



## Spontaneous recovery of motion and face aftereffects<sup>☆</sup>



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### ARTICLE INFO

#### Article history:

Received 18 March 2013

Received in revised form 25 June 2013

Available online 19 July 2013

#### Keywords:

Adaptation

Motion aftereffect

Face aftereffect

Spontaneous recovery

### ABSTRACT

The ability of the visual system to rapidly adjust to changing environmental conditions is one of its key characteristics. Environmental changes can occur over a variety of timescales, however, and it remains unknown how the visual system adapts to these. Does a single mechanism control adaptation across all timescales, or is adaptation subserved by multiple mechanisms, each of which is tuned to its preferred duration? To address this question, we conducted three experiments in which subjects viewed motion (Exp. 1 and 2) or faces (Exp. 3) in a sequence designed to produce opposing aftereffects. A first adapter was presented for a relatively long duration, while a second one was presented only long enough to extinguish the effects of the initial adapter. Continued measurement of aftereffects revealed a spontaneous recovery of adaptation caused by the initial, longer-lasting adapter in all three experiments. This pattern of results suggests that adaptation in the visual system generally reflects a combination of multiple temporally-tuned mechanisms.

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### 1. Introduction

One of the hallmarks of the visual system is its ability to rapidly fine-tune itself to optimize processing of the current environment, a phenomenon known as visual adaptation. For example, viewing a moving stimulus (e.g. a waterfall) initially induces a strong response in direction sensitive neurons, but during continued viewing, the response gradually weakens over time (e.g. Barlow & Hill, 1963; Kohn & Movshon, 2003; Vautin & Berkley, 1977). One effect of such adaptation is to bring the firing rate of the neural population down from a nearly saturated level, allowing neurons to more efficiently signal changes in stimulus strength (e.g. Fairhall et al., 2001; Laughlin, 1981; Sharpee et al., 2006; Wainwright, 1999). Salient byproducts of adaptation are perceptual aftereffects. For example, following the viewing of motion, a static pattern may appear to move; this illusory motion is known as the motion aftereffect (MAE; for reviews see Clifford, 2002; Mather, Verstraten, & Anstis, 1998; Mather et al., 2008).

Adaptation has been studied extensively using a wide range of visual stimuli, revealing aftereffects in perception of both simple attributes such as contrast and color, and more complex patterns such as faces (see reviews by Clifford et al., 2007; Kohn, 2007;

Webster, 2011) Since adaptation contributes to most stages of visual processing, understanding it is a necessary part of understanding vision more generally.

The majority of studies to date have examined effects of a single episode of adaptation. However, real environments often go through multiple changes over a short period, and thus it is important to understand how the visual system deals with sequences of adaptation episodes.

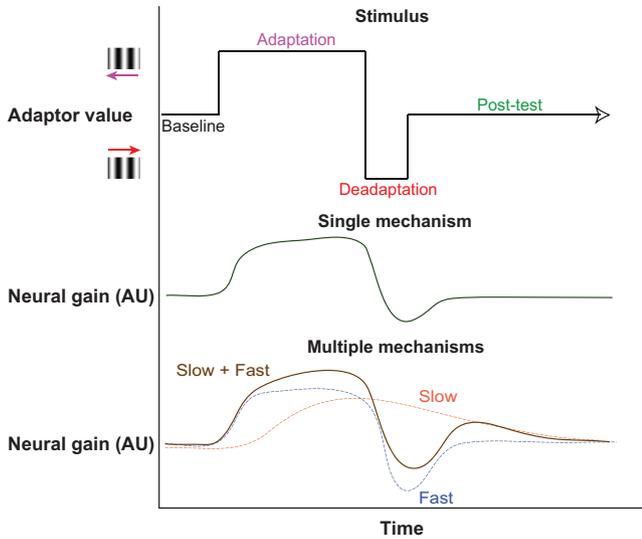
For example, because some environmental changes last a relatively long time, while others are more transient, it would be desirable to adjust to brief changes without erasing the adaptation history to the longer-term environmental features (Kording, Tenenbaum, & Shadmehr, 2007). Imagine you are driving across the country. As you look ahead, your visual system is exposed to a long-lasting characteristic pattern of optic flow to which it needs to adapt. Looking in the rear view mirror, however, the optic flow pattern is opposite, requiring its own adaptation. If adaptation to one pattern were to cancel out the previous state of adaptation, then your visual system would need to readjust from scratch every time you switch between looking ahead and using the rear view mirror. On the other hand, if adaptation states corresponding to longer and shorter-term patterns do not cancel each other out, then the visual system might be able to retain a memory of the effects associated with looking ahead, while still being able to adjust to the transient changes that arise from glancing in the rear view mirror.

One way to implement such a memory is for shorter and longer durations of adaptation to have different controllers in the brain, which we will refer to as mechanisms. We assume that the mech-

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**Fig. 1.** Single and multiple mechanism accounts of adaptation. Adaptation time courses of the two conceptual models of adaptation (bottom two plots; in arbitrary units) are shown in response to a series of adaptor stimuli (top panel). Adaptors are chosen such that the effects of “deadadaptation” cancel previously induced effects. Adaptation is controlled by mechanisms whose response is assumed to be proportional to neural gain or perceptual aftereffect strength. Both models respond equivalently throughout the baseline, adaptation, and deadadaptation periods of the paradigm. However, the multiple mechanisms model (bottom panel; solid line) predicts spontaneous recovery of adaptation effects in the post-test period, while a single mechanism model (middle panel) does not. Total response of the multiple mechanisms model is plotted in black, and the red and blue curves plot the responses of the slow and fast mechanisms. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

anisms determine how responsive a population of neurons is to a visual stimulus, most likely by modifying neural gain (i.e. scaling the relationship between stimulus and response). For example, prolonged viewing of motion in one direction might cause a mechanism to become active and reduce the gain of the motion selective neurons preferring that direction. Currently, almost all models of adaptation assume only a single such mechanism. Alternatively, multiple mechanisms may have preferred rates of environmental change, which cause them to be employed mainly when exposure to a new stimulus matches a particular duration (Kording, Tenenbaum, & Shadmehr, 2007; Pekny, Criscimagna-Hemminger, & Shadmehr, 2011; Vul, Krizay, & MacLeod, 2008). For example, a “fast” mechanism could become active quickly, while a “slow” one would be employed only if a stimulus remains present for a long time. When the environment changes again as an adaptor is removed, the fast mechanism would become inactive quickly,

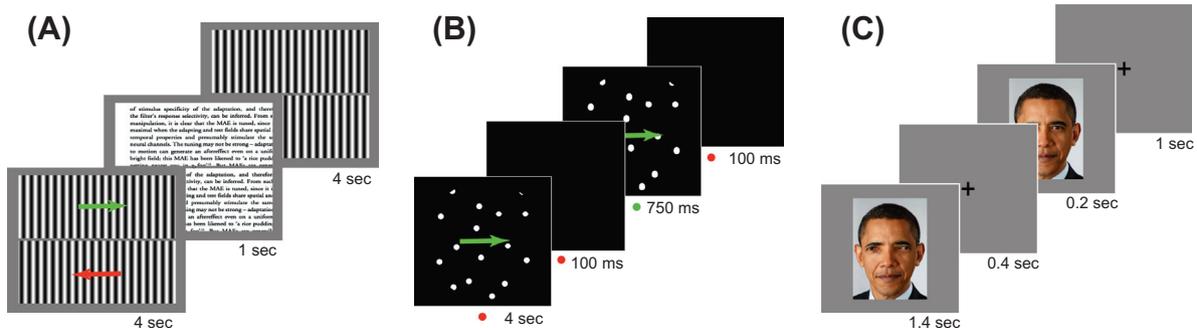
while the slow mechanism would remain active, returning relatively slowly to its initial state. Evidence for multiple temporally tuned adaptation mechanisms has been reported in motor learning (Kojima et al., 2004; Smith, Ghazizadeh, & Shadmehr, 2006) and a few recent cases in vision (see Bao & Engel, 2012 for contrast adaptation; Vul, Krizay, & MacLeod, 2008 for McCollough effect). Here we show evidence for such mechanisms in two other aspects of vision, establishing that multiple temporally tuned mechanisms may be a general feature of the visual system.

Classic experiments on animal learning (e.g. Bouton, 1993; Rescorla, 2004) and recent ones on motor adaptation (Kojima et al., 2004; Smith, Ghazizadeh, & Shadmehr, 2006) have demonstrated how to test for the presence of multiple temporally tuned mechanisms. Fig. 1 shows the experimental paradigm (top panel), which measures effects of consecutive episodes of adaptation. Subjects view two stimuli, one of which is presented for a relatively long duration (“adaptation”), while the second one (“deadadaptation”) is presented only briefly. The stimuli are carefully selected such that the first stimulus causes gain changes that are opposite to those caused by the second stimulus. As a consequence, adaptation elicited by the second stimulus effectively cancels out that caused by the first stimulus.

Single and multiple-mechanism models make different predictions about how much adaptation will be present during the period following deadadaptation, the “post-test”. If adaptation is controlled by a single mechanism (Fig. 1, second panel), then any gain changes caused by the first stimulus are eliminated as the mechanism adjusts the gain in response to the second stimulus. A single controlling mechanism thus predicts that during the post-test, gain will be close to its baseline level, with any residual effects quickly decaying away.

On the other hand, if adaptation reflects the sum of two controlling mechanisms, each of which operates over a different timescale (i.e. “fast” and “slow” mechanisms), then the two adaptation periods will engage these mechanisms differently (bottom panel). The initial adaptation period will cause strong responses in both the “fast” and “slow” mechanisms, since it is presented for a relatively long duration. However, because the “deadadaptation” period is very brief, the fast mechanism will adjust to it much more strongly than the slow one. In order to bring net gain down, the fast mechanism will have to produce strong negative effects that cancel the ongoing responses in the slow mechanism. After the deadadaptation period ends, because the fast mechanism adjusts quickly, its effects will decay rapidly and effects of the slow mechanism (which persist longer) will become unmasked, a phenomenon termed “spontaneous recovery.”

Here we adapted this paradigm to test for the presence of multiple temporally tuned mechanisms controlling motion and face adaptation. In the first experiment, subjects viewed a grating translating



**Fig. 2.** Trial structures. (A) Experiment 1: A pair of sinusoidal gratings translating in opposite directions was shown for 4 s, followed by a 1 s test trial. Subjects reported their perception of (illusory) motion. (B) Experiment 2: A 4 s moving dot display was followed by a brief blank interval and a test display. Subjects indicated whether they perceived the dots as moving coherently. (C) Experiment 3: A face adapter was shown for 1.4 s, followed by ISI and a test face. Subjects indicated whether the test face appeared to have eyes too close together or too far apart.

in one direction for 10 min, followed by brief “deadadaptation” in the opposite direction. The first stimulus induced perception of illusory motion, a motion aftereffect (MAE), which was eliminated by the period of reversed motion. In subsequent testing, subjects reported experiencing a return of the original MAE elicited by the initial 10 min stimulus, a pattern consistent with multiple temporally-tuned adaptation mechanisms. We observed similar spontaneous recovery phenomena for stimuli that induced changes in subjective motion coherence thresholds (Experiment 2), and in adaptation to faces (Experiment 3). Together, our findings extend upon the previous evidence for multiple temporally-tuned mechanisms in contrast adaptation (Bao & Engel, 2012), and McCollough effect (Vul, Krizay, & MacLeod, 2008), and suggest that such mechanisms may be a general feature of visual processing.

## 2. Experiment 1

In the first experiment, we investigated whether different durations of motion adaptation engage distinct temporally-tuned mechanisms. Subjects viewed two translating grating patterns moving in opposite directions, a first adapter presented for a relatively long duration, and a second, “deadadapter” shown only briefly (Fig. 1). Because the adapters moved in opposite directions, they produced opposing motion aftereffects. We tested whether the MAE elicited by the initial adapter, but extinguished during deadadaptation, would spontaneously recover. Such recovery would provide evidence that the deadadapter affected a different mechanism than initial adaptation.

### 2.1. Methods

#### 2.1.1. Participants

Seven volunteers (4 males and 3 females) participated in the experiment. All participants in all experiments had normal or corrected-to-normal vision, and procedures in all experiments were approved by the University of Minnesota Office for the Protection of Research Subjects.

#### 2.1.2. Stimuli

Participants viewed two rectangular patches of a sine wave grating, centered 2.8° above and below a central fixation mark. Each patch subtended 11 × 5.4° of visual angle. The full contrast gratings translated at a rate of 4 Hz, and their spatial frequency was 1.82 cycles per degree. Stimuli were presented on an LCD monitor, with a mean luminance of 31.3 cd/m<sup>2</sup>, in a dimly lit room. We coded all experiments using the Psychophysics Toolbox for MATLAB (Brainard, 1997; Pelli, 1997).

#### 2.1.3. Procedure

Subjects initially viewed leftward motion continuously for 10 min, while fixating on the central mark. Following this adaptation period, the motion reversed, and subjects were asked to report their perception of the motion aftereffect. Every 4 s, a physically static display (of text, see Fig. 2A) was presented for 1 s, and subjects indicated, using keypresses, whether the display appeared to move leftward, rightward, or to be stationary. This “deadadaptation” period continued until the MAE direction reversed from its initial direction for two consecutive trials. Subsequently, the static display was shown continuously and subjects were prompted to report their MAE perception every 4 s. This “post-test” period lasted 90 s.

#### 2.1.4. Analysis

Due to the variable duration of deadadaptation, time courses were aligned to the last trial of deadadaptation. For plotting, means and

standard errors were computed individually for the four trials preceding this point and all subsequent trials.

## 2.2. Results

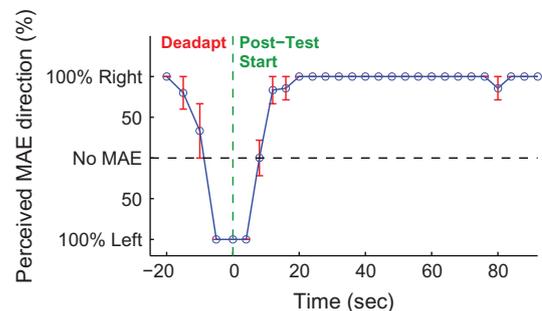
The results of Experiment 1 showed strong spontaneous recovery of adaptation. Fig. 3 plots subjects’ reported percent of motion while viewing the physically static display. All ( $N = 7$ ) subjects initially perceived rightward illusory motion, induced by the 10 min of adaptation to leftward motion, a traditional MAE. By the end of the deadadaptation period (mean duration, 29.3 s; ranging between 25–35 s), all participants reported a direction reversal of their MAE (i.e. to the leftward direction). This pattern indicates that the relatively brief period of reversed grating motion completely eliminated the behavioral marker of the original adaptation. In the post-test, however, where a static display was displayed, the MAE rapidly reversed back to the rightward direction for all subjects, corresponding to effects of the initial adaptation. The probability of observing these unanimous reports by chance is less than 0.01 (sign test).

Although these data are consistent with multiple mechanisms tuned to different durations (Fig. 1), an alternative account exists. The grating translating leftward and rightward could have caused adaptation in two distinct *direction-tuned* populations, where adaptation decay was proportional to induction time. The prolonged leftward motion could have produced longer lasting gain changes in the leftward-preferring neural population and the relatively brief rightward motion could have produced produced shorter-lived gain changes in the rightward-preferring population. As a consequence, during the post-test, gain changes in the rightward-tuned population might have decayed first and revealed more slowly decaying effects in the leftward-tuned population, and produced spontaneous recovery (for a similar effect in the orientation domain, see Magnussen & Johnsen, 1986).

In order to rule out this alternative account, Experiment 2 was designed to engage only a single direction-sensitive neural population. Both adaptation and deadadaptation used the same motion direction and speed, though the two conditions differed in strength of the motion signal.

## 3. Experiment 2

We used random-dot displays in which motion coherence varied. Adaptation to high coherence has previously been shown to lead to increases in motion coherence detection thresholds (Raymond, 1993). Subjects viewed a sequence of adapters, one containing high and one containing low coherence. We tested whether



**Fig. 3.** Results of Experiment 1. Percentage of subjects reporting the MAE in each direction as a function of time is plotted relative to the beginning of the post-test period. Deadadaptation reversed the direction of perceived MAE, but the original MAE direction quickly recovered in the post-test, and remained stable. Because of variability in the duration of the deadadaptation period, the results only show the average of the final 20 s of deadadaptation. Error bars plot  $\pm 1$  s.e. and are absent when identical responses obtained across all subjects.

coherence threshold changes observed during the adaptation period would spontaneously recover following their extinction in the deadadaptation stage.

### 3.1. Methods

#### 3.1.1. Participants

Three participants (2 males and 1 female) volunteered for the experiment. Two were authors and one was naïve to the purposes of the experiment.

#### 3.1.2. Stimuli

Subjects viewed 8.6° circular displays placed 4.6° above a central fixation mark. The displays contained dots 11 min in size, a fraction of which moved at a rate of 5.7 deg/s either leftwards or rightwards, with direction counterbalanced across experimental sessions. Before the presentation of each frame, a percentage of the dots were randomly selected to move coherently, while the remaining dots were re-drawn at new random locations. Because of this design, the coherent dots had no pre-determined lifetime and their probability of remaining within the coherently moving set depended solely upon the coherence percentage. The dots had a luminance of 72.8 cd/m<sup>2</sup> and were presented on a black background using a CRT monitor in a dark room. The displays were programmed using MATLAB code generously shared by the laboratory of Michael Shadlen.

#### 3.1.3. Procedure

We used a “top-up” adaptation design in which 4 s adapting displays were interleaved with 750 ms test displays (see Fig. 2B). The motion coherence of the adapter varied as described below. The motion coherence of the test was controlled using a one-up, one-down staircase procedure. On each trial, subjects viewed the test stimulus and pressed one of three keys to indicate whether or not they perceived motion in a direction specified at the beginning of the session. Following “yes” responses, coherence was reduced by 2.5% on the subsequent trial, and following “no” responses test coherence was increased by the same amount. Subjects were also allowed to use “strong yes” responses, which resulted in a decrease of test coherence of twice the usual size. This procedure converged to a 50% subjective motion coherence threshold. A chin rest was used throughout the experiment to minimize head motion.

Each experimental session had four parts, the baseline, adaptation, deadadaptation, and post-test periods (Fig. 1). The staircase procedure tracked subjects’ motion coherence thresholds throughout all four stages. In the initial 4 min baseline period, subjects viewed displays with 25% motion coherence adapters. This baseline was used to ensure that subjects’ thresholds would have room to both rise and fall during subsequent periods of the experiment.

Next, during the adaptation period, subjects viewed 90% coherence motion adapters for 10 min, which was followed by the deadadaptation period where adapters were 5% motion coherence. Deadadaptation had variable duration and lasted until the test coherence, controlled by the staircase, decreased below the baseline period threshold level for three trials. Finally, in a 3 min post-test stage, subjects again viewed 25% motion coherence.

Each subject participated in 4–5 sessions, separated by at least 4 h, and each session contained all four stages. A separate control experiment used procedures that were identical, except that the deadadaptation stage was removed, and the post-test stage was extended by 2 min.

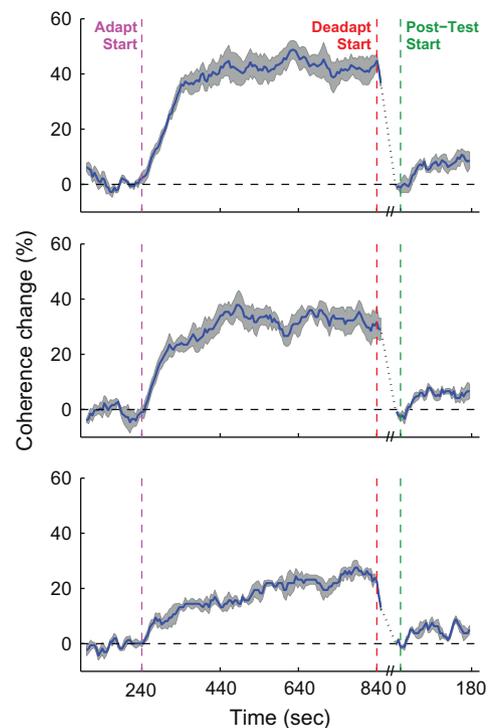
### 3.2. Results

Results again showed clear evidence of spontaneous recovery of motion adaptation. Fig. 4 plots mean motion coherence as a function of time for all participants. All subjects reached a stable coherence threshold during the baseline period; the figure plots data as change scores relative to this threshold. During adaptation, participants’ coherence thresholds increased rapidly, a traditional adaptation effect. These increases were robust and highly reliable (ranging between 25–40% dot coherence for the last 100 s of adaptation;  $t$  values  $> 7.5$ , and  $p < 0.01$  for all subjects).

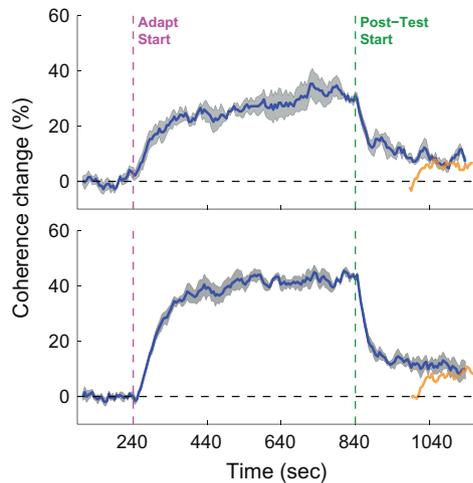
Deadadaptation eliminated effects of the initial adaptation, as thresholds returned back to their baseline values. This period ended following three trials where test coherence was below the baseline threshold, and its duration was considerably briefer than the adaptation phase (118.5 s on average, across observers; ranging between 45–295 s).

Following deadadaptation, subjects again viewed a 25% adapter, and subjective thresholds rose above baseline levels and remained elevated until the end of the experiment. The size of this “spontaneous recovery” effect was on average 18.7% of the 10 min adaptation effect and was statistically reliable in each subject ( $t(3) = 4.4$ ,  $p < 0.03$ ;  $t(3) = 5.6$ ,  $p < 0.02$ ,  $t(4) = 3.5$ ,  $p < 0.03$ ). This recovery cannot be explained by adaptation in different direction selective mechanisms, and so likely indicates the presence of more than one temporally tuned mechanism of adaptation.

A control experiment, which was identical to Experiment 2, but without a deadadaptation period, was conducted to verify that adaptation to coherent random-dot displays produces a typical pattern of aftereffect decay. Results, summarized in Fig. 5, show a similar pattern to the experimental condition up until the end of the adaptation period. Due to the lack of deadadaptation, the post-test results began with elevated coherence thresholds that decreased



**Fig. 4.** Results of Experiment 2. The graphs plot change in coherence threshold relative to the baseline threshold (dashed horizontal line). The three plots correspond to different subjects. Note that because the deadadaptation stage had variable duration, only its initial and final trials are shown. The gray error region plots  $\pm 1$  s.e. of the mean.



**Fig. 5.** Results of the random-dot motion control experiment. Plotting conventions are the same as in Fig. 4; the blue curve plots adaptation and its decay in the absence of a deadadaptation period. The orange line replots results from the post-test of the main random-dot experiment. Without deadadaptation, adaptation effects decayed to about the same level to which they spontaneously recovered following deadadaptation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

rapidly, but remained significantly elevated (ranging between 7–10% in last 100 s;  $t(3) = 8.6, p < 0.01$ ;  $t(4) = 4.2, p < 0.02$ ). These results are comparable to a typical pattern of aftereffect decay observed in past adaptation research, suggesting that shifts in motion coherence thresholds reflect similar gain changes as other forms of aftereffects.

To estimate the time constants of adaptation, we fit a linear model from Vul, Krizay, and MacLeod (2008) to our individual subject data. In the model, the net aftereffect corresponds to the sum of two independent mechanisms with distinct time constants. Fitting the model to the data produced estimates of exponential time constants that ranged between 28–62 s for the fast mechanism, while the time constant of the slow mechanism was an order of magnitude larger, between 350–700 s. The fast mechanism in this paradigm appears to be slightly slower than the one measured by Vul, Krizay, and MacLeod (2008) for the McCollough effect, which had a time constant of around 25 s. The slow mechanism was clearly faster than that for the McCollough effect, which can last for weeks and was estimated to have a time constant approaching infinity. Differences in both procedure and the underlying phenomena likely account for the differences in estimated time constants.

## 4. Experiment 3

In the final experiment, we assessed the existence of multiple temporally-tuned adaptive mechanisms in higher level vision, specifically face perception. Here, subjects viewed two faces with opposite spatial distortions. Adaptation to such faces has been shown to cause shifts in the perception of physically undistorted faces away from the adapter's distortion (Webster & MacLin, 1999). As in previous experiments, we were interested in whether perceptual shifts elicited by a longer-duration adapter would spontaneously recover following their cancellation by a briefer deadadaptation period.

### 4.1. Methods

#### 4.1.1. Participants

Eight participants (4 males and 4 females; 4 naïve to the purposes of the experiment) volunteered for the experiment.

#### 4.1.2. Stimuli

Subjects viewed distorted versions of a picture of president Obama subtending  $12.2 \times 16.3^\circ$  of visual angle and presented surrounding a central fixation mark. The effect of the distortion was to increase or decrease the distance between the two eyes in the image. Eleven images were generated, each with a different inter-eye distance (IED), ranging from  $2.15^\circ$  to  $5.45^\circ$  apart (measured pupil to pupil). The images were shown on an LCD monitor in a dimly lit room, and had a mean luminance of  $30.3 \text{ cd/m}^2$ .

#### 4.1.3. Task

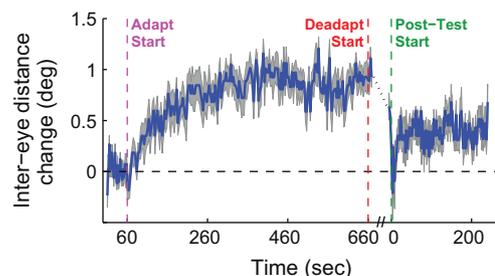
On each trial (see Fig. 2C), subjects viewed a “test” face, and pressed one of two keys to indicate whether its eyes appeared to be closer together or farther apart than in a normal face. The test face was displayed for 200 ms. In trials without an adapter, it was preceded by 1.4 s presentation of a uniform mean gray field. In trials with an adapter, it was preceded by a 1.4 s presentation of an “adapter” face, and a 400 ms presentation of the gray field. The test face presentation was followed by a 1 s display of the gray field.

A staircase procedure tracked the IED that appeared undistorted to subjects throughout the experiment. A one-up one-down procedure adjusted the inter-eye distance of the test face; this procedure asymptoted at the inter-eye distance that was perceived as undistorted. To avoid low-level adaptation, the position of the adapter was shifted randomly by  $0^\circ$  to  $1.1^\circ$  from the center of the display on each trial.

The experimental session had the same four stages as in Experiment 2: baseline, adaptation, deadadaptation, and post-test. The initial baseline period contained trials with no adapter and lasted 1 min. In the subsequent 10 min adaptation period, subjects viewed an adapter face with a very large inter-eye distance of  $5.45^\circ$ . During deadadaptation, the adapter had a small inter-eye distance of  $2.15^\circ$ . Deadadaptation lasted until the test inter-eye distance decreased for a single trial below the baseline value computed as the mean of all reversal trials during the baseline period. Finally, during the 4-min post-test period, subjects once again only performed trials without an adapter.

### 4.2. Results

Results again showed spontaneous recovery of adaptation. Fig. 6 plots the deviations of the test IEDs from the baseline value, averaged across subjects. 10 min adaptation to a distorted face caused the face that appeared normal to shift towards the distortion. By the last 60 s of adaptation, this effect was on average  $0.92^\circ$  of IED. These effects were then rapidly eliminated by deadadaptation. Deadadaptation took, on average, only 37.3 s (12–114 s range). Finally, in the post-test stage, the test IED shifted back from baseline toward the initial adaptation effect, and remained high until



**Fig. 6.** Results of Experiment 3. The figure plots the inter-eye distance perceived as undistorted, relative to the average of staircase reversals in the baseline period. The discontinuity in the plot is again due to deadadaptation having variable duration between subjects. The gray error region plots  $\pm 1$  s.e. of the mean.

the end of the session. In the final 60 s of the post-test stage, this effect corresponded to  $0.4^\circ$  ( $t(7) = 4.33$ ,  $p < 0.01$ ), which is 43% of the effect observed during the adaptation period.

## 5. Discussion

Three experiments tested for multiple temporally-tuned mechanisms in adaptation to motion and faces. In all three experiments, an initial 10 min of adaptation induced robust behavioral aftereffects, which were subsequently eliminated by a brief period of deadadaptation. During continued testing, however, the original aftereffect returned. We termed this phenomenon spontaneous recovery, by analogy to the animal learning literature.

The simplest explanation of these results is that adaptation and deadadaptation engaged distinct mechanisms. In this account, long-term adaptation engaged a “slow” mechanism tuned to longer time-scales, while the brief deadadaptation produced an opposing response in a “fast” mechanism tuned to shorter time-scales. Thus, deadadaptation masked, but did not eliminate, the long-term effects produced by the initial adaptation period. The spontaneous recovery reflected the rapid decay of the short-term mechanism, which revealed ongoing longer-lasting effects due to the slower mechanism. A model containing only a single mechanism cannot produce such effects; without a second component to remember the original adaptation, deadadaptation will completely erase the effects of the initial adaptation (Fig. 1).

Our first experiment resembles an unpublished experiment from a dissertation thesis (Kwas, 1999) in which subjects first adapted to motion in one direction for 60 s and then to the opposite direction for 15 s. Subjects’ initial MAE corresponded to the 15 s deadadaptation, but a delayed test revealed a reversal of the MAE direction to reflect the initial adaptation. While suggestive of multiple temporally-tuned mechanisms, these results, like those from our first and third experiment, can also be explained by two temporally untuned mechanisms operating for each of the two opposing directions.

Spontaneous recovery has been reported in a variety of other domains. The phenomenon was originally described in the animal learning literature (Pavlov, 1927), where habits taught to animals that have been extinguished can spontaneously recover in the absence of reinforcement (for a review, see Bouton, 1993). More recently, it has been reported for human motor learning (e.g. Smith, Ghazizadeh, & Shadmehr, 2006), and inspired by this work, Bao and Engel (2012) demonstrated spontaneous recovery in the visual system by measuring the tilt aftereffect following 4 h of contrast adaptation.

Multiple adaptive mechanisms have also been uncovered in a variety of neurophysiological paradigms, which demonstrate that adaptation can occur separately at multiple stages in the processing hierarchy. For example, neurons in macaque LGN show contrast adaptation effects originating in retina (Solomon et al., 2004) where multiple timescales of adaptation have been measured as well (reviewed in Rieke & Rudd, 2009). Similar results have been shown in motion processing, where dissociable adaptation effects have been identified in V1 and area MT (Kohn & Movshon, 2003, 2004). Within V1, adaptation may also have differential effects on classical receptive fields and suppressive surrounds (Dhruv et al., 2011; Patterson, Wissig, & Kohn, 2013; Wissig & Kohn, 2012).

Evidence for multiple mechanisms has also been found psychophysically. Contrast adaptation shows spontaneous recovery following both longer and shorter durations (Bao & Engel, 2012; Bao et al., *in press*), as well as a “spacing effect” that is also suggestive of multiple temporally tuned mechanisms (Magnussen and

Greenlee (1986)). Similarly, the McCollough effect has been demonstrated to reflect the sum of effects in two temporally-tuned mechanisms (Vul, Krizay, & MacLeod, 2008). Adaptation to motion has been shown to contain multiple mechanisms (Stocker & Simoncelli, 2009) including a very rapid phase, operating over fractions of a second, that may be distinct from longer-term motion aftereffects (Glasser et al., 2011; Roach & McGraw, 2009). Face adaptation also likely results from the combined effects of multiple mechanisms, some of which may arise earlier in the processing stream than others, and the latter may adapt very rapidly (for a review, see Zimmer & Kovacs, 2011).

Our results may be explainable by theories proposing that the visual system adapts to environmental changes in an optimal way (e.g. Grzywacz & Balboa, 2002; Stocker & Simoncelli, 2006; Wainwright, 1999; Wark, Fairhall, & Rieke, 2009). Kording, Tenenbaum, and Shadmehr (2007) have shown that the dynamics of motor adaptation can be accurately modeled in a Bayesian framework. In their model, when one adapts to an environmental change, the motor (or sensory) system faces the task of making an inference about the causes of this environmental change. Specifically, the system infers whether the cause is likely to be a long-lasting event (e.g. an injury affecting a muscle) or a shorter duration event (e.g. momentary fatigue). Causes of all durations are expected to happen simultaneously, and the net adaptation level is determined as a combination of gain changes inferred across all time-scales. Spontaneous recovery occurs essentially when the system infers that a long-lasting event is ongoing, despite having been momentarily counteracted by a shorter duration event.

Our results are broadly consistent with this interpretation. During the 10 min of adaptation, visual system might gain confidence that the adapter properties are likely associated with a relatively long-lasting event. In contrast, because of its brief duration, deadadaptation may be interpreted to have a transient cause. As a consequence, during the post-test period, the initial long-term adapter is still considered to be a relatively likely event, while deadadaptation is not. The net gain thus shifts back towards the level optimized for processing of the longer-term adapter (reflected in the response of the slow mechanism), producing spontaneous recovery.

This account is also generally consistent with the theory that adaptation can induce shifts in perceptual norms, the stimuli that elicit a neutral response in a given neural population (Leopold, Bondar, & Giese, 2006; Webster, 2011; Webster & Leonard, 2008). Norm shifts are thought to occur when changes in visual conditions are stable and long-lasting, and so could be controlled by gain changes within the slow mechanism.

It should be noted, however, that our results are also consistent with more simple models that posit two fixed discrete linear adaptation mechanisms with different time-constants (short for a fast mechanism and long for a slow one) whose sum is the net adaptation level (Vul, Krizay, & MacLeod, 2008). The purpose of our experiments was simply to provide clear demonstration of multiple temporally-tuned adaptation mechanisms in motion and face adaptation, rather than to distinguish between competing models of such mechanisms, and further research will be required to determine the precise nature of the mechanisms and how their effects combine.

While spontaneous recovery is consistent with the existence of multiple temporally-tuned adaptation mechanisms, it can also be explained by mechanisms that are specific to the adapters. Different mechanisms for leftward and rightward motion could explain the spontaneous recovery in our Experiment 1 and Kwas (1999). The spontaneous recovery of face adaptation in our Experiment 3 may also be explained in this way. For example, if inter-eye distance is encoded by populations of neurons tuned to different IEDs, then the two different adapters could cause gain changes in two

different sets neurons. Differential decay rates of adaptation in these neurons, due to distinct adaptation durations, could have produced spontaneous recovery.

We ruled out adapter-specific mechanisms for motion in Experiment 2, which used random dots with identical velocity for both adaptation and deadaptation. Current understanding of facial attribute encoding is still limited (e.g. see review by Webster & MacLeod, 2011), making it difficult to assess how likely adapter-specific effects are for faces, and how to rule them out.

A more general version of the adapter-specific hypothesis also remains untested here. It is possible that some part of the visual system is sensitive to different adapter statistics, such as motion coherence level, even if they are not explicitly coded by early sensory areas. Because of these differences, adapter stimuli in the adaptation and deadaptation periods might be considered by some part of the visual system to be distinct visual environments or “contexts”, each of which could be assigned its own adaptation mechanism. This account of adaptation appears to be supported by recent motor adaptation literature (Pekny, Criscimagna-Hemminger, & Shadmehr, 2011) and future research should look for further ways to distinguish between temporally- and contextually-tuned mechanisms in sensory adaptation.

Finally, given that evidence for temporally-tuned adaptation mechanisms has now been found in three visual domains, contrast, motion, and face adaptation, it seems likely they may be a general property of sensory function. Similar effects to those observed here should likely be observable in adaptation within the auditory and somatosensory systems, with possible applications to important “real-world” phenomena. For example, while eating a large meal leads to a feeling of satiety, people often briefly regain the sense of hunger for additional treats, and then return back to feeling full. Although such phenomena may not be often considered in terms of adaptation, studying them within this framework may be fruitful.

## Acknowledgments

This research was supported by Grant NSF BCS-1028584. We thank Sheng He, Gordon Legge, and Edward Vul for helpful comments, and Scott Luisi for research assistance.

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