



Decoding the motion aftereffect in human visual cortex



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ARTICLE INFO

Article history:

Accepted 8 June 2013

Available online 15 June 2013

Keywords:

Motion aftereffect

fMRI

Multivariate pattern classification

Visual motion processing

ABSTRACT

In the motion aftereffect (MAE), adapting to a moving stimulus causes a subsequently presented stationary stimulus to appear to move in the opposite direction. Recently, the neural basis of the motion aftereffect has received considerable interest, and a number of brain areas have been implicated in the generation of the illusory motion. Here, we use functional magnetic resonance imaging in combination with multivariate pattern classification to directly compare the neural activity evoked during the observation of both real and illusory motions. We show that the perceived illusory motion is not encoded in the same way as real motion in the same direction. Instead, suppression of the adapted direction of motion results in a shift of the population response of motion sensitive neurons in area MT+, resulting in activation patterns that are in fact more similar to real motion in orthogonal, rather than opposite directions. Although robust motion selectivity was observed in visual areas V1, V2, V3, and V4, this MAE-specific modulation of the population response was only observed in area MT+. Implications for our understanding of the motion aftereffect, and models of motion perception in general, are discussed.

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Introduction

The motion aftereffect (MAE) is a much-studied visual illusion in which adaptation to motion causes a subsequently presented stationary pattern to appear to move. The stationary pattern appears to move in the opposite direction of the original, physically moving stimulus. For example, after looking at a stationary point in a waterfall, upon fixating the adjacent rocks, those rocks will appear to drift upwards (Addams, 1834; Anstis et al., 1998). The MAE has been argued to result from an imbalance in oppositely tuned motion detectors (Barlow and Hill, 1963; Wohlgenuth, 1911; but see Sutherland (1961) and below). Adapted neurons respond relatively less strongly to a new stimulus than their oppositely-tuned counterparts. As a result, the balance of activity between the two opponent directions favors the unadapted direction, and an illusory motion percept occurs.

The neuronal basis of the MAE has been the topic of substantial recent study. Direction-selective motion-sensitive neurons are present in multiple visual areas (including V1, V2, V3, and V4; Kamitani and Tong, 2006), and numerous brain areas have been shown to be involved in the MAE (Taylor et al., 2000). Nonetheless, the majority of interest has focused on the possible role of human motion area MT+ in generating the illusory motion percept. Work in non-human primates suggests that cells in this area have appropriate characteristics: for example,

Petersen et al. (1985) demonstrated direction-specific adaptation of motion-sensitive cells in owl-monkey MT. Tootell et al. (1995) first presented evidence from human observers implicating MT+ activity in the MAE, and demonstrated that the time-course of activation in MT+ mirrors the time-course of the perceptual illusion. He et al. (1998) showed that both the MT+ activation and the perceptual MAE depend on the stationary test pattern being in the same retinal position as the preceding adaptation. Culham et al. (1999) noted that MT+ activation increased even when adaptation and test phases were separated by a storage period. Subsequent studies continued to implicate MT+ in perception of the MAE (Hautzel et al., 2001; Théoret et al., 2002).

Huk et al. (2001) called into question whether MT+ activity actually underlies the perceptual MAE. They argued that attention to the MAE, rather than the MAE per se, explains elevated MT+ activity. In a series of experiments, they demonstrated that when attention is controlled for, no difference in MT+ activation is observed between conditions in which a MAE is perceived and conditions in which it is not. However, Castelo-Branco et al. (2009) noted that in this study, attention was controlled for by having observers carry out a task on concurrent real motion. They argue that this might interfere with any MAE-related signal in MT+. After replicating Huk et al. (2001) using an attention-to-motion stimulus, they demonstrate that MT+ does in fact show elevated activity during the MAE when attention is allocated to a non-motion feature, such as orientation or color. Accordingly, there seems to be considerable evidence for a MAE-related motion signal in MT+.

A net change in cumulative neural activity is just one way in which a neural population might affect motion perception (e.g. Treue et al.,

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2000). However, most computational models of motion perception propose that it is the relative activity of populations of neurons with different direction tuning that underlies the percept of motion (the distribution shift model; e.g. Mather, 1980; Mather and Harris, 1998; Simoncelli and Heeger, 1996; Sutherland, 1961). In support of this view, adapting to motion does selectively adapt subpopulations of neurons in MT+, even under conditions of directed attention (Huk et al., 2001). This suggests that although an increase in mean MT+ activity does not generate the MAE, neural populations in MT+ might nonetheless be involved in generating the illusion.

An important question then arises: if a shift in the relative activity of neural subpopulations in area MT+ causes the illusory motion percept observed in the MAE, how does that pattern of neural activity compare to the neural activity observed in those same populations when observing real motion? In other words, is illusory motion coded in a similar way to real motion? Three general hypotheses can be formulated:

The first possibility is that the same neural populations are active during real and illusory motions in a particular direction. This might be expected in areas involved in integrating motion signals (such as MT+; e.g. Snowden et al., 1991), since the direction of the resulting motion percepts is similar. In this case, neural activity during illusory motion would be comparable to neural activity during real motion in the same direction (Fig. 1C).

A second possibility is that the MAE is the result of an imbalance in oppositely tuned motion detectors. In this case, MAE motion would be expected to be encoded as a relative suppression of activity corresponding to the adapting direction, together with enhancement of the activity coding for the direction of illusory motion (Fig. 1D).

The third possibility is that the motion percept in the MAE results from a different underlying pattern of neural activity than the motion percept elicited by real motion. This would be expected in early motion processing stages, before any integration occurs. However, it might also be expected in later stages if the direction of motion is encoded as the ensemble activity of motion detectors tuned to all

directions, rather than as the imbalance of opponent neurons (Treue et al., 2000). In this case, the MAE could result directly from suppression of the adapted motion direction, in line with findings from neurophysiological recordings in non-human primates (Van Wezel and Britten, 2002). Its neural signature would then be quite different from real motion in the same direction (Fig. 1E). This in turn could explain why the MAE (using a stationary test pattern) is easy to distinguish from real motion, despite both containing motion energy in the same direction (Hiris and Blake, 1992).

The existence of directionally selective subpopulations in human MT+ as well as in earlier visual areas (V1, V2, V3, and V4) can be inferred from functional magnetic resonance imaging (fMRI) studies using pattern classification techniques (Kamitani and Tong, 2006). Using this analysis approach, subtle irregularities in the distribution of direction-selective neurons allow the perceived direction of motion that an observer is viewing to be decoded on the basis of ensemble activity, even when individual voxels contain on the order of a million neurons (Solnick et al., 1984). Importantly, the classification approach works because patterns of neural activity evoked by motion in the same direction are more similar than patterns of activity evoked by motion in different directions. This makes classification performance an effective metric for evaluating the similarity of patterns of neural activity.

Here, we use fMRI in combination with multivariate pattern classification to directly compare the neural activity underlying the illusory motion percept observed during the MAE with neural activity evoked by observing real motion. To do so, we train a classifier on the pattern of fMRI activity in individual visual areas while observers view real motion in one of the four directions. This classifier subsequently categorizes fMRI acquisitions in which observers view a MAE into one of these four directions. The pattern of classification results will allow us to distinguish between these three hypotheses (schematic predictions of each hypothesis are illustrated in Fig. 1).

Methods

Observers

Four observers participated in the experiment. All observers had normal or corrected to normal vision and had previous experience as observers in psychophysical and neuroimaging experiments. All observers gave informed consent before participating. This study was approved by the local ethics committee (Commissie Mensgebonden Onderzoek region Arnhem-Nijmegen, Netherlands).

Stimuli

Stimuli were presented on a translucent screen at the head-end of the scanner bore, which the observer viewed at an effective distance of 80 cm by means of a mirror mounted on the head coil. Stimuli were generated and synchronized with the scanner using a PC running Matlab 7.04 (The Mathworks, Inc) with PsychToolbox 2.54 extensions (Brainard, 1997; Pelli, 1997). The scanner room was darkened such that the display was unaffected by ambient light.

Motion stimuli consisted of maximum contrast grayscale random pixel arrays presented in an annulus surrounding a central fixation point, with an inner radius of 2.4° and an outer radius of 10.1°. Both the inner and the outer edge of the annulus were softened with a cosine window of 1.2° wide. Within the annulus, pixel arrays moved in one of the four cardinal directions (up, down, left, and right) at a fixed speed of 3.7°/s. Motion stimuli were presented on a 50% gray background.

Test stimuli consisted of two counter-phasing sparse pixel arrays presented in the same annulus as the motion stimuli (Fig. 2). Each array was presented on a black background, with 20% of pixels within the annulus assigned a random luminance up to 20% of maximum. The two arrays were modulated in sine and cosine phases with a

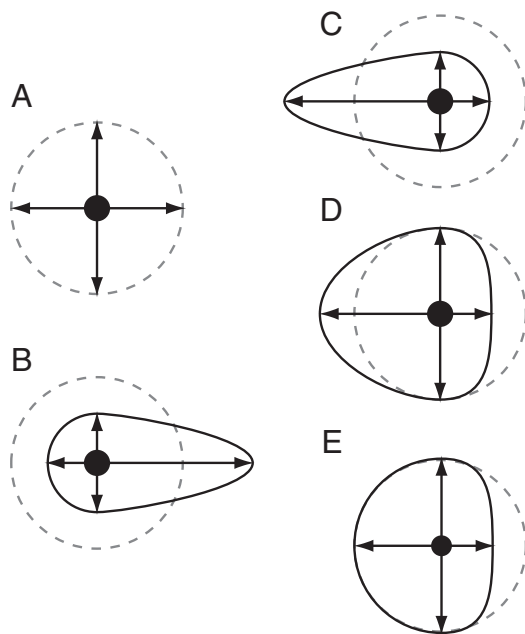


Fig. 1. Schematic illustration of three models of the motion after-effect. Arrows indicate the level of activity of direction-selective neural populations coding for the indicated direction. Ensemble activity is shown with a solid envelope in B–E. A. Response to a dynamic test pattern containing motion in all directions, without previous adaptation to motion. B. Response to an adapting stimulus containing strong rightward motion. C. Hypothetical response during the MAE if the MAE is encoded as the integrated direction of motion. D. Hypothetical response during the MAE if the MAE is encoded as an imbalance of opponent pairs of motion detectors. E. Hypothetical response during the MAE if the MAE is encoded as the ensemble activity of motion detectors tuned to all directions.

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