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Research report

Post-saccadic updating of visual space in the posterior parietal cortex in humans

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Abstract

Updating of visual space takes place in the posterior parietal cortex to guarantee spatial constancy across eye movements. However, the timing of updating with respect to saccadic eye movements remains a matter of debate. In the present study, event-related potentials (ERPs) were recorded in 15 volunteers during a saccadic double-step task to elucidate the time course of the updating process. In the experimental condition updating of visual space was required, because both saccade targets had already disappeared before the first saccade was executed. A similar task without updating requirements served as control condition. ERP analysis revealed a significantly larger slow positive wave in the retino-spatial dissonance condition compared to the control condition, starting between 150 and 200 ms after first saccade onset. Source analysis showed an asymmetry with respect to the direction of the first saccade. Whereas the source was restricted to the right PPC in trials with leftward first saccades, left and right PPC were involved in rightward trials.

The results of the present study suggest that updating of visual space in a saccadic double-step task occurs not earlier than 150 ms after the onset of the first saccade. We conclude that extraretinal information about the first saccade is integrated with motor information about the second saccade in the inter-saccade interval.

Keywords: Saccade; Updating; Spatial constancy; Parietal cortex

1. Introduction

Whenever we perform a saccadic eye movement, the retinal locations of objects in our environment change. To maintain perceptual stability the visual system needs to take into account amplitude and direction of the eye movements just made. Earlier work in humans and in monkeys has shown that the oculomotor system does not only use retinal error signals to guide saccades [15,28]. In a saccadic double-step task two successive saccades have to be performed to flashed targets. As both targets are presented within the latency of the first saccade, the retinal vector of the second target differs from the movement vector necessary to reach the target with the second saccade [15]. Monkeys and humans are able to accurately perform this task [15,28]. The oculomotor system therefore needs to have access to extraretinal information about the metrics of a saccade, probably by using efference copy or corollary discharge information of the saccadic movement command [4,42,45,50].

The posterior parietal cortex (PPC) is an ideal candidate for the so-called updating of visual space in conjunction with eye movements, because it is located between sensory and motor areas of the brain. Lesion and imaging studies in humans as well as single cell recordings in monkeys have shown that PPC regions are recruited in tasks which require the integration of visual and motor information [9,14,16–18,25].

The time course of updating with respect to saccade onset is still a matter of debate. In the lateral intraparietal area (LIP) of monkeys, neurons have been found, which show predictive remapping. They respond to visual stimuli appearing

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in their post-saccadic receptive field, before a typical visual response, as measured in a fixation task, would be expected [9,24]. Some neurons respond to visual stimuli in their future receptive field even before the saccade starts.

In other behavioural paradigms the time course of the updating process seems to be different. Evidence from single-cell recordings during a double-step task shows that activity in many LIP neurons codes for the direction of the next saccade and not for the location of visual stimuli. Thus the updating process seems to take place in the inter-saccade interval, when activity shifts to the neurons which code for the direction of the second saccade [29].

In humans, data concerning the time course of updating of visual space in the PPC are sparse [1,23,38]. A lateralized component over the occipito-parietal cortex about 70 ms after saccade onset was found, when subjects performed single horizontal saccades in complete darkness [38] and when moving stimuli with different velocities were presented during a saccade [23]. This component is dependent upon saccade direction and is discussed in terms of an efference copy signal of the just executed eye movement reaching the parieto-occipital cortex. By contrast, a centrally positive component over parieto-occipital cortex at about 120 ms after the onset of horizontal saccades with and without visual stimulation was described in another study, possibly reflecting incoming saccade-related efference copy information [1].

The present study aimed to elucidate the time course of updating of visual space in connection with two successive saccades. In the experimental condition retino-spatial dissonance was induced, i.e. the first saccade started after the second target had already disappeared. Updating of the second target's location was thus necessary to correctly perform the second saccade. The experimental condition will be referred to as retino-spatial dissonance condition (RDC). A similar task which requires two visually guided saccades served as control condition (CC). Electroencephalography (EEG) was used to provide the high temporal resolution necessary for the fine-graned analysis of brain processes. In addition, source analysis techniques were applied to further explore the brain regions involved in updating.

2. Materials and methods

2.1. Subjects

Fifteen healthy subjects took part in the experiment. Mean age was 28.27 years (S.D. = 5.11, range 22–38 years). All were right-handed and had normal or corrected-to-normal vision. Subjects signed an informed consent form before the experiment was started. The study was approved by the Ethics Committee of the Ruhr-University of Bochum.

2.2. Stimuli and task

On RDC and CC trials, subjects were instructed to perform a saccadic double-step task, i.e. they had to perform two successive saccades to flashed targets. At the beginning of each trial, a central fixation point appeared on the computer screen. After an unpredictable delay (1200–1800 ms), the fixation point disappeared and the first saccade target came on. It was located either 7.5° visual angle to the left or right of the fixation point. After the presentation of the first target the second target was presented on the screen. It was located 7.5° visual angle upward or downward from the first target. Thus subjects were required to first perform a horizontal saccade and then a vertical saccade. The presentation times of the first and the second target were 120 and 50 ms, respectively. On RDC trials, the second target was presented immediately after the first target. On CC trials, there was a delay of 250 ms between the offset of the first and the onset of the second target (see Fig. 1 for the sequence of events in both conditions). The fixation point and the saccade targets were red dots of 0.5° visual angle diameter.

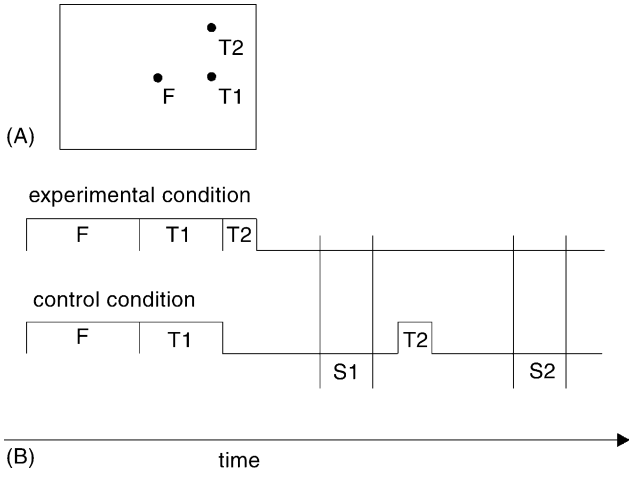

Fig. 1. (A) Locations of fixation point and target stimuli in a given trials. (B) Sequence of stimuli and saccades in the double-step task. In the experimental condition both targets are flashed in succession, so that they have already disappeared before the first saccade is executed. In the control condition there is a delay between the presentations of targets 1 and 2, in which the first saccade can be executed (F: fixation point; T: target; S: saccade).

In addition to these conditions, there was a fixation condition, in which the stimulation was exactly the same as on RDC trials. Subjects were asked to keep their eyes on the location of the central fixation point. To ascertain that they were still attending to the stimuli, subjects were asked to press one of two buttons, when the location of the second target was above the location of the first target and to press the other button, when it was below the first target. Each subject performed nine blocks of trials, three per condition. Each block consisted of 60 trials. Trials with different target locations were presented in random order.

2.3. Data recording

Throughout the experiment, EEG was recorded from 30 scalp sites according to the International 10–20 System (F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, T7, C3, Cz, C4, T8, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, PO7, PO3, POz, PO4, PO8), referenced to linked mastoids. Silver–silver chloride electrodes were used and they were fixed using an elastic cap.

Subjects were seated 57 cm in front of a computer monitor (LCD-display), on which the visual stimuli were presented. A chin rest was

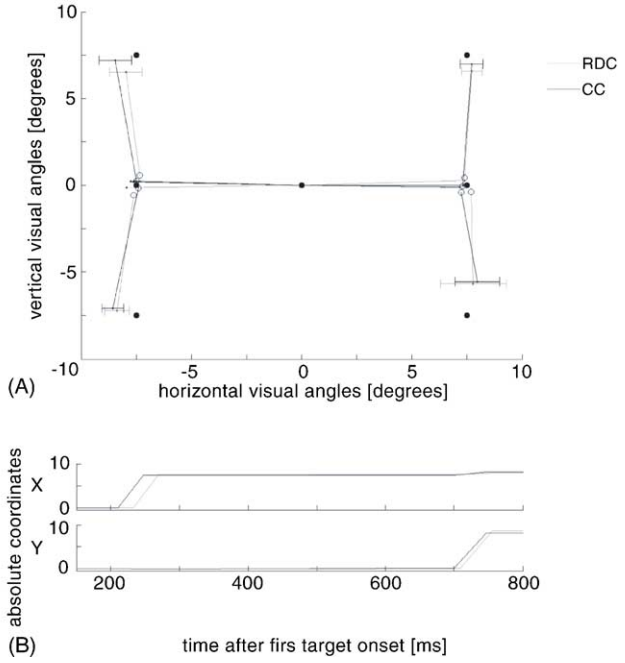

Fig. 2. Saccade data of five subjects in the experimental and control condition. (A) Mean saccade directions and amplitudes to all possible target locations. (B) Mean latencies of first and second saccades for all trials.

used to stabilize head position. The experiment was conducted in the dark. A circular frame was put in front of the screen, so that the frame of the monitor could not be used as external reference.

EOG was recorded from electrodes at the outer canthi of both eyes and above and below the left eye to determine the onset of horizontal and vertical eye movements. A Neuroscan Synamps System and the appropriate software were used for recording. All data were sampled at a rate of 500 Hz. The impedance was kept below 5 kΩ.

To explore whether subjects were able to perform correct saccades on RDC and CC trials, saccade accuracy was tested in five subjects using an EyeLink video system (SMI, Sensorimotor Instruments, Germany) in a separate experiment. The signal was sampled with 250 Hz. Subjects performed four blocks of 40 trials each, two blocks of RDC trials and two blocks of CC trials. Four of the five subjects also took part in the EEG experiment.

Saccades were performed with a similar degree of accuracy in both conditions and there was no evidence of systematic mislocalisation (Fig. 2A). As revealed by paired-samples *t*-test, there were no significant differences between conditions for horizontal or vertical deviations of saccade endpoints from target locations. The only near-significant between-condition difference ($P = 0.069$) emerged for vertical shifts of first saccade endpoints: On RDC trials, endpoints of first saccades tended to shift slightly into the direction of the second target. However, the mean difference between conditions on this measure was very small, about 0.1° visual angle.

As can be seen in Fig. 2B, the timing of first and second saccades was also very similar in both conditions. Neither for first, nor for second saccade latencies there was a significant difference between conditions (both $P > 0.19$). The conditions did not differ significantly with respect to the delay between first and second saccade ($P = 0.90$).

2.4. Procedure

Subjects were told that the study aimed to assess brain activity related to eye movements. For the conditions, in which eye movements were required, participants were instructed that they would see a central fixation point on the screen, followed by a first and a second target stimulus. They were asked to make two successive eye movements to the target positions as fast and as accurately as possible. For the fixation condition, they were asked to look at the position of the central fixation point during the whole block of trials. They would see two successive stimuli flashed on the screen. They were instructed to attend to the target stimuli and to press one of two buttons, when the second target stimulus was above the first target stimulus and to press the other button, when it was below.

Saccade accuracy was assessed in five subjects in a separate testing session a few days before the EEG-experiment. The instructions were the same as for the saccade tasks in the EEG-experiment.

2.5. Analysis of EEG- and saccade-data

Data were analyzed off-line. The first steps of analysis were performed using the Brain Vision Analyzer Software Package. Raw data were filtered with a 0.1 Hz high-pass and a 40 Hz low-pass filter. Then segments were created, ranging from 600 to 1500 ms after onset of the first target. After ocular correction was performed, segments were baseline corrected based on the average signal in the first 400 ms of the time epoch, i.e. from 600 to 200 ms before the onset of the first target.

The raw data of all 60 trials per block were then exported and further analyzed using MATLAB. For the experimental and control conditions an algorithm was used to detect saccadic eye movements. Saccades were detected, whenever the EOG-signal increased or decreased in 10 or more consecutive time frames (20 ms) and when the amplitude of the signal changed by more than 40 μV during this interval. If the signal returned to baseline at a similar rate, it was considered a blink rather than a saccade.

Only trials with two successive saccades in the correct directions entered the final analysis. In addition, the timing of the saccades was considered: In the experimental condition, only trials were included in which retino-spatial dissonance was involved, i.e. the first saccade had to start after the second target had already disappeared. In the control condition only those trials entered analysis in which the first saccade was already executed when the second target was presented, so that there was no retino-spatial dissonance. For both conditions there had to be a minimum duration of 200 ms between the onsets of both saccades. Trials with artefacts were detected automatically: Segments with a maximal difference between the highest and the lowest data point exceeding 150 μV were excluded.

In the next analysis step, every segment fulfilling the criteria mentioned above was realigned with respect to the beginning of the first saccade, with every new ERP-segment starting 400 ms before and ending 500 ms after saccade start. Then ERPs of all remaining trials per subject and condition were averaged, separately for leftward and rightward trials, i.e. trials with leftward and rightward first saccades. Data for trials with upward or downward second saccades were pooled.

To induce retino-spatial dissonance only on RDC trials and not on CC trials, it could not be avoided that the two conditions differed in the timing of the second target stimulus (see above).

ERPs from the fixation condition showed that both target stimuli caused a clear negative visual evoked potential (VEP) at about

180 ms after stimulus onset, which will be referred to as N180. This component cannot be observed in the traces aligned to first saccade onset, because the timing of the stimuli with respect to saccade onset is different from trial to trial, depending on saccade latencies. Additionally, the average timing of stimuli from saccade onset differs between subjects. Nevertheless, it might be possible that the temporally dispersed visual N180 contributes to possible differences in saccade-locked ERPs between RDC and CC trials.

Visual stimulation in the fixation condition matched the visual stimulation on RDC trials. On CC trials the second target stimulus was presented, when subjects already had performed the first saccade. Therefore the retinal location of the second target stimulus in the control condition differed from the retinal location of the second target stimulus in the experimental and fixation conditions. In four subjects, visual ERPs in response to the second target stimulus could be obtained on CC trials, because they showed frequent omissions of second saccades and many trials with large inter-saccade intervals. In these subjects, the average visual N180 in response to the second target stimulus was very similar for the control and fixation conditions, indicating that the retinal location of the second target stimulus did not have a significant effect on visual ERPs. ERPs from the fixation-condition were therefore used to correct for possible effects of visual input on RDC and CC trials.

To remove the VEP from the traces, a repeated sum of the mean VEP from the fixation condition was formed for every subject, dispersed according to the histogram of the timing of stimuli in relation to first saccade onset [44]. Grand-average ERPs were obtained for every condition, separately for rightward and leftward trials.

2.6. Statistical analysis

Initially, grand-average ERP-data were inspected visually. As activity in the parietal cortex was most relevant, nine parietal electrodes were chosen for ERP-analysis (CP3, CPZ, CP4, P3, PZ, P4, PO3, POZ and PO4). A repeated measures ANOVA with the factors condition (RDC and CC), row (anterior, middle, posterior) and line (right, middle, left) was performed on peaks and areas, in which activity on RDC and CC trials potentially differed. To determine the onset of areas of significant amplitude differences, a previously described method was used [36].

2.7. LORETA-analysis

Mean amplitudes of the areas, for which significant differences between RDC and CC trials emerged, entered LORETA (low resolution brain electromagnetic tomography) source analysis [35]. Although the spatial distribution of brain activity cannot be derived from extracranial measurement of electrical activity, multi-channel EEGs contain sufficient information to determine an approximate distribution. The method is based on computation of the current density at each grey matter voxel of a reference brain as a linear, weighted sum of the scalp electrical potentials. The smoothest of all possible current density configurations is chosen, the only constraint being that neighbouring voxels should have maximally similar activity. LORETA-images represent electrical activity at each voxel as squared current density.

For both conditions and for every subject, LORETA-images were generated for the ERP-components in question. The images were converted (http://www.ihb.spb.ru/~pet_lab/L2S/L2SMain.htm) and further analyzed using SPM99 (http://www.fil.ion.ucl.ac.uk/spm/). A PET/SPECT design with a two-sample *t*-test was performed with the following parameters: Global normalisation with proportional scaling to a mean of 50, absolute threshold masking with a threshold of 5 and global calculation of mean voxel value (within per image).

The level of significance was set to $P = 0.05$. The coordinates of the foci of significant differences between conditions were transformed into Talairach coordinates [43] with the algorithm suggested by Brett (http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml).

3. Results

3.1. Number of trials

As we aimed to induce retino-spatial dissonance in the experimental condition, but not in the control condition, saccades had to fulfill different timing criteria in both conditions (see Section 2).

The number of trials fulfilling the timing criteria and thus entering ERP-analysis was very similar in both conditions. On leftward trials, i.e. trials with a leftward first saccade, on average 64.3 (S.D. = 58.9) RDC trials and 58.8 (S.D. = 27.4) CC trials entered analysis. For rightward trials, the mean numbers of trials were 60.3 (S.D. = 26.8) and 66.4 (S.D. = 26.9), respectively. For both directions of first saccades there were no significant differences between the conditions (both $P > 0.42$).

3.2. Saccade characteristics

Fig. 3 shows onset latencies of first and second saccades, both with respect to the onset of the first target, in trials with leftward and rightward first saccades for RDC and CC trials. ANOVA with factors condition and side on first and second saccade latencies did not yield any main effects or interactions (all $P > 0.15$).

Since ERPs were time-locked to the onset of the first saccade, the duration between first and second saccade onset was of particular interest for those trials finally entering analysis. The inter-saccade interval was on average 450 ms (S.D. = 125 ms) on rightward RDC trials and 455 ms (S.D. = 152 ms) on leftward RDC trials. The corresponding intervals for CC trials were 470 ms (S.D. = 161 ms) and 485 ms (S.D. = 176 ms), respectively. There were neither significant main effects of condition or side, nor was there a significant interaction between the factors (all $P > 0.24$).

3.3. ERP-effects

Figs. 4 and 5 show grand average ERPs of all electrodes for RDC and CC trials, time-locked to first saccade onset on rightward and leftward trials, respectively.

Positive and negative peaks occurring at about 5 and 25 ms after first saccade onset were analyzed. They were determined for every subject as the peak positive and negative

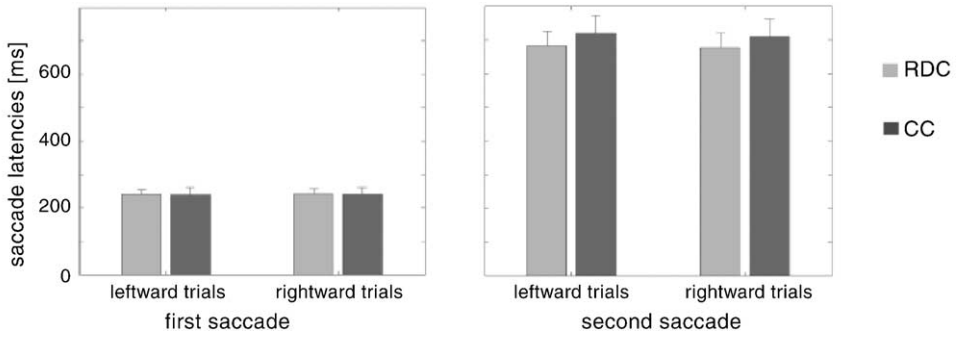

Fig. 3. Mean latencies of first and second saccades in leftward and rightward RDC and CC trials. Error bars indicate standard errors.

amplitudes in the −30 to 30 ms time range with respect to saccade onset. Then the peak-to-peak amplitudes were calculated. In rightward trials ANOVA with factors condition, row and line did not yield any significant main effects or interactions (all $P > 0.20$).

On leftward trials there was no main effect of condition and no interaction between condition and line (both $P > 0.43$). There was a significant interaction between the factors condition and row ($P = 0.049$). Further analysis showed that in the last row of electrodes the interaction between the factors condition and line approached significance (PO3, POZ, PO4; $P = 0.082$). However, neither for the whole row of electrodes nor for any of the single electrode sites was there a significant amplitude difference between the conditions (all $P > 0.10$). For the other rows, there were no significant main effects or interactions (all $P > 0.47$).

For both leftward and rightward trials, the most obvious difference between conditions is a more positive mean amplitude on RDC compared to CC trials, starting around 150 and 200 ms after first saccade onset. To explore onset latencies of significant differences between conditions, *t*-tests were performed for each time point (every 2 ms) at each electrode site [13,36]. Consistent with the procedure described by Rugg et al. [36], the onset latency for a given electrode was defined as the time point from which at least 15 consecutive *t*-tests were significant at the 0.05 level. Black bars above grand-average ERPs in Figs. 4 and 5 indicate regions of significant amplitude difference.

On rightward trials, the mean amplitude on RDC trials is significantly more positive in many frontal and parietal sites. In most cases, the area of significant differences is restricted to the time window from 150 to 350 ms after first saccade

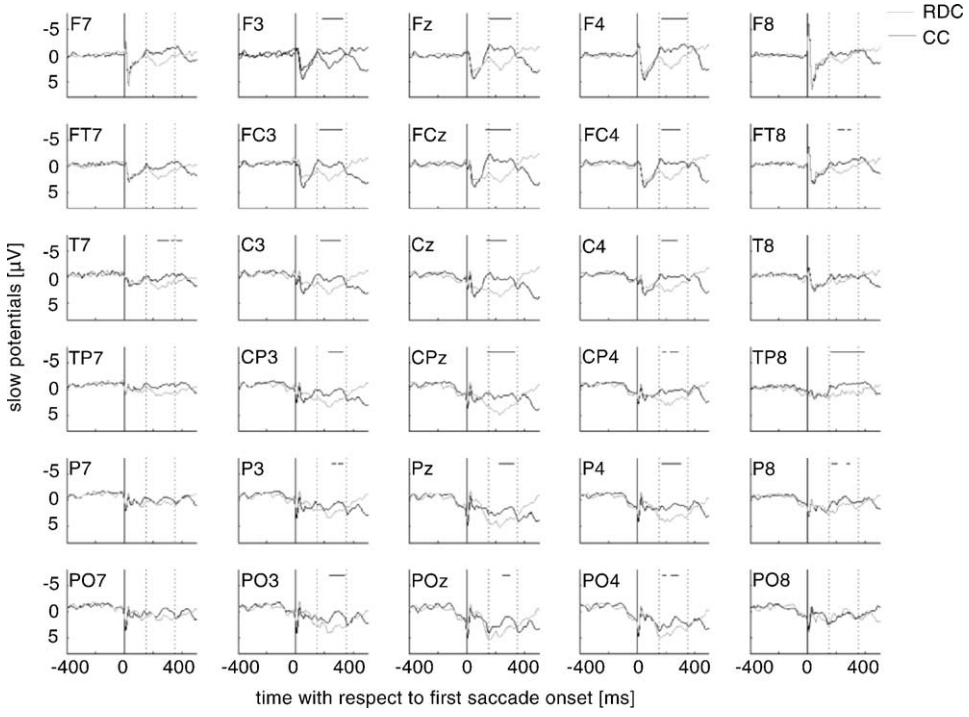

Fig. 4. Grand-average ERPs of RDC (in grey) and CC trials (in black) for rightward trials. ERPs are aligned to first saccade onset. Black bars above the traces indicate areas of significant difference between conditions.

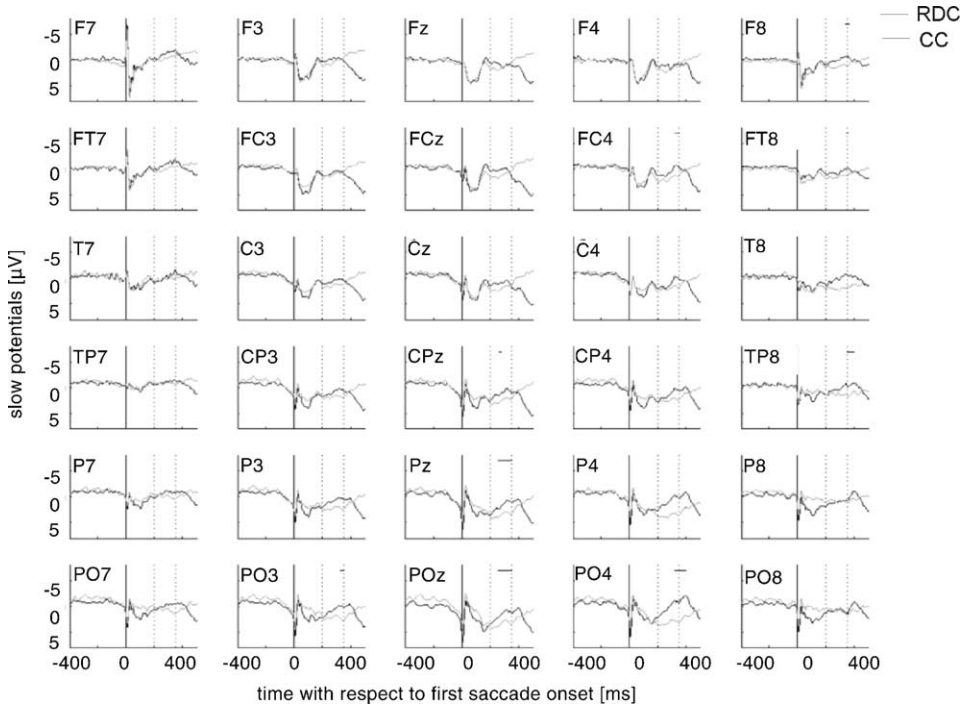

Fig. 5. Grand-average ERPs of RDC (in grey) and CC trials (in black) for leftward trials. ERPs are aligned to first saccade onset. Black bars above the traces indicate areas of significant difference between conditions.

onset. An ANOVA with factors condition, row and line for nine parietal electrodes (CP3, CPZ, CP4, PO3, POZ, PO4, P3, PZ, P4) on the mean amplitude in this time window revealed a significantly more positive amplitude on RDC as compared to CC trials ($P < 0.01$). The two- and three-way interactions did not reach significance (all $P > 0.19$).

For leftward trials, a similar pattern emerges. However, the positivity on RDC trials starts later than in rightward trials and the differences between grand-average ERPs in both conditions are not as pronounced as for rightward trials. Significant differences between conditions can only be found in central parietal electrodes. Although areas of significant differences begin even later, the larger positivity on RDC trials starts at about 200 ms for most of the sites. For frontal electrodes, the area of amplitude differences (not significant) ends at about 350 ms. Thus the time window between 200 and 350 ms was analyzed for leftward trials. As for rightward trials, the mean amplitude for nine parietal electrodes was significantly more positive on RDC relative to CC trials ($P = 0.029$). None of the interactions reached significance (all $P > 0.19$).

3.4. Source analysis

To determine the sources of activity responsible for differences between the conditions, the ERP activity in the time windows of significant between-condition effects entered analysis. Data from all electrode sites were considered. In Fig. 6 results of RDC–CC contrasts are shown separately for rightward and leftward trials. Table 1 lists Talairach coordinates of source centres.

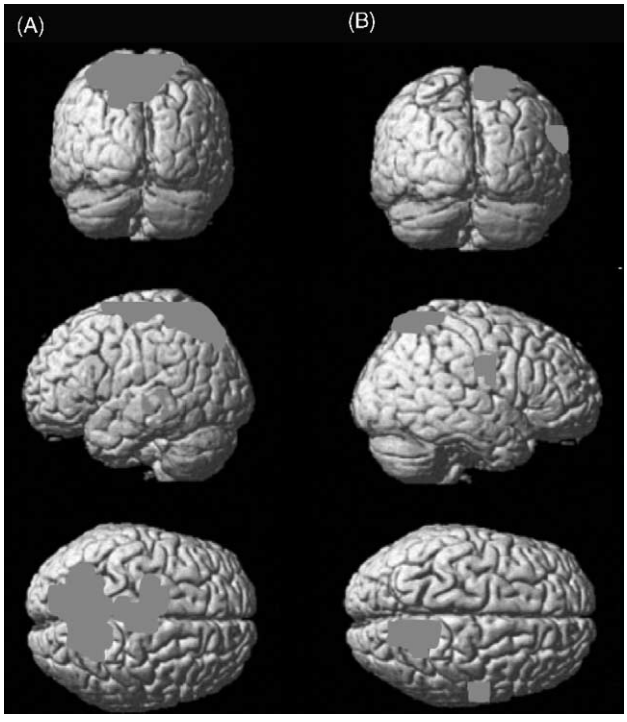

Fig. 6. Results of LORETA source analysis. Uniformly grey areas indicate source locations (A) RDC–CC contrast for the mean amplitude in the time window between 150 and 350 ms after first saccade onset for rightward trials. (B) RDC–CC contrast for leftward trials; time window 200–350 ms.

Table 1
Results of LORETA source analysis

	Brodmann area	*x*	*y*	*z*	*P*
RDC vs. CC rightward trials (150–350 ms)					
Superior parietal lobule (left)	7	−17	−62	62	0.011
Postcentral gyrus (right)	7	11	−48	68	0.033
Medial frontal gyrus (left)	6	−3	−21	66	0.027
RDC vs. CC leftward trials (200–350 ms)					
Superior parietal lobule (right)	7	18	−62	62	0.027
Precentral gyrus (right)	6	59	−3	27	0.024

The table shows probable Brodman area, Talairach space coordinates and levels of significance for source centres.

For rightward trials, the contrast between RDC and CC was calculated for the time window of 150–350 ms after onset of the first saccade. The main source of activity is in the left superior parietal lobule (SPL) and in the precuneus in Brodman's area 7, contralateral to the direction of the first saccade in the double-step task. But the source is not limited to this area. It extends into the right parietal lobe. The source centre is located in Postcentral Gyrus, but most of the source originates in the SPL in Brodman's area 7. In the left hemisphere, the source extends into the medial and superior frontal gyri (Brodman's area 6).

For leftward trials, the between-condition contrast involved the time window of 200–350 ms after first saccade onset. Here two small sources were found. One is located in the parietal lobe. Again the centre of activation is in the SPL contralateral to the direction of the first saccade. For leftward trials the source emerges only in the contralateral hemisphere.

The other source of activity for leftward trials is located in the lateral precentral gyrus of the right hemisphere in Brodman's area 6.

4. Discussion

In bringing a visual stimulus on the fovea, the oculomotor system accounts for intervening saccades by integrating information about eye displacement with information about the retinal error of the stimulus. The classical task is the double-step task, in which two targets are flashed very briefly before the execution of the first saccade [15]. As the vector of the movement necessary to reach the second target is different from the visual vector, under which the target is seen, the retinal location of the second target needs to be recalculated after the first saccade. To examine the temporal dynamics of this updating process, EEG was recorded while subjects performed a double-step task. A task with similar saccade requirements, in which both saccades were visually guided, served as control condition.

In the experimental condition, which required updating of visual space after the first saccade, a slow positive wave was observed, starting at about 150 ms after first saccade onset for rightward trials and at about 200 ms for leftward trials. For both leftward and rightward trials activity originated mainly in the superior parietal lobule contralateral to the direction of the first saccade, with activation for rightward trials extending into contralateral frontal cortex and ipsilateral parietal cortex.

Saccade characteristics did not differentially affect ERPs in the experimental and control conditions: The average inter-saccade interval as well as the saccade-related EOG-signal amplitudes were very similar in both conditions.

It is also unlikely that the clear ERP-differences between RDC and CC trials were caused by differences in visual stimulation in both conditions. First, the effects of visual stimulation were removed using a subtraction technique [44]. Second, if the corrected ERPs still reflected differences in visual stimulation, one would expect to find sources in the visual areas of striate and extrastriate cortex. Instead, source localisation revealed sources in parietal cortex, indicating that the slow positive wave on RDC trials may be related to updating of visual space.

Both lesion and neuroimaging studies have provided convincing evidence for the functional involvement of the PPC in visual space updating. Patients with PPC lesions were impaired at taking contralateral first saccades into account when performing a sequence of two saccades [10,17,18]. In a single case study, a patient with a bilateral extrastriate lesion involving the intraparietal sulcus was unable to compensate for retinal background movement, when a stimulus had to be tracked with a smooth pursuit eye movement [14]. Studies using functional magnetic resonance imaging (fMRI) also yielded PPC activations, but in subregions different to the areas emerging in the present LORETA analysis: Activations were observed in a region in the middle part of the intraparietal sulcus, which is considered the functional homologue of the monkey LIP, responsible for providing spatial constancy [16,37,46].

The localisation results of the present study have to be interpreted with caution, because of the relatively limited spatial resolution of the EEG source-localisation technique.

Interestingly, the asymmetries in parietal activation observed in the present study correspond to those found in imaging studies. Two studies reported pronounced right-sided posterior parietal activity related to updating of visual space when trials with leftward and rightward first saccades were pooled, possibly due to the involvement of the right PPC in saccades in both directions [16,46]. A functional asymmetry in terms of a more pronounced right hemisphere contribution to visual space updating was also confirmed by

our results. The right hemisphere therefore does not only seem to play a dominant role in visuospatial processing and attention [5,32], but also in providing spatial constancy across saccadic eye movements. It should also be noted that neglect of extrapersonal space is observed much more frequently following lesions of the right parietal cortex [8,48]. Interestingly, deficits in spatial short-term memory caused by failure in updating spatial representations across saccades have been described as one component of the neglect syndrome [26]. It has been shown that a deficit in updating visual space exacerbates the severity of symptoms in neglect patients [21].

The main purpose of the present study was to elucidate the time course of the visual space updating process in connection with saccades. Previous studies of intrasaccadic visual processing described post-saccadic ERP components, which have been discussed in terms of an incoming efference copy signal in the parietal cortex [1,23,38]. However, the exact timing of the ERP component differed from the present study. Parieto-occipital components with latencies from 65 to 120 ms after saccade onset emerged when saccades were performed in complete darkness or evoked by visual stimuli [1]. These results are not directly comparable to the present findings, since they involved only a single saccade. However, fMRI evidence has shown that updating in the parietal cortex can occur in connection with such tasks [30].

A recent study applying transcranial magnetic stimulation (TMS) to the parietal cortex, while subjects performed a double-step task, is more directly comparable to our study [49]. Subjects were unable to compensate for variability in their first saccade amplitude by adjusting the amplitude of the second saccade, when TMS-pulses were given at least 150 ms after first saccade onset. Earlier pulses had no disruptive effect. These findings are consistent with the present results, suggesting that the critical processing for updating of visual space in a double-step task occurs in the between-saccades interval.

In contrast to the sparse evidence from human studies, comprehensive evidence has accumulated from animal work. In the monkey, activity in many LIP visual neurons reflects predictive remapping [9]. These neurons anticipate the retinal consequences of a planned eye movement by responding to visual stimuli appearing in their future receptive field. The response latency is shorter than a typical visual latency measured in a fixation task. The mechanism of predictive remapping seems to provide a continuous retinocentric representation of space. Predictive remapping was not only found in LIP, but also in the frontal eye field (FEF), the superior colliculus (SC) and in different extrastriate cortex regions [34,47,51]. The receptive field shift is not instantaneous; before saccade onset LIP neurons decrease responding to stimuli in the old, pre-saccadic receptive field and increase responding to stimuli in the new, post-saccadic receptive field [24]. The authors also discussed possible implications of their findings for the perception of the second target in a double-step task. A given target excites two sets of neurons when it is presented shortly before a saccade. For one population of neurons, the stimulus is in the old receptive field, and for another one in the new, post-saccadic receptive field. It is unclear, how the visual system uses these signals for correct stimulus localisation.

The phenomenon of predictive remapping provides evidence of updating of visual space around the time of a saccade, with remapped responses in some neurons occurring even before saccade start. Updating is seen as a perceptual phenomenon, independent of task requirements. Within this context, the role of area LIP in sensorimotor integration is to encode the location of visual stimuli in a retinal frame of reference.

Findings from single cell recordings during a double-step task provide evidence for an alternative view of the role of area LIP: It might be more related to motor plans than to visual coding. Similarly to the present results of enhanced inter-saccade positivity, activity in many parietal neurons was enhanced between the first and the second saccade [2,11].

When delays between stimulus presentation and saccade execution were introduced, most LIP neurons showed sustained activity, coding for the next saccade, which was unrelated to sensory memory of stimulus location [29]. Before the first saccade in a double-step task, only neurons with movement fields relevant to the direction of the first saccade discharge. Between first and second saccade, activity shifts to the neurons with the movement fields relevant for the second saccade. Only few neurons discharge in response to stimuli in the receptive fields which are not targets for the next saccade. Neurons with similar properties have also been found in other oculomotor regions. In the FEF, visual, visuomotor and movement-related neurons discharge in the inter-saccade interval in a double-step task, when the second saccade is directed into the receptive or movement field of the neuron [12]. This finding is particularly surprising for the purely visual neurons, which discharge, although none of the stimuli appear in their receptive field. The so-called quasi-visual neurons in the SC also have similar properties [27].

Activity in LIP is also observed in connection with planning the next saccade, irrespective of its actual execution [3]. LIP neurons have also been found to discharge before intended arm movements, with saccade- and arm movement-related neurons being anatomically segregated [39]. Given these findings, it was concluded that LIP generally codes for intended movements.

The present data do not allow a clear differentiation of parietal positivity in terms of perceptual updating of the location of the second target stimulus or updating in motor coordinates for the second saccade. However, the timing of the positivity suggests that it is more related to the latter. If parietal activity in the present study reflected predictive remapping and thus perceptual updating of the second target stimulus, an earlier correlate of updating would be expected [9]. It is also unlikely that parietal positivity in the present study just reflects sensory memory of the location of the second target stimulus, although it has been shown that the PPC is involved in

performing memory-guided saccades [33]. As reported above, the vast majority of LIP cells codes for the direction of the next saccade rather than for stimulus location in a double-step task [29].

The enhanced parietal activity observed in the updating condition of the present study might thus reflect the preparation of the second saccade. Although the control condition also involved a second saccade, it could not be initiated before the presentation of the second target stimulus. In the experimental condition, the second target had already been presented and activity could thus directly shift to the neurons coding for the direction of the second saccade. Nevertheless, parietal activity on RDC trials is also related to the first saccade. Asymmetries in parietal sources revealed by LORETA indicated processing differences for leftward and rightward first saccades, probably related to asymmetries in space updating. Parietal activity may thus reflect the integration of information about the first saccade and information about the planned second saccade.

It remains to be elucidated, whether the updating processes in tasks with single saccades, requiring perceptual updating, and in double-step tasks, requiring updating of oculomotor coordinates, differ. Psychophysical investigations in human subjects have so far not yielded clear evidence for a dissociation between perceptual and oculomotor mechanisms in updating [6,7,15,19,20,22,31].

An efference copy or corollary discharge of the motor command to move the eyes is considered to underlie extraretinal information in the double-step task [40,41]. However, alternative explanations cannot be ruled out. Exocentric cues of relative localisation of saccade targets may also provide extraretinal information (see [7]). It might also be argued that the updating process is influenced by practice or prior knowledge about the task. The grand-average ERPs of subjects, who completed the present double-step task on a separate occasion several days before the EEG-experiment, did not differ from ERP traces of naive subjects, and practice therefore seems to play a negligible role.

In summary the results of the present study support the hypothesis that activity in the PPC in oculomotor tasks is more related to spatial accuracy of movement than to perceptual processes. The mechanism, by which eye movement information is integrated with perception, has yet to be explored in detail. Efference copy or corollary discharge of the oculomotor command clearly plays an important role. The present study indicates that during the performance of sequences of saccades with insufficient retinal information, the critical updating of visual space occurs in the intersaccade interval.

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