

Visual motion transforms visual space representations similarly throughout the human visual hierarchy



Ben M. Harvey^{a,b,*}, Serge O. Dumoulin^{a,1}

^a Experimental Psychology, Helmholtz Institute, Utrecht University, Utrecht, Netherlands

^b Faculty of Psychology and Education Sciences, University of Coimbra, Coimbra, Portugal

ARTICLE INFO

Article history:

Received 4 June 2015

Accepted 29 November 2015

Available online 5 December 2015

Keywords:

Vision

Motion

7 T fMRI

Population receptive field

ABSTRACT

Several studies demonstrate that visual stimulus motion affects neural receptive fields and fMRI response amplitudes. Here we unite results of these two approaches and extend them by examining the effects of visual motion on neural position preferences throughout the hierarchy of human visual field maps. We measured population receptive field (pRF) properties using high-field fMRI (7 T), characterizing position preferences simultaneously over large regions of the visual cortex. We measured pRFs properties using sine wave gratings in stationary apertures, moving at various speeds in either the direction of pRF measurement or the orthogonal direction. We find direction- and speed-dependent changes in pRF preferred position and size in all visual field maps examined, including V1, V3A, and the MT+ map TO1. These effects on pRF properties increase up the hierarchy of visual field maps. However, both within and between visual field maps the extent of pRF changes was approximately proportional to pRF size. This suggests that visual motion transforms the representation of visual space similarly throughout the visual hierarchy. Visual motion can also produce an illusory displacement of perceived stimulus position. We demonstrate perceptual displacements using the same stimulus configuration. In contrast to effects on pRF properties, perceptual displacements show only weak effects of motion speed, with far larger speed-independent effects. We describe a model where low-level mechanisms could underlie the observed effects on neural position preferences. We conclude that visual motion induces similar transformations of visuo-spatial representations throughout the visual hierarchy, which may arise through low-level mechanisms.

© 2015 Elsevier Inc. All rights reserved.

Introduction

Visual motion can affect the visuo-spatial responses of neurons in the visual hierarchy. Motion can also affect the perceived position of visual stimuli (Whitney, 2002). For example, when moving patterns are presented within stationary apertures, aperture position appears displaced in the direction of motion (Ramachandran and Anstis, 1990; De Valois and De Valois, 1991).

These changes in perceived position likely result from changes in neural representations of visual space. Neural mechanisms acting at various levels of the visual hierarchy have been proposed to explain these perceptual effects. These mechanisms are not mutually exclusive. First, displacement of the receptive field by motion may affect perceived position. Support for this hypothesis is provided by direction selective cells in cat primary visual cortex (V1) that have their receptive field

preferred positions displaced against the direction of motion (Fu et al., 2004). This displacement is proposed to reflect asymmetries to the receptive field inputs in the representation of starting and continuing motions. Increased neural response amplitudes at the start of the motion trajectory may induce these asymmetries, and bias visual field map activation (Whitney et al., 2003; Liu et al., 2006; Maloney et al., 2014). Second, these perceptual effects may arise in specialized motion processing areas like MT+, where patterns of fMRI activation follow the perceived position of the stimuli rather than their retinal position (Fischer et al., 2011; Maus et al., 2013). Indeed, feedback connections from MT to V1 have been implicated in motion-induced changes in perceived position (De Valois and De Valois, 1991; Nishida and Johnston, 1999). Third, high-level mechanisms such as motion-dependent shifts in spatial attention have also been proposed (Baldo and Klein, 1995). Fourth, perceived position may change through predictive coding, so that the neural representation of position follows expectations from previous experience (Roach et al., 2011; Maloney et al., 2014; Schellekens et al., 2014). Finally, extraclassical effects may facilitate neural responses beyond the stimulus in the direction of motion and thereby cause direction-dependent changes in neural activation (Watamaniuk and McKee, 1995; Ledgeway and Hess, 2002; Ledgeway et al., 2005).

* Corresponding author at: Faculty of Psychology and Education Sciences, University of Coimbra, Rua do Colégio Novo, Coimbra 3001-802, Portugal.

E-mail addresses: b.m.harvey@uu.nl (B.M. Harvey), s.o.dumoulin@uu.nl (S.O. Dumoulin).

¹ Experimental Psychology, Utrecht University, Heidelberglaan 2, Utrecht, 3584 CS, Netherlands.

Here we aim to unify these neurophysiological and fMRI results, and extend them by asking: how visuo-spatial response preferences are affected by motion in visual stimuli; where in the visual processing hierarchy these effects occur; and how they progress throughout the hierarchy. To do this, we characterize population receptive field (pRF) properties measured with different stimulus motion speeds and directions in several visual field maps, including V1, V3A and the MT+ map TO1 (Amano et al., 2009). We find direction-specific and speed-dependent changes in pRF properties in all visual field maps examined, with effects increasing up the visual hierarchy. Across visual field maps and within visual field maps, the extent of pRF changes was approximately proportional to pRF size. We propose a model in which these changes in pRF properties may straightforwardly result from larger response amplitudes to appearing than continuing motions, consistent with established changes in response amplitude along the motion trajectory. We also demonstrate perceptual displacements using the same stimulus configuration, though these displacements do not change strongly with motion speed. Therefore, motion transforms the neural representation of visual space similarly throughout the visual processing hierarchy. These effects on the neural representation of visual space may underlie motion's effects on position perception, though aspects of neural and perceptual effects differ.

Methods

Subjects

Four subjects participated in the fMRI experiment (one female, age range 25–44 years). All subjects had normal or corrected-to-normal visual acuity. All experimental procedures were cleared by the medical ethics committee of University Medical Center Utrecht.

pRF mapping stimuli

pRF mapping stimuli were generated in Matlab (Mathworks, Natick, MA, USA) using the PsychToolbox (Brainard, 1997; Pelli, 1997). Visual stimuli were gamma-corrected (using the output of a PR650 colorimeter, Photo Research Inc., Chatsworth, CA, USA) and presented by back-projection onto a 15.0×7.9 cm screen inside the MRI bore. The subject viewed the display through prisms and mirrors, and the total distance

from the subject's eyes (in the scanner) to the display screen was 41 cm. This gave a visual angle of 11° for the vertical (smallest) dimension of the display. Visible display resolution was 1024×538 pixels.

The pRF mapping paradigm was similar to that described in previous studies (Dumoulin and Wandell, 2008; Amano et al., 2009; Levin et al., 2010; Winawer et al., 2010; Harvey and Dumoulin, 2011; Hoffmann et al., 2012; Zuiderbaan et al., 2012). The stimulus (Fig. 1A) consisted of bar-apertures at various orientations stepping across the visual field. The stimulus had a radius of 5.5° . After every volume acquisition (TR, 1500 ms), the bar-aperture stepped 0.55° across this visual field. So the bar-aperture took 20 TRs (30 s) to cross the stimulus area. The bar-aperture passed through the stimulus area alternating between cardinal and diagonal directions, with a 20 TR (30 s) blank display period following each cardinal direction bar pass (Fig. 1B).

We presented all stimuli at 99% Michelson contrast, the maximum possible with the display. The contrast of the bar-aperture faded at its edges following a 1° wide raised cosine to avoid hard edges that would increase the range of spatial frequencies present in the stimulus. Including these edges, the bar-aperture was 2° wide. Within this bar-aperture, we showed a sine wave grating with a spatial frequency of 1 cycle/ $^\circ$ (Fig. 1A). We measured pRFs across four runs, in which gratings moved at one of four speeds (1.25°/s, 2.5°/s, 3.75°/s and 5°/s) in the direction of pRF measurement (using a grating with the same orientation as the bar-aperture) (see Experimental rationale Section). To determine the direction-specificity of these effects, we also measured pRFs while gratings moved at two speeds (2.5°/s and 5°/s) orthogonal to the direction of pRF measurement (using an orthogonally oriented grating). We measured responses to different speeds and directions in separate scanning runs in random order during the same session.

During each scanning run, subjects fixated a dot (0.125° radius) in the center of the display. This changed colors between red and green at random intervals. To ensure fixation and attention here, subjects pressed a button every time the color changed, on average every 3 s with a minimum change interval of 1.8 s. Subjects reported over 85% of these changes on every scanning run.

Because a moving pattern sometimes passed behind the fixation dot, we wanted to avoid involuntary motion tracking eye movements that would affect pRF parameter estimates. The fixation dot was surrounded by a white annulus (to 0.19° radius) to increase the contrast here. This was then surrounded by a mean luminance gray annulus (the same

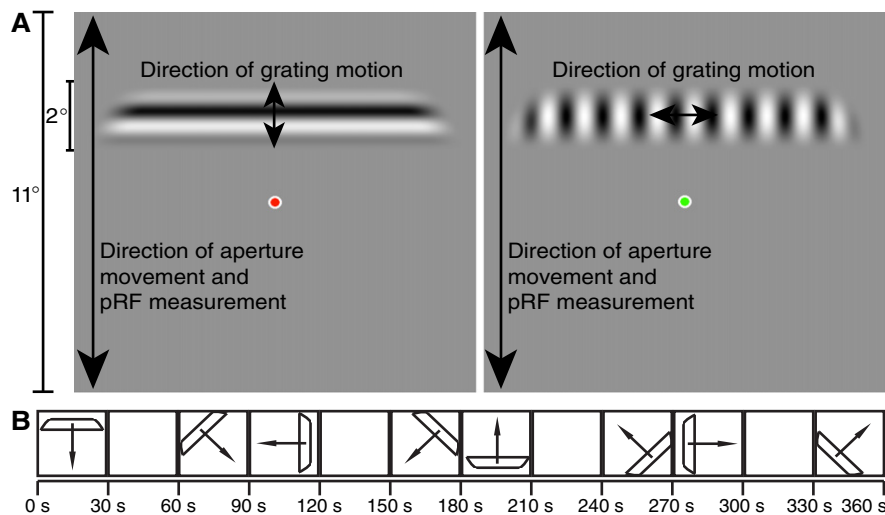


Fig. 1. pRF mapping stimuli. (A) The bar-aperture used for pRF measurement contained a grating moving in the direction of pRF measurement (left) or in the orthogonal direction (right). The grating moved in two opposite directions during presentation of each bar position, to avoid motion adaptation from prolonged presentation of the same motion direction. Grating orientation differed between motion directions so that the grating orientation was orthogonal to grating motion. Subjects fixated the colored dot in the center of the display and reported when its color changed. (B) The bar-aperture stepped once every volume acquisition (TR) across the subject's visual field. During the scanning run, the bar stepped through the visual field in eight directions, with each cardinal direction followed by a 30 s period (20 TRs) with no bar presented, allowing the fMRI signal to return to baseline.

Download English Version:

<https://daneshyari.com/en/article/6024555>

Download Persian Version:

<https://daneshyari.com/article/6024555>

[Daneshyari.com](https://daneshyari.com)