



Real-motion signals in human early visual cortex

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ARTICLE INFO

Keywords:

Visual motion
Eye movements
Early visual cortex
Visual stability
Self-motion
Human fMRI

ABSTRACT

Eye movements induce visual motion that can complicate the stable perception of the world. The visual system compensates for such self-induced visual motion by integrating visual input with efference copies of eye movement commands. This mechanism is central as it does not only support perceptual stability but also mediates reliable perception of world-centered objective motion. In humans, it remains elusive whether visual motion responses in early retinotopic cortex are driven by objective motion or by retinal motion associated with it. To address this question, we used fMRI to examine functional responses of sixteen visual areas to combinations of planar objective motion and pursuit eye movements. Observers were exposed to objective motion that was faster, matched or slower relative to pursuit, allowing us to compare conditions that differed in objective motion velocity while retinal motion and eye movement signals were matched. Our results show that not only higher level motion regions such as V3A and V6, but also early visual areas signaled the velocity of objective motion, hence the product of integrating retinal with non-retinal signals. These results shed new light on mechanisms that mediate perceptual stability and real-motion perception, and show that extra-retinal signals related to pursuit eye movements influence processing in human early visual cortex.

Introduction

When objects change their position in the visual field, the brain needs to infer whether the object moved ('Objective motion') or whether the eye moved and therefore shifted the visual field relative to the object ('Pursuit Motion'). Even though both options result in retinal motion, only the former is perceived as world-centered 'Real-motion'. Previous behavioral and electrophysiological studies suggest that the discrimination between these sources for visual motion is mediated by integrating efference copies of eye movement commands with visual input, reflected in responses of real-motion neurons (Galletti et al., 1984; von Helmholtz, 1867; von Holst and Mittelstaedt, 1950), allowing to separate self-induced from world-centered objective visual motion (Erickson and Thier, 1991; Galletti et al., 1990, 1988, 1984). Similar non-retinotopic coding of visual motion and visual locations has been found in various areas in the monkey brain such as MST (Ilg et al., 2004), V3A (Galletti et al., 1990), V6 (Galletti and Fattori, 2003), VIP (Duhamel et al., 1997)

and early visual areas V1 (Daddaoua et al., 2014; Galletti et al., 1984) and V2 (Galletti et al., 1988).

In the human brain, comparably few studies examined objective motion responses, and a systematic overview across visual regions is still missing. A recent functional magnetic resonance imaging (fMRI) study showed that human areas V3A and V6 respond almost exclusively to planar objective motion, suggesting a near complete integration of efference copies with visual input (Fischer et al., 2012). Both areas, along with hMST have also been shown to encode objective motion when visual stimuli simulate head motion (Arnoldussen et al., 2011; Goossens et al., 2006), and the same regions encode visual stimuli in a spatiotopic (head- or world-centered) reference frame at fixed eye-positions (Burr and Morrone, 2011; Crespi et al., 2011; d'Avossa et al., 2007). Among the motion responsive regions in the cingulate sulcus, areas Pc (Cardin and Smith, 2010) and CSv (Wall and Smith, 2008), the latter has been shown to encode objective motion to a limited extent (Fischer et al., 2011). Finally, there is evidence that human VIP (Merriam et al., 2003) as well

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<https://doi.org/10.1016/j.neuroimage.2018.04.012>

Received 24 November 2017; Received in revised form 6 April 2018; Accepted 8 April 2018

Available online 10 April 2018

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as several regions in the intraparietal sulcus (IPS) (Konen and Kastner, 2008) have access to both retinal and eye movement information and might hence show objective motion responses. While early visual cortex does respond to objective motion in monkey (Galletti et al., 1988, 1984), its involvement in the human brain has not been examined before.

To examine early visual cortex in this context and to provide the yet missing overview across the visual system, we used fMRI to investigate the responses of sixteen visual brain areas to objective motion during eye movements. We used retinotopic mapping (early visual areas V1-hV4, parietal regions IPS-0 to IPS-4) and dedicated motion localizers (hMT/V5, hMST+, V3A, V6, CSv, Pc, VIP) to independently identify these regions in every participant prior to examining their objective motion responses.

We used planar dot motion and a moving fixation disc to induce different objective motion velocities while pursuit speed as well as retinal motion were matched. Given that early as well as high level visual motion responses have previously been shown to be speed tuned (Arnoldussen et al., 2011; Chawla et al., 1999, 1998; Pitzalis et al., 2012) we expected different objective motion velocities to yield differential responses. Eye tracking was employed throughout the experiment and participants conducted an independent task at fixation to keep attention balanced across conditions. We specifically tested which regions were involved in perceptually relevant estimation of objective motion velocity while physical input parameters were exactly matched. This estimation can only be achieved by the multi-modal integration of efference copies with visual signals, and it is essential to maintain a stable perception of the visual environment during self-motion.

Methods

Participants

A total of 18 participants (7 male, 11 female) participated in this study (23–34 years of age, normal or corrected to normal vision, no neurological pathologies). Prior to scanning, participants were instructed about the experiment in spoken and written form, performed several test trials and gave written consent. The study was approved by the joint ethics committee of the university clinics Tuebingen and the Max Planck Institute Tuebingen.

Stimulus

The stimulus was written in MATLAB 2013b (<http://www.mathworks.de/>) using Psychtoolbox (<http://psychtoolbox.org/>) and was projected onto a translucent screen in a back-projection setup via a gamma corrected NEC PE401h projector. The display covered 22×16.4 visual degrees. The stimulus (Fig. 1) consisted of a fixation disc (light grey, 0.9° in diameter) as well as a random dot pattern (black and white dots, 100% contrast) on a grey background (mean luminance: 10 participants with 487 cd/m^2 , 8 participants with 244 cd/m^2). The luminance split between participants was due to technical reasons and unlikely to affect any question of interest). The planar random dot pattern consisted of an average of 1540 dots varying randomly in size between 0.08 and 0.2° , with all dots moving coherently and simultaneously while keeping their relative distances fixed. The random dots hence moved together as one background image, inducing global planar visual motion. Both fixation disc and the random dots in the background moved on a circular trajectory with a radius of 4.1° (quarter of the screen height). The random dot pattern could however move at different velocities relative to the fixation disc, yet always on the same trajectory (see experimental conditions below). The motion radius was chosen such that the area of controlled visual stimulation was maximal: the nearest border to the screen edge was at all times further away than 4 visual degrees, leading to controlled visual stimulation within at least 8×8 visual degrees (Fischer et al., 2012). The rotation direction and starting point of the fixation disc was randomized and counter balanced across trials within each participant.

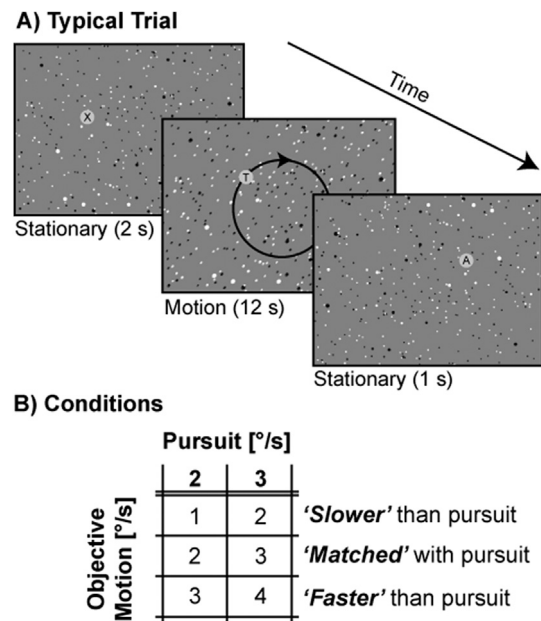


Fig. 1. Illustration of stimulus timeline and experimental conditions. A) Stimulus timeline across a typical trial. Each trial started with a stationary background and stationary fixation disc, shown for 2 s. This was followed by the condition-specific motion (of background and fixation) for 12 s. Note that the circular trajectory of fixation disc and background plane were identical, but that background motion could be faster, matched, or slower relative to pursuit. Trials ended with a stationary period lasting 1 s. B) At two different pursuit speeds ($2^\circ/\text{s}$ and $3^\circ/\text{s}$) we presented objective motion that was $1^\circ/\text{s}$ slower ('Slower' conditions), matched ('Matched' conditions) or $1^\circ/\text{s}$ faster ('Faster' conditions) relative to pursuit. Data was pooled across pursuit speeds to obtain the 3 (pursuit-speed invariant) conditions Faster, Matched and Slower.

Fixation task

Participants were instructed to always fixate the fixation disc on which we displayed a character repetition-detection task to balance attention across conditions. Random black characters (A-Z) were presented in random order with a frequency of 1 Hz. Every three to eight presentations one of these characters was repeated, which participants had to report via button press. As a control measure we recorded hit rate, false alarms rate and response time across all conditions. A button press was counted as a hit if occurred within 1 s after a character repetition; otherwise it was counted as false alarm. Response time depicts the time between a character repetition and the corresponding hit. For each of these measures we performed repeated-measures ANOVA to test for condition dependent effects.

Trial timeline

A typical trial started with a stationary stimulus for 2 s, followed by the movement of the stimulus for 12 s, ending with another stationary period of 1 s (Fig. 1). The motionless pre- and post-stimulus periods provided enough time to facilitate the saccade from the end-point of the fixation disc of the preceding trial to start-point of the current trial, as well as stable fixation before the actual motion stimulus was shown.

Experimental conditions

Pursuit eye velocity was experimentally determined through movement of the fixation disc and objective motion by movement of the background dots. Retinal motion is the difference between the two. We presented a total of nine conditions that resulted from combinations of two pursuit speeds and three objective motion speeds. Data was pooled

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