 135°). The induction gratings were 1.82 cycles/degree and filled the entire screen (36° in width, 27° in height). The adapting grating colors were always red and green (CIE chromaticity coordinates of [0.6168, 0.3449] and [0.2696, 0.6130], respectively). The red-green alternation yielded an averaged L- and M-cone modulation of 25% at a luminance of 16 cd/m^2 .

Each four-frame adaptation sequence was followed by a 300-msec test trial ([Figure 1](#)). The test field was a 15-degree diameter circle on a black background. The two adapting orientations were randomly assigned to appear in the left or the right half of the test field. Subjects were asked to indicate which side of the test field “looked redder.” 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 aftereffect colors while maintaining isoluminance at 45 cd/m^2 . The test field gratings on the first trial were neutral gray, and with each response the color contrast (L-cone contrast) between the orthogonal test gratings was increased or decreased by 0.001 in MacLeod and Boynton’s r chromaticity measure (MacLeod & Boynton, 1979;

roughly 0.1% L-cone, and 0.3% M-cone contrast), as dictated by the subject’s response. Thus, for any given trial, the aftereffect strength could be evaluated as the L-cone contrast between the red-adapted and green-adapted sides of the test field. Because subjects match chromaticity between orthogonal test gratings the null reflects a purely orientation-contingent aftereffect, as any retinal effects will apply to both orientations. During recovery periods (designed to measure aftereffect decay or the baseline aftereffect strength), the 3.8-second alternation of adapting gratings was replaced with a presentation of a neutral gray screen, followed as usual by a test stimulus. This structure of recovery testing minimizes exposure to test gratings that may themselves cause de-adaptation.

To minimize carryover between one adaptation period and the next, orientation set (cardinal or oblique) alternated between successive adaptation periods, and the color-orientation pairing (e.g., red-vertical, green-horizontal) alternated between every adaptation period of the same orientation set. So in an experiment with four adaptation periods, the color-orientation pairings in each period might be (red—vertical, green—horizontal), (red— 45° , green— 135°), (green—vertical, red—horizontal), and (green— 45° , red— 135°). This is the general scheme for all of our experiments, and we now need only specify the specifics of the durations and arrangement of adaptation and recovery periods.

Experiment 1

In [Experiment 1](#) our goal is to dissociate the two timescales suggested by previously seen data. We aim to separately characterize the slow and fast timescales by investigating how they each behave as a function of adaptation duration and decay at short time intervals.

Methods

To investigate build-up and decay of the McCullough effect, we chose three adaptation durations (10, 40, and 80 adaptation trials: roughly 40, 160, and 320 seconds of adaptation, respectively) and one decay duration (80 blank trials: 320 seconds). Nine observers were exposed to adaptation periods in order of increasing duration, with color-orientation pairings assigned randomly to the first period, and alternating as described in the [General methods](#). A 320-second recovery period followed each adaptation period.

Results and discussion

[Figure 3](#) shows the time course of build-up and decay of the McCullough effect for the three adaptation durations

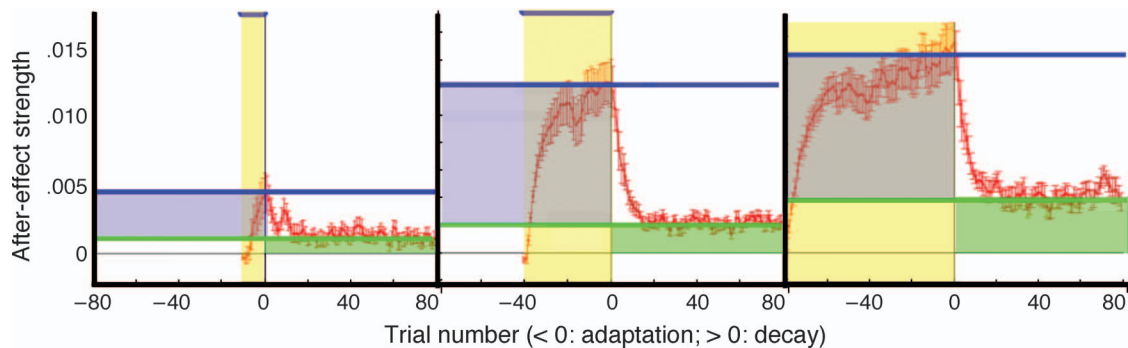


Figure 3. [Experiment 1](#) results: The build-up and decay of McCollough effect strength (L-cone contrast, plotted with ± 1 SEM across subjects) during adaptation (yellow) and recovery (white). The aftereffect does not decay to zero magnitude; instead, it decays to a shifted baseline corresponding to the long-term effect (green). The magnitude of the short-term effect can be inferred from the peak aftereffect reached during adaptation (blue/gray).

(40, 160, and 320 seconds). Here, and in all other figures, error bars in the graph represent the uncertainty due to the variation between subjects: they are the standard deviations for the distribution of settings over subjects divided by the square root of the number of subjects (standard error of the mean). In [Figures 2](#) and [3](#) for instance, the standard deviation of the effect across subjects of the shift in r chromaticity was about 0.002 or 14% of the average effect.

As evident in the decay phase, there appear to be two timescales involved in adaptation: one that decays quickly (the decay evident in trials 0 to 20 of the decay period), and another that decays slowly, if at all (evident in the flat baseline shift at the end of the decay period). That is, it appears as though the McCollough effect is the result of relatively quick adaptation, a mechanism that saturates within about 20 trials (80 seconds), and an infinite timescale of adaptation, a mechanism that may be likened to a perfect integrator: one that “remembers” all of the stimuli that were ever presented.

First, to test whether the apparently flat shifted baseline really is flat, we estimated the best-fitting line to the last 30 trials of the decay period for each adaptation duration. The 95% confidence intervals on the slope of this line were (in percent of the mean aftereffect): -0.0082 to 0.0059 for 40 seconds of adaptation, 0.0007 to 0.0108 for 160 seconds of adaptation, and 0.0054 to 0.0156 for 320 seconds of adaptation (positive values indicate a positive slope, meaning that the aftereffect strength is increasing, if anything). These intervals indicate that the shifted baseline at the end of the decay period is very unlikely to be decaying at any considerable rate.

Second, it is somewhat surprising that the time constant of decay of the fast timescale appears to be constant regardless of adaptation duration. Models of memory consolidation and forgetting suggest that exposure duration should alter the effective time constant of decay. To test whether the rate of decay of the fast phase of recovery

is independent of the duration of adaptation, we fit an exponential decay curve,

$$M = a + (b - a)(1 - \exp(-t/\tau)), \quad (1)$$

to the decay periods (trials 1–80) for each of the adaptation durations. The 95% confidence intervals for the best-fitting exponential time constants for the fast phase of recovery were between 22.5 and 28.5 seconds for all adapting durations (time constants for 40, 160, and 320 seconds were 25.5, 24.8, and 24.8, respectively). Mechanisms of consolidation occurring during the prolonged adaptation periods would make the pace of recovery slower (McGaugh, 2000). However, no such slowing is evident: the only effect of longer adaptation is a greater magnitude of the baseline shift.

Finally, if the flat, shifted baseline is the result of an adaptation process operating on a very long timescale (such as a perfect integrator) while the quick adaptation is produced by a separate process, one would expect to find different rates of increase of the adaptation magnitude at each timescale as a function of adaptation time. Specifically, as adaptation duration increases, the “infinite” timescale should show no diminishing returns and increase linearly, while the fast timescale should reach an asymptote. We can estimate the magnitude of the persisting component of adaptation from the baseline shift observed at the end of the decay period. We can then estimate the magnitude of the transient component by the aftereffect strength at the end of the adaptation period that cannot be accounted for by the magnitude of the persisting component. Thus, the fast component magnitude may be defined as the difference between the final aftereffect reached during the adaptation period and the magnitude of the persisting component. These two quantities are illustrated on the graphs in [Figure 3](#). We plot the inferred magnitude of adaptation at the fast and slow timescale as a

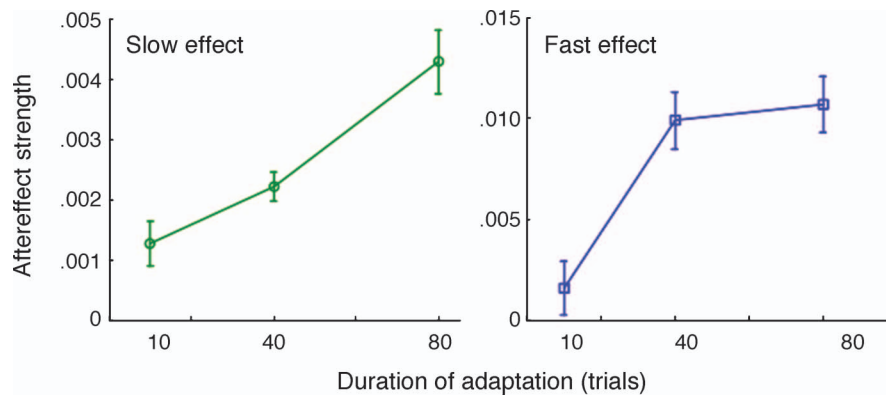


Figure 4. **Experiment 1** results: The magnitude of adaptation of the slow and fast timescales (± 1 SEM across subjects) as a function of number of adaptation trials (each one roughly 4 seconds long). The slow timescale grows linearly with adaptation time, showing no diminishing returns, while the fast timescale saturates within the first 40 trials.

function of adaptation duration in Figure 4. The fast timescale saturates within 40 trials or 160 seconds (in that its magnitude does not change significantly from 40 to 80 trials), while the slow timescale shows no signs of diminishing returns and increases linearly with adaptation duration.

Experiment 2

Experiment 1 suggests that the McCollough effect is the result of two timescales of adaptation: one decaying with a time constant of 25 seconds, and the other operating as a perfect integrator. Previous work on the time course of McCollough effect induction and decay has produced mixed yet suggestive results (for a review, see Skowbo, Timney, Gentry, & Morant, 1975).

Several findings are in favor of a perfect integrator: magnitude of the aftereffect increases with adaptation durations up to 2.5 hours (Riggs, White, & Eimas, 1974), and the effect may persist for weeks (Jones & Holding, 1975; Stromeyer, 1978). On the other hand, MacKay and MacKay (1975) reported that the McCollough effect may be attenuated by even diffuse light, suggesting that the McCollough effect may be very sensitive to subsequent stimuli. However, others suggest that exposure to uniform light or natural viewing conditions attenuates the effect only slightly compared to exposure to aligned gratings (Skowbo et al., 1975) and it may be the case that the slow (10 minutes) matching procedures used in those studies produced extended exposures to test gratings and thus caused the apparent decay. Indeed there is evidence that the slow matching procedures employed in the prior literature are partly responsible for the decay: Skowbo et al. (1975) showed that 50 minutes of post-adaptation stimulation plus five tests resulted in more than 30%

decay, while the same 50 minutes of stimulation with only one test produced only 10% decay. This indicates that the bulk of the observed decay was caused by the testing procedure rather than the intervening stimulation. Thus, the question remains open whether color-orientation neutral exposure causes a decay of the McCollough effect.

In **Experiment 2** we tested the permanence of the persisting shift further by asking whether it is affected by intervening blocks of adaptation to stimuli of unrelated orientation (oblique after cardinal axes, or vice versa). Since the interposed adapting stimuli are always symmetrical in their differences from the preceding and following adapting set, they would not be expected to disturb the match established by a perfect orientation-contingent integrator but might cause decay if each orientation's chromatic null point is reset by chromatically symmetrical stimulation.

Methods

To assess these issues, we added measurements of the baseline before each adaptation block. As in **Experiment 1**, we interposed adaptation at different orientations sets (e.g., adaptation at 45 and 135 degrees when the adaptation of interest is at 90 and 180 degrees). However, in this experiment the added measures of baseline adaptation before the later block at a particular orientation set allowed us to assess whether a persistent color-contingent aftereffect can be modulated by exposure to the same colors at non-adapted orientations.

Subjects were exposed to adaptation durations of 10, 20, 40, and 80 trials (40, 80, 160, and 320 seconds) in the following order. As discussed before, “blank” trials are test trials with the same interval spacing as adaptation trials, but with a uniform screen instead of an adapting pattern between the test trials:

1. 40 blank trials of orientation set A (baseline)
2. 10 adaptation trials of orientation set A; color-pairing A
3. 80 blank trials of orientation set A (decay)
4. 40 blank trials of orientation set B (baseline)
5. 20 adaptation trials of orientation set B; color-pairing A
6. 80 blank trials of orientation set B (decay)
7. 40 blank trials of orientation set A (baseline)
8. 40 adaptation trials of orientation set A; color-pairing B
9. 80 blank trials of orientation set A (decay)
10. 40 blank trials of orientation set B (baseline)
11. 80 adaptation trials of orientation set B; color-pairing B
12. 80 blank trials of orientation set B (decay)

Orientation set and color pairing were assigned randomly for the first block and then alternated as described in the [General methods](#).

With this adaptation order, we could measure the baseline aftereffect strength before the onset of a particular bout of adaptation. This design allowed us to precisely measure (1) the persistence and susceptibility to interference of the long-term aftereffect by seeing how much, if at all, it decayed from the previous decay period to the baseline (i.e., from blocks 3 to 7, or blocks 6 to 10);

and (2) the baseline shift by measuring the baseline before adaptation.

Results and discussion

In [Figure 5](#) we plot the aftereffect strength for each coupled orientation set: top row corresponds to blocks 1–3, then 7–9, while the bottom row reflects blocks 4–6 and 10–12. We see that even after up to 8 minutes of adaptation and measurement at an unrelated adaptation, there are no signs of decay of the slow timescale. The 95% confidence intervals on the change of aftereffect strength from the last 30 trials of the decay period to the last 30 trials of the following baseline measurement were -0.0022 to 0.0016 for the decay of 40 second adaptation and -0.0024 to 0.0021 for the decay of 160 second adaptation.

Aside from assessing the persistence of the aftereffect, the baseline measure before each adaptation period allows us to more accurately estimate the magnitude of adaptation at each timescale. We could thus assess the amount of adaptation at the slow timescale as the shift in aftereffect strength from the pre-adaptation baseline to the end of the decay period. Again, the magnitude of the fast timescale adaptation corresponds to the difference between the aftereffect strength at the end of the

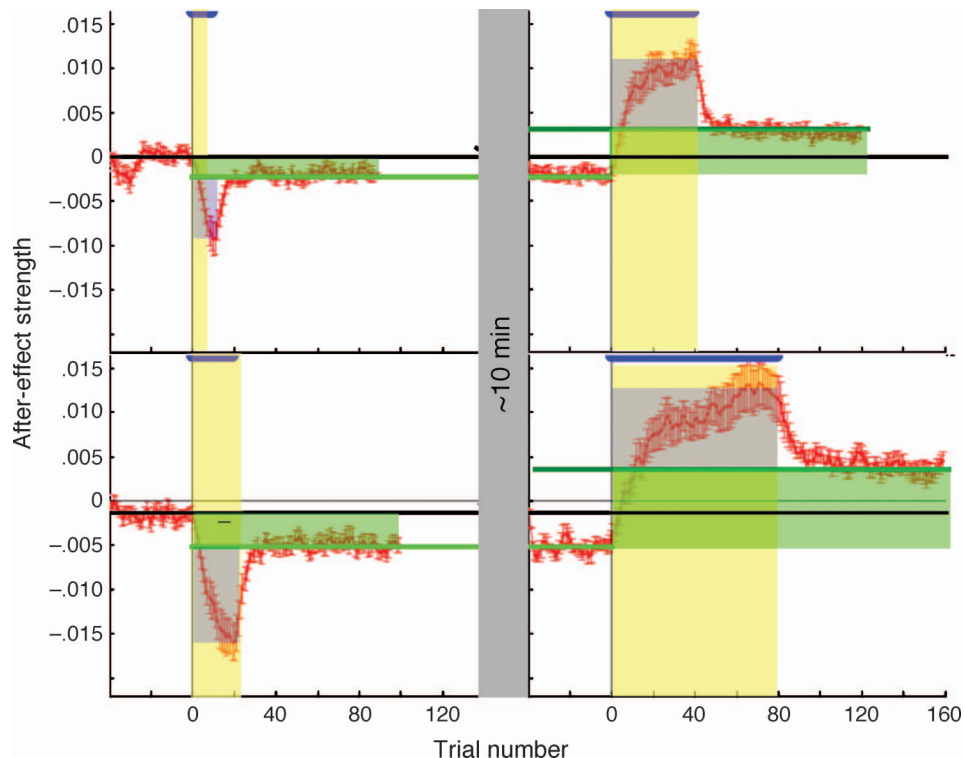


Figure 5. [Experiment 2](#) results: McCollough effect build-up and carry-over across blocks of unrelated adaptation (oblique orientations for cardinal adaptation, and vice versa). The shifted baseline (long-term effect) does not decay through 8 minutes of unrelated adaptation. The magnitude of the long-term effect (green) and short-term effect (gray) may be inferred from the peak aftereffect and the baseline shift.

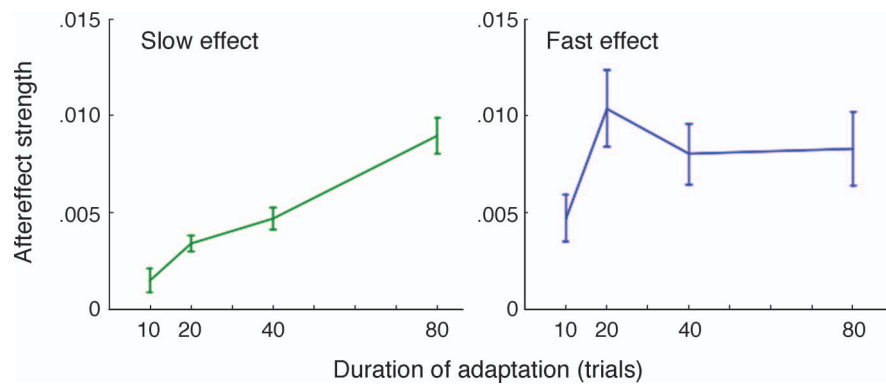


Figure 6. Experiment 2 results: The magnitude of the long-term and short-term effects: the long-term effect does not saturate, the short-term effect saturates within 20 trials (80 seconds).

adaptation period and that at the end of the decay period (shown in Figure 5).

Again we find (Figure 6) that the slow timescale shows no signs of decay or diminishing returns, suggesting that within the durations we have tested, it acts as a perfect integrator. It is presumably this infinite timescale of adaptation that underlies the renowned persistence of the McCollough effect—a process that does not “forget” unless it encounters de-adapting stimulation.

Experiment 3

Several models of adaptation and learning imply that the timescales at which learning takes place may interact non-linearly. One plausible model, the serial multi-rate model of adaptation at multiple timescales (Smith et al., 2006), would arrange the timescales serially such that the slow adaptation processes adapts to the output of the faster adaptation processes. For example, the short-term aftereffect might reflect changes in synaptic connectivity or presynaptic transmitter depletion (Kohn, 2007), while the long-term effect depends on modulation of protein synthesis at the cell body through the activation of CREB or some similar transcription factor (Tully, Preat, Boynton, & Del Vecchio, 1994; Yin & Tully, 1996). In such a two-stage system, adaptation for long periods without breaks will reduce the output of the first stage to a level lower, on average, than is produced by stimulating an initially unadapted system in bursts for the same total adapting duration. Thus, the longer timescale process would benefit from “spacing,” an effect observed in learning wherein the same amount of training produces better long-term memory when it is “spaced” over a period of time rather than presented all together, or “massed” (Cepeda, Pashler, Vul, Wixted, & Rohrer, 2006). In other words: if induction were spaced, one would expect a greater long-term aftereffect. Indeed, in studies of the cellular basis of

long-term memory and learning, modulation of gene expression at the cell nucleus typically shows a marked benefit of spacing (Tully et al., 1994). We tested for a spacing benefit in an experiment designed to maximize spacing by minimizing the saturation of the fast timescale.

Methods

Subjects adapted to 4 minutes of a particular color-orientation pairing either spaced (4 seconds on, then 4 seconds off for 8 minutes), or massed (all 4 minutes on), then 4 minutes of the opposite color-orientation pairing with the opposite spacing condition. After a 4-minute delay, the persisting effect was measured. Any deviation from baseline in the final testing period would indicate that adaptation at the two timescales is non-linear. An aftereffect in the direction of spaced adaptation would suggest that the serial model of learning applies to the timescales of the McCollough effect. An aftereffect in the massed direction would imply a preference toward persistent exposure. Finally, no difference would indicate a perfectly linear system, such that the same total amount of adaptation has an equal effect regardless of its distribution in time.

The arrangement of adaptation periods had the following structure:

1. 20 blank trials, orientation set A (baseline A)
2. 20 blank trials, orientation set B (baseline B)
3. 60 massed adaptation trials; orientation set A; color-pairing A (massed A)
4. 1 blank trial, followed by 1 adaptation trial, 60 times (120 trials total); orientation-set B, color-pairing A (spaced B)
5. Spaced A (orientation-set A; color-pairing B)
6. Massed B (orientation-set B; color-pairing B)
7. 60 blank trials, orientation-set A (final test A)
8. 60 blank trials, orientation-set B (final test B)

Thus, across both orientation sets, we counterbalanced whether the massed or spaced trials came first, and the temporal proximity of massed and spaced trials to the final test. The delay between massed and spaced was held constant to 120 trials, and the delay between final adaptation and final test was held constant to 60 trials.

Results

Figure 7 shows that our spacing manipulation successfully prevented saturation (or any considerable build-up) of the fast component: the aftereffect reached at the end of the O1M block is substantially greater than that reached in the O2S block. In the Linear model, this is an expected result of the fast process's leaky integration (the model fits the data of Figure 7 with $R^2 = 0.95$, RMSE = 0.0018): the less frequent topping up of adaptation makes it less effective than the same duration of adaptation introduced more rapidly, just as a leaky bucket is harder to fill with short separate bursts than with a continuous flow. If the slow process adapts to input from the fast process and spacing successfully precludes adaptation of the fast process, then we should expect to see a spacing effect: a greater net aftereffect in the spaced direction during the testing trials.¹ Figure 7 shows the time course of the aftereffect build-up and the testing block. The measurements of the effect at the final test show no advantage for the spaced direction and no deviation from baseline. The 95% confidence interval for the magnitude of the effect at the final test (where positive values are in favor of the spaced direction) is -0.0044 to 0.0012 . This shows no evidence of a spacing benefit, indicating that the two timescales documented above interact linearly. It is not the case that the system “trades off” assignment of learning between the timescales, nor is it the case that the slow timescale takes its input from the output of the

fast timescale adaptation. Thus, a parallel, linear, multi-rate model is supported.

The fact that the system operates in parallel rules out several plausible models of how the two timescales may be instantiated. Namely, “parallel” as we have operationally defined it means that input to the fast and slow processes is independent of any adaptation that may be present. Thus, it is not the case that fast adaptation occurs at earlier stages of processing that provide input to slower adaptation mechanisms at later stages of processing. This extends to the level of single cells: it cannot be the case that fast adaptation occurs at the afferent synapse, while slower adaptation occurs at the cell body or the axon terminals. We can rule out this class of models. However, there is a larger set of plausible models in which input to the fast and slow timescales is independent of ongoing adaptation. This may be achieved at the level of a single cell (if both types of adaptation are occurring simultaneously at different dendritic arbors), a single cortical area (if different cells with identical input are substrates for the fast and slow adaptation), or different visual areas (if common input is sent to both areas independently). Thus, we are limited in the anatomical conclusions we may draw; however, we can draw conclusions about the functional properties of the system: namely that input to the fast and slow timescales is independent of ongoing adaptation.

Is there a very fast component?

In our experiments thus far, induction and decay appear to involve distinct processes, one with a time constant less than a minute, and the other one integrating over time without loss. But suppose that in addition, a third

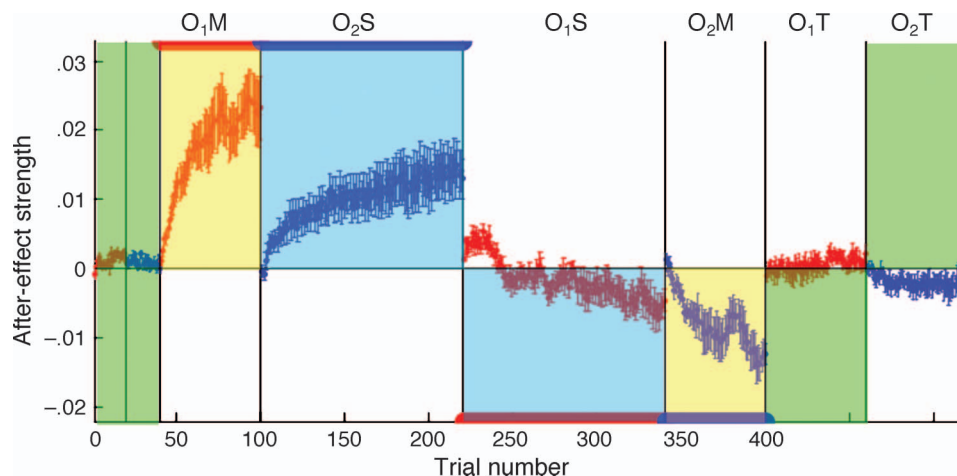


Figure 7. McCollough effect build-up and decay for unrelated orientations (O1 and O2; red and blue graphs) during spaced (blue blocks) and massed (yellow blocks) adaptation. There was no tendency towards greater effects in the spaced direction during the final testing periods (green blocks), indicating that the long-persisting aftereffect depends on a simple accumulation of adapting effects over time.

component of the orientation-contingent color aftereffect decays very rapidly, say in less than one second. Such a process would not be easily detectable in experiments where recovery is sampled at intervals of a few seconds. To investigate the possibility that an orientation-contingent color aftereffect can be induced and decay on a timescale on the order of one second, we exploited the fact that even very rapid alternation of the orthogonal pair of inducing gratings can produce an effect (Vul & MacLeod, 2006). Large McCollough effects are obtained when orientation alternates at 2 Hz; this makes it possible to alternate opposite color-orientation pairings at rates up to 0.5 Hz, with each pairing realized by a single four-frame sequence.

In this adapting stimulus, the color-orientation correlation is itself a square wave, alternating between positive and negative at 0.5 Hz. Test trials were interposed after an integer number of complete cycles.

Thus, the colors seen in a test trial represent the net effect that results from a succession of equal numbers of alternating brief positive and negative cycles of McCollough effect induction. The test for a rapidly induced and rapidly decaying aftereffect was made by comparing trials of two kinds. For example, a trial that began with a red-horizontal correlation would finish with a green-horizontal correlation, and vice versa. If there were a rapid aftereffect component, these two conditions would yield (briefly) different null settings, determined in each case by the correlation exhibited at the end of the pre-adapting sequence. But we could find no consistent difference between the two conditions, using color-orientation pairings that alternated at frequencies of 0.125 Hz or 0.5 Hz (an effect was detectable at 0.0625 Hz—when the fast timescale we previously described would be expected to be noticeable). On this evidence, there is no very rapidly induced and rapidly decaying component in the induction of orientation-contingent color aftereffects.

Linear model

Since we showed that the two timescales sum linearly (Experiment 3), the current data should be well accounted for by a simple two-timescale linear model. We constructed such a model and evaluated the best fitting parameters. That is, we constructed a model with two timescales represented by leaky integrators with amplitudes and time constants that could be adjusted to fit the data. Here we write the convolution of the leaky integrators with the induction stimuli as an integral:

$$M(t) = \sum_i \int_0^{\infty} A(t - \tau) w_i(\tau) d\tau. \quad (2)$$

Here $M(t)$ is the McCollough effect strength at time t ; A is the time series reflecting the entire history of induction stimuli; and w_i is the impulse response function of timescale i , a decaying exponential leaky integrator with time constant γ_i and amplitude α_i :

$$w_i(\tau) = \alpha_i \exp(-\tau/\gamma_i). \quad (3)$$

The definition of the input A warrants further discussion. Informally it could be expressed as the correlation between orientation and color in the sequence of stimulation within a brief time window centered on a particular time. Thus, a zero input, $A(t) = 0$, means that the stimulus sequence around time t had no difference in color between the alternating orthogonal orientations of interest. The sign of $A(t)$ depends on which of the gratings is redder, and the magnitude is proportional to the L-cone contrast between the orthogonal gratings. Addition of achromatic gratings to the sequence will reduce A if A is understood strictly as a correlation measure, but not if it is understood as a covariance. The first choice is in some respects a more natural one since achromatic gratings reduce the evidence for orientation-contingent bias in color perception. Moreover, this form of the linear model correctly predicts that the McCollough effect can be reduced by testing (e.g., Skowbo, 1988). This distinction is not strongly relevant for the present experiments, and for the sake of simplicity, we have simply omitted the brief (300 msec) test stimuli from the descriptive model. However, it must be noted that a complete model should not only take the test stimuli into account but will also need to treat achromatic gratings as a potential de-adapting stimulus, as they reduce the time-windowed correlation between orientation and color.²

Equations 2 and 3 lead to an exponential solution of the form shown in Equation 1. In addition, we provided a term, β , to the model that could modulate the input to the slow timescale proportionally to the magnitude of adaptation at the fast timescale, thus changing Equation 2 to the following pair of equations:

$$M_1(t) = \int_0^{\infty} A(t - \tau) w_1(\tau) d\tau, \quad (4)$$

$$M_2(t) = \int_0^{\infty} [A(t - \tau) - \beta(M_1(t - \tau))] w_2(\tau) d\tau, \quad (5)$$

$$M_A(t) = M_1(t) + M_2(t). \quad (6)$$

By evaluating β , we could again test whether there is any evidence that the slow timescale takes its input from the output of the fast timescale adaptation.

This linear model provides an excellent fit to the data described in the three experiments above, as well as several other experiments we have conducted that are not reported here (Figure 8). Notably, although the model does not provide for any interaction of adaptation effects over time, such as would yield a difference between massed and spaced adaptations, the results of Figure 7 contrasting massed and spaced adaptations are qualitatively well predicted.

The fast timescale in the linear model has a time constant of 32 seconds and reaches an asymptote at 4.7% of the induction contrast, while the slow timescale approached infinity and builds up at a rate of 0.014% of the induction contrast per second.³ β , the parameter that would modulate input into the slow timescale by the output of the fast timescale, was essentially 0 (-0.009 ; a marginal estimate of the posterior distribution over all settings of parameters allowed us to estimate the 95% confidence interval on β as -0.42 to 0.55). This means that the induction contrast that the slow timescale operates over is reduced by (at most) half of the magnitude of adaptation of the fast time constant. A purely serial model would predict that the chromatic contrast of the input to the slow process (i.e., the output of the fast process) would be reduced by the full magnitude of the fast timescale adaptation: β would be 1. We can confidently rule out this alternative.

Given these results, we compared a three-parameter model where β is constrained to be 0, and the slow timescale time constant (τ_2) is constrained to be infinitely high. This model provided an identically good fit to the data: in both the five parameter, and the three parameter models, RMSE = 0.0014, and $R^2 = 0.9602$.

We conclude that the McCollough effect is the result of parallel adaptation of a relatively fast timescale (a leaky integrator with a time constant of roughly 30 seconds) and a perfect integrator, wherein the net adaptation is just the linear sum of the adaptation at these two timescales.

Discussion

We showed that the McCollough effect is a product of two distinct and separable timescales of learning in early visual cortex: a transient one, corresponding to a leaky integrator with a time constant of roughly 30 seconds; and an infinite one, which appears to be a perfect integrator in that it shows no signs of decay or saturation. These timescales operate and sum purely linearly. The best way to account for these data is a dynamic linear system comprised of two integrators, which take the same input, and sum to produce the output measured as an aftereffect.

It is interesting to speculate about the generality of these timescales. The 30-second (fast) timescale appears consistent (although on the slow end of the range) with classic work on contrast adaptation dynamics. Blakemore and Campbell (1969), Bodinger (1978), and Lorenceau (1987) all reported a component of contrast adaptation at roughly the fast scale that we report here, suggesting the possibility of a common mechanism. However, it would be misleading to suggest that there is something unique about the 30-second timescale we observed. A recent review of adaptation cites timescales ranging over five orders of magnitude (Kohn, 2007), and there is no shortage of visual aftereffects with timescales at any point in that range. So, the fast timescale we see is well within the commonly reported range, but this range is so large, that it is not parsimonious to postulate a special role for the specific fast timescale we observe here. However, this is not the case of our slow timescale of adaptation.

The “infinite” timescale we observed appears to show no signs of diminishing returns with increasing duration of adaptation: the color bias is simply proportional to adapting duration. It is presumably this permanent component that has been measured in classic studies of the persistence of the McCollough effect (e.g., Jones & Holding, 1975). The apparent permanence of this effect

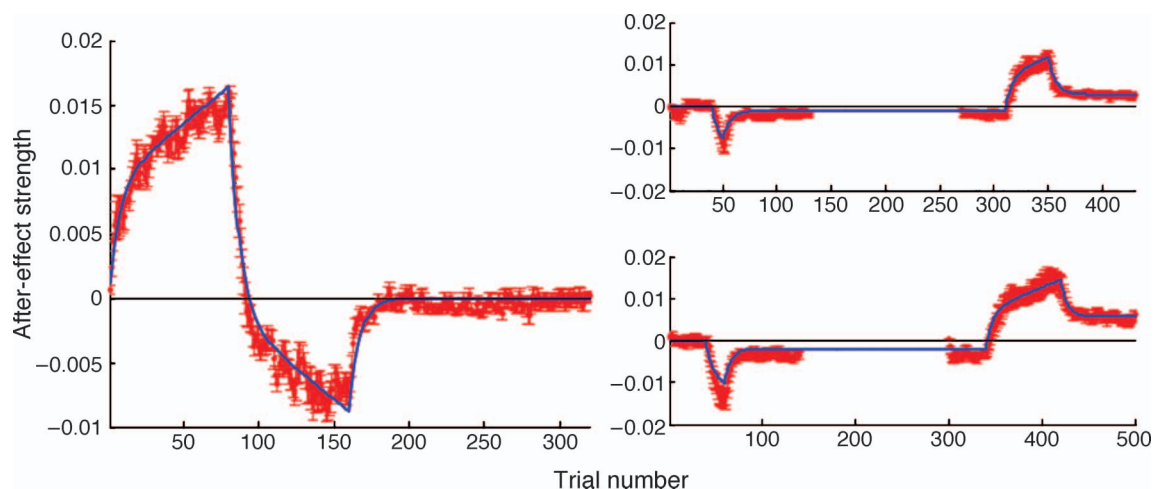


Figure 8. A fit of a two-timescale linear model to the data presented in Figures 2 and 4. One timescale has an infinite time-constant (a perfect integrator), the second timescale has a time-constant of 30 seconds.

seems quite counterintuitive for a system that is compensating for errors in itself, or in the environment. However, adaptation that lasts forever is well suited to compensate for the correlation of color and orientation that may occur due to the combination of astigmatism and chromatic aberration—the effects of which are permanent without the corrective optics that were unavailable to our evolutionary ancestors.

It remains possible (indeed likely) that the build-up of the slow adaptation does saturate as the magnitude of the aftereffect approaches the color contrast of the inducing stimulus. However, to show such an effect would require adaptation for many hours and would likely violate ethical protocols (since the effect does not decay naturally, it would require an equally long time to de-adapt).

The McCollough effect is one of many peculiarly long-lasting aftereffects. Most of these effects are in the domain of color: orientation contingent color aftereffects (Jones & Holding, 1975), motion-contingent color aftereffects (Hepler, 1968), attentional selection for color (Tseng et al., 2004), even adaptation to global color statistics resulting from exposure to chromatically filtered illumination (Neitz, Carroll, Yamauchi, Neitz, & Williams, 2002) or chromatic bias induced by cataracts (Delahunt, Webster, Ma, & Werner, 2004). As such, it seems that the long-lasting nature of the McCollough effect and thus the very slow timescale of adaptation is not an isolated case. It is possible that such long-term adaptation is present for only color aftereffects. However, there are documented effects outside the realm of color that last as long as the McCollough effect (e.g., spiral motion; Masland, 1969). Our interpretation is that in the cases of contingent aftereffects, the contingencies and thus de-adapting stimuli are simply very rare in the world. Thus, these aftereffects last longer than “normal” aftereffects simply because they have no opportunity to de-adapt. Of course, this implies that more common aftereffects may also have a long-lasting component which has proven difficult to detect simply because it is too easy for subjects to de-adapt. If this is the case, the multiple timescales of learning (particularly the slow timescale) we observed for the McCollough effect should not be seen as a peculiarity of the McCollough effect, but rather a clear test case in which these timescales may be isolated and measured. Of course, whether such a permanent component exists in many other adaptation phenomena remains an open question.

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Footnotes

¹A less obvious account of how two timescales might interact (McLoughlin, 2005) would suggest that the fast adaptation sets the maximum level of adaptation the slow timescale might reach, thus resulting in increased slow-timescale adaptation in the massed condition.

²The effects of physically achromatic test gratings, as opposed to the perceptually achromatic ones used in our nulling experiments, should in principle differ very slightly because of their slight difference in chromaticity. We ran control experiments to check this point and could detect no difference between the speed of decay as measured by nulling and matching.

³These values correspond to the maximum-likelihood parameters for the fit to all but Experiment 3. In Experiment 3, the best fitting magnitudes of the timescales are both 50% greater than for other experiments. However, the time constants, and relative magnitudes of the two timescales remain unchanged. This may reflect differences in subjects in this experiment.

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