Perceptual and neural consequences of rapid motion adaptation

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AUTHOR SUMMARY

Nervous systems adapt to the prevailing sensory environment, and the consequences of this adaptation are observed in perception and in the responses of single neurons (1). Examples include the desensitization of the somatosensory system to constant stimuli (e.g., clothing) and the visual system's adjustments to changes in light levels. Given the variety of time scales underlying events in the natural world, determining the temporal characteristics of adaptation is a key step in understanding how the nervous system adjusts to its sensory environment. Traditionally, perceptual adaptation has been studied over long time periods, with adapting stimuli presented for seconds or longer. Neurophysiological work, however, has shown that adaptation occurs at a variety of time scales and can be observed following stimulus exposures as brief as tens of milliseconds (1-3). Although this rapid adaptation has strong implications for neural



Fig. P1. Consequences of rapid motion adaptation. Illustration of the stimuli and the task used in the main MAE experiment. On each trial, a brief high-contrast moving adapter was followed by a low-contrast stationary test stimulus at variable ISIs. At the end of each trial, observers indicated the perceived direction of the test stimulus motion. Importantly, we used adapting stimuli whose motion direction could not be correctly discriminated, ensuring that observers' reports of test stimulus motion constitute an objective measure of MAE presence. The results show that, although the motion direction of these brief adapting stimuli could not be perceived, observers nonetheless perceived the motion aftereffect.

studied following seconds or even minutes of motion adaptation (4), and consequently the relevance of adaptation processes that generate MAEs to natural vision is unclear: Although the MAE seemingly requires prolonged periods of adaptation, everyday sensory experience involves moving objects that change position rapidly. Hence, our initial goal was to objectively establish the shortest adaptation duration that is sufficient to produce a perceivable MAE. In the first experiment, seven observers adapted to a moving grating presented for 67 ms, which was followed by the presentation a stationary test stimulus at one of four interstimulus intervals (ISIs; Fig. P1). At the end of each trial, observers indicated the perceived direction of the test stimulus motion. If brief motion adaptation is sufficient to generate an MAE, the test stimulus should appear to move in the opposite direction from

coding of sensory stimuli (1–3), relatively little is known about its perceptual effects. We addressed this question in the context of visual motion-a perceptual modality characterized by rapid temporal dynamics. Here, we demonstrate that just 25 ms of motion adaptation is sufficient to alter perception of subsequently presented stationary objects. Specifically, we show that brief exposure to motion is sufficient to generate a motion aftereffect (MAE), an illusory sensation of movement experienced when a stationary pattern is viewed following exposure to adapting motion (4). This rapid adaptation occurs regardless of whether the adapting motion is perceived, indicating involvement of low-level visual processes. In a parallel study, we examined the neural basis of rapid motion adaptation by recording in the middle temporal (MT) area, a cortical region critical for motion processing (5). We found that, following brief exposures to motion, MT neurons respond to the subsequent stationary stimuli in a directionally selective manner. Overall, we show that the MAE is not merely an intriguing perceptual illusion, but rather a consequence of rapid neural and perceptual processes that can occur essentially every time we experience natural motion.

We first used behavioral approaches to study rapid motion adaptation in human subjects. Specifically, we investigated a compelling and extensively studied perceptual consequence of motion adaptation: the MAE. The MAE, however, is typically the adapting motion. Crucially, the adapting stimuli were configured so that their direction could not be discriminated (Fig. P1), ensuring that observers did not know the expected MAE direction. The results showed that, for short ISIs, observers consistently perceived the test stimuli as moving in the opposite direction from the adapting motion. In a subsequent experiment, we further shortened the duration of the adapting stimuli and found that perceivable MAEs can be generated with as little as 25 ms of motion adaptation. These results objectively demonstrate that the MAE can be observed following adaptation periods that are sufficiently brief to affect perception during typical visual experience.

These findings show that conscious perception of adapting motion direction is not necessary for that motion to generate direction-specific MAEs. To directly test the role of perceptual

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visibility in rapid motion adaptation, we investigated how changes in the discriminability of adapting motion affected the resulting MAEs. If the buildup of rapid adaptation depends on the perceptual visibility, MAE strength should increase with improved visibility of the adapting motion. However, we found just the opposite: MAE weakened with increased discriminability of adapting motion. The robust dissociation between perceptual visibility and adaptation suggests involvement of neural mechanisms occurring at the earliest stages of motion processing. In the full manuscript, we describe additional experiments that provide support for this hypothesis.

Next, we characterized how changes in stimulus parameters (such as contrast and size) affect rapidly generated MAEs. The main goal of these experiments was to generate predictions for subsequent neurophysiological recordings. We found that the MAE strength decreased with increasing ISI and with increasing test stimulus contrast. However, MAE strength increased with increasing stimulus size, suggesting involvement of mechanisms that integrate motion signals over space.

These behavioral experiments were followed by neurophysiological recordings in the macaque. We focused on cortical area MT, an area known to be causally involved in motion perception (5). MT neurons can reflect adaptation occurring at earlier stages of processing and integrate motion signals over large regions of space. Motion adaptation in area MT has been studied over a variety of time scales (1), but it is not known how MT neurons respond to stationary stimuli following exposure to adapting motion. We therefore recorded responses from 106 MT neurons to brief stimuli that were designed to correspond to those used in our behavioral experiments. The results show that brief motion adaptation yields direction-selective responses to subsequently presented stationary stimuli. A simple model shows that these MT responses can account for our perceptual results and their dependence on stimulus parameters. Specifically, our experimental manipulations of the contrast, size, and timing of the stationary test stimulus reveal similar effects on perceptually observed MAEs and MT responses. Crucially, the strength of the direction selectivity evoked by stationary test stimuli did not depend on neural selectivity to the adapting motion. This

nicely dovetails with our psychophysical results, which showed that perceptual visibility of adapting motion did not affect the strength of the ensuing MAE.

In conclusion, we show that the MAE is a consequence of a fast adaptation process that can occur essentially every time we experience motion. These findings indicate that the adaptation mechanisms underlying rapid generation of MAEs are likely an integral part of sensory responses to natural motion stimuli, which typically occupy a given retinal location for only a fraction of a second. One feature of these results is that perceptual MAEs following brief motion exposure occur only for a limited set of test stimuli. Significantly, this does not indicate that rapid motion adaptation occurs only in those special cases, but only that revealing its consequences in the form of MAEs requires carefully chosen test stimuli. It is currently unknown whether the rapid motion adaptation processes that we have revealed by using MAEs have other functional consequences for our perception. The broader functional role of rapid adaptation is supported by neurophysiological work showing that the visual system quickly recalibrates its stimulus sensitivity in response to stimulus changes (1-3), but behavioral support for this hypothesis has been mixed and limited to adaptation durations longer than 1 s (1). One possibility is that the past use of longer adapting periods introduced changes in sensory sensitivity that masked beneficial effects of rapid adaptation. Thus, determining how shorter adapting periods affect subsequent perception is an important direction for future research that will elucidate the role of adaptation during natural vision and possibly strengthen links between neurophysiological and behavioral findings.

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