

Linking apparent position to population receptive field estimates using a visual field projection model

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Abstract

In illusions called motion-induced position shifts (MIPS), a coherent motion signal shifts the apparent location of a stimulus in the direction of motion. MIPS allow for studying the perception mechanism underlying object localisation because they dissociate the physical from the perceived position of a stimulus. Here, we propose a bottom-up approach to modelling position perception that links apparent position to population receptive field estimates motivated by empirical data. We recorded psychophysical and functional magnetic resonance imaging (fMRI) data while systematically varying two factors: the motion direction of the stimulus carrier pattern (inward, outward and flicker motion) and the contrast of the mapping stimulus (low and high stimulus contrast). We observed that, while physical positions were identical across all conditions, presence of low-contrast motion, but not high-contrast motion, shifted perceived stimulus position in the direction of motion. Correspondingly, we found that pRF estimates in early visual cortex were shifted against the direction of motion for low-contrast stimuli but not for high stimulus contrast. We propose a model built on the assumption that activation of pRF units can be linked to apparent position via visual field projections. Our model replicates the perceptual position shifts.

Keywords: visual neuroscience; position perception; population receptive fields; visual field projections

Introduction

A wide range of psychophysical studies shows that motion signals lead to systematic localisation biases (Ramachandran & Anstis, 1990; De Valois & De Valois, 1991; Arnold, Thompson, & Johnston, 2007; Kwon, Tadin, & Knill, 2015). For example, when drifting Gabor patches are presented within a stationary aperture, the stimulus appears shifted in the direction of motion (De Valois & De Valois, 1991; Chung, Patel, Bedell, & Yilmaz, 2007; Arnold et al., 2007). Such illusion are called motion-induced position shifts (MIPS). They raise the question of how the human visual system encodes location and how, in the case of MIPS, the apparent position shift can be explained. Furthermore, they offer a dissociation between the physical and the perceived position of a stimulus that can

clarify which neuronal and perceptual processes correspond to the apparent position of the stimulus.

To investigate these questions, we presented human observers ($n=5$) with motion stimuli that were systematically varied along two factors: the motion direction of the stimulus carrier pattern (3 levels: inward, outward and flicker motion) and the contrast of the stimulus (2 levels: low and high stimulus contrast), resulting in $3 \times 2 = 6$ conditions. We then obtained psychophysical, functional magnetic resonance imaging (fMRI), and in-silico simulation data for each of the 6 stimulus conditions. First, we collected psychophysical measurements to determine the direction and extent of perceptual position shifts. Second, we recorded fMRI responses from early- and mid-level visual areas to obtain population receptive field (pRF) estimates. Finally, we explored the link between perceptual position shifts and changes in pRF position in form of a visual field projection model.

Results

How do stimulus motion and contrast influence perceived position?

Figures 1A and B show group-averaged psychometric functions for high- and low-contrast stimuli, respectively. For high-contrast stimuli, the fitted psychometric functions are very similar for the different carrier motion combinations and we do not observe a systematic shift in perceived position. By contrast, for low-contrast stimuli the fitted psychometric functions are clearly separated and the arrangement of the curves is consistent with previous studies that reported a shift of perceived position in the direction of motion (De Valois & De Valois, 1991; Chung et al., 2007; Arnold et al., 2007).

Figures 1C and D plot the group mean PSEs (and 95% confidence intervals) obtained from psychometric functions that were fitted to each participant and pattern combination individually for high- and low-contrast stimuli. In the low-contrast condition, mean PSE for the outward-flicker combination was 0.20 ± 0.14 and was significantly different from the veridical position difference, i.e., $PSE = 0$. Reversely, mean PSE for the inward-flicker combination was -0.21 ± 0.07 and also significantly different from 0. In the high-contrast condition, no mean PSE for any combination was significantly different from 0. Furthermore, the mean PSEs for the outward-flicker as well as the inward-flicker combination were both positive with 0.10



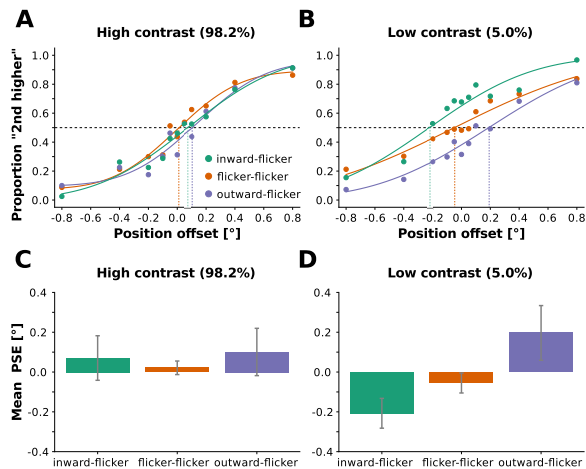


Figure 1: Displacement of perceived stimulus position in the direction of motion only observed for low-contrast stimuli. We varied the physical position offset between two subsequently presented stimuli. Participants indicated whether they perceived the first or second stimulus as higher. **(A)** Data and fitted psychometric functions for high-contrast stimuli averaged across participants. Dots represent data and curves represent fitted functions. The fitted curves represent responses for the sequence of inward then flicker motion (green), flicker then flicker motion (orange) and outward then flicker motion (violet). **(B)** Data and fitted psychometric functions for low-contrast stimuli. **(C)** Point of subjective equality (PSE) for high stimulus contrast. Bars represent average PSE across subjects. Error bars represent 95% confidence interval. **(D)** PSE for low stimulus contrast.

± 0.12 and 0.07 ± 0.11 , respectively. We thus did not find the perceived position to be shifted in any systematic direction for the high-contrast data.

How do stimulus motion and contrast influence pRF properties?

We found that the effect of carrier motion on pRF properties differed depending on the stimulus contrast and visual field map (Figure 2). For high stimulus contrast, we found no substantial changes in eccentricity for areas V1 - V3, replicating Lie et al. (2006). For higher visual field maps, starting from V3ab, however, we observed higher preferred eccentricity values for outward compared to inward motion - with the highest difference, 0.7, in field map TO. Flicker motion led to values intermediate to those obtained for inward and outward motion. For pRF sizes we observed a systematic decrease for outward as compared to inward motion across all visual field maps, with increasingly higher differences for higher visual field maps. Beyond V3, these effects were substantial with differences from 0.76 in V3a/b to 2.83 in TO. Percent signal change was decreased for outward compared to inward motion, which is consistent with a bias for motion towards fixation.

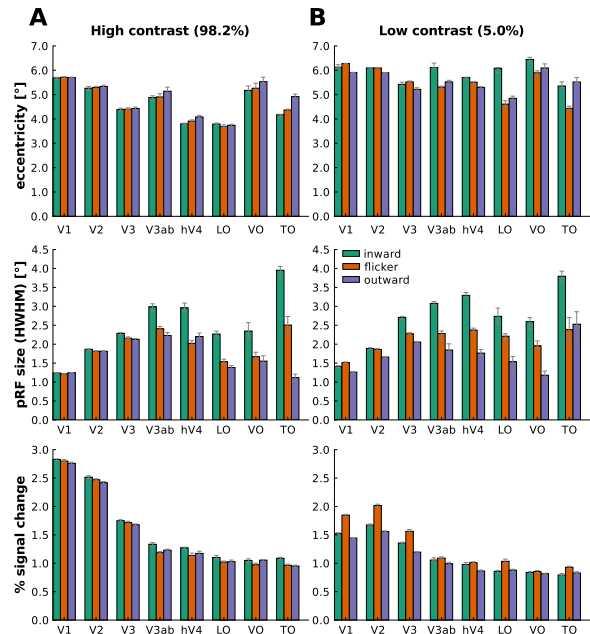


Figure 2: Effect of carrier motion on pRF properties depends on stimulus contrast and visual field map. Each bar represents a pRF property (median across voxels of all participants \pm 68% confidence interval) in different visual field maps (V1 to TO) during one of three motion conditions: inward (green), flicker (orange) and outward (violet) motion. Panels **(A)** and **(B)** show results for high- and low-stimulus contrast. Different rows show different pRF properties: eccentricity of the pRF center (in of visual angle), pRF size (HWHM, of visual angle) and approximated % signal change.

For low stimulus contrast, we found lower preferred eccentricity values for outward as compared to inward motion across all visual field maps, with the notable exception of area TO. This corresponds to a shift of the pRF center in the direction opposite to motion, consistent with results from the animal literature (Fu, 2004). Eccentricity decreases were consistent across voxels (indicated by small error bars) and in the order of 0.20 to 1.23. We also observed systematic decreases of pRF sizes across all visual field maps for outward as compared to inward motion. These decreases were higher for higher visual areas and in the range from 0.15 to 1.53. Percent signal change was decreased for outward compared to inward motion.

Can pRF center shifts account for perceptual shifts?

If the pRF center shifts in the direction opposite to motion, as they do for low-contrast stimuli, how can we account for the observation that, perceptually, the apertures appear displaced in the direction of motion? Figure 3 offers an explanation in form of a model centered on visual field projections. The model makes two assumptions: (i) during MIPS, pRF centers in lower-level visual areas are shifted against the direction

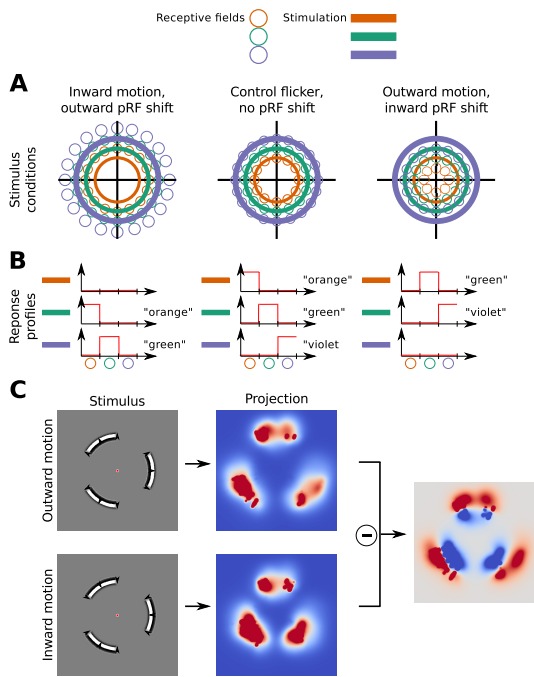


Figure 3: Simulated perceptual consequences of pRF shifts in the direction opposite to motion. **(A)** Assumed pRF center positions during inward (left column), flicker (middle column) and outward motion (right column). **(B)** During inward (outward) motion pRF units send a population level code that signals a position of the stimulus at slightly lower (higher) eccentricities than its actual position. For example, during peripheral (“violet”) stimulation with inward motion, the neuron population will send a more foveal (“green”) code. **(C)** Shifted population level codes can be turned into quantifiable perceptual predictions via visual field projections.

of motion; (ii) at the same time, retinotopy is *not* flexible in the sense that connections from lower- to higher-level visual areas are not dynamically updated during stimulus presentation.

Figure 3A and B demonstrate how, given pRF shifts opposite to motion direction, lower-level visual areas send position codes that indicate a shift in the direction of motion. During natural viewing conditions, pRF centers are not displaced and lower-level visual voxels send position codes congruent with the physical position of a stimulus (middle column). However, during inward (outward) motion, pRFs will be shifted outward (inward) meaning that units will now respond to eccentricities slightly higher (lower) than usual. At the population level, the code that lower-level voxels of different eccentricities will send will signal a position of the stimulus that is slightly more foveal (peripheral) than the actual physical stimulus (see Figure 3B).

Figure 3C simulates the perceptual consequences of shifted population position codes. We assume the activation of pRF units is connected to perceived stimulus position via

a visual field projection. The projection describes the mapping between the activation of a unit and the perceived presence of a stimulus at a certain position of the visual field. The mapping is learned during natural viewing conditions and assumed not to change during inward (outward) motion because connections between low-level and high-level neurons do not reorganise at the time scale of stimulus presentation. Consequently, if during inward (outward) motion a population of units in a lower-level visual area signals a more foveal (peripheral) code than usual, this will be interpreted (perceived) as the presence of a more foveal (peripheral) stimulus.

We tested the visual field projection model by turning the observed pRF center shifts into predictions about perceptual displacements. Figure 4A shows the results of our simulation. We obtained perceptual shifts in the order of 0.1 to 0.5 depending on the visual field map. For early visual field maps V1-V3 the simulated perceptual shifts were too small to account for our empirical findings (which were in the order of 0.4). However, the simulated perceptual shifts obtained in higher visual field maps approximate the perceptual shifts found empirically. We also investigated the effect of pRF size changes on perceptual shifts since we observed larger pRF sizes for inward compared to outward motion. Figure 4B shows that if we assume pRF size differences in addition to pRF center shifts, the simulated perceptual shift is enhanced.

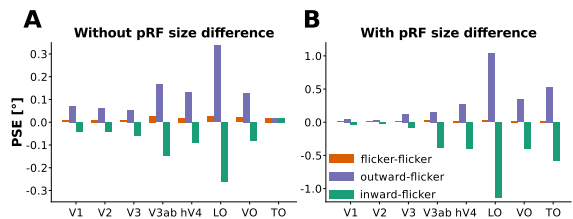


Figure 4: Simulated perceptual consequences of pRF shifts based on the visual field projection model. **(A)** Point of subjective equality (PSE) for simulated psychophysics data. The three bar conditions represent simulated responses for the sequence of inward then flicker motion (green), flicker then flicker motion (orange) and outward then flicker motion (violet). We assumed that the eccentricity of the pRF shifted with the same magnitude that was observed empirically (see Figure 2, upper row). The pRF size was assumed to remain fixed. **(B)** PSE for simulated psychophysics data. Same conventions as in **(A)** but this time, in addition to shifting the pRF center, we also changed the pRF size in accordance with the pRF size difference that we observed empirically (see Figure 2, middle row). Note the different scale between the y-axes in **(A)** and **(B)**.

Conclusion

We found that perceptual position shifts in the direction of motion coincide with pRF center shifts in the direction opposite the direction of motion. We link these two seemingly contradictory findings proposing a visual field projection model.

Methods

Participants Five healthy participants with corrected-to-normal vision took part in the study. All participants gave informed, written consent to participate in the experiment. The study was approved by the ethics committee of the Faculty of Psychology and Neuroscience at Maastricht University.

Stimuli Stimuli were presented either at 5% or at 98.2% Michelson contrast. During inward and outward motion conditions, stationary apertures revealed a radial square wave grating (spatial frequency: 1 cycle per) drifting 5 of visual angle per s inward or outward, respectively. During the flicker condition, apertures revealed a dartboard pattern (Dumoulin & Wandell, 2008). All stimuli were presented for brief periods of 400 ms to avoid adaptation to motion direction (Fu, 2004),

Psychophysics The psychophysics session followed a similar procedure as that described by (Harvey & Dumoulin, 2016). We used the method of constant stimuli and a two-interval forced choice paradigm. On a given trial we presented two stimuli in temporal succession and systematically varied the vertical distance between them (either no offset or 0.05, 0.1, 0.2, 0.4, or 0.8). Subjects judged whether they perceived the first or second stimulus as higher.

MRI acquisition T2*-weighted functional data were acquired on a 7 T Magnetom scanner using a 2D gradient echo echo planar image sequence (TE/TR = 20/2000 ms; in-plane FoV 144 x 144 mm²; matrix size 120 x 120; slices = 35; voxel resolution = 1.2 mm isotropic; nominal FA = 82; echo spacing = 0.78 ms; GRAPPA factor = 2, partial Fourier = 6/8).

pRF modelling The pRF mapping data were analyzed as described in (Dumoulin & Wandell, 2008), i.e., voxel time courses were assumed to be generated by an isotropic 2D Gaussian in visual space. We also employed established extensions of the standard pRF model (Zuiderbaan, Harvey, & Dumoulin, 2012; Kay, Winawer, Mezer, & Wandell, 2013).

Visual field projection model To simulate perceptual displacements, we applied systematic shifts to the pRF centers obtained in an independent mapping experiment in the order that was observed empirically. Using these shifted pRF parameters, we simulated responses for each voxel that would be produced by the stimuli shown during the psychophysics experiment. The simulated response patterns were projected into the visual field by calculating the 2D projection M as

$$M = \sum_{v=1}^V g_v \bar{r}_v / \sum_{v=1}^V \bar{r}_v \quad (1)$$

where $g_v = g(x, y | \mu_x, \mu_y, \sigma)$ is the 2D Gaussian for a pRF with μ_x , μ_y , and σ , \bar{r}_v is the simulated response and V is the total number of voxels in a given field map.

This resulted in one visual field projection M per psychophysics stimulus, motion condition and field map. For every projection we calculated the expected eccentricity value $E(Ecc)$ and its variance $Var(Ecc)$. Intuitively, when we com-

pare two projections M_1 and M_2 for two stimuli s_1 and s_2 then the stimulus for which the projection has a higher expected eccentricity value should be perceived as higher on a proportion of trials $p > 0.5$. This intuition was captured via a cumulative Gaussian function (Van Humberck, Putzeys, & Wagemans, 2016) and we calculated the proportion p of trials where the second stimulus is perceived as higher than the first for all stimulus pairs shown in the psychophysics experiment. In a second pass, we repeated the analysis above but this time, in addition to assuming shifts in pRF center, we also assumed differences in pRF size between motion conditions in the order observed empirically.

Acknowledgments

We would like to thank Dimo Ivanov for help with adjusting the MP2RAGE sequence and Mario Senden and Brian Wandell for valuable advice. This work was financed by the Netherlands Organisation for Scientific Research (NWO)

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