Parallax-sensitive remapping of visual space in occipito-parietal alpha-band activity during whole-body motion

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Author contributions: conceived the experiment: TG, LS, WPM; collected the data: TG; analyzed the data: TG; wrote the manuscript: TG, LS, WPM.

Running head: Parallax-sensitive remapping during whole-body motion
Abstract

Despite the constantly changing retinal image due to eye, head and body movements, we are able to maintain a stable representation of the visual environment. Various studies on retinal image shifts caused by saccades have suggested that occipital and parietal areas correct for these perturbations by a gaze-centered remapping of the neural image. However, such a uniform, rotational, remapping mechanism cannot work during translations when objects shift on the retina in a more complex, depth-dependent fashion due to motion parallax. Here we tested whether the brain’s activity patterns show parallax-sensitive remapping of remembered visual space during whole-body motion. Under continuous recording of electro-encephalography (EEG), we passively translated human subjects while they had to remember the location of a world-fixed visual target, briefly presented in front or behind the eyes’ fixation point prior to the motion. Using a psychometric approach we assessed the quality of the memory update, which had to be made based on vestibular feedback and other extraretinal motion cues. All subjects showed a variable amount of parallax-sensitive updating errors, i.e. the direction of the errors depended on the depth of the target relative to fixation. The EEG recordings show a neural correlate of this parallax-sensitive remapping in the alpha band power at occipito-parietal electrodes. At parietal electrodes, the strength of these alpha band modulations correlated significantly with updating performance. These results suggest that alpha-band oscillatory activity reflects the time-varying updating of gaze-centered spatial information during parallax-sensitive remapping during whole-body motion.
Keywords: spatial updating, EEG, alpha, whole-body motion, remapping

Introduction

We perceive the world as a stable reality, despite the ubiquitous changes in visual input due to our own movements. We do not perceive a visual shift when we make a saccade, even though the image of the world moves briskly on our retinas (Helmholtz, 1867; Bridgeman and Nardello, 1994; Schlag and Schlag-Rey, 2002). Also when we walk around, our perception seems not to be disturbed by the even more complex changes in the optic flow on our retinas (Angelaki and Hess, 2005 for review). How does our brain create this percept of visual stability?

There is evidence that the brain codes dynamic visual representations of the environment, which are remapped in gaze-centered coordinates when the eyes move. Various cortical and subcortical regions have been implicated in this remapping during saccadic eye movements, in both primates (Duhamel et al., 1992; Colby and Goldberg, 1999) and humans (Medendorp et al., 2003a; Merriam et al., 2003; Bellebaum and Daum, 2006; Morris et al., 2007). Behavioral studies and preliminary neurophysiological reports have also provided evidence for gaze-remapping during smooth pursuit eye movements (Blohm et al., 2003, 2005; Dash et al., 2012). Do such mechanisms, involved in saccadic or smooth pursuit remapping with the head immobilized, also operate to enable visual stability during head and body motion, taking into account vestibular and other signals? When the body is brought in motion, like when driving a car, vestibular feedback informs the brain about the motion (Li and Angelaki, 2005; Li et
al., 2005; Klier et al., 2008), but how these signals contribute to visual remapping has not been revealed.

In geometric terms, when the body translates through space, world stationary objects move at different speeds and in different directions relative to the retina, depending on their distance from the eyes' fixation point (Van Pelt and Medendorp, 2007). This geometric property, called motion parallax, does not play a role in visual remapping during saccades, but must be taken into account by a gaze-centered remapping mechanism during body translations. Do the neural mechanisms for visual stability show this level of sophistication or does the brain resort to a different gaze-independent mechanism?

Recent behavioral studies have made inferences about the nature of the computations by measuring the errors in the updating behavior during body translations. A gaze-independent mechanism could operate by storing and updating in Cartesian body-centered coordinates, which simply requires the amount of updating to be the same for each object: the opposite of the amount of body translation (Medendorp et al., 1999). If the translation is misjudged in this case, updating errors arise that have the same magnitude and the same sign irrespective of the depth of the target relative to the fixation. However, we recently falsified this model by showing that updating errors during active and passive body translations increase with depth from fixation and reverse in sign for objects presented at opposite depths from fixation (Van Pelt and Medendorp, 2007; Clemens et al., 2012). Thus, these gaze-centered errors indicate that the internal remapping mechanism accounts for the geometry of motion parallax, although not perfectly. The neural correlate of such a parallax-sensitive updating mechanism, however, has not been revealed.
In the present study, we recorded electroencephalographic (EEG) signals while human subjects had to retain object locations during whole-body translation. We focused our analysis on spectral power in the alpha band (8 – 12 Hz), which is not only the dominant frequency band in the brain, but has been shown to remap across hemispheres when saccadic eye movements reverse the side of the remembered target relative to gaze (Van Der Werf et al., 2013).

Here, by exploiting the direction selectivity of alpha band power, we tested whether internal representations of remembered visual objects are remapped trans-hemispherically when their representation reverses side relative to gaze due to passive whole body translation dependent on their depth relative to the fixation point. We further investigated whether a relationship exists between the observed alpha power modulations during this remapping and the behaviorally observed errors.
Materials and methods

Participants

Sixteen healthy participants (nine female, age range 18-31 years), free of any known vestibular or neurological disorder and with normal or corrected-to-normal vision gave their informed consent to participate in the experiment. All but one were right-handed. During analysis, data of five participants were discarded, resulting in 11 datasets (see section Analysis – EEG for details).

The study was approved by the local ethics committee. Participants never received any feedback about their performance.

Setup

Subjects were seated in a custom-made linear sled designed to impose body motion along a lateral track of 800 mm. The sled, powered by a linear motor (TB15N, Technotion, Almelo, The Netherlands), was controlled by a Kollmorgen S700 (Danaher, Washington, DC) drive. Motion kinematics of the sled were controlled with an accuracy better than 50 μm, 2 mm/s, and 150 mm/s2. The sled was configured such that participants were seated on the sled with their interaural axis aligned with the motion axis. Participants were restrained using a 5-point seat belt. Head motion was restrained using a modified over-ear headphone fixed to the sled. Emergency buttons at both sides of the sled chair enabled subjects to stop the sled motion immediately if needed. Psychophysical responses were recorded using a joystick, which was operated with the subject’s right hand.
Positions of both eyes were continuously recorded at 500Hz using an Eyelink II system (SR Research, Kanata, Canada, accuracy < 0.5º). Its camera system, which was mounted to the sled, remained stable with respect to the head during the entire experiment.

The sled was further equipped with a 96-channel active electrode electroencephalography (EEG) system (Brain Products GmbH, Gilching). EEG data were recorded continuously during the experiment. The over-ear headphone prohibited EEG recordings from electrodes located around the ears (FT9/10, T7/8, TP7/8 and TP9/10), leaving 88 active recording sensors. Additionally, horizontal and vertical electrooculograms (EOG) were recorded using electrodes placed below and above the right eye and at the bilateral outer canthi. Impedance of all electrodes was kept below 20kΩ, an adequate level for this active system. EEG and EOG signals were sampled at 1000Hz (amplifier bandwidth: 0.016-1000Hz, internal sampling rate 5kHz), and then saved to disk.

Visual stimuli were presented using red light-emitting diodes (LEDs). A single LED served as an earth-stationary fixation point (FP) and was located 1200mm from the eyes when the sled was at the center of its movement range. Furthermore, a 450mm wide array of LEDs, consisting of 180 LEDs, with a spatial separation of 2.5 mm (center-to-center), was used to present target and probe stimuli (see paradigm). The LEDs were approximately square (2mm x 2mm), usb-powered with a luminance of 1 lumen or less. This array was oriented in parallel with the sled movement axis, at a distance of either 287mm in front of fixation (913mm from the eyes) or 535mm behind fixation (1735mm from the eyes), such that the retinal eccentricity was the same for targets behind- and in front of fixation (2.9 degrees). This way, the angle of rotation (and thus the ‘speed of
movement’ of the remembered target) was kept identical for target behind and in front of fixation. The fixation point and LED array were displaced vertically by a few mm, such that they did not occlude each other and were approximately at eye level. The experiment was controlled using custom software programmed in a Delphi environment (CodeGear RAD Studio, Embarcadero Technologies, San Francisco USA). EEG and eye movement data were recorded using separate computers, controlled by the main stimulus computer. Triggers were sent by the main stimulus computer to the EEG computer to synchronize task events and EEG data.

**Task**

The experiment took place in a completely darkened room, except for the stimulus lights. Subjects performed a forced-choice (left/right) spatial updating task, illustrated in Figure 1. This paradigm is similar to that of Clemens *et al.* (2012), but with discrete sled motion (i.e. a single 400mm movement with a minimum jerk profile) to the left and right, as opposed to the continuous sinusoidal sled motion. A trial started with the sled 200 mm displaced from its center position, either to the right or left. The central fixation point (FP), now 9.5 degrees away from the body midline, was turned on and had to be fixated until a probe appeared (0-3s). Next, after 1 s, the target was flashed (50ms) either in front of or behind of the fixation point. Both the fixation point and target were located on a line perpendicular to sled motion axis at the center of the sled motion range. After a second delay (1s), the chair moved with a bell-shaped velocity profile (peak velocity 0.75 m/s, duration 1 s) over a distance of 400 mm to the opposite position relative to center of the motion range. Next, after another delay (1s), a probe stimulus was flashed for 50ms, after which fixation constraints were released. Using a left-right joystick response,
subjects had to indicate whether the probe was located left or right in space relative to
the remembered target. After the response, the next trial started with the current position
of the sled as the new starting position.

< FIGURE 1 ABOUT HERE >

The subject’s task was thus to encode the initial target, update its memorized
location over the course of the sled motion and compare the internally updated location
with the location of the probe. The retinal position of the target was jittered slightly (+/-
0.6 degrees) across trials to deter stereotyped responses. Targets of the present trial
were thus not informative about the location on the previous trial, avoiding possible
feedback on the previous trial performance. Thirteen fixed target-probe differences were
tested (equally spaced between -4.6 and +4.6 degrees, 8 repetitions for each
difference), with a pseudo-randomized target-probe difference in each trial. This fixed
interval psychometric procedure provided an estimate of the bias and precision of spatial
updating across whole-body motion.

In total, there were four task conditions: two motion directions (left/right) and two
depths of the target and probe (535mm behind or 287mm in front of fixation). Left and
right trials alternated continuously, while target and probe depth alternated every two
blocks.

The experiment aimed to capture activity related to updating of remembered
spatial locations with intervening motion. In order to obtain a baseline for the EEG
recordings that captures activity evoked by the translation itself, subjects were asked to
keep fixation, while their body was translated but no targets or probes were shown.

The experiment consisted of eleven blocks, 4 blocks of trials with targets/probes
in front of fixation (the ‘front’ condition), 4 blocks with targets/probes behind fixation (the
‘behind’ condition) and 3 baseline blocks. Conditions alternated every two blocks.
Baseline blocks followed after every two task blocks. A task block consisted of 52 trials
(26 left- and 26 rightward motion), while baseline blocks consisted of 70 trials (35 left-
and 35 rightward motion). As such, each of the four task conditions had 104 repetitions,
while the baseline had 105 repetitions. The total experiment consisted of 626 trials,
lasting approximately one hour, see Figure 1C.

**Analysis - behavior**

All analyses were performed using Matlab (Mathworks, Natick, Massachusetts, U.S.A).
The forced-choice joystick responses were used to estimate the likelihood of a left
response by fitting a logistic function

\[ f(x; \mu, \sigma) = \left(1 + \exp\left(-\frac{2\ln(1/\alpha - 1)}{\sigma}(x - \mu)\right)\right)^{-1} \]

with \( \alpha=0.1 \), using a Bayesian inference approach for each task condition using Psignifit 3.0
(Fründ et al., 2011). The mean of this function (\( \mu \)) represents the bias (positive value
corresponds to a leftward bias). The width of the curve (\( \sigma \)), determined over the interval
in which the function rises from 0.1 (\( \alpha \)) to 0.9 (1-\( \alpha \)), is inversely related to precision and
serves as a measure of the participant’s variability in the updating task.

To obtain a measure of updating performance independent of motion direction
and target/probe depth, the observed biases were converted into an updating gain. Our
previous study has shown that biases can be consistently explained by a gaze-centered
updating model with a non-unity gain factor between the actual \( (\vec{T}) \) and perceived \( (\vec{T}') \) lateral translation (Clemens et al., 2012). In brief, let \( \vec{0F} \) be the vector from the cyclopean eye to the fixation point and \( \vec{0R} \) the vector from the cyclopean eye to the reference target. This allows us to express the true translation as the angle through which the eye rotates \( (\sin(\phi_F) = \frac{T}{|\vec{0F}|}) \) and that the reference target moves through \( (\sin(\phi_R) = \frac{T}{|\vec{0R}|}) \). Then, if we drop the sine because of small angles, to compensate for the translation, the target needs to be internally rotated by \( \vec{\phi} \equiv \gamma \cdot T \left( \frac{1}{|\vec{0R}|} - \frac{1}{|\vec{0F}|} \right) \) relative to gaze. However, if the perceived translation has a non-unity gain \( \gamma \), it follows that \( \vec{\phi} = \gamma \cdot \vec{\phi} \), which results in angular bias \( \vec{\phi} - \vec{\phi} \) (see Clemens et al. 2012 for further details). This angular bias can be expressed in Cartesian coordinates and thus \( \mu \) of the psychometric function fits, by \( \mu = (\vec{\phi} - \vec{\phi})|\vec{0R}| = (\gamma - 1) \cdot T \left( 1 - \frac{|\vec{0R}|}{|\vec{0F}|} \right) \). Provided that \( \vec{0R} \), \( \vec{0F} \), and \( \vec{T} \) are controlled parameters in our experiment and \( \mu \) comes from our psychometric curves, we can calculate the translation gain. As can be noted, the bias flips sign according to presenting the target in front (\( \vec{0R} < \vec{0F} \)) of or behind (\( \vec{0R} > \vec{0F} \)) the fixation point, following the geometry of motion parallax.

**Analysis – EEG**

Analyses of EEG data were performed using the FieldTrip toolbox (Oostenveld et al., 2011) to obtain topographic maps of alpha activity and time-frequency representation of the lower frequency bands. All trials were manually checked for bad channels and/or artifacts in the time-domain. While conditions were not blinded during artifact rejection, no electrode location (and thus laterality) could be derived from the raw traces. EOG recordings were used to detect blinks, loss of fixation and saccades towards the targets.
or probes. Trials containing artifacts during the critical 3 second period ranging from target onset until probe presentation (e.g. blinks, saccades, muscle twitches, signal loss, jumps) were removed and bad channels were interpolated using a distance-weighted nearest neighbor approach. Eye tracking data were used to check for residual eye movements in the cleaned data. Two subjects showed excessive blinks and eye movements, leading to a trial rejection above 50% and were excluded from further analysis. Due to the importance of keeping fixation in this task we chose to delete these trials, rather than using a correction method. In three subjects, the behavioral data could not be fitted due to poor performance in one or more conditions. This was mainly because the biases (µ) of these subjects were beyond the range of sampled probe locations. Because our analyses require a coupling between the EEG data and behavior, these subjects were excluded from further analysis. This resulted in 11 datasets. Of the remaining subjects, mean trial rejection rate was 20.5% (SD 9.0) for task trials and 25.9% (SD 8.2) for baseline trials. Rejection rates of the task trials did not significantly differ between left or right direction, or target depth (all p>0.29) For the remaining trials, EEG signals were low-pass filtered offline at 80Hz and high pass filtered at 1Hz. A two-pass band-stop filter (48-52Hz) was applied to reduce line noise. Before frequency analysis, the data were re-referenced to ‘average reference’ (Bertrand et al., 1985).

The full power spectrum was calculated for each 4s trial, aligned to the presentation of the target (or the equivalent time point in the baseline trials) using Morlet wavelets (σ=7, resulting in an average frequency resolution of 2.8Hz and a 222ms wavelet length in the alpha range), over a frequency range of 1-80 Hz. Data were averaged and z-transformed. For each condition, the corresponding baseline condition
was subtracted; effectively subtracting out task-irrelevant activity, such as low-level vestibular processing (e.g. baseline condition moving left was subtracted from the task conditions containing leftward motion). Data were further analyzed in two different ways: first, to show the average task-evoked activity and second, to isolate the lateralized components.

The analyses focused on power modulations in the alpha band (~8-12Hz). For each subject, average power spectra were calculated to locate the peak alpha frequency. The mean alpha peak was centered at 10.3 Hz (sd 0.46).

To distinguish the task-evoked activity, baseline-corrected data were pooled by mirroring conditions with opposite visual input and averaged over conditions. Thus, in this analysis, data of the front-right (FR) condition (motion to the right with targets presented in front of fixation) and the behind-left (BL) condition (leftward motion, target behind fixation), which both have the initial target in the right visual hemifield, were mirrored according to the anterior-posterior midline (left and right hemisphere was swapped), and summed with the front-left (FL) and behind-right (BR) conditions. Thus, the task-evoked component was computed as (FL + FR* + BL* + BR)/4, in which * indicates a mirror flip of the data. Here, the right hemisphere is contralateral to initial target presentation.

To isolate the lateralized components, conditions with opposite initial visual input were subtracted, i.e. data of the FR condition were subtracted from the FL condition, as were the data of BR condition from the BL condition data. These two datasets were then subtracted again. So, the lateralized component was calculated as (FL - FR) – (BL - BR). Here also, the right hemisphere is contralateral to the initial target presentation.
To assess whether the observed power modulations in the alpha band are due to spatial updating performance, we correlated the power difference before and after the motion with the individual subjects’ behavioral gains. To this end, a function was fitted describing the time course of alpha power per electrode, for all conditions. The function assumes a constant alpha power over the pre-motion period; a linear change in alpha power after motion onset and again a constant alpha power in the post-motion baseline period. The pre- and post-baseline amplitude, change onset and post-baseline onset were free parameters. The difference in alpha power pre- and post-motion, reflecting the alpha modulation during the trial, was used in an independent samples regression analysis against the gain factor. Statistical significance testing was done using cluster based statistics and Monte Carlo permutation tests to correct for multiple comparisons (Maris and Oostenveld, 2007).

**Results**

We tested whether the neural mechanism for visual stability takes the geometry of motion parallax into account when updating target locations during translational body motion. Subjects had to remember the location of a target, briefly flashed in front or behind the eyes’ fixation point. After an intervening whole-body translation, they had to report the memory of this location using a left/right choice response (i.e., whether a probe was perceived left or right of the memorized target). We first summarize the behavioral results, followed by an analysis of spectral power modulations in the alpha band and the link between these two.
Behavior

Figure 2A shows the psychometric data of a typical subject, separately for the front and behind conditions (top vs bottom panel). The respective panels plot the fraction of leftward responses (indicated by the circles) as a function of horizontal probe location relative to the initial target, together with the fitted psychometric function. If updating performance were perfect, the psychometric curves would be centered at zero. However, the actual results show consistent biases, which flip between front and behind condition, as well as for leftward versus rightward motion. A body-centered updating model would imply that updating errors should have the same sign for targets in front of and behind the fixation point, depending only on the position of the target relative to the body. However, the depth-dependent error reversals that are seen indicate that targets are coded and updated relative to gaze. In other words, these observations suggest that the updating mechanism simulates the geometry of motion parallax, by coding and updating targets relative to gaze.

We derived estimates of the bias (μ) values in each of the four conditions. Figure 2B depicts these values for all subjects (dots), in top-view panels, separately for leftward and rightward motion. Bias values range approximately between -13 to 13 cm, and

< FIGURE 2 ABOUT HERE >
generally reverse for targets presented in front versus behind fixation. Bias values were entered in a repeated measures ANOVA with motion direction (leftward/rightward) and target location (front/behind) as factors. While there were no significant main effects (all \( p>0.21 \)), it revealed a significant MOTION DIRECTION x TARGET LOCATION interaction (\( F(1,10)=7.15, \ p=0.023, \ \text{partial } \eta^2=0.42 \)). Post-hoc analyses showed that conditions that differ in either motion direction or target location, but not both are significantly different (all \( p=<0.036 \)) while conditions that differ in both are not (all \( p>0.14 \)). This supports the notion that updating is performed in a gaze-centered reference frame, consistent with the findings of Clemens et al. (2012).

To determine the quality of updating, we applied the gaze-centered model described in the methods to calculate the gain value for each individual subject. Figure 2C depicts the resulting gain values, which range from 0.2 to 1.4 across subjects. In other words, the subject group is not homogenous with respect to gain; there are good (gain near 1) and less good performers (median split by gain 0.71). Furthermore, the gain did not significantly differ among the four conditions (repeated measures ANOVA, \( p=0.15 \)), which means that the model also correctly accounts for the sign of the updating bias, reversing dependent on target depth. Thus, the geometry can explain the bias across all four conditions, suggestive of a gaze-centered parallax-sensitive mechanism underlying visual stability. The question is: can these results be linked to a neural mechanism that reflects these principles?

\textit{Alpha band power simulates motion parallax}
The behavioral observations above, as well as previous physiological work on head-fixed saccade and smooth pursuit remapping, predict that certain brain areas should have an activity pattern that evolves during body motion in a way that depends on object depth. In the present paradigm, remembered targets at opposite depths from fixation reverse (left-right) with respect to gaze direction during the body motion. We exploited the direction selectivity of spectral power to test whether these physical shifts are accompanied by a change in focus of alpha band power from one hemisphere to the other to internally simulate this shift.

<FIGURE 3 ABOUT HERE>

Figure 3 shows the group average scalp topography of the power modulations of the alpha band in the four task conditions relative to baseline, averaged across subjects, during 4 non-overlapping time intervals, each covering a 0.5 s interval. Power reductions are coded in cooler colors; power enhancements in warmer colors. Fig 3A plots power during the leftward motion trials, with the target presented at t=0 s in front of fixation, in the left visual field (‘front left condition’). This stimulus response, observed in the subsequent, pre-motion time interval (0 – 0.5 s), is reflected by a clear power reduction at the occipito-parietal electrodes with an inclination to the right, contralateral hemisphere. During the acceleration phase of the motion, from 1 – 1.5 s, the reduction diminishes and shifts focus to the left hemisphere during the deceleration phase of the motion (1.5 – 2 s), which is the hemisphere contralateral to updated target location.
relative to gaze. The left hemisphere power reduction is maintained during the post-
motion delay (2.5 – 3 s) until the probe appears (at 3 s).

Using the same format, Figure 3B plots the results of the leftward motion trials
with the target presented behind the fixation point, in the right hemifield (‘behind left
condition’). Compared to Fig 3A, the pattern is now reversed; although weaker, the initial
stimulus-related power reduction of the left hemisphere is remapped to the right
hemisphere in response to the intervening body translation.

The two bottom panels show the power modulations during rightward motion
trials, in the same format as figure 3 (‘front right’ and ‘behind left’ conditions). Again, both
panels show an initial power reduction due to the initial stimulus. After the intervening
motion, this suppression is reorganized from the hemisphere contralateral to the initial
target location to the hemisphere ipsilateral to the initial target location for the front right
condition (C). This pattern is less prominent for the behind right condition; while the
initial power reduction of the contralateral hemisphere still vanishes during the motion,
no clear reduction of the ipsilateral hemisphere has emerged. (D). The relatively weaker
lateralization in the behind condition may be due to larger variability in remembered
target position, which can be seen in the behavior as well (figure 1B). Because all four
panels show data relative to baseline (i.e. the same motion without updating targets),
their general result can be interpreted as indicative of a gaze-centered trans-
hemispheric remapping of target representations during translational motion.

To show the consistency of these patterns, figure 4A shows the scalp topography
of the common task-evoked, subject specific alpha component that is shared across all
four conditions relative to the baseline condition. Note that, in plotting this contrast, the
convention is that left and right hemispheres are ipsilateral and contralateral to the gaze-
centered location of the initial stimulus, respectively. Regions with warmer (red) colors indicate a relative power increase; regions with cooler color (blue) represent a relative power decrease. The scalp topography is shown at the same time intervals as in figure 3. The initial, stimulus driven, response observed in the pre-motion time interval 0 – 0.5 s, is reflected by a clear decrease in power in the contralateral hemisphere, extending to the central parietal electrodes. During motion, the power reduction becomes weaker, and shifts focus to the left hemisphere, which is contralateral to the gaze-centered location of the updated stimulus location. To test this further, a parieto-occipital ROI was defined for each hemisphere (P1/2, P3/4, P5/6, P7/8, PO3/4, PO7/8, PO9/10, PPO9/10, O1/2 and O9/10), the mean activities of which were extracted for a pre-motion time window (0-0.5s) and post-motion time window (2.5-3s). These values were entered in an ANOVA with factors TIME (pre/post) and HEMISPHERE (ipsilateral/contralateral with respect to initial target). This revealed a significant TIME x HEMISPHERE interaction effect (F(1,10)=15.98, p=0.003, partial $\eta^2=0.62$), supporting the idea that the target representation is actually remapped.

To further analyze the laterality of these activity patterns, the lateralized components were isolated as the power differences between the two hemispheres. Figure 4B shows the scalp topography of the lateralized components. Here also, an initial reduction can be seen in the right, contralateral hemisphere. Subsequently, tracking the topography across the various time intervals indicates a polarity reversal during the translation, i.e. when targets must be remapped to the ipsilateral side of gaze. To test the significance of the remapping effect, we compared the difference in power before and after the motion (time windows 0-0.5s and 2.5-3s) using a dependent samples t-test with cluster permutation correction. As shown in Fig 4C (central panel),
this revealed a significant bilateral (mirror symmetric) cluster, as marked by the asterisks (p<0.002). To demonstrate the temporal dynamics of the remapping effect in more detail, figure 4C (outer panels) depicts the time-frequency plots of the lower frequency band of the lateralized component contrast. Again, the contralateral hemisphere (right plot) shows initial power reduction in the post-stimulus phase before motion onset. This reduction is remapped to the ipsilateral hemisphere (left plot) during motion (t=1 – 2 s) and is sustained after motion ends.

< FIGURE 4 ABOUT HERE >

Alpha band modulations correlate with updating gain

If the observed power modulations in the alpha band are indeed part of a gaze-centered updating mechanism, they should vary in relation to updating performance. The behavioral performance of our subjects varied between low and high gain (see figure 2). Figures 3-4 show that the updating process is reflected in a difference in alpha-band activity before and after translation. To quantify this, the modulation in the alpha band over time was calculated for all electrodes per subject and averaged according to hemisphere (contra- or ipsilateral). This pre-post difference value was entered in a regression analysis with the gain factor. This yielded a significant cluster of electrodes (p<0.025 cluster-corrected), as shown in figure 5A. This bilateral parietal cluster shows a significant negative correlation with updating performance. This means that a larger difference between the alpha power before and after motion is associated with a higher
gain factor, i.e. better performance. This is illustrated in figure 5B, where the alpha modulation data has been median-split into a high and low performance group. As can be seen, ‘good’ performers (gain > 0.71) show larger alpha modulations at more anterior, central parietal electrodes, whereas ‘poor’ performers show more posterior modulations at occipital electrodes. This shows that reductions in the alpha band at parietal electrodes during task performance are clearly associated with accurate spatial updating.

Discussion

Using saccadic updating paradigms, it has been suggested that the brain stores dynamic visual representations within a gaze-centered reference frame to maintain visual stability (Medendorp et al., 2003a; Merriam et al., 2003; Bellebaum and Daum, 2006; Van Der Werf et al., 2013). Here, we studied whether similar gaze-centered mechanisms are recruited for visual stability across whole-body motion. For gaze-centered updating mechanisms to be veridical under whole-body motion during world-stationary fixation, parallax geometry needs to be taken into account. Importantly, our subjects could not see the effects of parallax geometry but had to simulate it internally based on vestibular motion signals and other extraretinal motion cues, combined with estimates of fixation and target depth. Our focus was on the role of alpha band oscillations, which have been implicated in saccadic updating (Van Der Werf et al.,
2013). By exploiting the direction selectivity of alpha band power, we show parallax-sensitive, trans-hemispheric remapping of alpha band power when remembered targets cross hemifields relative to the fixation point, dependent on their depth. At parietal electrodes, the strength of these remapping modulations correlated significantly with the quality of the visuospatial updating, pointing to a crucial role of this region in maintaining visual stability.

Our behavioral results show that subjects are able to perform (although not perfectly) the necessary update of spatial location for an intervening passive whole-body motion, which is in line with previous studies (Medendorp et al., 2003b; Li et al., 2005; Van Pelt and Medendorp, 2007). The direction of the systematic errors, or biases (a deviation to the left or right of the veridical location) depended on the depth of the target and motion direction of the subject, consistent with the findings of Clemens et al. (2012). Thus, from the behavior we infer that the brain employs a gaze-centered mechanism to internally update remembered visual space during whole-body translations, taking the geometry of motion parallax into account.

The behavioral data could be explained by a gaze-centered updating model with a gain factor on the translation. Gain factors were below 1 (mean ~ 0.7) indicating a general underestimation of translation, which is in line with a general underestimation of distance traveled (Tremblay et al., 2013). However, performance was better than previously found with passive sinusoidal translations (Clemens et al., 2012), suggesting that the content of vestibular feedback (sinusoidal versus transient) and task conditions affect updating performance. Other studies, using active motion (i.e. where additional information is available in the form of a motor command copy), show a close to ideal performance (Medendorp et al., 2003b; Van Pelt and Medendorp, 2007), suggesting that
visual stability essentially requires a multimodal solution (Klier and Angelaki, 2008; Medendorp, 2011).

The incorporation of the geometry of motion parallax was not only observed in the behavioral biases. Here, for the first time, we show a neural correlate in terms of time-varying alpha band activity over occipito-parietal areas. By choosing a baseline that included the translation, but no updating of spatial targets, activity was isolated that reflected spatial updating. In all our four updating conditions, presentation of the initial target is followed by a contralateral decrease in alpha power over occipital and occipito-parietal electrodes in the pre-motion phase. This initial power decrease is driven by the visual input of the target. Importantly, after the intervening motion, alpha power reduction is sustained in the opposite hemisphere during the post-motion phase, contralateral to the updated location of the reference target in gaze coordinates, in absence of direct visual stimulation of this hemisphere. Our results show that the location of the target is reflected in lateralized alpha reductions that remap trans-hemispherically during the updating task. This reversal in lateralization is similar to saccadic updating, where a trans-hemispheric remapping of power reductions from the hemisphere contralateral to the initial target before the saccade, to the hemisphere contralateral to the updated target with respect to gaze after the saccade, has been shown (Van Der Werf et al., 2013). However, in the present experiment an internal simulation of motion parallax is needed to work out the location of the updated target in gaze coordinates.

In the current paradigm, a spatial target had to be stored in memory and updated throughout the trial. Low-frequency oscillations, such as the alpha band (8-12Hz) and the theta band (5-8 Hz), have been implicated in working memory processes (Jensen et al., 2002; Raghavachari et al., 2006; Sauseng et al., 2009). Whereas theta band
oscillations seem to be involved in sequential processing (Hsieh et al., 2011; Roberts et al., 2013; VanRullen, 2013), the alpha band seems to be more specific for (visuo)spatial memory tasks (Fries et al., 2001; Sauseng et al., 2005; Roux and Uhlhaas, 2014), which is consistent with the present observations.

Various studies have further shown a negative coupling between power in the alpha band and power in the gamma band (Fries et al., 2001; Osipova et al., 2008). This frequency coupling is suggested to establish a coherent neuronal group representing a location in working memory (Salazar et al., 2012). Unfortunately, we were unable to obtain reliable measurements in the gamma band. Although the head was fixed relative to the body, the acceleration of the chair caused increased tension in the neck muscles, creating artifacts in the higher frequencies. In future work, it would be interesting to see if gamma is indeed phase locked to alpha during spatial updating performance and whether it is similar to saccadic updating (Van Der Werf et al., 2013).

Could the present results be explained as a purely attentional phenomenon? In the literature, alpha band power has been strongly linked to visuospatial attention (Foxe et al., 1998; Worden et al., 2000, see for reviews Foxe and Snyder, 2011; Jensen et al., 2012). Attending a visual hemifield results in laterialized increases and decreases in alpha power in the ipsi- and contralateral hemisphere, respectively. Indeed, while the initial reduction is likely a response to the visual stimulation, the ensuing alpha reductions may be indicative of covert attention. Following this notion, the power modulations in the alpha band seen over the occipito-parietal areas may be an implementation of an ‘attentional pointer’ to the remembered location in gaze coordinates (Cavanagh et al., 2010) and instantiate one of the mechanisms that contributes to the updating process. However, the update of this attentional pointer still
requires an internal simulation of motion parallax, which is accompanied by time-varying spatial-selective alpha power reductions in the posterior brain.

We found that alpha band activity at parietal electrodes correlated significantly with spatial updating performance for whole-body motion. Even though no source localization was performed and thus no anatomical structures can be implicated, we suggest that the resulting pattern of activity may have arisen from the neuronal computations that have to take place in parietal cortex. Particularly, this may stem from lateral intraparietal area (LIP), which is known to contain neurons with gaze-centered receptive fields that predictively remap the neural image to anticipate the visual consequences of saccades (Duhamel et al., 1992; Kusunoki and Goldberg, 2003). Similar observations have actually also been made for the frontal eye fields (Sommer and Wurtz, 2006). It is further known that the receptive fields of LIP neurons are three-dimensional, meaning that they are tuned to a combination of target direction and target depth (Gnadt and Mays, 1995; Genovesio and Ferraina, 2004). It is well possible that such neurons with 3D receptive fields play a role in parallax-sensitive updating provided they also integrate vestibular or other extraretinal information about the motion. Indeed, there are pathways that transmit vestibular signals to parietal cortex (Kaufman and Rosenquist, 1985; Meng et al., 2007; Shinder and Taube, 2010), supporting this proposal. Also human studies have explicitly implicated parietal cortex in self-motion processing based on caloric vestibular stimulation (Suzuki et al., 2001; Dieterich et al., 2003, for review Lopez et al., 2012) and optic flow signals (Kovács et al., 2008; Wolbers et al., 2008). It seems plausible that the intersubject differences in alpha modulation in parietal cortex reflect the neural basis for more veridical integration of vestibular signals
into the updating process, as the larger modulation is associated with better updating
performance.

As pointed out by Van Pelt and Medendorp (2007), vestibular and retinal signals
are not the only relevant signals to implement spatial updating in the present study. Also
changes in eye position to keep the eyes at the fixation point during the translation – the
version and vergence eye movements – provide cues for the updating mechanism.
These signals have also been observed in parietal cortex (Andersen et al., 1985; Gnadt
and Mays, 1995; Gnadt and Beyer, 1998; Prevosto et al., 2009; Chang and Snyder,
2010), where they need to be integrated with vestibular signals, as well as target depth
and direction information, in order to compute the evolving representation of
remembered 3-D space during self-motion that we have shown.

Taken together, our results suggest that during passive motion, the
representation of a remembered and updated target is reflected in lateralized alpha
band activity. The pattern of activity in the alpha band is in line with a gaze-centered
updating mechanism, necessitating inclusion of motion parallax effects. Activity at the
posterior parietal electrodes shows a strong relation to updating performance, possibly
indicating a crucial role for the PPC in updating locations in the world under passive
motion conditions.

Grants: This work is supported by grants from the European Research Council (EU–
ERC 283567), EU-FP7-FET grant (SpaceCog 600785), and the Netherlands
Organisation for Scientific Research (NWO–VICI: 453–11–001; NWO-VENI: 451-10-
017).
Disclosures: The authors declare no competing financial interests.


Legends

Figure 1

Schematic depiction of the setup and paradigm. A) Top view of the experimental setup. A typical trial started with the subject on either side of the central position. While keeping fixation (depicted as a green dot) a target is flashed either in front of- or behind the fixation point at t=0. Here, the target is presented behind fixation, thus to the right of gaze (see inset, star represents target). Subjects moved at t=1 with a bell-shaped velocity profile (distance 400mm, duration 1s) while keeping track of the (invisible) remembered target. Here, after the motion, the remembered target location (depicted as a dotted circle) is to the left of gaze. At t=3 a probe stimulus is flashed at the same depth which could be left or right of the target. B) Time course of the experiment and position of the sled in an example trial. C) Example of condition order. Two blocks (52 trials) with fixation either behind ('B') or in front of fixation ('F') were alternated with a baseline block ('Bl') in between. Start condition (B/F) was randomized across subjects.
Figure 2

Behavioral results. A) Psychometric curve fits for a single subject for the left and rightward motion conditions with the targets presented in front of fixation (top) or behind fixation (bottom). Bias (µ) values (see dotted vertical lines), corresponding to the 0.5 probability point, were extracted for every subject. To construct the curve, all task trials were included (104 per condition). B) Bias (µ) of the psychometric curve fit for the two target/probe depths and left and right motion directions for all subjects. The data point marked with a red circle corresponds to the single subject data in A. Fixation depth is shown as a dotted red horizontal line. C) Gain factors for the four task conditions.

Figure 3

Group average scalp topography of alpha band power at four different time intervals, separately for the four conditions of the experiment. The first time interval (0-0.5s) shows the oscillatory response to the visual presentation of the target. At t=1 motion commences (lasting 1s) and thus the second and third time interval reflect the first and second half of motion, respectively. The fourth time interval (2.5-3s) reflects activity just before the presentation of the probe stimulus, when the subject is in a stationary situation again. The right column shows a lateralization index over time, calculated as the normalized difference in alpha reduction for the left and right hemisphere. Positive
laterality index indicates a right hemisphere bias, negative a left hemisphere laterality bias.

**Figure 4**

Isolating the group average task-evoked activity and the laterialized components of the alpha band activity across all conditions. A) Task-evoked activity during the four time intervals of figure 3. Warmer colors, increase in alpha power; cooler colors, decreases in power. Plotting convention: right hemisphere is contralateral to the initially presented target and the left hemisphere is contralateral to the updated target position relative to gaze. B) Lateralized components, illustrated by a subtraction of all conditions. Plotting conventions as A. C) (middle) Electrodes that show a significant (p<0.002) difference between alpha power before (0-0.5s) and after (2.5-3s) the motion in the subtraction. (bottom left and right) Time-frequency plots of the lower frequency band of the laterialized components for these significant electrodes (TPPP7/8h, P3/4, P5/6, P7/8, P9/10, PO3/4, PO7/8, PO9/10, PPO9/10h, O9/10, O1/2h, O1/2).

**Figure 5**

Linking behavioral and neural correlates. A) Electrodes showing a significant correlation between power modulations in the alpha band and psychometrically determined updating gain. Color map, t-values from the regression analysis. (right) Relationship between alpha power and updating performance at significant sensors (Pz, P1, P3, P4,
CCP3h and PO4). B) Scalp topography plot of the alpha modulation (pre-post motion difference) over time as used in the regression analysis with gain for 'good' (left) and 'bad' (right) performers (median split, gain>0.71 considered 'good'). Cooler colors indicate a greater pre- minus post motion difference and thus a greater modulation of alpha over time.
A

Task-evoked activity

B

Lateralized components

C

Pre-post modulation

Left Hemisphere (ipsilateral)

Right Hemisphere (contralateral)
High Gain subjects vs. Low Gain subjects: 

- **A** Behavioral correlation

  - Heatmap showing brain activity patterns with a significant p-value of less than 0.025.

- **B** Comparison of High Gain and Low Gain subjects

  - Heatmaps highlighting different brain activity levels between the two groups.