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Storage of an oculomotor motion aftereffect

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Abstract

Adaptation to motion produces a motion aftereffect (MAE), where illusory, oppositely-directed motion is perceived when viewing a stationary image. A common hypothesis for motion adaptation is that it reflects an imbalance of activity caused by neuronal fatigue. However, the perceptual MAE exhibits storage, in that the MAE appears even after a prolonged period of darkness is interposed between the adapting stimulus and the test, suggesting that fatigue cannot explain the perceptual MAE. We asked whether neural fatigue was a viable explanation for the oculomotor MAE (OMAE) by testing if the OMAE exhibits storage. Human observers were adapted with moving, random-dot cinematograms. Following adaptation, they generated an oculomotor MAE (OMAE), with both pursuit and saccadic components. The OMAE occurred in the presence of a visual test stimulus, but not in the dark. When the test stimulus was introduced after the dark period, the OMAE reappeared, analogous to perceptual MAE storage. The results suggest that fatigue cannot explain the OMAE, and that visual stimulation is necessary to elicit it. We propose a model in which adaptation recalibrates the motion-processing network by adjusting the weights of the inputs to neurons in the middle-temporal (MT) area. © 2006 Elsevier Ltd. All rights reserved.

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1. Introduction

The motion aftereffect (MAE) occurs when an observer adapts to motion that is viewed for an extended time. It is commonly manifest as the perception that a static surface moves opposite the direction of the adapting motion. The MAE has been extensively studied (e.g., Addams, 1834; Bex, Bedingham, & Hammett, 1999; Gibson, 1937; Levinson & Sekuler, 1976; Purkinje, 1820; Spigel, 1960, 1962a, 1962b, 1964; Thompson & Wright, 1994; Verstraten, Fredericksen, Grusser, & Van de Grind, 1994; Wohlgemuth, 1911), however the neural substrate of this phenomenon remains unknown. An early theory suggested that fatigue occurs in neurons that encode the direction of the adapting stimulus, leading to an imbalance in activity favoring the opposite motion direction. This has been hypothesized to

* Corresponding author. *E-mail address:* scott.watamaniuk@wright.edu (S.N.J. Watamaniuk). occur because the fatigued neurons are unable to sustain high firing rates for a long time, or neurotransmitters are depleted, resulting in the fewer action potentials (Barlow & Hill, 1963; Wohlgemuth, 1911). A competing theory is that the synaptic weights of the neuronal network subserving motion processing are recalibrated by adaptation (Gibson, 1937; Harris, Morgan, & Still, 1981; Wiesenfelder & Blake, 1992).

Many physiological studies have assessed V1 (Giaschi, Douglas, Marlin, & Cynader, 1993; Hammond, Mouat, & Smith, 1985, 1986; Maffei, Fiorentini, & Bisti, 1973; Marlin, Hasan, & Cynader, 1988; Vautin & Berkley, 1977; vonderHeydt, Hänny, & Adorjani, 1978) and MT neurons (Kohn & Movshon, 2004; Petersen, Baker, & Allman, 1985; van Wezel & Britten, 2002) during the course of adaptation but the results are mixed and do not clearly differentiate between the fatigue and recalibration models. However, the perceptual phenomenon of MAE storage is strong evidence against neuronal fatigue as the mechanism of adaptation. Storage occurs when a period of darkness is imposed

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between the adapting stimulus and the test stimulus, postponing the MAE until the test stimulus appears (Spigel, 1960, 1962a, 1962b, 1964; Thompson & Wright, 1994; Verstraten et al., 1994; Wohlgemuth, 1911). This occurs even when the duration of the dark period is much longer than that of the usual MAE, and can leave the strength of the MAE relatively undiminished. If neuronal fatigue was the mechanism of adaptation, the adapted neurons should recover their activity level during the dark period thus preventing the expression of an MAE at a later time.

Evidence of a smooth pursuit MAE, which has characteristics similar to the perceptual MAE, has been found recently (Braun, Pracejus, & Gegenfurtner, 2006; Gardner, Tokiyama, & Lisberger, 2004). One might expect that the pursuit MAE would also exhibit storage, because motion pathways in the middle temporal/medial superior temporal (MT/MST) complex that are commonly thought to underlie motion perception provide input to the pursuit system (Komatsu & Wurtz, 1988; Newsome, Wurtz, & Komatsu, 1988). Moreover, smooth pursuit has been shown to reflect motion perception (Beutter & Stone, 1998; Heinen & Watamaniuk, 1998; Stone & Krauzlis, 2003; Watamaniuk & Heinen, 1999). However, these results cannot be taken as unequivocal evidence that neuronal changes that underlie the smooth pursuit MAE are restricted to the motion pathways that subserve perception. Changes in the pursuit system itself, including fatigue, could contribute to the pursuit MAE. To determine if neuronal fatigue is involved in the pursuit MAE, we investigated whether adaptation was preserved following a period of no visual stimulation.

2. Method

All experiments were approved by the California Pacific Medical Center institutional review board. Three human observers (two naïve) gave informed consent and participated in the experiments.

2.1. Stimuli

The adapting stimulus was a random-dot cinematogram (RDC) with component dots displayed at a density of 3.0 dots/deg². The pursuit stimulus was also an RDC (0.05 deg dot diameter, dot luminance = 14.4 cd/m²) that moved against a dark background. Stimuli were presented on a 17 in. high-resolution computer monitor (1.76 min arc/pixel) at a rate of 60 Hz and RDCs were viewed through a 20 deg diameter aperture. The background luminance was (0.46 cd/m²) and all stimuli were viewed from a distance of 80 cm. When the stimulus was an RDC, all dots moved in the same direction and at the same speed and virtually "wrapped around" when the border of the RDC was reached.

2.2. Procedure

Two separate types of trial blocks were used, *no-gap* and *gap*. Each block of trials began with the observer fixating a spot in the center of the screen (see Fig. 1). Simultaneous with the appearance of the spot, the adapting RDC appeared with component dots that moved upward at 10 deg/s. After 60 s, the RDC was turned off. On *no-gap* trials, the adapting RDC was followed immediately by a second RDC, the pursuit target, with component dots that moved at 0.5 deg/s. One way to minimize the chance that observers will predict the stimulus is to include, in a block of trials, stimuli that move at several different speeds in the same or opposite direc-



Fig. 1. Schematic representation of the adaptation protocol for experiments without and with a gap period. Each block of trials began with 60 s adaptation (a static spot was provided for fixation). (a) When there was no gap, a 1.5 s RDC pursuit stimulus moving orthogonal to the adaptation stimulus was next presented. Each trial was immediately followed by 10 s of top-up adaptation. (b) In the gap condition, a blank, dark screen (1 s) was presented immediately following the initial and top-up adaptation epochs, followed by a 1 s pursuit stimulus. The pursuit stimulus in all conditions moved in one of five directions spaced every 10 deg from -20 to +20 deg, centered about rightward (0 deg). In control trials, the stimulus presentation was the same except the adapt stimuli were static.

tion of the adapt stimulus, a technique used by previous investigators to reveal a pursuit MAE (Braun et al., 2006). However, anticipatory pursuit movements that are based on previous motion occur even when target motion is unpredictable (Heinen, Badler, & Ting, 2005; Kowler, Martins, & Pavel, 1984), and could add noise to the measured velocity. Therefore, while we adopted the multiple velocity paradigm, we modified it so that the principle direction of the test stimuli was orthogonal to the upward adapt stimulus so that anticipatory eye velocity generated by the adapt stimulus would have a direction roughly orthogonal to the test. Pursuit target motion direction was randomly set to one of five possible directions (-20, -10, 0, 10, 20 deg), with zero being directly rightward. Observers were required to follow the target with their eyes, which they did with a combination of smooth pursuit and saccades. After 1500 ms, the pursuit RDC disappeared and the next trial began. Gap trials were identical to nogap trials, except that a 1000 ms blank period was interposed between the adapting and pursuit stimuli, and the pursuit RDC was presented for only 1000 ms.

All trials after the first trial were preceded by a 10 s "top-up" adaptation period to maintain the level of motion adaptation. Control trial blocks were also performed for both *no-gap* and *gap* conditions. These were the same as the adapt blocks except that the adapting RDC was stationary. To avoid possible long-term adaptation effects, control blocks were never run sooner than 30 min after completion of an adapt block. The first trial from every block was excluded from the data analysis, due to possible "surprise" effects from the sudden appearance of the target after Download English Version:

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