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**Directional anisotropy of motion responses in retinotopic cortex**

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6

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**Abstract:**

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5 Recently, evidence has emerged for a radial orientation bias in early visual cortex. These results predict that  
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7 in early visual cortex a tangential bias should be present for motion direction. We tested this prediction in a  
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9 human imaging study, using a translating random dot pattern that slowly rotated its motion direction 360°  
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11 in cycles of 54 s. In addition, polar angle and eccentricity mapping were performed. This allowed the  
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13 measurement of the BOLD response across the visual representations of the different retinotopic areas. We  
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15 found that in V1, V2 and V3, BOLD responses were consistently enhanced for centrifugal and centripetal  
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17 motion, relative to tangential motion. The relative magnitude of the centrifugal and centripetal response  
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19 biases changed with visual eccentricity. We found no motion direction biases in MT+. These results are in  
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21 line with previously observed anisotropies in motion sensitivity across the visual field. However, the  
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23 observation of radial motion biases in early visual cortex is surprising considering the evidence for a radial  
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25 orientation bias. An additional experiment was performed to resolve this apparent conflict in results. The  
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27 additional experiment revealed that the observed motion direction biases most likely originate from  
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29 anisotropies in long range horizontal connections within visual cortex.  
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**Introduction:**

Visual motion processing is a fundamental capability of the visual system of humans and animals. Motion sensitive neurons can be found throughout the cortex including in visual areas V1, V2, V3 and the middle temporal visual area (MT+) (Albright 1984; Orban et al. 1986; Felleman and Van Essen 1987; Levitt et al. 1994). A motion sensitive neuron selectively responds to a preferred direction and speed of motion, and motion direction is encoded in the pattern of activity across a pool of differently tuned neurons. It is generally thought that direction tuning of a neuron is directly related to its orientation tuning, or to that of its inputs, because only motion orthogonal to the preferred orientation can be signaled unambiguously. Cells in area MT of the macaque indeed show such a close correspondence between orientation tuning and direction tuning (Albright, 1984).

Recently, a functional magnetic resonance imaging (fMRI) study observed a large response bias for radial orientations as compared to tangential orientations in early visual cortex in humans and monkeys (Sasaki et al. 2006). This finding leads to the expectation that motion sensitivity in early visual cortex should be anisotropic as well, with a bias towards tangential motion relative to the fovea. The possible presence of directional biases are further supported by human psychophysical studies (Georgeson and Harris 1978; Ball and Sekuler 1980; Edwards and Badcock 1993; Raymond 1994; Giaschi et al. 2007) and electrophysiological recordings in monkeys in MT (Albright 1989), parietal cortex (Steinmetz et al. 1987), and the frontal eye fields (FEF) (Xiao et al. 2006).

Directional anisotropies of the motion response are not necessarily based on local inhomogeneities in cells that are tuned for a specific motion direction. E.g. it is known that visual information can be integrated across hypercolumns by means of horizontal connections within early visual cortex. Horizontal connections extend between cells with a similar tuning in adjacent locations within the visual field (Ts'o et al. 1986). For motion perception, such cells could facilitate motion detection through recruitment effects along the path of motion (van Doorn and Koenderink 1984). If anisotropies are related to horizontal connections, then the length of the motion stimulus would have a strong effect on directional biases.

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3 The presence of any systematic directional biases would have important consequences for recent fMRI  
4 studies have used multivoxel pattern analysis of visual areas to predict perceived motion direction  
5 (Kamitani and Tong 2006; Serences and Boynton 2007a; Serences and Boynton 2007b). Suggestions have  
6 been made that these decoding strategies exploit subvoxel inhomogeneities in direction sensitivity  
7 (Kamitani and Tong 2005; Kamitani and Tong 2006). This notion implicitly assumes equal responses for  
8 all motion directions across the visual field. Large scale anisotropies in the motion response would have  
9 implications for this interpretation. To test whether early visual cortical areas change their response with  
10 motion direction, we measured the BOLD response with fMRI across the retinotopic visual field  
11 representations of V1, V2, V3 and MT+, in human subjects observing translating coherent motion for a full  
12 complement of motion directions.  
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25 The current study demonstrates that indeed systematic motion direction biases exist in early visual cortex in  
26 humans. Activation enhancements were observed for radial motion directions and the relative magnitude of  
27 the bias for centrifugal and centripetal motion changed as a function of visual eccentricity. This result is in  
28 conflict with a tangential motion direction bias that would be expected on the basis of a radial orientation  
29 bias. An additional experiment was performed to resolve this apparent conflict in results by testing the  
30 notion that directional biases are caused by anisotropies in the modulation of neuronal activation along the  
31 path of motion. The results from the additional experiment revealed that the observed motion direction  
32 biases most likely originate from anisotropies in long range horizontal connections within visual cortex.  
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#### 43 **Methods:**

#### 44 **Subjects:**

45 12 healthy subjects that where recruited from Utrecht University participated in the experiment. All  
46 subjects gave informed consent for participation (approved by the local ethics committees of Utrecht  
47 University or the University of Birmingham). 9 subjects performed the fMRI experiment at Utrecht  
48 University, and 3 subjects performed the experiment at the University of Birmingham with concurrent  
49 measurement of eye movements. 10 subjects performed the additional experiment.  
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**Scanning protocol:**

At both locations scanning was performed on a Philips Achieva 3T scanner (Philips Medical Systems, Best, the Netherlands) with a Quasar Dual gradient set. For functional images, a navigated 3D-PRESTO pulse sequence was used (van Gelderen et al. 1995; Ramsey et al. 1998). The acquisition parameters were: TR=30 ms (time between 2 subsequent RF pulses); effective TE=43.87 ms; FOV(anterior-posterior, inferior-superior, right-left)= 65\*200\*160 mm; flip angle=10 degrees; matrix: 26\*80\*64 slices; voxel size 2.5 mm isotropic; 8 channel head coil; SENSE factors=2.0 (left-right) and 1.8 (anterior-posterior). A new volume was acquired every 540 ms, and encompassed the posterior 65 mm of the brain. A T1 weighted structural image of the whole brain (voxel resolution=0.875\*0.875\*1.00 mm; FOV=168\*224\*160 mm) was acquired at the end of the functional series. Immediately before the T1 image, an additional PRESTO image of the same volume of brain tissue was acquired with a high flip-angle (27 degrees, FA27) for the image coregistration routine (see below).

**Stimuli:**

For task presentation we used a desktop PC, a projection screen, and a video-projector system. All stimuli were programmed in C++ software (Bjarne Stroustrup, 1983, Bell Laboratories, USA). The start of each series of stimuli was triggered by the scanner. During all stimuli, there was a red central fixation dot (radius of 0.08° visual angle) that was surrounded by a circular aperture (radius of 0.4° visual angle). Subjects were requested to maintain fixated on the fixation dot regardless of the presented stimuli. The average luminance of the entire screen was constant during all stimuli and was 42.2 cd/m<sup>2</sup>.

For eccentricity mapping, we used an expanding ring with a maximum eccentricity of 7.5° visual angle (Figure 1A). After the ring was fully expanded, it returned to its minimum eccentricity (0.4° visual angle). The width of the ring was 1/5<sup>th</sup> of the maximum stimulus radius. There was 1 series (900 images) with 8 cycles of 54000 ms (100 images) and there was a blank period with only the fixation dot during the first and last 27000 ms (50 images) of the series. For polar angle mapping, we used a rotating wedge (45° circular angle) that extended to a maximum eccentricity of 7.5° visual angle (Figure 1B). There was 1 series (900 images) with 8 full clockwise rotations that lasted 54000 ms (100 images) each. The screen was

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3 blank during the first and last 27000 ms (50 images) of the series, except for the central fixation dot. Both  
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5 the rotating wedge and the expanding ring contained a checkerboard pattern with white and black squares  
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7 that reversed contrast every 125 ms.  
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11 The main stimulus was a random dot pattern with dots that translated at a constant speed of  $4.81^\circ/\text{s}$  within a  
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13 circular aperture with a radius of  $6.08^\circ$  visual angle (Figure 1C). The direction of translation changed  $360^\circ$   
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15 in cycles of 54000 ms (100 images). During one series the direction of translation rotated clockwise, in the  
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17 other series it rotated counter clockwise. There were 8 full rotations in translation direction during each  
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19 series of 900 images. The dots were static during the first and last 27000 ms (50 images) of each series.  
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23 The control stimulus consisted of 2 random dot patterns, one in the left, and one in the right hemifield,  
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25 within a circular aperture with a radius of  $6.08^\circ$  visual angle (Figure 1D). In one condition, the dots of the  
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27 two patterns were moving outwards, parallel to the horizontal meridian (always  $4.81^\circ/\text{s}$ ). In the other  
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29 condition, they were moving inwards, parallel to the horizontal meridian. There were 8 blocks of 19980 ms  
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31 (37 images) of each condition which were orderly alternated and separated by 12420 ms (23 images)  
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33 periods where all dots were static. Responses were measured along the horizontal and vertical meridian.  
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35 The control stimulus is less likely to induce shifts in spatial attention or eye movements than the main  
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37 stimulus.  
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41 The stimulus of the additional experiment was largely similar to the stimulus of the main experiment. The  
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43 important difference was an occlusion of part of the random dot pattern with grey bars with a width of  
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45  $0.71^\circ$  each, and a  $1.43^\circ$  gap between bars (Figure 1E). The random dot pattern was moving in blocks of  
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47 16200 ms (30 images) with a constant speed ( $4.81^\circ/\text{s}$ ) and direction. The direction of motion could be  
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49 upward, downward, leftward, or rightward and blocks of motion were always interrupted with 16200 ms  
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51 (30 images) periods where the dots were static. In the first session (960 images) the direction of motion was  
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53 always parallel to the bars, in the second session (960 images) the direction of motion was always  
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55 orthogonal to the bars. Furthermore, the radius of the stimulus was increased to  $7.50^\circ$ , as results from the  
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57 main experiment indicated that there were no spatial shifts in representation of the stimulus (see further  
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3 below). During the additional experiment, there was an attentional control task within the aperture at  
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5 central fixation. A white cross ( $0.25^\circ$  visual angle) was presented every 1000 ms for a duration of 300 ms.  
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7 During 25% of the presentations, one of the bars of the cross became an arrow (up, down, left, right) by the  
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9 placement of a small rectangle ( $0.05^\circ$  visual angle) at one of the extremities. Subjects had to press the  
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11 button on a button box (up, down, left, right) that corresponded to the indicated direction of the arrow.  
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17 Random dot patterns contained an equal number of white and black dots ( $0.14^\circ$  visual angle). On average,  
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19 there were 4300 dots visible at a particular moment in time. When dots reached the border of the pattern,  
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21 they were replotted at the other extremity.  
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#### 23 24 25 **Eye movements:**

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27 Eye movements were measured at 60 Hz during the main stimulus in 3 out of 12 subjects and using the  
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29 ASL EyeTrac 6 MR-compatible video based eye tracker (Applied Science Laboratories, Bedford, USA) at  
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31 the University of Birmingham. Blinks and low frequency drifts ( $<0.00926$  Hz.  $\sim 2$  cycles of the main  
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33 stimulus) were removed. At each time point during the stimulus, eye position and displacement were  
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35 recalculated in terms of eye position and displacement relative to the motion direction of the stimulus.  
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37 Saccades were detected by identifying any sample in which the velocity exceeded  $30^\circ/s$ .  
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#### 39 40 41 **Statistical Analysis:**

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43 All preprocessing steps were done using SPM5 (<http://www.fil.ion.ucl.ac.uk/spm/>). After realignment, the  
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45 functional images were coregistered and resliced to the FA27 volume, using the first functional volume as a  
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47 source. The T1 structural image was also coregistered to the FA27-image, thereby providing spatial  
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49 alignment between the structural image and the functional volumes. Low frequency noise in the fMRI data  
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51 was modeled and removed from the data using a GLM and a design matrix containing the mean of each  
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53 image, and 8 cosine functions forming a high-pass filter with a cutoff at  $8.2 \times 10^{-1}$  Hz.  
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3 For polar angle and eccentricity mapping, a vector was created that represented cyclic activation during  
4 presentation of wedges and rings (7200 ms activation every 54000 ms) and was convolved with a  
5 hemodynamic response function (Friston et al. 1995). The cross correlation between the fMRI data and this  
6 vector was calculated for every voxel and for 100 lags (0-99; i.e. every image within a cycle) and the peak  
7 cross correlation determined the receptive field location of the voxel in polar angle and eccentricity. Polar  
8 angle and eccentricity measures of voxels were interpolated to 8 steps (45° circular angle) and 5 steps  
9 (1.42° visual angle) respectively. The activated voxels ( $p < 0.05$ ; Bonferroni corrected) formed a visual field  
10 representation that consisted of 40 segments (8 x 5), which was further subdivided in V1, V2, V3, and MT+  
11 (see further below). For each subject, the average BOLD response was calculated in these segments during  
12 cycles of the main stimulus and the second control stimulus. Average BOLD responses were shifted 7  
13 images back in time to account for the delay of the hemodynamic response. Subsequently, responses for  
14 clockwise and counterclockwise changing translation direction were averaged and rescaled to 'translation  
15 direction' over the x-axis (0°-360°), and 'percent signal change' over the y-axis. Effects of translation  
16 direction on the BOLD response were analyzed for each segment using repeated measures General Linear  
17 Models (100 layers ~ number of images in each cycle) and results were Bonferroni corrected for the total  
18 number of tested segments in each comparison ( $p < 0.05$ ).

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37 Average BOLD responses during cycles of the control stimulus and the additional experiment were also  
38 generated for each segment. The amplitude of the responses were estimated by fitting a BOLD response  
39 model of block activation followed by a rest period (Friston et al. 1995).

#### 40 41 42 43 44 **Segmentation of retinotopic areas:**

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46 The T1 image was corrected for intensity inhomogeneities using the segmentation utility in SPM5  
47 (Ashburner and Friston 2005). The bias corrected T1 images were then imported in the Computerized  
48 Anatomical Reconstruction and Editing Tool Kit (CARET) (Van Essen et al. 2001). T1 images were  
49 resliced to a 1 mm isotropic resolution, manually placed in Talairach orientation, and subdivided in left and  
50 right hemisphere. All subsequent steps were done per hemisphere. The intensity of the grey/white matter  
51 border was determined, followed by automatic extraction of the cortex. A white matter segment was  
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3 generated and was automatically corrected for topological errors. Remaining topological errors were  
4 removed manually. A surface reconstruction was generated and inflated. Several cuts were applied on the  
5 inflated surface, amongst others along the calcarine fissure and the medial wall. The surface was flattened  
6 and geometric distortions were reduced. Results of the polar angle mapping were mapped to the anatomical  
7 surface using the 'enclosing voxel' algorithm. Retinotopic areas V1, V2, and V3 were manually segmented  
8 by drawing borders along the reversals in the change of the polar angle representation. The resulting flat  
9 segments were converted back to volumetric format and used as ROIs in further analysis.  
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19 For identification of MT+, the voxel time-series of the control stimulus were entered into a GLM, with a  
20 one factor representing BOLD activation during inward motion, and one factor representing BOLD  
21 activation during outward motion. A volume of t-values was generated for the contrast representing  
22 activation during both inward and outward motion. MT+ was defined as the bilateral clusters of significant  
23 voxels in the ascending limb of the inferior temporal sulcus ( $p < 0.05$ ; Bonferroni corrected)  
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### 31 **Results:**

#### 32 **Main Experiment:**

33 We presented translating motion that slowly changed direction (Figure 1C), and measured the BOLD  
34 response across the visual field representations of V1, V2, V3, and MT+, which were all subdivided in 40  
35 segments (8 polar angles \* 5 eccentricities). All except 3 of the total of 120 segments in V1, V2 & V3  
36 demonstrated a systematic group-wise effect on brain activation ( $F_{(99,1089)} > 1.60$ ;  $p < 0.05$ ). Thus, there were  
37 systematic anisotropies in V1, V2, and V3. However, there were no significant effects anywhere in MT+.  
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46 To further investigate the nature of the anisotropies, we averaged over eccentricities, and found a  
47 significant effect of motion direction in all 8 polar angle segments of V1, V2 and V3 ( $F_{(99,1089)} > 1.51$ ;  
48  $p < 0.05$ ), but not in MT+. The mean BOLD responses for each motion direction in the 8 polar angle  
49 segments of V1, V2, and V3 are depicted in figure 2. It can be seen that the direction bias in the BOLD  
50 response corresponds to enhanced radial motion sensitivity. The direction bias regularly rotates with polar  
51 angle relative to the fovea. These results show that the motion direction relative to the fovea is an important  
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3 determinant of the amplitude of the BOLD response. In areas V1, V2 and V3 BOLD responses were  
4 enhanced for centrifugal and centripetal motion, relative to tangential motion. In area MT we found no  
5 significant variation of the BOLD response as a function of motion direction.  
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11 For investigating effects of eccentricity on this bias, the BOLD responses per segment were first rescaled  
12 to motion direction relative to polar angle over the x-axis ( $0^\circ$ =centripetal motion,  $-90^\circ/90^\circ$ =tangential  
13 motion,  $-180^\circ/180^\circ$ =centrifugal motion), and subsequently averaged over the 8 polar angles per eccentricity.  
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15 The average responses per eccentricity and visual area are depicted in figure 3. There were significant  
16 effects of motion direction for all eccentricities of V1, V2 & V3 ( $F_{(99,1089)} > 1.47$ ;  $p < 0.05$ ), and these effects  
17 consisted of either a centrifugal and/or centripetal response biases. Again, no significant effects were  
18 observed in MT+.  
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27 To estimate how the amplitudes of the centrifugal and centripetal response biases changed with eccentricity  
28 in the retinotopic areas, the responses in each subject were fitted with a linear combination of two peaks  
29 (based on a cosine function) using a multiple regression analysis. The amplitude fits of the centrifugal and  
30 centripetal response are depicted in figure 4. Effects of eccentricity (5 layers; 5 steps of  $1.42^\circ$ ), motion  
31 direction (2 layers; centrifugal/centripetal motion), and retinotopic area (3 layers; V1, V2 & V3) were  
32 analyzed using a repeated measures general linear model. The test revealed a main effect of motion  
33 direction ( $F_{(1,11)} = 30.99$ ;  $p < 0.001$ ), and an interaction effect between eccentricity and motion direction  
34 ( $F_{(4,44)} = 51.33$ ;  $p < 0.001$ ). Centripetal biases were larger than centrifugal biases, and this difference between  
35 centrifugal and centripetal biases depended on eccentricity. Between  $0.40^\circ$  and  $1.82^\circ$ , and between  $4.66^\circ$   
36 and  $7.50^\circ$ , there was a combination of a centrifugal and centripetal bias. Between  $1.82^\circ$  and  $4.66^\circ$ , there  
37 was a large centripetal bias and nearly absent centrifugal bias.  
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#### 50 **Control Experiment:**

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52 As the full-field stimulus (Figure 1C) that we used could have induced eye movements or shifts in spatial  
53 attention, we investigated whether the same effects were also present during the control stimuli (Figure 1D  
54 and 1E). In the control stimulus the visual field was bisected across the vertical meridian and we showed  
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opponently moving random dot patterns in the two halves. Together with the absence of motion in the central 0.40° degrees this minimizes consistent effects of eye movements or shifts in attention. We investigated the BOLD responses in the segments along the horizontal meridian during this stimulus (Figure 5). Amplitude fits of the BOLD response were entered into a repeated measures GLM (motion direction \* eccentricity \* retinotopic area; similar as for the main stimulus). The results followed the same pattern as for the main stimulus. This consisted of larger responses for centrifugal motion at the lowest eccentricity, and larger responses for centripetal biases at higher eccentricities. The differences between centrifugal and centripetal motion were somewhat larger during the control stimulus than during the main stimulus (88% in V1, 35% in V2, and 19% in V3). Again, there were no differences in MT+.

#### **Additional Experiment:**

In the additional experiment, the motion stimulus was interrupted either parallel to the path of motion or orthogonal to the path of motion (1E). BOLD responses were measured along the horizontal and vertical meridians for motion parallel to the bars and motion orthogonal to the bars. BOLD responses were classified as centrifugal, centripetal, or tangential, dependent on the position in the visual field relative to the motion direction. BOLD responses were averaged over retinotopic areas (V1, V2 & V3), as the results of the main experiment and control experiment demonstrated no qualitative differences in directional biases between visual areas. Amplitude fits of the BOLD response were entered into a repeated measures GLM (motion direction \* eccentricity \* condition (parallel/orthogonal interruption). There was a significant interaction effect between motion direction and condition ( $F_{(2,72)}=17.44$ ;  $p<0.001$ ) and a significant interaction effect between motion direction, eccentricity, and condition ( $F_{(8,72)}=3.24$ ;  $p=0.003$ ). These effects were best described as the presence of a centripetal motion direction bias when the stimulus was interrupted parallel to the path of motion, but absent direction biases when the stimulus was interrupted orthogonally to the path of motion (except for the lowest eccentricity, where there were no biases in both conditions).

Furthermore, the performance on the attentional control task during the additional experiment was not different for the stimulus with interruptions parallel or orthogonal to the path of motion considering reaction times (mean RT parallel  $\pm$  SD = 782  $\pm$  99 ms; mean RT orthogonal  $\pm$  SD = 776  $\pm$  101 ms; paired

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3  $t_{(7)}=1.20$ ;  $p=.27$ ) or the proportion of correct responses (mean correct parallel  $\pm$  SD =  $0.86 \pm 0.11$ ; mean  
4 correct orthogonal  $\pm$  SD =  $0.87 \pm 0.09$ ; paired  $t_{(7)}= -0.70$ ;  $p=0.50$ ). Subjects reported that they were fully  
5 engaged in optimally performing the task. Behavioral data of two subjects was lost due to a defective  
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### Eye movement control:

In addition to the split-field stimulus as a control we also measured eye-movements for three subjects during the main experiment. Eye movement recordings showed no deviations in fixation position with changing motion direction (mean deviation from central fixation was  $0.04^\circ$  visual angle, in the direction of '+ $14^\circ$  of polar angle relative to the motion direction'). In addition, no saccades (see Methods) were detected in all three subjects for the entire duration of the stimulus.

To further analyze if there was a systematic relationship between motion direction and direction of micro-saccades or smooth pursuit (e.g. as a part of optokinetic nystagmus), the absolute displacement parallel to the direction of motion and perpendicular to the direction of motion was calculated between each sample. Nystagmus e.g. would on average induce a larger amount of eye displacement parallel to the path of motion compared to orthogonal to the path of motion. This analysis revealed a mean displacement during the stimulus of  $0.12^\circ$ /sample parallel to the motion direction, and  $0.12^\circ$ /sample perpendicular to the direction of motion, indicating no relation between direction of eye movements and motion direction. The three subjects with simultaneous eye movement acquisition had fMRI results that were largely similar to the group mean (Figure 4)

### Discussion:

We found strong evidence for directional anisotropies of motion responses across the visual field representations of V1, V2 and V3 when observing whole field coherent translating motion. In all three retinotopic areas, the amplitude of the motion response depended on the motion direction relative to polar angle and the eccentricity relative to the fovea. All biases consisted of enhanced responses for centrifugal and centripetal motion, relative to tangential motion. The centripetal bias was present for all except very low eccentricities. The centrifugal bias was present for low eccentricities, and for eccentricities beyond

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3  $\pm 4.5^\circ$ . The response to centripetal motion was larger than the response to centrifugal motion, except for low  
4 eccentricities. The results from the control experiment, where the left and right visual field contained  
5 opponent motion directions, confirmed the results from the main experiment. We did not observe any  
6 significant motion direction biases in MT+. Our additional experiment showed that these directional biases  
7 did not occur when the motion stimulus was interrupted orthogonally to the path of motion.  
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15 On first sight, the current finding of a radial motion bias is unexpected. Motion perception of gratings and  
16 random dot patterns are both thought to be based on orientation detection in space and time (Skottun et al.  
17 1994). As it is known that the preferred motion directions of cells is orthogonal to their orientation  
18 preference (Albright, 1984), the previously reported radial orientation bias should therefore predict a  
19 tangential motion bias (Sasaki et al. 2006). In our study we found the opposite. However, the additional  
20 experiment shows that it is highly unlikely that the directional biases are related to local anisotropies in  
21 orientation sensitivity. If the currently observed directional biases were based on classical receptive field  
22 effects, then the additional stimulus would have produced a directional bias whether the stimulus was  
23 interrupted parallel or orthogonal to the direction of motion. Even when the stimulus was interrupted  
24 orthogonally, the length of each motion path was  $1.43^\circ$ , thereby still far exceeding receptive field sizes in  
25 the central  $15^\circ$  of the visual fields in V1 and V2 (Dumoulin and Wandell 2008). Directional biases however  
26 completely disappeared when the length of the motion path was  $1.43^\circ$ .  
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41 Anisotropies in extraclassical receptive field effects are thus producing the bias, which means either long  
42 range horizontal (lateral) connections within the visual areas, or interareal feedback connections. Although  
43 fMRI does not have the temporal resolution to completely resolve this issue, we believe that the data from  
44 the additional experiment indicate that anisotropies in horizontal connections are the most likely candidate.  
45 Interareal feedback signals would originate from areas upstream containing motion sensitive neurons with  
46 large receptive field sizes. Neurons that are responding to motion in a large portion of the visual field  
47 would be largely indifferent to whether motion is interrupted parallel or orthogonal to the path of motion,  
48 as the total amount of motion information across large portions of the visual field remains the same.  
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56 Anisotropies were however only observed for interruptions parallel to the path of motion. Horizontal  
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3 connections would be better suited to generate modulations that are specifically dependent on the length of  
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5 the path of motion.  
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9 Horizontal connections in visual cortex have been implicated in the facilitation of the detection of spatial  
10 contours based on signals from local orientation detectors (Gilbert and Wiesel 1983; Schmidt et al. 1997).  
11 Their role in visual motion processing has been far less investigated. These lateral connections could play a  
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13 role in motion information integration across regions beyond the classical receptive field sizes, which could  
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15 contribute to solving the aperture problem. Guo et al. found activation modulation in V1 neurons when the  
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17 stimulation within the classical receptive field was identical, but the global direction of the stimulus  
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19 movement was different (Guo et al. 2006). Such connections could also play a role in defining shapes of  
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21 objects that are defined by motion. The current study would predict that the strength of modulations  
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23 through horizontal connections would be different along the path of motion compared to orthogonal to the  
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25 path of motion. Moreover, our study suggests that modulations along the path of motion are anisotropic  
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27 across the visual field.  
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33 A couple of factors could have confounded the current results. Although eye movements are unlikely to  
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35 have accounted for the data, the motion stimulus could have induced covert shifts in spatial attention.  
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37 Spatial attention is known to locally enhance the visual response at the focus of attention (Tootell et al.  
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39 1998; Jack et al. 2006). The single translating random dot pattern may have induced drifts in the focus of  
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41 spatial attention, which could account for the currently observed data. However, there are several  
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43 arguments that oppose such an explanation. Biases were also present when subjects were fully engaged in a  
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45 in an attentional control task. Furthermore, attentional shifts would most likely enhance the signal in the  
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47 direction of motion as a result of attentional tracking, and not opposite to the direction of motion as was  
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49 observed in this study. In addition, during the control stimulus where two opponently moving random dot  
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51 patterns were presented simultaneously, there were similar differences between centrifugal and centripetal  
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53 motion, although such a stimulus would be far less effective in inducing attentional shifts. Although it is  
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55 technically possible that this stimulus would have induced two separate attentional spotlights, divided  
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57 attention roughly halves the amount of activation per spotlight (McMains and Somers 2004). This would  
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3 result in lower biases for the control stimulus compared to the main stimulus, but we observed the opposite.  
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5 Furthermore, the additional experiment produced only biases when the stimulus was interrupted parallel to  
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7 the path of motion, whereas both the stimulus with orthogonal and parallel interruptions would to some  
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9 extent be effective in inducing attentional shifts.  
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13 Psychophysical studies have extensively addressed direction biases in motion sensitivity. These studies  
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15 have predominantly tested and found differences between centrifugal and centripetal motion. While some  
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17 studies have reported increased sensitivity for centripetal motion (Edwards and Badcock 1993; Raymond,  
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19 1994; Giaschi et al. 2007), other studies have reported a centrifugal bias (Scott et al. 1966; Georgeson and  
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21 Harris 1978; Edwards and Badcock 1993; Lewis and McBeath 2004). However, see also van de Grind et  
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23 al., who observed a tangential motion bias at eccentricities beyond 24° when measuring detection  
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25 thresholds for different motion directions across the visual field (van de Grind et al. 1993). This apparent  
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27 conflict in results may originate from differences in the eccentricity at which the motion direction biases  
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29 are measured. Centripetal biases have been reported for stimuli that were presented at relatively low  
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31 eccentricities and the centripetal bias decreases with increasing eccentricity (Edwards and Badcock 1993).  
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33 Contrary to the centripetal bias, the centrifugal bias increased with increasing eccentricity (Ball and Sekuler  
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35 1980). The larger centripetal bias in this study was observed at relatively low eccentricities, which is thus in  
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37 line with previous psychophysical studies.  
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40 Surprisingly, in our study we did not observe any effects of motion direction on activation in MT+ in spite  
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42 of it's well known involvement in perception of coherent motion (Braddick et al. 2000; Braddick et al.  
43  
44 2001). Contrary to our findings, Giaschi et al. (Giaschi et al. 2007) measured activation differences in MT+  
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46 during horizontal and vertical centrifugal and centripetal motion and observed a centripetal response bias.  
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48 This contradiction could be the result of the difficulties that are present when defining the retinotopy of  
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50 MT+ (Smith et al. 2006). However, the control stimulus that was used in the current experiment was  
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52 roughly similar to a stimulus that was used by Giaschi et al., and measurement of centrifugal vs. centripetal  
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54 response biases with this stimulus does not depend on the retinotopy of MT+. Still, our control stimulus did  
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56 not produce a centripetal response bias. A more likely other explanation is that the motion stimuli of  
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3 Giaschi et al. were presented at 25% and 75% coherence level respectively, compared to 100% in our  
4 study. The centripetal motion bias that they observed in MT+ was only significant for stimuli near the  
5 detection threshold (25% coherence). Detection of motion at low coherence levels may require attention to  
6 motion which enhances activation levels in MT+. Thus direction biases could very well be present in MT+,  
7 but not for fully coherent motion stimuli as in our experiment. For early visual cortex, we would expect no  
8 qualitatively different results for incomplete coherence as these areas are thought to be less influenced by  
9 attention. Furthermore, incomplete coherence (and also limited lifetime) of dots does not truly interrupt a  
10 motion stimulus. An uninterrupted motion stimulus will produce the directional bias.  
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21 The currently observed directional anisotropy of the motion response has implications for the interpretation  
22 of earlier studies in which perceived motion directions were predicted with multivoxel pattern analysis  
23 (Kamitani and Tong 2006; Serences and Boynton 2007a; Serences and Boynton 2007b). Kamitani and  
24 Tong have argued that the use of multivoxel pattern analysis provides the ability to detect activation  
25 differences as a result of random fluctuations in the number of columns within a voxel that are tuned for a  
26 particular motion direction (Kamitani and Tong 2005; Kamitani and Tong 2006). Although the acquired  
27 form of our data did not allow for multivoxel pattern analysis, our results suggest that large scale  
28 anisotropies across the visual field may have contributed to decoding in these studies. This view is further  
29 supported by the finding that discrimination with support vector machines was worse for opposing motion  
30 directions, and worse in MT+ (Kamitani and Tong 2006). Both observations are in line with the notion that  
31 the currently observed anisotropies have contributed to the results of previous decoding studies, in addition  
32 to possible subvoxel inhomogeneities. The removal of these global effects requires a full correction per  
33 presented motion direction for the mean activation within each eccentricity by polar angle segment of the  
34 visual field.  
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50 In conclusion, we found consistent anisotropies of the BOLD response across the visual field  
51 representations of V1, V2 & V3, which are most likely related to anisotropies in horizontal connections.  
52 Horizontal connections could thus make a substantial contribution to the fMRI signal in visual cortex. It  
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3 would be interesting to see whether the contribution of these horizontal channels can also be isolated for the  
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5 perception of orientations.  
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**Legends:**

Figure 1:

Schematics of the presented stimuli: Colored arrows and lines are for illustration purposes only. A: An expanding circle for eccentricity mapping. B: A clockwise rotating wedge for polar angle mapping. C: A moving random dot pattern which slowly changed translation direction in cycles of 54000 ms. During the first functional series the translation direction of dots changed clockwise (as indicated by the dotted green arrows), in the second series it changed counter clockwise D: Two random dot patterns, one in each hemifield (the dotted green line marks the border). During one condition, dots were moving outwards (blue arrows), during the other condition they were moving inwards (red arrows), parallel to the horizontal plane. E: A random dot pattern that was regularly interrupted. In one condition the interruptions were parallel to the path of motion (blue arrow), in the other condition they were orthogonal to the path of motion (red arrow).

Figure 2:

Mean (n=12) BOLD responses during 360° cycles of motion directions for the 8 polar angle segments of V1, V2 & V3. There was an effect of motion direction on the BOLD response in all these segments ( $p < 0.05$ ; Bonferroni corrected). The minimum in each graph corresponds to the lowest response within each segment. Gridlines in the radial plots indicate 0.5 % signal change relative to the minimum BOLD response. All average responses could be fitted by a combination of a centrifugal and centripetal response bias. Note that these plots are not meant to represent actual direction tuning curves of the segments. Due to the dispersion of the BOLD response relative to the neural response, underlying neural response biases may be more specifically tuned. In addition, the plotted BOLD response is not absolute, but relative to the minimum response in each segment. In MT+ (not displayed) there were no significant effects of motion direction in any of the 8 polar angle segment.

Figure 3:

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3 Average BOLD response ( $n=12$ ) as a function of the motion direction relative to centripetal motion for  
4 different eccentricities in areas V1, V2 & V3, and MT+. The  $0^\circ$  label signifies centripetal motion, and  
5  $180^\circ/-180^\circ$  signifies centrifugal motion. Different colored lines indicate different eccentricities. Bars  
6 indicate standard error of the mean. The amplitude of the BOLD response is in percent signal change  
7 relative to the mean signal for all stimulated motion directions. Note that the outer ring corresponds to the  
8 population receptive field where the centre is located outside the border of the stimulus. This was to check  
9 whether anisotropies could originate from spatial shifts in the representation of the stimulus, which are  
10 suggested in previous research (Whitney et al. 2003; Whitney and Bressler 2007). As anisotropies are not  
11 larger at the borders of the stimulus, this explanation is very unlikely.  
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23 Figure 4:

24 Average amplitudes ( $n=12$ ) of the centrifugal and centripetal response biases as a function of eccentricity in  
25 areas V1, V2 & V3 as estimated by fitting cosine functions. Bars indicate standard error of the mean.  
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27 Dotted lines represent the mean effects of the 3 subjects that performed the task with simultaneous  
28 acquisition of eye movement data.  
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35 Figure 5:

36 Average BOLD responses during presentation of the control stimulus (Figure 1D) for different  
37 eccentricities in the segments along the horizontal meridian in V1, V2, V3 & MT+ ( $n=12$ ). During the first  
38 19980 ms of each series, the two random dot patterns were either moving inward or outward. During the  
39 last 12420 ms, the random dot patterns were static. Error bars indicate standard error of the mean. The  
40 eccentricity between  $1.82^\circ$  and  $3.24^\circ$  of MT+ was not represented in all subjects, resulting in unreliable  
41 estimates.  
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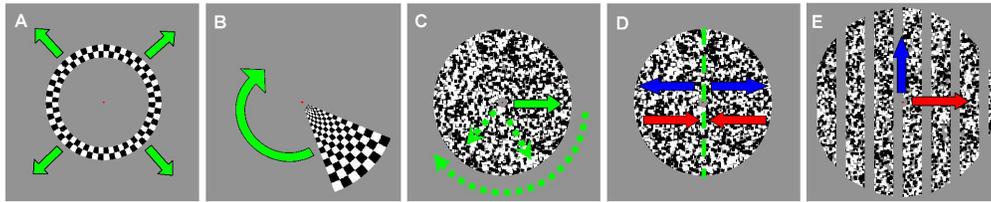
50 Figure 6:

51 Average BOLD responses ( $n=10$ ) during presentation of the additional stimulus (Figure 1E) for different  
52 eccentricities for motion parallel to the bars (6A) and motion orthogonal to the bars (6B). Responses are the  
53 average over all meridians (horizontal & vertical) and visual areas (V1, V2, V3). During the first 16800 ms  
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of each series, the random dot pattern was moving. During the last 16800 ms, the random dot pattern was static. Error bars indicate standard error of the mean.

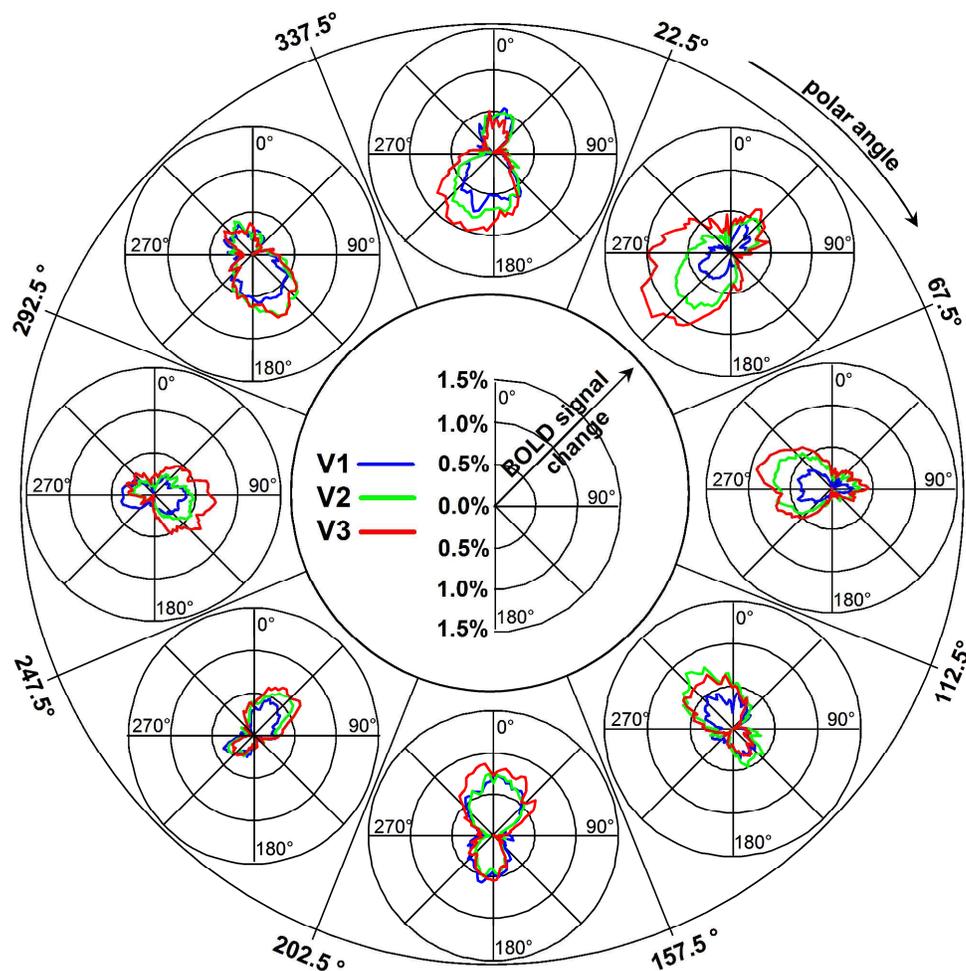
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Schematics of the presented stimuli: Colored arrows and lines are for illustration purposes only. A: An expanding circle for eccentricity mapping. B: A clockwise rotating wedge for polar angle mapping. C: A moving random dot pattern which slowly changed translation direction in cycles of 54000 ms. During the first functional series the translation direction of dots changed clockwise (as indicated by the dotted green arrows), in the second series it changed counter clockwise. D: Two random dot patterns, one in each hemifield (the dotted green line marks the border). During one condition, dots were moving outwards (blue arrows), during the other condition they were moving inwards (red arrows), parallel to the horizontal plane.

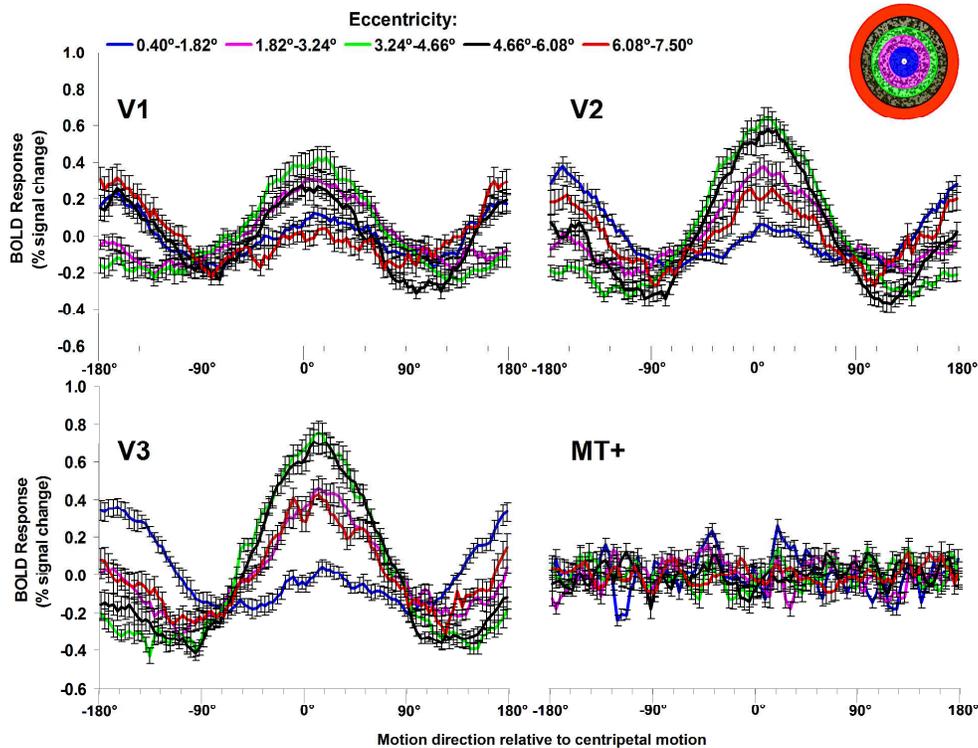
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Peer Review



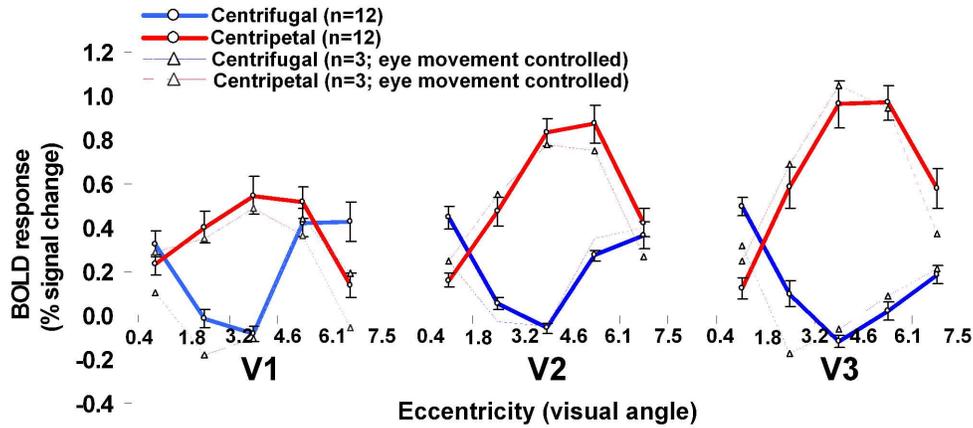
Mean ( $n=12$ ) BOLD responses during 360° cycles of motion directions for the 8 polar angle segments of V1, V2 & V3. There was an effect of motion direction on the BOLD response in all these segments ( $p<0.05$ ; Bonferroni corrected). The minimum in each graph corresponds to the lowest response within each segment. Gridlines in the radial plots indicate 0.5 % signal change relative to the minimum BOLD response. All average responses could be fitted by a combination of a centrifugal and centripetal response bias. Note that these plots are not meant to represent actual direction tuning curves of the segments. Due to the dispersion of the BOLD response relative to the neural response, underlying neural response biases may be more specifically tuned. In addition, the plotted BOLD response is not absolute, but relative to the minimum response in each segment. In MT+ (not displayed) there were no significant effects of motion direction in any of the 8 polar angle segment.

175x172mm (600 x 600 DPI)



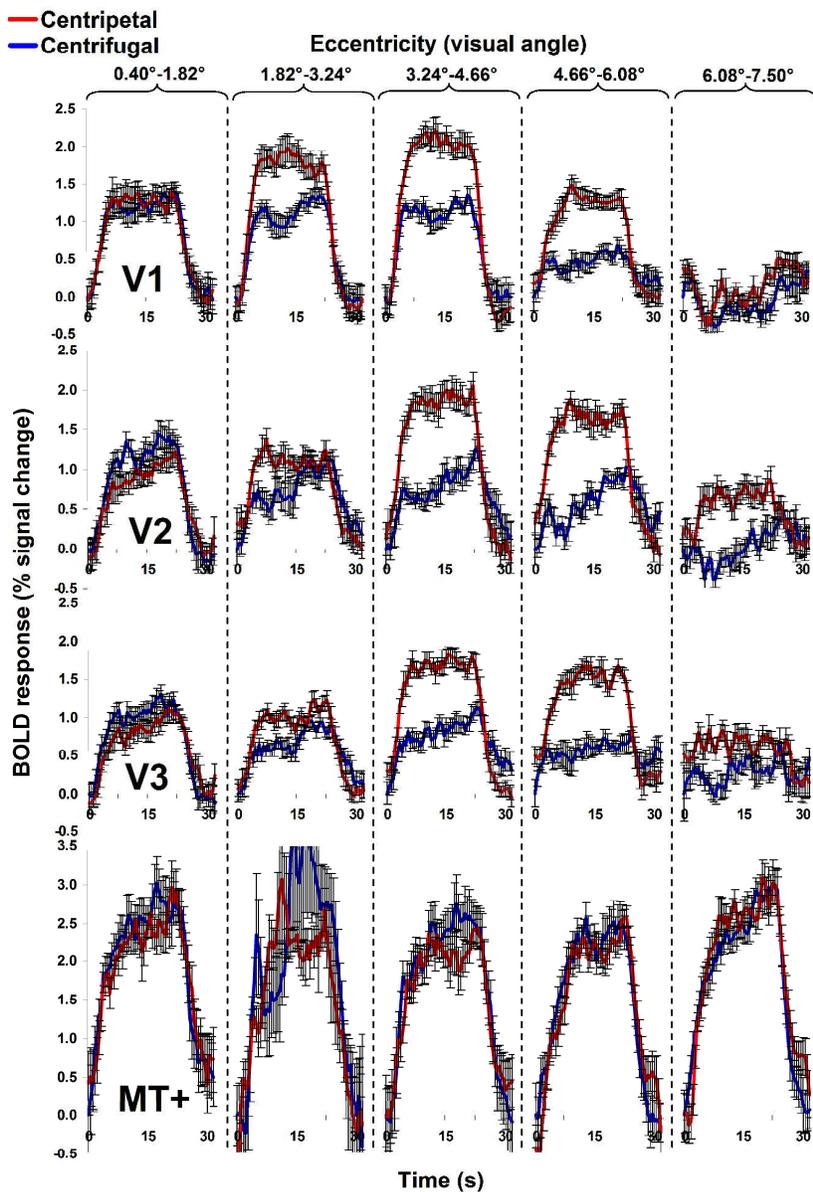
Average BOLD response ( $n=12$ ) as a function of the motion direction relative to centripetal motion for different eccentricities in areas V1, V2 & V3, and MT+. The 0° label signifies centripetal motion, and 180°/-180° signifies centrifugal motion. Different colored lines indicate different eccentricities. Bars indicate standard error of the mean. The amplitude of the BOLD response is in percent signal change relative to the mean signal for all stimulated motion directions. Note that the outer ring corresponds to the population receptive field where the centre is located outside the border of the stimulus. This was to check whether anisotropies could originate from spatial shifts in the representation of the stimulus, which are suggested in previous research (Whitney et al. 2003; Whitney and Bressler 2007). As anisotropies are not larger at the borders of the stimulus, this explanation is very unlikely.

166x130mm (600 x 600 DPI)



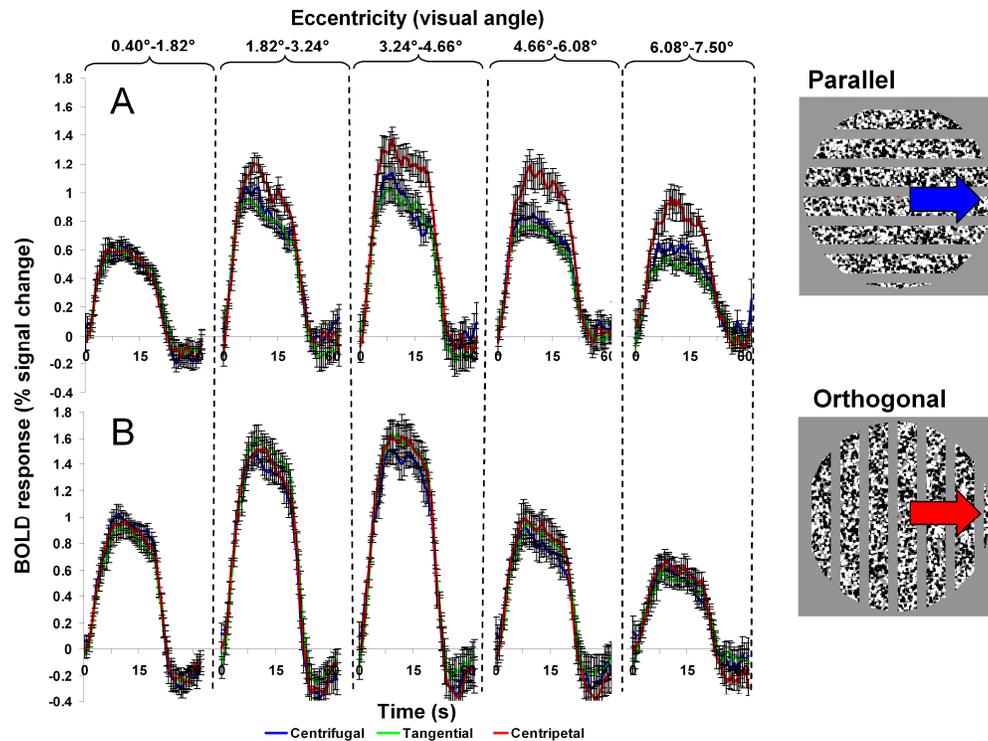
Average amplitudes (n=12) of the centrifugal and centripetal response biases as a function of eccentricity in areas V1, V2 & V3 as estimated by fitting cosine functions. Bars indicate standard error of the mean. Dotted lines represent the mean effects of the 3 subjects that performed the task with simultaneous acquisition of eye movement data.

175x89mm (600 x 600 DPI)



Average BOLD responses during presentation of the control stimulus (Figure 1D) for different eccentricities in the segments along the horizontal meridian in V1, V2, V3 & MT+ (n=12). During the first 19980 ms of each series, the two random dot patterns were either moving inward or outward. During the last 12420 ms, the random dot patterns were static. Error bars indicate standard error of the mean. The eccentricity between 1.82° and 3.24° of MT+ was not represented in all subjects, resulting in unreliable estimates.

175x246mm (600 x 600 DPI)



34 Average BOLD responses ( $n=10$ ) during presentation of the additional stimulus (Figure 1E) for  
 35 different eccentricities for motion parallel to the bars (6A) and motion orthogonal to the bars (6B).  
 36 Responses are the average over all meridians (horizontal & vertical) and visual areas (V1, V2, V3).

37 During the first 16800 ms of each series, the random dot pattern was moving. During the last  
 38 16800 ms, the random dot pattern was static. Error bars indicate standard error of the mean.

39 175x134mm (600 x 600 DPI)

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