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Contents lists available at ScienceDirect

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Visual field biases for near and far stimuli in disparity selective columns in human visual cortex

Shahin Nasr [a,b,*], Roger B.H. Tootell [a,b]

[a] Athinoula A. Martinos Center for Biomedical Imaging, Massachusetts General Hospital, Boston, MA, USA
[b] Department of Radiology, Harvard Medical School, Boston, MA, USA

ARTICLE INFO

Article history:
Accepted 6 September 2016

Keywords:
Statistics of natural scenes
Stereopsis
Depth perception
Extrastriate cortex
7T fMRI

ABSTRACT

When visual objects are located in the lower visual field, human observers perceive objects to be nearer than their real physical location. Conversely, objects in the upper visual field are viewed farther than their physical location. This bias may be linked to the statistics of natural scenes, and perhaps the ecological relevance of objects in the upper and lower visual fields (Previc, 1990; Yang and Purves, 2003). However, the neural mechanisms underlying such perceptual distortions have remained unknown.

To test for underlying brain mechanisms, we presented visual stimuli at different perceptual distances, while measuring high-resolution fMRI in human subjects. First, we localized disparity-selective thick stripes and thick-type columns in secondary and third visual cortical areas, respectively. Consistent with the perceptual bias, we found that the thick stripe/columns that represent the lower visual field also responded more selectively to near rather than far visual stimuli. Conversely, thick stripe/columns that represent the upper visual field show a complementary bias, i.e. selectively higher activity to far rather than near stimuli. Thus, the statistics of natural scenes may play a significant role in the organization of near- and far-selective neurons within V2 thick stripes and V3 thick-type columns.

Introduction

In humans and many other terrestrial animals, visual objects that appear below the line of sight (i.e. in the lower visual field) are typically located closer than objects appearing in the upper visual field (Yang and Purves, 2003). This typical difference in object distance can affect human judgments. Consistent with these statistics of natural scenes, humans are known to systematically underestimate the distance of objects below the line of sight, perceiving them nearer than their actual distance (Ooi et al., 2001; Philbeck and Loomis, 1997; Wallach and O'Leary, 1982; Yang and Purves, 2003). Analogously, observers overestimate object distance when such objects are located in the upper visual field (Breitmeyer et al., 1977). Thus far, the neural mechanisms underlying these behavioral biases have been obscure.

A main cue for estimating visual object distance is binocular disparity. Images from the two eyes are 'crossed' for objects located further than the center of gaze ('far' distances), or 'uncrossed' for objects located nearer than that ('near' distances). At least in macaque monkeys, this distinction is fundamental enough that neurons that respond selectively to such 'near' and 'far disparities are grouped together in segregated columns within visual cortex (Adams and Zeki, 2001; Chen et al., 2008; Tanabe et al., 2005). Consistent with these results from monkeys, a recent fMRI study also suggested that near and far selective neurons are clustered within one area in human visual cortex, named V3A (Goncalves et al., 2015). However, it has not been tested whether near and far columns are located preferentially in the cortical representation of the upper vs. lower visual fields (respectively), i.e. consistent with the bias in depth perception.

Here we show evidence for such a neural bias. We conducted high-resolution, high field (7T) fMRI measurements in human subjects during presentation of visual stimuli in near vs. far conditions (see Section 2). Consistent with the reported bias in human depth perception, we found that near stimuli evoked stronger activity in disparity selective columns in the lower (compared to upper) visual field representations, within each of the two most retinotopically-organized extrastriate cortical areas.

Methods

Participants

Six human subjects (3 females), aged 21–32 years, participated in this study. All subjects had normal or corrected-to-normal

* Correspondence to: Building 149, 13th street, Charlestown, MA 02129, USA.
E-mail address: shahin@nmr.mgh.harvard.edu (S. Nasr).

http://dx.doi.org/10.1016/j.neuroimage.2016.09.012
1053-8119/

visual acuity and radiologically normal brains, without history of neuropsychological disorder. All experimental procedures conformed to NIH guidelines and were approved by Massachusetts General Hospital protocols. Written informed consent was obtained from all subjects prior to the experiments.

General procedures

Each subject was scanned in multiple sessions, on different days, in a high field scanner (Siemens 7 T whole-body system, Siemens Healthcare, Erlangen, Germany). Initial sessions localized stereo-selective ('thick') and color-selective ('thin') stripes/columns, in each subject. Subsequent scans measured fMRI activity evoked by random dot stereograms ((RDS) (Anzai et al.,2011; Bela Julesz, 1971; Minini et al., 2010; Nasr et al., 2016; Tsao et al., 2003)) of either crossed ('far') or uncrossed ('near') binocular disparity (see below). All subjects were also scanned in a 3T scanner (Tim Trio, Siemens Healthcare) in one additional session, for structural and retinotopic mapping.

Visual stimuli

Stimuli were presented via an LCD projector (1024 × 768 pixel resolution, 60 Hz refresh rate) focused on a rear-projection screen, viewed through a mirror mounted on the receive coil array. Matlab 2013a (MathWorks, Natick, MA, USA) and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) were used to control stimulus presentation.

During all experiments, stimuli were presented in a blocked-design procedure. Subjects were required to maintain fixation on a small (0.1° × 0.1°) central spot. To control the level of attention during the scans, subjects were required to simultaneously perform an unrelated ('dummy') task, reporting changes in color (red-to-green or vice versa) and shape (square-to-circle or vice versa) of the fixation spot during 'near vs. far' and localizer scans (see below), by pressing a key on a keypad.

Near vs. far disparity

Disparity-varying stimuli were sparse (5% bright) RDS based on red or green dots (0.09° × 0.09°) presented against a black background, extending 20° × 20° in the visual field. Subjects viewed the two RDS (each either red or green) through custom anaglyph spectacles, using Kodak Wratten filter No. 25 (red) over one eye, and 44 A (cyan) over the other. Two RDS were overlaid and fused within all experiment blocks. In 'near' and 'far' conditions, stimuli formed a stereoscopic percept of a regular array of cuboids that varied sinusoidally in depth between 0° and 0.22°, either 'in front' or 'behind' a fronto-parallel plane that intersected the fixation target. In a control condition, the fused percept was limited to that fronto-parallel plane (i.e. zero depth).

Each experimental run included 9 stimulus blocks (24 s per block). Additionally, each run began and ended with control conditions of 12 s of uniform gray ('blank'). Each subject participated in two separate scan sessions, with 12 runs (960 functional volumes) per session.

Localizing thick and thin stripes/columns

Details of the stimuli and experimental procedure used to localized thin and thick stripes are reported elsewhere (Nasr et al., 2016). Briefly, V2 thick stripes and V3 thick type columns were localized using RDSs based on red or green dots (0.09° × 0.09°) presented against a black background, extending 20° x 20° in the visual field. As described above, subjects viewed the stimulus through custom anaglyph spectacles. Stimuli formed a stereoscopic percept of a regular array of cuboids that varied sinusoidally in depth, with independent phase. However, in contrast to the main experiment in which stimuli were presented either in front or behind the fixation target, here the stimuli spanned the full depth range (i.e. ± 0.22°) within each experimental block. As a control, in separate blocks, RDS stimuli were presented at zero disparity. Each experimental run began and ended with 12 s of uniform gray ('blank') and included 8 stimulus blocks (24 s per block). Each subject participated in three scan sessions (12 runs per session) during which 2592 functional volumes were collected.

Color-selective ('thin') stripes and columns were localized in V2 and V3 in separate scan sessions, using sinusoidal gratings (20° × 20° of visual angle) which varied in either color or achromatic luminance, in independent blocks (Nasr et al., 2016). Grating stimuli were also presented in systematically varied orientations (either 0°, 45°, 90° or 135°), drifting in orthogonal directions (reversed every 6 s) at 4°/s. In each run, these blocks included 9 stimulus presentation blocks (24 s per block). Each run began and finished with an additional block (12 s) of uniform gray of equal mean luminance. Each subject participated in 1–2 scan sessions (12 runs per session). 1008 functional volumes were collected in each scan session.

Retinotopic mapping

Details of retinotopic mapping are reported elsewhere (Nasr et al., 2011). Briefly, stimuli were colored images of scenes and faces, which were presented within retinotopically limited apertures, against a gray background. The retinotopic apertures included wedges aligned along the horizontal and vertical meridian meridians (radius = 10°, polar angle = 30°), a foveal disk (radius = 1.5°) and a peripheral ring (inner-outer radius = 5–10°). For one subject, we also mapped retinotopic areas using counter-phased, radially scaled checkerboard stimuli, rather than scenes and faces.

To confirm the V1/V2/V3 borders, in 2 subjects we also used phase-encoded, continuously rotating rays or continuously expanding/contracting ring stimuli for retinotopic mapping, each filled with contrast-reversing (1 Hz) checkerboards that were scaled in size with eccentricity. Details of this procedure are described previously (Sereno et al., 1995).

Imaging

7T sessions

The main experiments were conducted in a 7 T Siemens whole-body scanner equipped with SC72 body gradients (70 mT/m maximum gradient strength and 200 T/m/s maximum slew rate) using a custom-built 32-channel helmet receive coil array and a birdcage volume transmit coil (Keil et al., 2010). Voxel dimensions were nominally 1.0 mm, isotropic, except as noted below. Single-shot gradient-echo EPI was used to acquire functional images with the following protocol parameter values: TR = 3000 ms, TE = 28 ms, flip angle = 78°, matrix = 192 × 192, BW = 1184 Hz/pix, echo-spacing = 1 ms, 7/8 phase partial Fourier, FOV = 192 × 192 mm, 44 oblique-coronal slices, acceleration factor $R = 4$ with GRAPPA reconstruction and FLEET-ACS data (Polimeni et al., 2015) with 10° flip angle. The field of view included occipital cortical areas V1, V2, V3, and usually the posterior portion of V4.

3T sessions

High spatial resolution was not necessary to map the borders of retinotopic areas. Instead, retinotopic mapping was conducted using a 3 T Siemens scanner (Tim Trio) and the vendor-supplied 32-channel receive coil array. That functional data was acquired using single-shot gradient-echo EPI with nominally 3.0 mm isotropic voxels using the following protocol parameters: TR = 2000 ms, TE = 30 ms, flip angle = 90°, matrix = 64 × 64, BW = 2298 Hz/pix, echo-spacing = 0.5 ms, no partial Fourier,

Please cite this article as: Nasr, S., Tootell, R.B.H., Visual field biases for near and far stimuli in disparity selective columns in human visual cortex. NeuroImage (2016), http://dx.doi.org/10.1016/j.neuroimage.2016.09.012