



Determinants of motion response anisotropies in human early visual cortex: The role of configuration and eccentricity



Ryan T. Maloney^{a,b,c,*}, Tamara L. Watson^d, Colin W.G. Clifford^{a,b,c}

^a School of Psychology, UNSW Australia, Sydney, New South Wales, Australia, 2052

^b School of Psychology, The University of Sydney, Sydney, New South Wales, Australia 2006

^c Australian Research Council Centre of Excellence in Vision Science, The University of Sydney, Sydney, New South Wales, Australia 2006

^d School of Social Sciences and Psychology, The University of Western Sydney, Bankstown, New South Wales, Australia 2200

ARTICLE INFO

Article history:

Accepted 24 June 2014

Available online 1 July 2014

Keywords:

Motion perception
Direction selectivity
fMRI
Optic flow
Radial bias

ABSTRACT

Anisotropies in the cortical representation of various stimulus parameters can reveal the fundamental mechanisms by which sensory properties are analysed and coded by the brain. One example is the preference for motion radial to the point of fixation (i.e. centripetal or centrifugal) exhibited in mammalian visual cortex. In two experiments, this study used functional magnetic resonance imaging (fMRI) to explore the determinants of these radial biases for motion in functionally-defined areas of human early visual cortex, and in particular their dependence upon eccentricity which has been indicated in recent reports. In one experiment, the cortical response to wide-field random dot kinematograms forming 16 different complex motion patterns (including centrifugal, centripetal, rotational and spiral motion) was measured. The response was analysed according to preferred eccentricity within four different eccentricity ranges. Response anisotropies were characterised by enhanced activity for centripetal or centrifugal patterns that changed systematically with eccentricity in visual areas V1–V3 and hV4 (but not V3A/B or V5/MT+). Responses evolved from a preference for centrifugal over centripetal patterns close to the fovea, to a preference for centripetal over centrifugal at the most peripheral region stimulated, in agreement with previous work. These effects were strongest in V2 and V3. In a second experiment, the stimuli were restricted to within narrow annuli either close to the fovea (0.75–1.88°) or further in the periphery (4.82–6.28°), in a way that preserved the local motion information available in the first experiment. In this configuration a preference for radial motion (centripetal or centrifugal) persisted but the dependence upon eccentricity disappeared. Again this was clearest in V2 and V3. A novel interpretation of the dependence upon eccentricity of motion anisotropies in early visual cortex is offered that takes into account the spatiotemporal “predictability” of the moving pattern. Such stimulus predictability, and its relationship to models of predictive coding, has found considerable support in recent years in accounting for a number of other perceptual and neural phenomena.

© 2014 Elsevier Inc. All rights reserved.

Introduction

Functional magnetic resonance imaging (fMRI) has recently been proven a useful technique for uncovering broad anisotropies in the tuning properties of visual cortex (in humans and other mammals) to the spatial and spatiotemporal structure of images. These anisotropies have been identified as early as primary visual cortex (V1) for a range of systematically-varied stimulus attributes presented across the visual field, including orientation (Freeman et al., 2011; Furmanski and Engel, 2000; Mannion et al., 2010a; McDonald et al., 2012; Sasaki et al., 2006; Swisher et al., 2010), complex polar form (Mannion and Clifford, 2011; Mannion et al., 2010b) and direction of motion (Beckett et al., 2012;

Clifford et al., 2009; Giaschi et al., 2007; Maloney et al., 2013; Raemaekers et al., 2009; Schellekens et al., 2013; Wang et al., 2013). Such anisotropies provide a functional signature of the processing of these attributes across entire populations in visual cortex and have the potential to reveal the strategies used by the visual system to achieve an efficient processing of its inputs.

The focus of the present report is on directional anisotropies, and in particular radial motion biases, in the processing of visual motion in early retinotopic cortex. Pure radial motion is described as either centrifugal (expanding outwards) or centripetal (contracting inwards), and, when centred at the fovea, it describes a trajectory that runs through a range of eccentricities at a single visual field polar angle. Evidence from various sources suggests that the visual system is highly sensitive to this type of motion. Extracellular recordings in non-human primates have indicated radial motion preferences in the middle temporal area MT/V5 (Albright, 1989), V4A (Pigarev et al., 2002), the

* Corresponding author at: School of Psychology, UNSW Australia, Sydney, New South Wales, Australia, 2052. Fax: +61 29385 3641.

E-mail address: r.maloney@unsw.edu.au (R.T. Maloney).

frontal eye fields (Xiao et al., 2006) and posterior parietal cortex (Steinmetz et al., 1987). There is also an over-representation of neurons tuned to centrifugal motion over other complex motion patterns in the dorsal aspect of the medial superior temporal (MSTd) cortex (Duffy and Wurtz, 1991a, 1991b; Graziano et al., 1994; Lagae et al., 1994; Orban et al., 1992; Tanaka and Saito, 1989; Tanaka et al., 1989). In humans, psychophysical biases for radial motion have been reported (Beardsley and Vaina, 2005; Burr et al., 2001; Morrone et al., 1999), although of the radial motions mixed accounts suggest sensitivity is greater for either centripetal (Edwards and Badcock, 1993; Edwards and Ibbotson, 2007; Giaschi et al., 2007; Raymond, 1994) or centrifugal motion (Ball and Sekuler, 1980; Beardsley and Vaina, 2005; Meese and Anderson, 2002). Further, fMRI studies have shown greater activation for radial over tangential motions in human cortical areas V1–V3 (Beckett et al., 2012; Clifford et al., 2009; Raemaekers et al., 2009; Schellekens et al., 2013; Wang et al., 2013), while fMRI and magnetoencephalography (MEG) studies have indicated that activity in the V5/MT+ complex (the putative human homologue of macaque areas V5/MT and MST; Tootell et al., 1995; Zeki et al., 1991) is enhanced for radial compared to uniformly translating motion (Giaschi et al., 2007; Holliday and Meese, 2005, 2008; Koyama et al., 2005; Morrone et al., 2000; Wall and Smith, 2008; Wall et al., 2008). Functionally, these radial motion biases likely serve important roles in computations related to ego-motion and navigation, such as heading perception and time-to-contact estimation (for reviews see Britten, 2008; Lappe, 2000; Vaina, 1998).

The work of Raemaekers et al. (2009) documented systematic patterns of bias in the response of human early visual cortex to direction of motion. They presented wide-field patterns of coherently-translating random dots that changed their direction of motion a full 360° across a cycle of 100 images, and found that in areas V1, V2 and V3 (but not V5/MT+) the amplitude of the fMRI blood-oxygenation level-dependent (BOLD) response was enhanced for motion radial to the point of fixation (i.e. parallel to the visual field polar angle) compared to tangential (rotational) motion (see also Clifford et al., 2009). A key observation made by Raemaekers and colleagues was that these anisotropies were not uniform across eccentricity. At low eccentricities the strongest responses in areas V1–V3 were elicited by centrifugal motion. At higher eccentricities, however, the responses to centripetal motion tended to be stronger (see also Schellekens et al., 2013; Wang et al., 2013). Raemaekers et al. (2009) note that this dependency on eccentricity may have influenced motion response anisotropies as measured in previous psychophysical and/or fMRI studies, either because the effect was summed or cancelled across eccentricity or because of the particular location in the visual field where the responses were measured. They do not however explore in detail the possible reasons for this change in the anisotropies as a function of eccentricity.

Here, using two different spatial (and temporal) stimulus configurations in two experiments, anisotropies in the response to complex patterns of motion were measured using fMRI in functionally-defined human visual cortical areas V1, V2, V3, V3A/B, hV4 and V5/MT+. Complex motions are parameterised in polar coordinates by the flow angle (relative to a zero degree, radial baseline) typically centred at the point of fixation, whereby motions are characterised as centrifugal, centripetal, rotational or spiral (Clifford et al., 1999; Graziano et al., 1994; Meese and Anderson, 2002; Morrone et al., 1999). The use of complex patterns of motion thus provides a direct manipulation of global motion direction relative to the fovea. In contrast, the uniform translational motion stimuli used previously (e.g. Giaschi et al., 2007; Raemaekers et al., 2009; Schellekens et al., 2013; Wang et al., 2013) provide indirect evidence for radial biases, because they require reference to precise retinotopic cortical maps in order to effect a transformation into polar co-ordinates.

In the first stimulus configuration, wide-field complex motion patterns that systematically changed in flow angle (centred at the fovea) were presented. Anisotropies in the BOLD response to these patterns

were apparent, marked by a bias towards the radial motions that depended strongly on eccentricity (particularly in V2 and V3), as with Raemaekers et al. (2009). At the lowest eccentricities, the strongest response was to centrifugal motion patterns and the weakest to centripetal patterns. As eccentricity increased, this pattern gradually shifted to almost the exact opposite pattern: the strongest response was to centripetal motion while the response was weakest to centrifugal motion.

This shift in response bias for motion as a function of eccentricity could be due to the “predictability” of the moving spatial pattern with respect to position in the visual field; such motion predictability is known to have a powerful influence on both perception (Roach et al., 2011; Schwiedrzik et al., 2007; Zhang et al., 2013) and activity in visual cortex (Alink et al., 2010; Kok et al., 2013). In a second experiment, the stimuli were restricted to narrow annuli either close to the fovea or further in the periphery, an arrangement that was intended to reduce the predictability of the moving spatial pattern whilst keeping the local motion information within those annuli the same as it was under the first set of wide-field stimuli. The results were consistent with a radial motion bias in areas V2 and V3 that depended neither on eccentricity nor on whether the motion was centripetal or centrifugal. The results from the two experiments demonstrate a characteristic processing anisotropy in early visual cortex (particularly V2 and V3) for complex motion. This was marked most prominently by radial biases where, for wide-field stimuli but not narrow annuli, the type of radial motion preference (centrifugal or centripetal) depended upon eccentricity. A novel interpretation of these results is provided that emphasises recent developments in theories of predictive coding (e.g. Alink et al., 2010; Enns and Lleras, 2008; Roach et al., 2011; Spratling, 2010; Summerfield and Egner, 2009; Yuille and Kersten, 2006) and how these interactions likely reflect the differential importance of radial motion in the control of ego-motion.

Methods

Subjects

A total of 8 subjects took part in two experiments (ages 24–46 years, 3 female) including the three authors and five who were naive to the theoretical motivations of the study. There were six subjects per experiment, four of whom were common to both. All were experienced in visual psychophysics and fMRI experiments, with corrected-to-normal visual acuity. The experimental protocol came with the approval of the University of Sydney Human Research Ethics Committee.

Stimuli

Visual stimuli consisted of random dot kinematograms (RDKs) presented at 100% coherence and generated with the PsychToolbox 3.0.9 (Brainard, 1997; Pelli, 1997) for MATLAB (7.10 R2010a; The MathWorks, Natick, MA). The RDKs were pre-generated and saved as AVI files, and ranged in flow angle in 16 steps of 22.5°, relative to the radial angle (0°). Thus a flow angle of 0° produced centrifugal motion, $\pm 180^\circ$ gave centripetal motion, 90° counter-clockwise motion and -90° clockwise motion (see Fig. 1C). Flow angles intermediate to these four “cardinal” flows result in spiral motions of varying pitch (Beardsley and Vaina, 2005; Graziano et al., 1994; Meese and Anderson, 2002). All were centred at the fovea and set against the mean background luminance of the display, and, in the wide-field configuration, within an annular region with an inner border at 0.75° and an outer border at 6.28° (Figs. 1A–B). The outer edge of the stimuli was slightly less than the maximum possible on the display apparatus (a radius of 7.15°; see below). Stimuli in the second experimental configuration were identical to those in the wide-field configuration except that the RDKs were presented (in separate runs) within much narrower annuli: an inner annulus of 0.75–1.88° and a more eccentric, outer annulus of 4.82–6.28° (Figs. 1E–F). The positions of these two annuli were the same as the

Download English Version:

<https://daneshyari.com/en/article/6026794>

Download Persian Version:

<https://daneshyari.com/article/6026794>

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