

Different spatial organizations of saccade related BOLD-activation in parietal and striate cortex

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Abstract

Voluntary saccades performed in total darkness provide the opportunity to investigate the brain system active during saccades without confounding effects caused by the saccade induced shifts of the retinal image. Using this approach saccade related activation has been demonstrated not only in parietal but also in striate cortex. Currently no information is available about the reference frame in which this activation is represented in parietal and in striate cortex. However, knowledge about how the brain codes spatial information about saccades in the absence of visual input is potentially relevant to our understanding of visually guided behaviour. The present study combines functional magnetic resonance imaging (fMRI) with simultaneous electrooculogram-recordings to provide evidence that volitional saccades executed in total darkness are represented in a retinotopic reference frame in a parietal brain area, the putative homologue of human LIP, and in a head/body centred egocentric reference frame in human V1. The potential co-existence of retinotopic and egocentric space representations in the primary visual cortex indicates that V1 may be involved in visuo-motor integration.

Section: Cognitive and Behavioral Neuroscience

Keywords: saccades, retinotopic reference frame, egocentric reference frame, parietal cortex, striate cortex, functional magnetic resonance imaging

Abbreviations: fMRI = functional magnetic resonance imaging; BOLD = blood oxygenation level dependent; EOG = electrooculogram;

1. Introduction

Every second we perform several saccades, fast ballistic eye movements, to reorient our centre of regard to a new target in the environment which may then become a target of yet another motor act, for example a grasp. Both motor acts require visuo-motor coordination but with different spatial organization. While saccades are planned and executed in a retinotopic reference frame, grasps are easily planned and executed in an egocentric, head body centred reference frame. Because saccades displace the origins of these reference frames relative to each other it becomes essential for visuo-motor coordination that saccade related brain activity is coded in retinotopic as well as in egocentric reference frames in the brain.

Recent functional magnetic resonance imaging (fMRI) studies in humans demonstrated retinotopically organized saccade related activation in parietal cortex (Schluppeck et al., 2005; Sereno et al., 2001) in a brain area that is the putative homologue to monkey LIP (Merriam et al., 2003; Sereno et al., 2001). Moreover, saccade related activation has been demonstrated in single neurons in striate cortex in monkey (Bartlett et al., 1976; Duffy and Burchfiel, 1975), a brain area considered as primary sensory. Human fMRI-studies found saccade related modulation of V1 activation even in the absence of visual input (Bodis-Wollner et al., 1999; Bodis-Wollner et al., 1997; Sylvester et al., 2005; 2006), suggesting a role of V1 in a saccade related brain network. What is currently unknown is whether saccade related activation in striate cortex reflects an egocentric or a retinotopic reference frame. The visual environment is represented retinotopically in primary visual cortex (Inouye, 1909; Talbot and Marshall, 1941; Tootell et al., 1988; Sereno et al., 1995; Engel et al., 1997). If V1 represented saccade related activation in an egocentric head/body centred reference frame it could serve as a first integration stage for

visuo-motor coordination. Accordingly, several models of visuo-motor coordination and perisaccadic neuronal processing, suppose that retinotopically and egocentrically coded neuronal information converge at early visual processing stages (Pouget et al., 1993; Quaia et al., 1998; Zipser and Andersen, 1988). However, such convergence has not been shown until now in V1.

In the present study we investigated perisaccadic hemodynamic activity in a parietal area and in striate cortex using event-related fMRI. Saccades were performed in total darkness to avoid confounds of pure saccadic activation with visual input related effects. This is important because many brain areas activated around saccades are also activated by visual input (Andersen et al., 1990; Wurtz and Mohler, 1976a; Wurtz and Mohler, 1976b). The results were analyzed in retinotopic and in egocentric reference frames. Fig. 1 illustrates the orthogonal difference of saccades coded in retinotopic versus egocentric coordinates. Our results indicate that V1 codes saccades in egocentric coordinates when visual input is absent and our data confirm previous reports that an area in parietal cortex codes saccades in a retinotopic reference frame (Duhamel et al., 1992; Schluppeck et al., 2005; Sereno et al., 2001). Our findings are germane for theories of visuo-motor integration that deal with the problem of eye movement induced relative shifts of the retinotopic reference frame coding visual space and the egocentric (head/body centered) reference frame coding motor space (e.g. Andersen and Buneo, 2003; e.g. Pouget and Snyder, 2000).

Insert Figure 1 here

2. Results.

2.1 Saccades in darkness

During fMRI-scanning participants performed saccades in total darkness to

remembered locations in a fixed sequence. The characterization of the same saccade as “left” or “right” can be in the retinotopic and egocentric head/body centered reference frame. This differentiation permits the analysis of the underlying neural activity with respect to the reference frame (detailed in Fig. 1). For example, a saccade starting at the left periphery and directed towards the horizontal head body midline would be a *rightward* directed saccade in the retinotopic reference frame, but this saccade is executed within the *left* egocentric hemispace (Fig. 1, saccade 1).

We measured eye movements during the fMRI measurements using the electrooculogram (EOG). The advantage of this method is that it does not require any light sources. The scanner related artefacts in the EOG time series were removed using a template matching method implemented in a commercial software package (BrainVision Analyzer, Brainproducts, Munich, Germany). Fig. 2. demonstrates the effectiveness of the method for a sequence of saccades.

Insert Figure 2 here

The start and end positions derived from the EOG as well as the saccade amplitudes and velocities were similar over the four saccade types (from the head/body midline to the left, from the left back to the midline, from the midline to the right, and from the right to the midline, see Fig. 1). The numerical results are shown in Table 1. On average 930 saccades were included in the analysis of the blood-oxygenation-level-dependent (BOLD)-responses for each of the four subjects.

Insert Table 1 here

2.2 MRI analysis. The analysis focused on the spatial organisation of saccade related activity in the parietal and striate cortices known to be retinotopically organized (Engel et al., 1997; Inouye, 1909; Sereno et al., 1995; Talbot and

Marshall, 1941; Tootell et al., 1988) and modulated in association with volitional saccades (Bodis-Wollner et al., 1997; Duhamel et al., 1992; Merriam et al., 2003; Schluppeck et al., 2005; Sereno et al., 2001; Sylvester et al., 2005; 2006).

Insert Figure 3 here

BOLD-activation with respect to retinotopic coordinates (saccades (1 & 2) vs. (3 & 4)) was consistently higher in the parietal cortex contralateral to the saccade direction in each subject (Fig. 3A). In Fig. 3B these BOLD-differences are overlaid on the individual brains of three subjects. Response clusters are located in the vicinity of the superior end of the occipito-parietal sulcus or slightly anterior to it in the Precuneus, in BA 7. The respective mean Talairach-coordinates over the three subjects are in the left hemisphere: -18.6, -68.8, 44.8, and 16.2, -69.5, 46.7 in the right hemisphere. These localizations fall close to the previously reported coordinates of the putative human homologue of LIP (Schluppeck et al., 2005; Sereno et al., 2001). The parietal cortex ipsilateral to the saccade direction showed no saccade-related BOLD-activation. These results confirm that an anatomically defined portion of the posterior parietal cortex codes perisaccadic activity in reference to the fixation centred retinotopic map (Duhamel et al., 1992; Schluppeck et al., 2005; Sereno et al., 2001). However, because these previous studies did not attempt to separate saccadic responses in retinotopic versus egocentric reference frames the conclusion about retinotopic coding in this parietal area was, although widely accepted, not necessarily evident. By discriminating between these reference frames we could provide further support and confirm the previous interpretation that the posterior parietal cortex codes saccades related activity in a retinotopic reference frame. The fundamentally new finding in the present study is that in contrast to the parietal

cortex V1 codes saccades in an egocentric reference frame.

Insert Figure 4 here

Insert Figure 5 here

The evaluation of BOLD-activation with respect to egocentric coordinates revealed higher occipital activations ipsilateral to the head/body hemifield in which the saccade was performed in every single subject (in eight out of eight hemispheres, Fig. 4A). The probability to obtain these results in eight out of eight hemispheres is $p < 0.004$ in a Binomial-test. Activation with reference to an egocentric reference frame fell close to the calcarine sulcus where striate cortex is located. For more precise localization of the saccade related BOLD-effects we determined the borders of V1 for three of the four subjects using retinotopic mapping. Fig. 5 shows example maps with the borders of V1, V2, and V3 delineated by an automated algorithm (see Experimental Procedure). We found that egocentric activation modulation fell indeed within area V1 (Fig. 4B) in every hemisphere investigated. The saccade related BOLD-averages show that saccades in ipsilateral egocentric hemispace increase the BOLD-response in V1 whereas saccades in contralateral egocentric hemispace slightly decrease the V1 BOLD-level (Fig. 6). We also tested if the average BOLD modulation in V1 discriminates between saccades within the left and the right hemifield of the egocentric reference frame. Therefore, we compared the group BOLD response between saccades performed within different egocentric hemispaces but with same retinotopic direction (saccades (1 vs 2) and (4 vs 3)). We found that the BOLD modulation in V1 indeed discriminates between saccades performed in the left and the right egocentric hemifield (left occipital hemisphere: $t(7)=2.6$; $p < 0.05$; right occipital hemisphere: $t(7)=2.6$; $p < 0.05$). Moreover, the egocentric saccade related

BOLD effects were almost exclusively lateralized to the ipsilateral hemisphere. Even with a relatively liberal threshold of $t > 2.5$ perisaccadic modulation was found in 3265 voxels in the hemisphere ipsilateral to the visual hemifield in which the saccades were performed. Only 152 voxels were observed in the contralateral V1. Detailed retinotopic eccentricity measurements in six hemispheres revealed both foveal (within 5 deg diameter) and extrafoveal V1 saccade related activation (Fig. 4B). If perisaccadic V1 activation represented solely fixational processes then the BOLD-effects would have been restricted to the foveal representation only. However, this is clearly not the case.

As an additional control, we evaluated whether the retinotopic saccade direction (see Fig. 1) had an influence on the BOLD-response in the striate cortex. We calculated the BOLD-differences between inward vs. outward saccades (saccades (1 vs. 4) & (3 vs. 2)) for the hemisphere ipsilateral and contralateral to the egocentric hemifield in which the saccades were executed. A significant paired t-test over subjects would suggest that the BOLD-response in V1 can be used to discriminate between the retinotopic directions of the saccades. However, we found no such evidence (ipsilateral ($t(7) = -1.6$, $p > 0.1$; contralateral ($t(7) = 0.4$, $p > 0.1$)). This result confirms the conclusion that V1 codes saccade related activity in an egocentric reference frame.

Insert Figure 6 here

3. Discussion.

Our results reaffirm that human V1 (Bodis-Wollner et al., 1999; Bodis-Wollner et al., 1997; Sylvester et al., 2005; Sylvester et al., 2006) and an area in parietal cortex (Schluppeck et al., 2005; Sereno et al., 2001) are modulated by voluntary saccades,

even when they are decoupled from visual input in absolute darkness. Because the saccades were executed in absolute darkness it can be ruled out that the results reflect an effect of visual input shifted on the retina by the saccade. The perisaccadic BOLD-activity we found is most likely related to the execution of the saccade per se. Our novel analysis of a routine saccadic paradigm allowed us to separate out retinotopic vs. egocentric reference frames because the same saccades elicit different activations when represented in different reference frames in the brain. Our results show that visual input independent perisaccadic activity is coded differently in V1 and in the parietal cortex. In concordance with previous studies we found that perisaccadic activity is represented in a retinotopic reference frame in the parietal cortex (Duhamel et al., 1992; Schluppeck et al., 2005; Sereno et al., 2001). In V1, however, we found that saccade related BOLD-modulation is represented in an egocentric reference frame.

Attentional factors are unlikely to explain our results in V1 because spatial attention is coded in a retinotopic reference frame in both parietal and striate cortex (Silver et al., 2005; Tootell et al., 1998), and we found retinotopic saccade related activation in parietal cortex but not in V1. Furthermore, Astafiev et al. (2004) have shown that orienting purposeful motor activity (such as looking and pointing) toward a target modulates the activity in visual areas stronger than attentional factors alone. These authors also found that BOLD-activation V1 is modulated by pointing finger movements extending previous studies reporting saccades related activation in V1 even when these were performed in total darkness (Bodis-Wollner et al., 1999; Bodis-Wollner et al., 1997; Sylvester et al., 2005). Visual imagery of the saccade targets is also an unlikely cause of the activation modulation we observed in V1. The

reason is that imagery related modulation in V1 is retinotopically organized (Slotnick et al., 2005). Therefore, this explanation is incompatible with the egocentrically organized activation modulation we found.

Moreover, the activity observed in V1 cannot be attributed to fixation alone. We found that BOLD-activation in V1 extended well beyond the foveal representation (5° visual angle) and in some hemispheres these activations were even separate from the fovea (Fig. 4A). Extrafoveal V1 activation reflects by definition interfixational processes, i.e. activation by the saccade. Therefore, we think that V1 activity may represent both fixational and perifixational activity either before or after fixation breaks. This motor-activity related interpretation of perisaccadic V1 activity converges with the results of a previous fMRI-study in which it was demonstrated that perisaccadic BOLD-activity only occurs in V1 when the saccade is actually performed, but not when it is only imagined (Bodis-Wollner et al., 1997).

Furthermore, this interpretation is consistent with electrophysiological evidence of intrasaccadic modulation of EEG activity in the dark (Bodis-Wollner et al., 2002; Forgacs et al., 2008).

Saccades performed in total darkness can, of course, modulate BOLD-responses in other brain regions than the ones we analyzed (e.g. Bodis-Wollner et al., 1997; 1999, Sylvester et al. 2005; 2006). Since the BOLD-measurements we took were restricted to occipital and posterior parietal cortex we focussed our analysis on the retinotopic saccade related modulation in posterior parietal cortex and the egocentric modulation in V1. Informally, we observed that the egocentric BOLD modulations extended into V2 in most hemispheres investigated, and sometimes even into V3. However, we

concentrated our analysis on V1 because of its pivotal role in the visual processing hierarchy, and because the egocentric BOLD modulations were most consistently found in this brain area. Of course, the results of our study do not preclude that other brain areas outside of the brain volume we investigated may show saccade related modulation or may represent other reference frames, e.g. object specific coding (Wilson et al., 2005).

Our result that V1 can code saccades in an egocentric reference frame raises the possibility that V1 is capable of constituting a vector required for describing the saccade induced displacement of the retinal image of a visual stimulus in head/body coordinates. This interpretation is in concordance with several studies in macaque monkeys showing that the response of a subpopulation of V1 neurons to visual stimuli is modulated by gaze direction (e.g. Guo and Li, 1997; Trotter and Celebrini, 1999). This modulation has been seen as an indication that V1 codes visual stimuli not only in a retinotopic reference but already integrates information about stimulus location in the egocentric head/body reference frame. The *saccade related V1* activation we found when voluntary saccades were executed in total darkness, without any visual input may reflect a prediction of the orbital eye position by a corollary discharge when the saccades are actually performed (Donaldson, 2000; Duffy and Burchfiel, 1975; Snyder, 2000; Wurtz and Sommer, 2004). Alternatively, but not necessarily exclusively, the signals may reflect input from the pulvinar which integrates visual and motor information in retinotopic and in head/body reference frames (Grieve et al., 2000) and is known to project to V1 in the macaque (Adams et al., 2000).

Several models of perisaccadic neuronal processing and visuo-motor coordination

aim to explain the effective compensation of the saccade related shift of the retinal image by incorporating eye position signals. The compensation of the self generated shifts helps to perceive the world as stable despite the changing retinal input. Shift compensation is also necessary for visually guided behaviour (e.g. grasping an object) because saccades shift the retinotopic reference frame, in which the location of a visual object is coded, relative to the egocentric reference frame, in which movement plans (e.g. grasping) are coded. These models assume the convergence of head/body centred information about eye position with retinotopic visual information at early processing stages (Pouget et al., 1993; Quaia et al., 1998; Zipser and Andersen, 1988). We propose that the representation of perisaccadic activity in V1 in egocentric coordinates in addition to the retinotopic representation of the space identifies area V1 as the earliest cortical area in the visual processing hierarchy with the possibility to compute the compensation of the saccade related shift of the retinal image. Our study now demonstrates in humans that this brain region may constitute an early locus in the circuit of visuo-motor integration.

4. Experimental Procedure.

4.1 Subjects

Four right-handed subjects with a mean age of 25 years participated in the experiment. All had normal or corrected to normal vision and gave their informed consent before the beginning of the experiment. The experiments were approved by the ethics committee of the Medical Faculty of the Otto-von-Guericke University. The subject's task was to perform a sequence of self-initiated eye movements in the absence of any visual input. Prior to each functional scan there was a practice session in the light. In this session a cartoon face was displayed on a screen and the

fixation cross jumped repeatedly on a horizontal line from the nose to the left eye, back to the nose, to the right eye and back to the nose again. The latency between jumps of the fixation cross varied between 3 seconds and 9 seconds, with approximately 80% short inter-saccade intervals. The subjects were instructed to memorize the position of the saccade targets and the frequency distribution of the inter-saccade intervals (not the order) and to imitate the saccade sequence during functional scanning in total darkness with eyes open. The practice sessions between trials also served to keep the light adaptation level approximately constant. Due to the immobilization of the subject's head during scanning it is not possible to distinguish between head and body centred reference frames. Therefore we subsume both under the label egocentric reference frame. Three of the subjects participated in an additional retinotopy scan on a different day.

4.2 Eye movements

We recorded the EOG during fMRI-scanning with an MR-compatible BrainAmp EEG-amplifier (Brainproducts, Munich, Germany). Using the EOG to record eye movements allowed us to measure them in total darkness, even without infrared light sources. Ag/AgCl electrodes were attached in a differential montage at the subjects' outer canthi of the left and right eyes. Three additional EEG-channels were used to measure the electrocardiogram (ECG). The ECG was used to remove the cardio-ballistic artefact in the EOG that is caused by unavoidable heartbeat related movements of the electrodes and cables in the scanner's magnetic field. Finally, a digital pulse provided by the scanner at the start of every volume acquisition was also recorded. The sampling rate was 5 kHz with an analogue low pass at 256 Hz and no high pass filter. A template matching method implemented in the software

package BrainVision Analyzer (Brainproducts, Munich, Germany) was used to remove the scanner-related and the cardioballistic artefacts (Fig. 2). Then the time series were digitally filtered at 70 Hz to suppress residual high frequency artefacts. The artefact reduced horizontal EOG time series was used to detect and classify saccades with a semi-automatic approach. Therefore a custom developed Matlab-software calculated a multi-scale wavelet decomposition of the EOG time-series with a complex Morlet-wavelet. The amplitudes of the time series of complex coefficients were used to detect the saccades and to localize them in time by comparing the phase alignment of the coefficients over scales. Candidate saccades found the algorithm that did not exhibit a clear step in the EOG (i.e. where the saccade velocity was too low) were rejected. Next, the saccades were classified according to the four saccade types shown in Fig. 1 based on the step start and end point and the direction of the step in the EOG. An example of the EOG recording of a sequence of saccades is shown in Figure 2. After the saccades were determined we averaged the EOG time series interval ± 700 ms around the saccades separately for each saccade type in a run. The average step size and the maximum slope were calculated from these averages. A calibration function determined prior to the start of each run from six horizontal saccades positions was used to convert the saccades parameters into degrees (saccade amplitude) and degrees per second (saccade velocity).

4.3 MRI

Imaging was performed on a 1.5T GE Signa Lx scanner with a 5" surface coil placed at the back of the subject's head. The subjects were in supine position with the head fixed in normal anterior orientation. Therefore, head and body reference frames were aligned throughout the scans. Functional images with blood oxygenation level

dependent (BOLD) contrast were recorded from 20 slices oriented approximately perpendicular to the calcarine sulcus. The slices covered the occipital and parietal cortex (gradient echo EPI-sequence, slice thickness = 3 mm, slice matrix = 64 by 64 pixels, field of view 180 mm, inplane resolution 2.81*2.81 mm, TR = 3 s, TE = 40 ms, flip angle = 80deg). All subjects were measured in at least six and up to eight functional scans (9 min each). The brain anatomy underlying the functional volumes was assessed with an additional T1 weighted volume that was acquired with a spin echo sequence in the same slice position (slice matrix 256 by 256 pixels, inplane resolution 0.7*0.7mm, TR = 500 ms, TE = 9 ms). This T1 weighted volume was used co-register the functional images with an individual high quality whole head anatomical T1 weighted scan measured in a separate session on a second day (3D-FSPGR-sequence, 124 sagittal slices with a 256 by 256 pixel matrix, voxel size 0.98*0.98*1.5 mm, TR=24 s, flip angle=30°). The whole head T1 weighted scan served as the individual anatomical standard space for the fMRI-analysis.

Great care was taken to ensure that no light reached the subjects eyes during the functional scans when the subjects performed saccades. For this purpose all lights in the scanner and in the control room were turned off during functional scanning. In addition, the front and back end of the magnet's bore was covered with thick black cloth. Two tests were performed in the scanner prior to the functional scans to confirm that no light reached the subjects' eyes. First the subjects were instructed to move their eyes and to report possible perceived visual displacements of any sort. Then they were asked to open and close their eyes and to report any sensation of visual change. None of the subjects reported any visual sensation or visual changes. Furthermore, the subjects were instructed to press an alarm ball if they had the

impression that light reached their eyes during the functional scans, which never happened.

The BOLD-data from the saccade-scans were analysed using SPM99 (Wellcome Department, London). The BOLD-weighted images were slice time and motion corrected and smoothed with a 6 mm FWHM gaussian kernel. The latencies of the saccades with respect to the start of the functional run and the saccade types were used to construct an event related model of the BOLD-response for each of the four saccade types (see Fig. 1). This model derived from the EOG-data recorded during the functional scans was estimated with SPM99. All analyses were performed individually at the single subject level to reach maximal accuracy.

The functional scans for the retinotopic mapping of the borders of early visual areas were acquired in a separate session on a second day. In these scans we presented a rotating wedge and an expanding ring stimulus to determine the borders of V1 according to previously described procedures (Engel et al., 1997; Sereno et al., 1995) using the mrVista-toolbox (<http://white.stanford.edu>). The spatial accuracy of the maps obtained with this method is well within the spatial resolution of the voxel size used here for fMRI-scanning (Engel et al., 1997). The cortical grey matter sheet was segmented in full head T1-weighted anatomies, flattened, and used to calculate the borders of visual areas V1, V2 and V3 with an automatic algorithm that fits a 2D model of the expected maps to the maps measured in the retinotopy scans (Dougherty et al., 2003). Furthermore, the full head scans served as an individual anatomical standard space to depict the statistical results of the saccade scans, and to superimpose them on the borders of V1. In addition, these full head scans were used to calculate Talairach-coordinates using the transformation implemented in the

mrVista-toolbox.

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Figures Captions:

Fig. 1 This figure exemplifies the different left/right classifications of saccades (arrows) in retinotopic (left panel) and egocentric (right panel) reference frames.

The four depicted saccades (marked 1 to 4) move the centre of gaze of the observer labelled "O" between the three positions (F1, F2 and F3). The white disks represent the starting points and the arrows point in the directions of the saccades. The arrow's colour indicates the saccade's classification: green and red, indicate whether they are classified "left" or "right", respectively. Note that the same saccade can have different classifications in the two reference frames indicated by the different colours of arrows representing the same saccade (e.g. saccade 1).

The saccade characterization according to the retinotopic reference frame is depicted in the left panel. The retinotopic reference frame (blue cross) is centred on the current fixation (white disk) and the saccade direction relative to the current fixation defines whether the saccade was left or right *independent* of the saccade's location in space. A saccade from the left to the head/body midline and a saccade from the head/body midline to the right is classified left retinotopic (green arrows, saccades 1 and 2). Saccades in the opposite direction, from the right towards the head/body midline and from there towards the left are classified right retinotopic (red arrows, saccades 3 and 4). Generally, left and right saccades in a retinotopic reference frame are directed towards the left or the right relative to the current fixation.

The saccade characterization according to the egocentric reference frame is depicted in the right panel. The egocentric reference frame is centred on the observer's head (yellow cross) and the head/body-midline separates left and right egocentric hemispaces (the red or green tinged areas respectively). Here the saccades are

characterized according to the hemispace in which they were performed *independent* of the saccade direction. Therefore, both saccades between fixation points F1 and F2 are classified left egocentric (red arrows, saccades 1 and 4 in the red tinged area) and right egocentric saccades are those that jump between fixation points F2 and F3 (green arrows, saccades 2 and 3 in the green tinged area).

In the present experiment we exploited the fact that the classification of a saccade as "left" or "right" can differ between the reference frames (indicated by the colour changes of same saccade between panels, e.g. saccade 1) to distinguish whether the saccade related BOLD-activation in the investigated brain areas follows an egocentric or a retinotopic coding scheme. In the analysis of the fMRI-data we grouped the saccade related BOLD-activation according to the egocentric and the retinotopic reference frame and contrasted "left" versus "right" saccades according to each reference frame.

Please note that head and body were held fixed during the MRI-scans and thus we use "egocentric" as a synonym for "head/body" reference frame since we cannot distinguish craniotopic and somatotopic reference frames.

Fig. 2 The EOG-artefacts produced by fMRI-scanning and a corrected EOG time series with marked saccades. A) The amplitudes of the artefacts caused by the functional scanning sequence exceed the EOG-signal caused by the saccade by approximately a factor of 20. The shape and timing of this artefact is highly deterministic. Thus it can be corrected by subtracting a model of the artefacts from the time series. B) The saccade steps (marked by the grey disks) in the EOG became apparent after the artefact removal. The four saccade types are clearly identifiable and indicated by numbers (1: left in, 2: right out, 3: right in, 4: left out, see also

Figure 1). To calculate the parameters reported in Table 1 the EOG-potentials were separately averaged for each saccades type and converted to degrees.

Fig. 3 A) Parietal activation related to saccade direction defined with respect to retinotopy was consistently found in the parietal cortex of all investigated eight hemispheres (indicated by the blue cross). The upper row shows where leftward saccades elicit a higher BOLD-response than rightward saccades, and the lower row depicts the results of the reverse comparison. The stars indicate the uncorrected p-value thresholds at voxel level applied to the images. The colourbars show the t-value code. B) This perisaccadic BOLD-modulation is located in the vicinity of the superior end of the occipito-parietal sulcus (indicated by the black circle). Data from three subjects are shown on 3D-renderings of the individual brains. Right hemispheres show higher activation for saccades towards the left from the current fixation, and left hemispheres exhibit the reverse preference. The small heads placed above the "right > left" contrast illustrate how saccade types were grouped and what groups were compared.

Fig 4 A) Occipital BOLD-modulation related to the egocentric space in which the saccades are performed was consistently found in all eight hemispheres (indicated by the blue cross). The upper row shows that saccades within left egocentric space elicit higher BOLD-responses in left occipital cortex than saccades in the right space. The lower row depicts the results of the reverse comparison that reveals activations in right occipital cortex. The stars indicate the uncorrected p-value thresholds at voxel level applied to the images. The colourbars show the t-value code. B) The BOLD-modulations overlaid on individual brains and restricted to V1 (blue). The green outline depicts the retinotopic representation of the fovea (5 deg diameter). The

perisaccadic BOLD modulation falls in many hemispheres in multiple clusters that are located within and beyond the foveal representation. The small heads below the "left > right" contrast illustrate how saccade types were grouped and what groups were compared. Although no retinotopy was available for subject 4 the marked activation clusters could be safely assigned to V1 because they fell within calcarine sulcus (see supplementary material).

Fig. 5 The phase maps of the BOLD-activation evoked by a rotating wedge stimulus in a retinotopy scan. Data from two hemispheres of two different subjects are shown. The colour code for the elevation angle is depicted in the lower left half disc. The colours cyan, magenta, and blue mark the lower vertical meridian, the upper vertical meridian and the horizontal meridian. Area V1 is outlined white on the flat maps (lower row). This area has a full hemifield and therefore contains the full range of phase angles. Areas V2 and V3 are outlined in yellow and red respectively. The top row presents the data rendered on the subject's individual anatomies. The borders of V1 follow approximately the calcarine sulcus.

Fig. 6 Event related averages of the BOLD-responses elicited in V1 by saccades executed in the ipsilateral (red) and the contralateral (black) hemispace. Averages over all eight hemispheres are shown and error bars indicate the standard error of the mean over hemispheres.

Figure 1 Rieger et al.

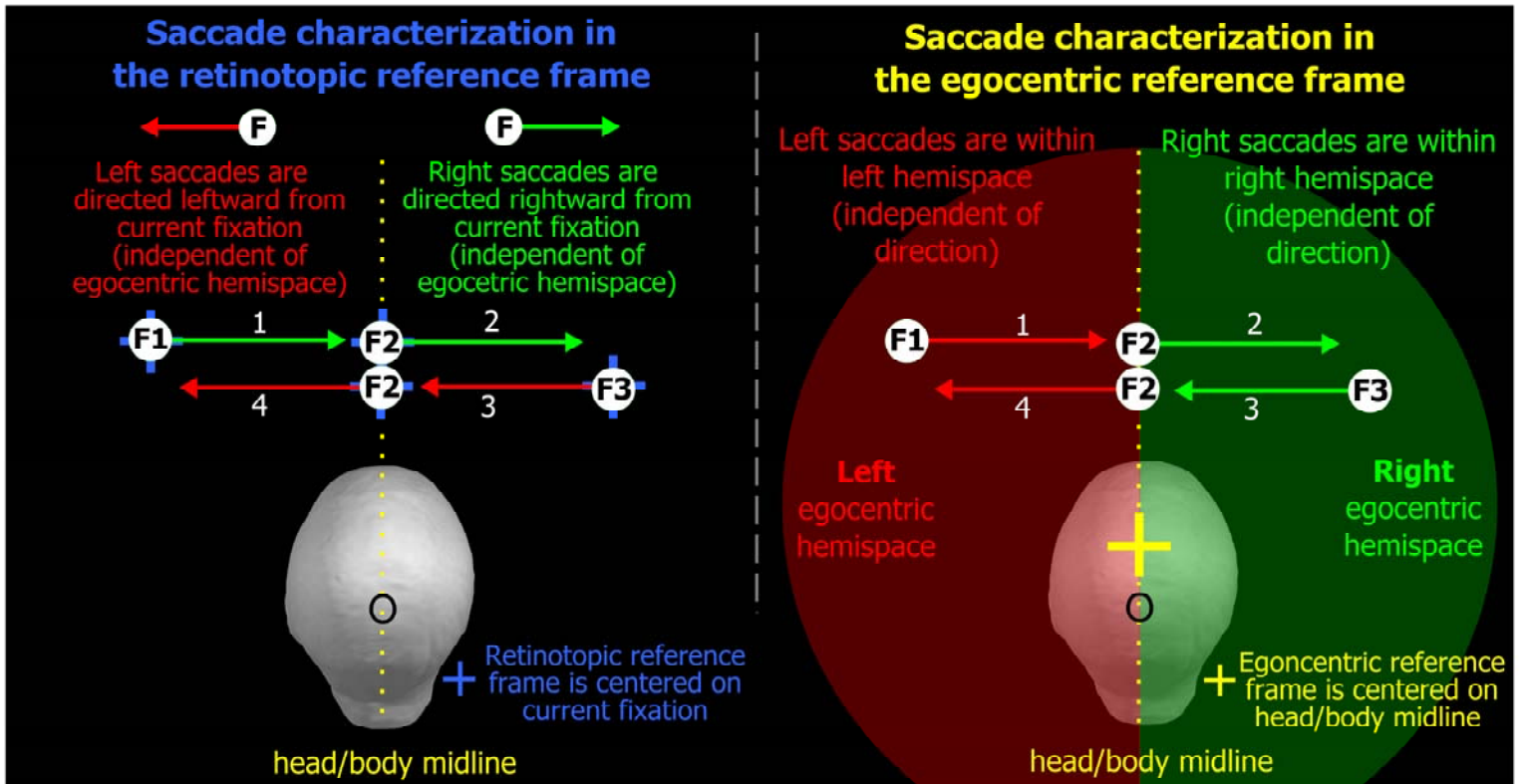


Figure 2 Rieger et al.

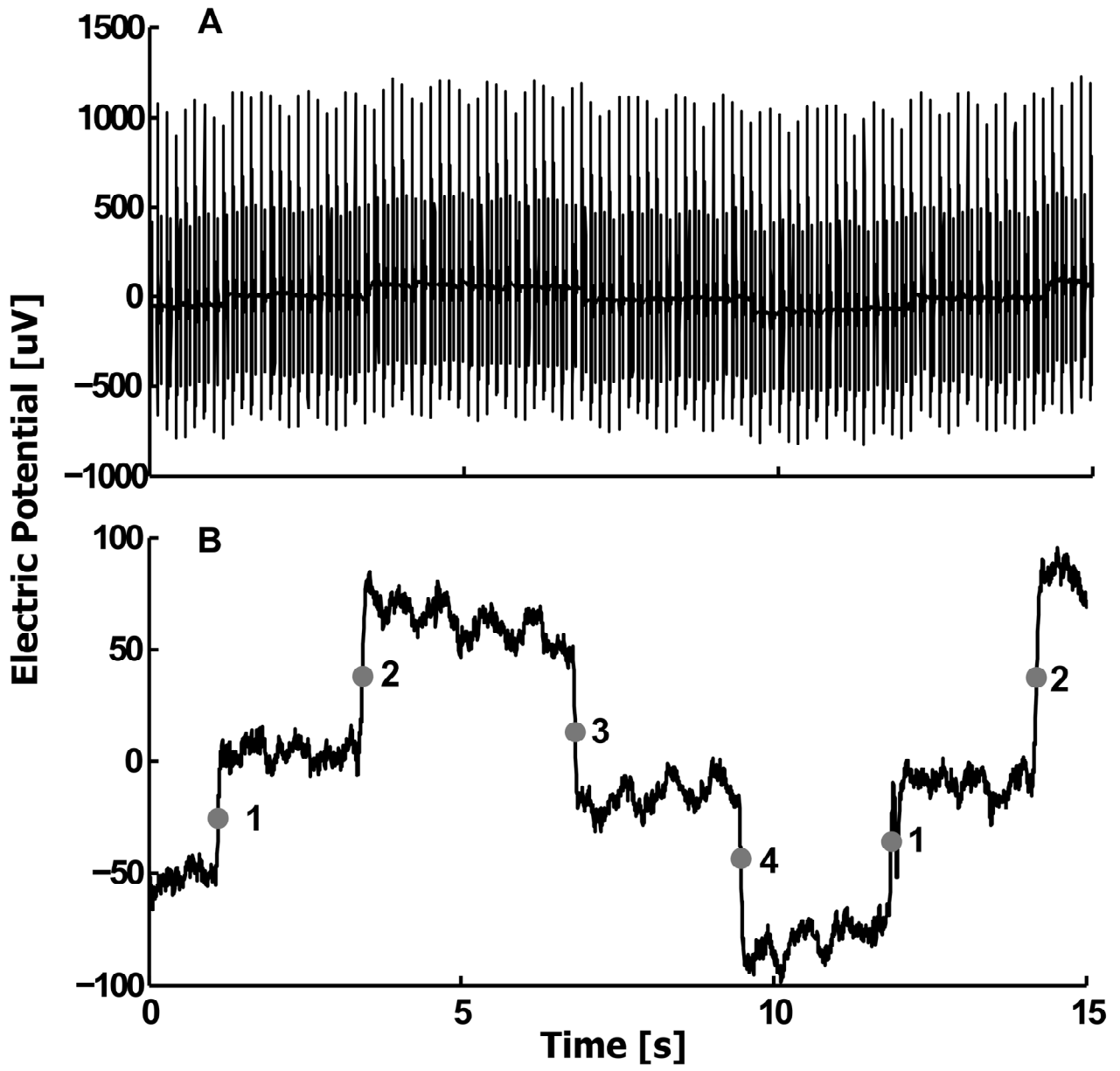


Figure 3 Rieger et al.

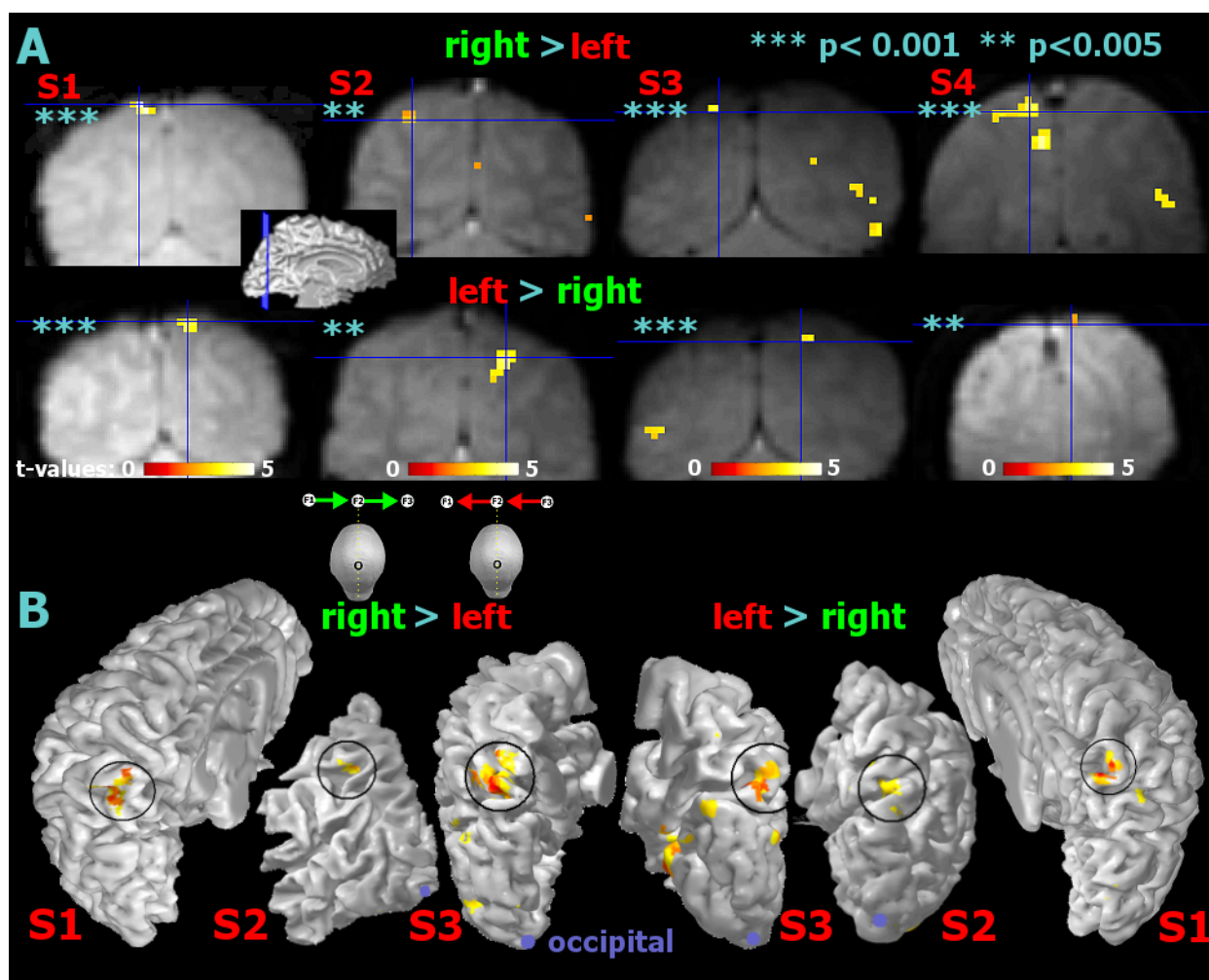


Figure 4 Rieger et al.

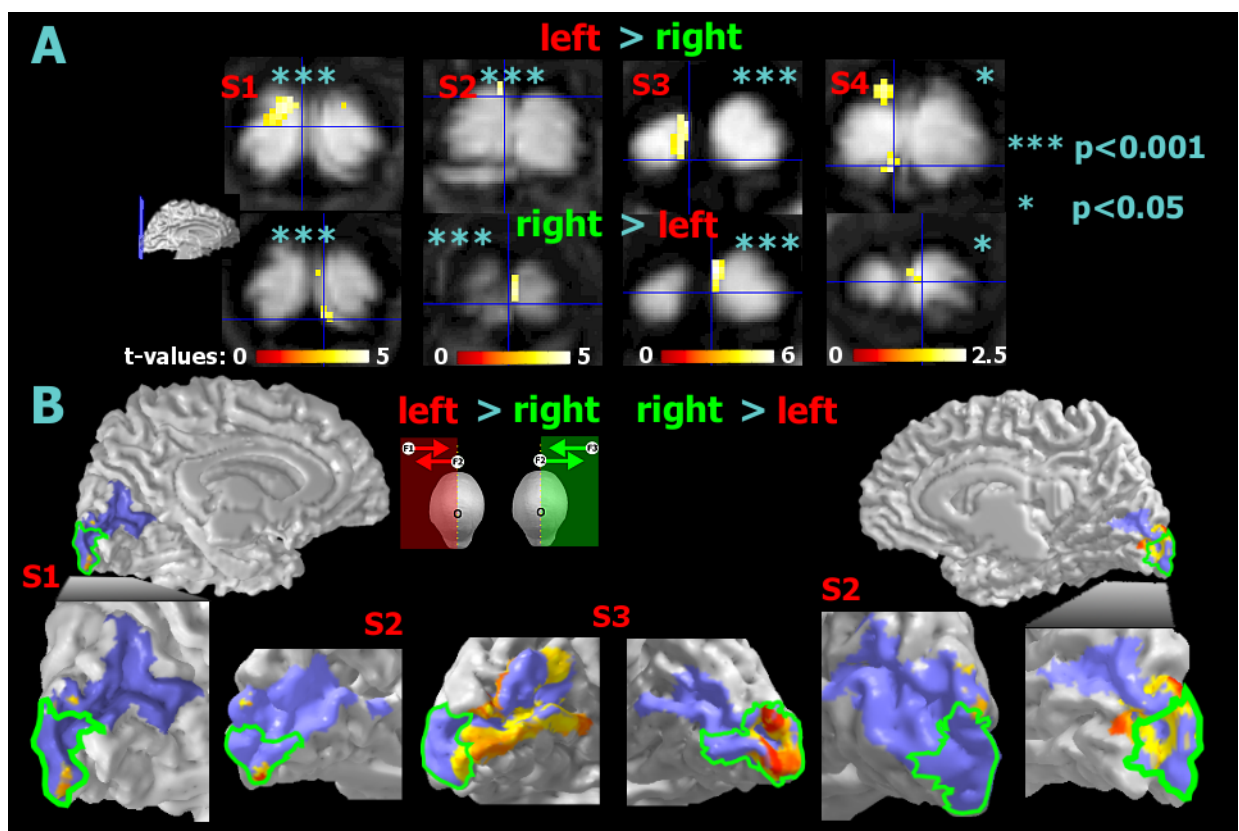


Figure 5 Rieger et al.

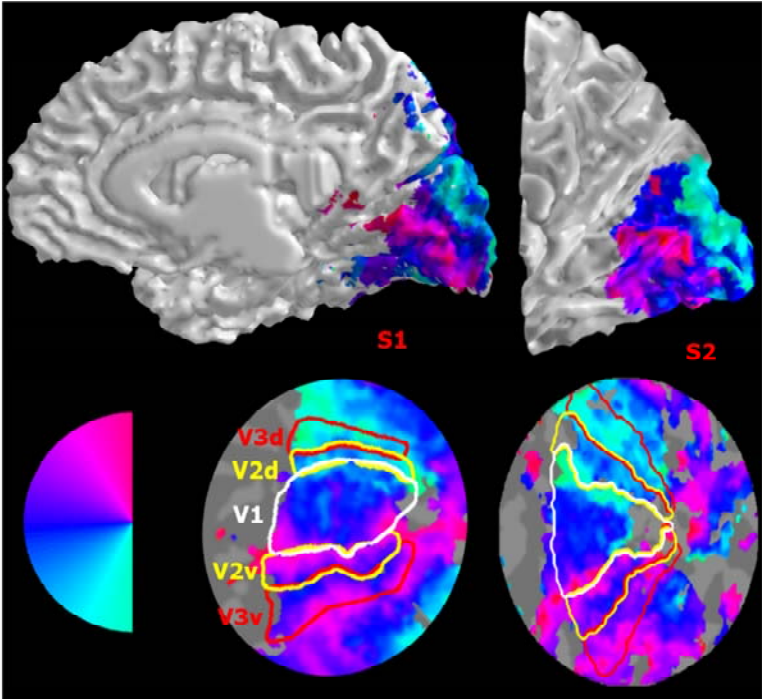


Figure 6 Rieger et al.

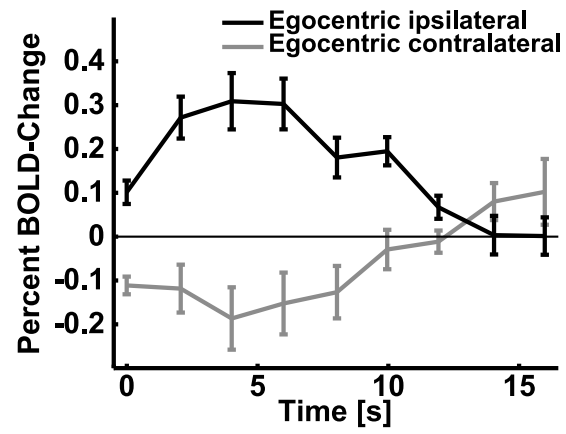
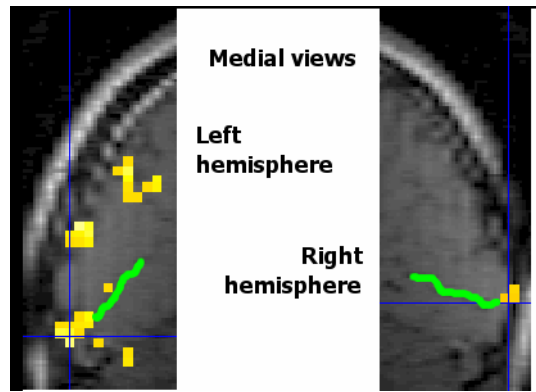


Table 1 The averaged parameters for the four saccade types

	Start position	End position	Distance	Max. speed in °/s	Average # per subject
Left in (1)	-27°	16°	43°	287	234.75
Left out (4)	-8°	-47°	-39°	262	232.25
Right in (3)	29°	-14°	-43°	297	233
Right out (2)	11°	44°	33°	243	230.5

Average start and end positions, amplitudes and velocities of the saccades performed in total darkness during the fMRI-measurements. All four saccade types are named according to an egocentric frame of reference (i.e. "left in" denotes a saccade from the left periphery towards the head/body midline). The numbers in parentheses relate to the saccade numbering in Fig. 1. Saccades directed towards the head/body midline (in) tended to have slightly higher amplitudes than saccades directed towards the periphery (out). There was no difference in the amplitudes ($t(7)=1.47$; $p>0.1$) and velocities ($t(7)=0.32$; $p>0.5$) of saccades performed in the left or right hemispace. The average inter-saccade interval was 3.9 s. The last column reports the average number of saccades per subject that went into the analysis.



Medial slices showing the BOLD modulations with respect to the egocentric reference frame found in subject 4 (see Figure 4A in the manuscript for the coronal slices). The occipital activation falls within calcarine sulcus where V1 is located. The calcarine sulcus is indicated by the green line.