



Research report

Premotor and occipital theta asymmetries as discriminators of memory- and stimulus-guided tasks

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ABSTRACT

The saccadic paradigm has been used to investigate specific cortical networks involving visuospatial attention. We examined whether asymmetry in theta and beta band differentiates the role of the hemispheres during the execution of two different prosaccadic conditions: a fixed condition, where the stimulus was presented at the same location; and a random condition, where the stimulus was unpredictable. Twelve healthy volunteers (3 male; mean age: 26.25) performed the task while their brain activity pattern was recorded using quantitative electroencephalography. We did not find any significant difference for beta, slow- and fast-alpha frequencies for the pairs of electrodes analyzed. The results for theta band showed a superiority of the left hemisphere in the frontal region when responding to the random condition on the right, which is related to the planning and selection of responses, and also a greater activation of the right hemisphere during the random condition, in the occipital region, related to the identification and recognition of patterns. These results indicate that asymmetries in the premotor area and the occipital cortex differentiate memory- and stimulus-driven tasks.

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1. Introduction

The ability to selectively direct our attention to a particular stimulus, stimulus feature or spatial location represents one of the most fundamental aspects of human (neural) information processing [33,13]. Saccades are one of the ocular movements responsible for this ability [19,14]. Saccadic eye movements (SEM) are controlled by a cortical and subcortical network composed of several oculomotor areas [19]. The execution of SEM also activates brain areas

involved in multisensory and sensorimotor integration. Recent studies shed light on the specific role of these networks [16,22].

Evidence suggests a bilateral cortico-cortical network that interconnects attention modulation and saccades [22,44]. Although attention processes are related to both left and right hemispheres, a greater activation of the right hemisphere during the execution of tasks involving attention has been observed [21]. These findings point to the existence of cerebral dominance for spatial attention, assuming that areas of the right hemisphere are modulators of attention for both ipsilateral and contralateral stimulation [25]. Brignani et al. [3] analyzed the electrocortical rhythms and found that eye movement control is not distributed equally to the left and right hemifields and that the two hemispheres cover the visual field asymmetrically.

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In a recent study [28] hypothesized that the neural basis of saccades in humans should be under right cerebral dominance. They identified a right asymmetrical activation in the lateral frontal eye fields (FEF), the anterior intraparietal sulcus (aIPS), the superior temporal sulcus (STS), the occipito-temporal junction (MT/V5 area), the middle occipital gyrus, and medially along the calcarine fissure (V1) during a task involving visually guided saccades. They also observed a left asymmetrical activation of a saccadic motor system in the medial FEF and in the motor strip eye field along the Rolando sulcus. These results demonstrate that, although bilateral by nature, the brain network involved in the execution of visually guided saccades presented specific right and left asymmetries that are not related to anatomical differences in sulci positions.

Most studies of electrophysiological correlates of SEM investigate the time domain. Thus, it would be of considerable interest to study how performing saccades modulates theta human activity in both hemispheres. We seek to fill this gap by focusing on the frequency domain, especially in slow waves such as theta band. Theta band (4.5–8 Hz) was chosen due to its involvement in various mental tasks, especially spatial navigation and attention [29,9]. Oscillations in theta band have been correlated with voluntary behavior, suggesting that it may reflect the integration of sensory information with motor response [2]. In addition, we found very up-to-date few studies that focus on the participation of slow waves in SEM [41]. On the other hand, beta band is a high frequency range between 13 and 30 Hz. Oscillations in beta band have been correlated to motor activity, attention and mental activity [26,32,34].

Therefore, this study aims to analyze electroencephalographic recordings through the asymmetries in theta and beta band frequency, in the cortical areas that participate in SEM during two different task conditions: a fixed one, where memory drives the performance of repetitive tasks, and a random condition, which is stimulus driven [39]. It is believed that these two patterns of stimulus presentation are useful to investigate the role of visual perception and its influence on SEM [4,38,14]. Among the variables of the EEG, asymmetry detects the energy balance between the cortical areas of both hemispheres and is defined by the difference in absolute power between the homologous electrodes [43]. As previously described, it has also been demonstrated that the two hemispheres participate differently, not only in visual-spatial attention, but also in the network related to SEM. Using this paradigm, we want to investigate the role of cortical areas (i.e., central, temporal, parietal, frontal, occipital) in the planning, execution and cognitive control of SEM. For this purpose, four questions are relevant: (1) which cortical areas are responsible for saccades and for visual-spatial attention? (2) Which cortical areas are responsible for discriminating among different kinds of visual-spatial attention? (3) Which hemispheres (left or right) participate more intensively in SEM? (4) How does the SEM condition modulate theta and beta band asymmetry?

2. Methodology

2.1. Subjects

Twelve healthy volunteers (3 male; mean age: 26.25; SD 4.13) were recruited for this study. All participants had normal or corrected-to normal vision and no sensory, motor, cognitive or attention deficits that would affect saccadic eye movement. Subjects signed a consent form which thoroughly described the experimental procedure. The experiment was approved by the ethics committee of the Psychiatric Institute of the Federal University of Rio de Janeiro (IPUB/UFRJ).

2.2. Tasks and procedures

Subjects sat in a comfortable chair in a darkened and noise-free room in order to minimize sensory interference. A bar composed of 30 light emitting diodes (LEDs) was positioned at the participants' eye level. Fifteen LEDs were located on the left side of the fixation point, and 15 on the right side. The bar was of 120 cm long. The LED bar was placed at a distance of 100 cm from the participants' eyes. Computer software controlled the LED bar and determined stimulus presentation. Participants were asked to keep their eyes fixed on the center of the bar, and to shift their eyes when they perceived one of the diodes lighting up. Participants were instructed to follow the LEDs with their eyes in such way that their heads remained static.

The SEM paradigm consisted of two different conditions: a fixed pattern and a random pattern. In the fixed pattern, the target-stimulus (target LED) always appeared at a pre-defined position, i.e., LED 12, of either the left or the right side, alternating between left and right. This condition is characterized by predictability; the stimulus appears at a pre-defined spatial location in the periphery of the visual field, and was thus considered to be memory-driven. In contrast, the random pattern presented a fully randomized series of target LEDs at completely unpredictable spatial positions across the central and both peripheral visual fields (the light could appear at any of the 30 LEDs). This experimental condition was considered purely stimulus-driven. Under both conditions, each LED remained lit for 250 ms, with an inter-LED-time of 2 s. Each participant underwent 12 consecutive blocks, including six blocks of fixed SEM and six blocks of random SEM, with 20 trials per block. The probability of a light appearing on the left or right side was counterbalanced within and across blocks, thus both were SEM conditions.

2.3. EEG data acquisition

The International 10/20 EEG electrode system [17] was used with a 20-channel EEG system (Braintech-3000, EMSAMedical Instruments, Brazil). The 20 electrodes were arranged on a nylon cap (ElectroCap Inc., Fairfax, VA, USA) yielding monopolar derivations using the earlobes as reference. Impedance of EEG and EOG electrodes was kept between 5 and 10 k Ω . The amplitude of the data recorded was less than 70 μ V. The EEG signal was amplified with a gain of 22,000 Hz, analogically filtered between 0.01 Hz (high-pass) and 80 Hz (low-pass), and sampled at 200 Hz. The software *Data Acquisition* (Delphi 5.0) from the Brain Mapping and Sensory Motor Integration Lab, was employed with the notch (60 Hz) digital filter.

2.4. Saccadic eye movement acquisition

Four additional electrodes of 9 mm in diameter mounted in a bipolar form were used to measure the electrooculogram (EOG). Electrodes were arranged horizontally from the outer canthi of both eyes to determine the horizontal EOG (hEOG) and vertically above both eyes to determine the vertical EOG (vEOG).

2.5. Data processing and analysis

We applied a visual inspection and Independent Component Analysis (ICA) to remove possible sources of artifacts produced by the task (i.e., blink, muscle and saccade-related artifacts). The data were collected using the bi-auricular reference and they were transformed (re-referenced) using the average reference after we conducted the artifact elimination using ICA. We removed those trials that clearly showed a blink and saccade-related artifacts "influence" through visual inspection, and for the ones containing blink and saccade-related artifacts "contamination" we used ICA. A

classic estimator was applied for the power spectral density (PSD), or directly from the square modulus of the Fourier transform (FT), which was performed by MATLAB 5.3 (Matworks, Inc.). The number of samples was 800 ($4\text{ s} \times 200\text{ Hz}$) with rectangular windowing. We extracted Quantitative EEG parameters within a time window between 500 ms before the stimulus presentation and 500 ms after the target stimulus LEDs (the selected epoch started 500 ms before and ended 500 ms after the trigger, i.e., moment 1 and moment 2, respectively). Thereafter, all raw EEG trials were visually controlled and trials contaminated with ocular or muscle artifacts were discarded. The FT resolution was $1/4\text{ s}$ to 0.25 Hz . To examine a stationary process, the “Run-test” and “Reverse-Arrangement test” were applied. The stationary process was accepted for each 4 s (epoch’s duration in this period). In this manner, based on artifact-free EEG epochs, the threshold was defined by the mean plus three standard deviations, not including epochs, with a total power higher than this threshold in the analysis.

We used a semi-automated method to detect the saccade reaction time. In particular, the saccades were determined at the start of the inflection point of the curve, always recognized from visual inspection. The saccade was sectored after stimulus presentation, in the period of 500 ms after the stimulus presentation. The highest velocity (first derivative) was detected at the point of deflection. From the moment that the LED lights were shown, we defined a period of 500 ms to seek the EOG inflection and mark the point that had the highest “acceleration” or the initiation (second derivate) of the EOG signal. Saccades with latencies of less than 70 ms and more than 500 ms were not considered.

Our data analyses revealed that the saccadic eye movements elicited in our study produce a slow electrical activity that mainly affects the delta band (0–3.5 Hz). We also conducted additional analyses to unravel the exact nature of saccade-related artifacts over the cortex.

2.6. Calculation of asymmetry

Statistical analysis was done according to the formula $Pa-Pb/Pa+Pb$ (Pa = right hemisphere and Pb = left hemisphere).

2.7. Statistical analysis

Theta (4.5–8 Hz), beta (13–30 Hz), slow- (8–10 Hz) and fast- (10–12 Hz) alpha asymmetry were the dependent variables of interest. The pairs of electrodes used for the analysis were FP1–FP2, F3–F4, F7–F8, C3–C4, T3–T4, T5–T6, O1–O2 and P3–P4 for theta and beta frequencies. And FP1–FP2, T3–T4, T5–T6, O1–O2 and P3–P4 for slow- and fast-alpha band. The statistical analyses were performed using a two-way repeated ANOVA measure with the factors SEM condition (2 levels: fixed versus random SEM), and time point (2 levels: pre- versus post-stimulus epoch).

We also analyzed saccade latency. The statistical analysis was performed using an Independent-sample t -test measure.

3. Results

We analyzed theta asymmetry over the prefrontal cortex and the fronto-temporal, parietal and occipital lobes, at the following pairs of electrodes: FP1–FP2, F3–F4, F7–F8, C3–C4, T3–T4, T5–T6, O1–O2 and P3–P4. The two-way repeated measure ANOVA revealed a main effect for condition on pairs F3–F4 ($p=0.007$) (Fig. 1) and O1–O2 ($p=0.023$) (Fig. 2). For the electrode pairs F3–F4 and O1–O2, we noticed higher asymmetry in the random condition when compared to the fixed condition. We found no significant results for the other electrode pairs.

The results of the statistical analysis showed a greater asymmetry in the random condition when compared to the fixed condition

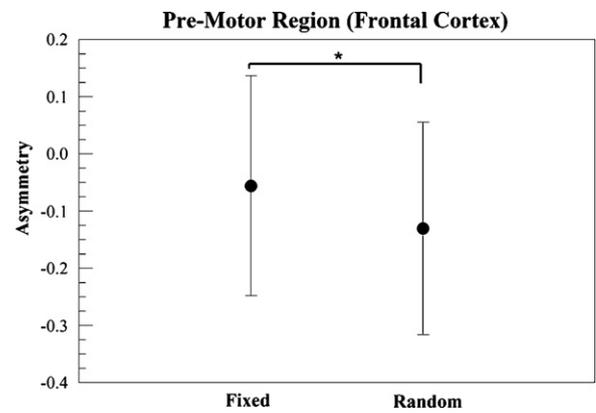


Fig. 1. Mean and standard deviation of theta asymmetry over premotor region at fixed and random condition. The statistical analysis revealed a main effect of time point ($p=0.007$).

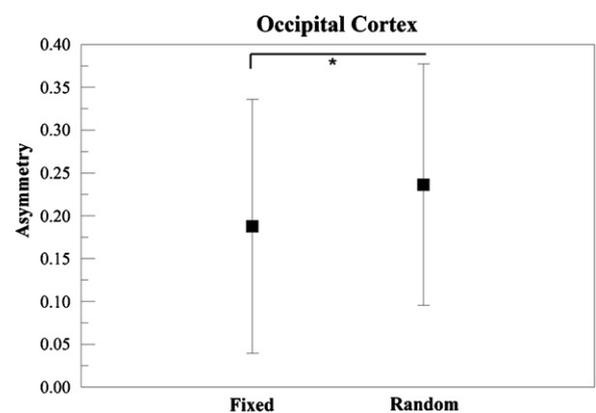


Fig. 2. Mean and standard deviation of theta asymmetry over occipital cortex at fixed and random condition. The statistical analysis revealed a main effect of time point ($p=0.023$).

for the electrode pair F3–F4. The results also indicated a greater negativity in the random condition, indicating the predominance of the left hemisphere over the right. However, we observed greater asymmetry under the random condition for the electrode pair O1–O2, where we noted positive values for both asymmetry conditions, with a predominance of the right hemisphere. For beta, slow- and fast-alpha we did not find any significant difference at the pair of electrodes observed.

We also analyzed saccade latency and found a difference in time reaction between the fixed and random condition ($p=0.005$; $F=8.077$) (Fig. 3). SEM latency for the fixed SEM condition

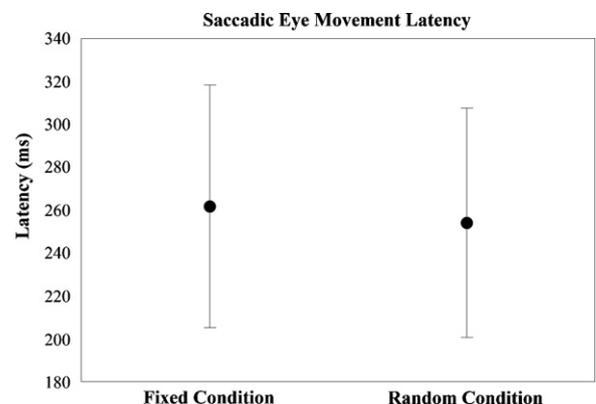


Fig. 3. Mean and standard deviation of saccadic eye movement latency (ms). The statistical analysis revealed a significant difference between conditions ($p=0.005$).

($x = 261.73$ ms; $SD = 56.57$) was significantly higher as compared to the random SEM condition ($x = 254.06$; $SD = 53.48$).

4. Discussion

The present study aimed to observe patterns of asymmetry in theta (4.5–8 Hz) and beta (13–30 Hz) band over the frontal, parietal, temporal and occipital cortical areas during the execution of an attention task involving saccadic eye movement. In the following subsections we will focus the discussion on the cortical areas where we observed significant statistical differences, as well as in the parietal cortex. We will also briefly discuss behavioral data. We also analyzed slow- and fast-alpha for the following pair of electrodes: FP1–FP2, T3–T4, T5–T6, O1–O2 and P3–P4; and we did not find a significant statistical difference. We also did not find a significant difference for beta band. Although beta asymmetry has been widely related to motor control [31,42], our data did not demonstrate that beta asymmetry discriminates fixed and random conditions during a SEM task.

We already have published the frontal alpha asymmetry data during the execution of our saccade paradigm (see Sanfim et al. [45]). In that manuscript we investigated slow- (8–10 Hz) and fast- (10–12 Hz) alpha asymmetry over F3–F4, F7–F8 and C3–C4 pair of electrodes. Our most important result was a main effect for condition over F3–F4, with a negative alpha (slow- and fast-) asymmetry (i.e., indicating the predominance of the left hemisphere over the right). We also found a main effect for condition over F7–F8 for slow-alpha asymmetry, with a positive asymmetry (i.e., indicating the predominance of the right hemisphere over the left). We concluded that slow- and fast-alpha asymmetry are associated with the planning and preparation of SEM. Specifically, we observed that asymmetry for these frequencies bands play an important role for attention network and integration of sensory information during a oculomotor response.

Our results in beta, theta, slow- and fast-alpha asymmetry demonstrated that theta, slow- and fast-alpha asymmetry over frontal areas (F3/F4) discriminates the two experimental conditions (i.e., fixed and random pattern of stimulus presentation). We observed that for these frequencies there is more engagement of the left hemisphere for the memory-driven. However, according to our results beta asymmetry is not sensitive to the pattern of stimulus presentation in the fixed and random condition.

4.1. Planning and response selection

Asymmetry in theta band was investigated in three distinct frontal regions: FP1–FP2, F7–F8 and F3–F4. Our results showed a main effect for condition in the F3–F4 pair of electrodes, and no significant results for the others pairs. The F3 and F4 electrodes are located over a cortical area called the premotor frontal region. Consequently, we found an increase of asymmetry for the stimulus-driven condition when compared to the memory-driven condition over the premotor frontal region. Or rather, we observed a greater imbalance between the hemispheres for the stimulus-driven condition. More importantly, we identified greater participation of the left hemisphere and lesser involvement of the right hemisphere under the stimulus-driven condition (Fig. 4a). For the memory-driven condition, although we verified an increased participation of the left hemisphere, the imbalance between the hemispheres was less (Fig. 4b). Thus, the results indicate a greater involvement of the left hemisphere (F3) for both conditions, with increased participation under the stimulus-driven condition. The left hemisphere is responsible for the preparation and execution of voluntary SEM in tasks involving sequencing and mechanisms related to visual motor attention [30]. One possible interpretation of these

findings would be that more intensive planning takes place over the frontal–premotor areas, which coordinate the search of the visual system in a task that is driven by environmental stimuli (random condition).

Previous studies have linked theta band to the integration of sensory information with motor response [18,40] and also associated it with the forced state of attention (concentration) required to maintain the performance of tasks [11]. Variations in theta band have been observed during exploration and navigation tasks that require spatial sensory integration [2,5]. Caplan et al. [6] demonstrated that the theta band oscillations underlying the coordination of sensory and motor brain activity modulate exploratory learning and navigation planning. Other studies have shown an association between the activity of theta band and the execution of different attention tasks and spatial navigation [39,10].

The supplementary visual field is located in the frontal cortex, and rostrally to the supplementary motor area [18]. Thus, a system of association of the supplementary visual field and the supplementary motor area suggests the involvement of the left frontal cortex in control saccades [12,22]. Our findings are consistent with other studies that observed the same pattern of theta band activity over the left hemisphere of the frontal cortex. In this context, the increased activity over the left frontal cortex found in our results is explained by the exclusive involvement of this region in the onset of motor sequence in eye movement. Specifically, our findings showed a greater asymmetry in the theta band for the random condition. This result can be interpreted according to the type of sequencing that is done under each condition. In the stimulus-driven condition, participants need to perform a visual search to detect the LED lights. This feature of the task involves the need for coordination between the stimulus (LED) and motor activity (i.e., saccadic movement) to find the target location, which reflects the involvement of attention on visuomotor integration [7]. In the performance of the memory-driven condition, the task becomes more predictable since the location of the target LED is always peripheral, appearing in a permanent position (LED 12) either on the left-hand or right-hand side (alternating between left and right). The unpredictability of the random sequence seems to have favored the participation of the left frontal cortex, and may be related to cognitive processes of visual exploration and expectation for the production of motor responses, reflecting the sensory stimulation of attention in visuomotor integration systems [30,23,8]. In conclusion, the different absolute power found in the theta band over the frontal electrodes F3 and F4, for the fixed and random conditions, provides great evidence that theta oscillations can discriminate between memory and stimulus driven movements. Our results are consistent with previous findings relating left hemispherical superiority over the right for the random condition.

4.2. Pattern identification and recognition

The occipital cortex is responsible for the first stage of information processing: the identification of the stimulus [27]. Particularly, in attention processes, this stage is associated with the selection of relevant stimuli [1,15]. Therefore, this region plays an essential role in the generation and direction of oculomotor movements [36]. Our study verified a greater asymmetry for the random condition when compared with the fixed condition for the electrode pair O1–O2 (Fig. 3a and b). Our findings also demonstrated that the right hemisphere (O2) is more involved in both conditions, especially under the random condition. Thus, theta band activity is concentrated over the right occipital cortex, particularly over the primary visual cortex (striate cortex), with a prevalence of activity during the execution of the random condition. These findings corroborate other studies demonstrating an increase in activation in the right primary visual cortex when the task required an update

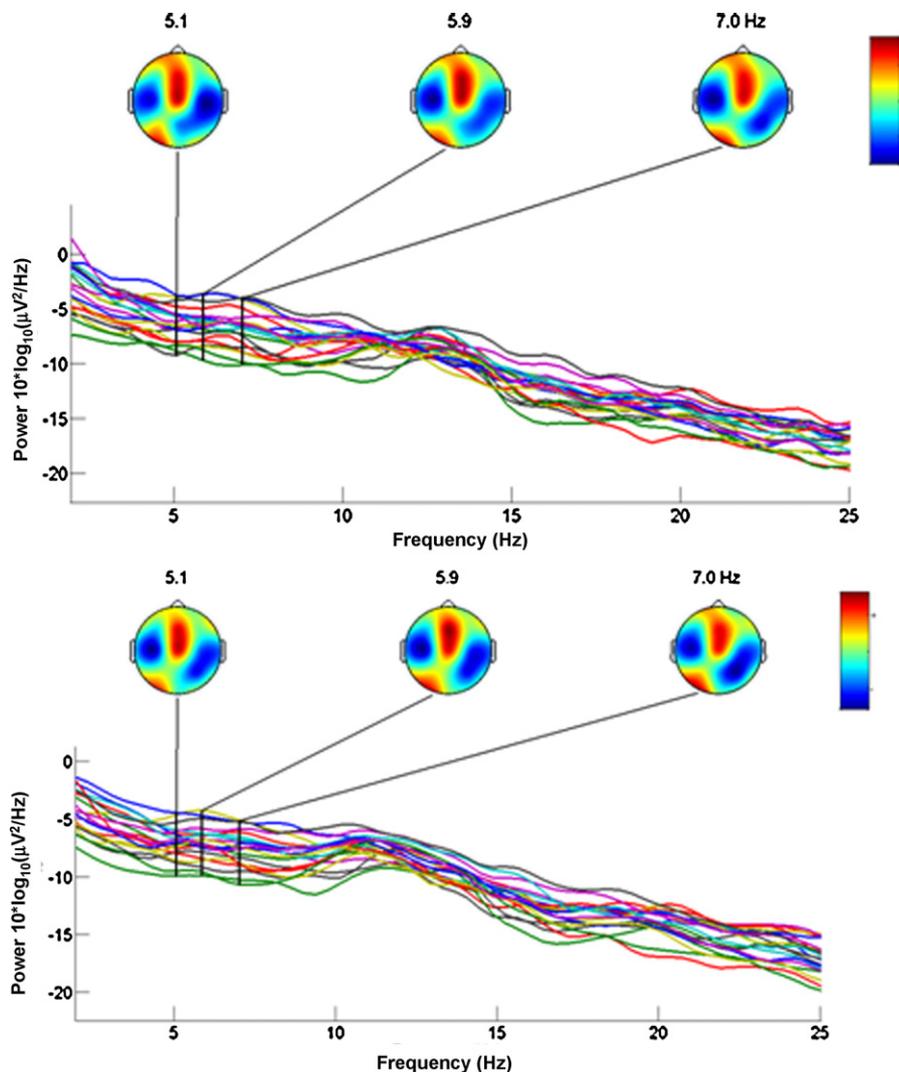


Fig. 4. Power activity of the cerebral cortex at three different frequencies, generated from the analysis of fast Fourier transform (FFT). (a) Random (stimulus-driven) condition. (b) Fixed (memory-driven) condition.

of the oculomotor motion parameters [20]. The right hemisphere could control the eye movements for the left or right field, while the left hemisphere preferentially controls the eye movements of the right contralateral visual field [24,35]. One study involving electroencephalography concluded that eye control movements cannot be distributed equally between the left and right hemifields and that the two hemispheres cover the visual field asymmetrically [3]. Accordingly, the electrode pair O1–O2 showed an increase in theta asymmetry under the random condition when compared to the fixed condition. We observed a larger gradient energy over the right hemisphere as this hemisphere participated more during the random condition.

Our results revealed that areas of the right hemisphere modulate attention in both the contralateral and the ipsilateral hemispheres, considering that the areas of the left hemisphere are directed only to the right contralateral hemisphere [25]. Thus, spatial exploration reflects the organization of cerebral lateralization, of which right brain dominance is present in spatial analysis, or rather in guided saccadic movements [37]. Their involvement is demonstrated by occipital activation in the primary visual area, extending through the ventral and dorsal striated pathways [22].

Although we did not find a significant difference between tasks on parietal sites P3–P4 ($p=0.241$), we did find a tendency towards

a greater positive asymmetry during the stimulus-drive condition. The increased activity in the right hemisphere is coherent with the type of sequencing that is done under this condition, where unpredictability calls upon visuospatial attention and search. We also found an increased asymmetry between moments ($p=0.058$).

Regarding SEM latency, both SEM conditions required participants to direct their gaze towards the target-stimulus once it was identified. Our SEM latency findings clearly revealed a significant difference between SEM condition, demonstrating that the change in SEM latency is significantly different between the fixed versus random pattern SEM condition. Specifically, the fixed SEM latency seems to be higher than random SEM latency, as expected.

In brief, analysis of the data revealed a superiority of the left hemisphere in the frontal region when responding to the random condition on the right, which is related to the planning and selection of responses, and also a greater activation of the right hemisphere during the random condition, in the occipital region, related to the identification and recognition of patterns. Although we did not find a significant difference between tasks on parietal sites, we did find a tendency towards a greater positive asymmetry during the stimulus-driven SEMs. The present findings suggest that the right hemisphere was dominant when the task required an update of the oculomotor motion parameters and that asymmetries in the premotor area and the occipital cortex differentiate memory- and

stimulus-driven tasks. Conflict of interest None declared. Funding source

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.brainresbull.2011.10.013.

References

- [1] M.S. Beauchamp, L. Petit, T.M. Ellmore, J. Ingeholm, J.V. Haxby, A parametric fMRI study of overt and covert shifts of visuospatial attention, *Neuroimage* 14 (2001) 310–321.
- [2] B.H. Bland, S.D. Oddie, Theta band oscillation and synchrony in the hippocampal formation and associated structures: the case for its role in sensorimotor integration, *Behav. Brain Res.* 127 (1–2) (2001) 119–136.
- [3] D. Brignani, C. Maioli, P. Maria Rossini, C. Miniussi, Event-related power modulations of brain activity preceding visually guided saccades, *Brain Res.* 1136 (2007) 122–131.
- [4] J.W. Brown, D. Bullock, S. Grossberg, How laminar frontal cortex and basal ganglia circuits interact to control planned and reactive saccades, *Neural Networks* 17 (May (4)) (2004) 471–510.
- [5] G. Buzsáki, Theta rhythm of navigation: link between path integration and landmark navigation, episodic and semantic memory, *Hippocampus* 15 (7) (2005) 827–840.
- [6] J.B. Caplan, J.R. Madsen, E. Schulze-Bonhage, R. Aschenbrenner-Scheibe, E.L. Newman, M.J. Kahana, Human theta oscillations related to sensorimotor integration and spatial learning, *J. Neurosci.* 23 (11) (2003) 4726–4736.
- [7] J.D. Connolly, M.A. Goodale, J.F. Desouza, R.S. Menon, T. Vilis, A comparison of frontoparietal fMRI activation during anti-saccades and antipointing, *J. Neurophysiol.* 84 (2000) 1645–1655.
- [8] M. Corbetta, J.M. Kincade, G.L. Shulman, Neural systems for visual orienting and their relationships to spatial working memory, *J. Cogn. Neurosci.* 14 (3) (2002) 508–523.
- [9] L.M.F. Doyle, K. Yarrow, P. Brown, Lateralization of event-related beta desynchronization in the EEG during pre-cued reaction time tasks, *Clin. Neurophysiol.* 116 (2005) 1879–1888.
- [10] A.D. Ekstrom, J.B. Caplan, E. Ho, K. Shattuck, I. Fried, M.J. Kahana, Human hippocampal theta activity during virtual navigation, *Hippocampus* 15 (7) (2005) 881–889.
- [11] S.H. Fairclough, L. Venables, A. Tattersall, The influence of task demand and learning on the psychophysiological response, *Int. J. Psychophysiol.* 56 (2) (2005) 171–184.
- [12] B. Gaymard, C. Pierrot-Deseilligny, S. Rivaud, S. Velut, Smooth pursuit eye movement deficits after pontine nuclei lesions in humans, *J. Neurol. Neurosurg. Psychiatry* 56 (7) (1993) 799–807.
- [13] B. Gaymard, C.J. Ploner, S. Rivaud-Peichoux, C. Pierrot-Deseilligny, The frontal eye field is involved in spatial short-term memory but not in reflexive saccade inhibition, *Exp. Brain Res.* 129 (2) (1999) 288–301.
- [14] A. Herwig, M. Beisert, W.X. Schneider, On the spatial interaction of visual working memory and attention: evidence for a global effect from memory-guided saccades, *J. Vis.* 10 (5) (2010) 8.
- [15] S.B. Hutton, Cognitive control of saccadic eye movements, *Brain Cogn.* 68 (3) (2008) 327–340.
- [16] F. Jagla, M. Jergelova, I. Rieckensky, Saccadic eye movement related potentials, *Physiol. Res.* 56 (2007) 707–713.
- [17] H. Jasper, The ten-twenty electrode system of international federation, *Electroencephalogr. Clin. Neurophysiol.* 10 (1958) 371–375.
- [18] E. Kandel, S. Schwartz, T. Jessel, *Principles of Neuroscience*, 4th ed., McGraw-Hill, New York, 2000.
- [19] Z. Kapoula, Q. Yang, O. Coubar, G. Daunys, C. Orssaud, Role of the posterior parietal cortex in the initiation of saccades and vergence: right/left functional asymmetry, *Ann. N. Y. Acad. Sci.* 1039 (2005) 184–197.
- [20] H.O. Karnath, A right perisylvian neural network for human spatial orienting, in: M.S. Gazzaniga (Ed.), *The Cognitive Neurosciences*, 4th ed., MIT Press, Cambridge, MA, 2009, pp. 259–268.
- [21] C.S. Konen, R. Kleiser, F. Bremmer, R.J. Seitz, Different cortical activations during visuospatial attention and the intention to perform a saccade, *Exp. Brain Res.* 182 (3) (2007) 333–341.
- [22] J.E. McDowell, K.A. Dyckman, B.P. Austin, B.A. Clementz, Neurophysiology and neuroanatomy of reflexive and volitional saccades: evidence from studies of humans, *Brain Cogn.* 68 (2008) 255–271.
- [23] W.P. Medendorp, H.C. Goltz, T. Vilis, J.D. Crawford, Gaze-centered updating of visual space in human parietal cortex, *J. Neurosci.* 23 (2003) 6209–6214.
- [24] W.P. Medendorp, H.C. Goltz, J.D. Crawford, T. Vilis, Integration of target and effector information in human posterior parietal cortex for the planning of action, *J. Neurophysiol.* 93 (2005) 954–962.
- [25] M.M. Mesulam, Spatial attention and neglect: parietal, frontal and cingulate contributions to the mental representation and attention targeting of salient extrapersonal events, *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 354 (1999) 1325–1346.
- [26] E. Niedermeyer, F. Silva, *Electroencephalography: Basic Principles, Clinical Applications and Related Fields*, 5th ed., Urban & Schwarzenberg, Baltimore, 2005.
- [27] R.J. Perry, S. Zeki, The neurology of saccades and covert shifts in spatial attention: an event-related fMRI study, *Brain* 123 (2000) 2273–2288.
- [28] L. Petit, L. Zago, M. Vigneau, F. Andersson, F. Crivello, B. Mazoyer, Functional asymmetries revealed in visually guided saccades: an fMRI study, *J. Neurophysiol.* 102 (5) (2009) 2994–3003.
- [29] G. Pfurtscheller, M. Woertz, G. Supp, F.H. Lopes da Silva, Early onset of post-movement beta electroencephalogram synchronization in the supplementary motor area during self-paced finger movement in man, *Neurosci. Lett.* 339 (2003) 111–114.
- [30] C. Pierrot-Deseilligny, R.M. Müri, T. Nyffeler, D. Milea, The role of the human dorsolateral prefrontal cortex in ocular motor behavior, *Ann. N. Y. Acad. Sci.* 1039 (2005) 239–251.
- [31] B. Pollok, J. Gross, A. Schnitzler, Asymmetry of interhemispheric interaction in left-handed subjects, *Exp. Brain Res.* 175 (2) (2006) 268–275.
- [32] C.E. Portella, J.G. Silva, V.H. Bastos, D. Machado, M. Cunha, M. Cagy, et al., Procedural learning and anxiolytic effects: electroencephalographic, motor and attentional measures, *Arq. Neuropsiquiatr.* 64 (2B) (2006) 478–484.
- [33] M.I. Posner, S.E. Petersen, The attention system of the human brain, *Annu. Rev. Neurosci.* 13 (1990) 25–42.
- [34] M. Sabate, C. Llanos, E. Enriquez, M. Rodriguez, Mu rhythm, visual processing and motor control, *Clin. Neurophysiol.* (2001) [Epub ahead of print].
- [35] D. Sava, M. Liotti, G. Rizzolatti, Right hemisphere superiority for programming oculomotion: evidence from simple reaction time experiments, *Neuropsychologia* 26 (1988) 201–211.
- [36] D. Schluppeck, P. Glimcher, D.J. Heeger, Topographic organization for delayed saccades in human posterior parietal cortex, *J. Neurophysiol.* 94 (2005) 1372–1384.
- [37] M.A. Silver, D. Ress, D.J. Heeger, Topographic maps of visual spatial attention in human parietal cortex, *J. Neurophysiol.* 94 (2005) 1358–1371.
- [38] L.S. Simó, C.M. Krisky, J.A. Sweeney, Functional neuroanatomy of anticipatory behavior: dissociation between sensory-driven and memory-driven systems, *Cereb Cortex* 15 (12) (2005) 1982–1991.
- [39] M.E. Smith, L.K. McEvoy, A. Gevins, Neurophysiological indices of strategy development and skill acquisition, *Brain Res. Cogn. Brain Res.* 7 (3) (1999) 389–404.
- [40] L.R. Squire, D. Berg, F. Bloom, S. Du Lac, *Fundamental Neuroscience*, 3rd ed., Elsevier, Oxford, 2008.
- [41] E.S. Tomilovskaya, A.V. Kirenskaya, V.Y. Novototski-Vlasov, I.B. Kozlovskaya, Event-related EEG changes preceding saccadic eye movements before and after dry immersion, *J. Gravit. Physiol.* 11 (July (2)) (2004) P33–P34.
- [42] T. Tsujimoto, T. Mima, H. Shimazu, Y. Isomura, Directional organization of sensorimotor oscillatory activity related to the electromyogram in the monkey, *Clin. Neurophysiol.* 120 (6) (2009) 1168–1173.
- [43] B. Velasques, S. Machado, C.E. Portella, J.G. Silva, P. Terra, C. Ferreira, et al., Cortical asymmetry. Catching an object in free fall, *Arq. Neuropsiquiatr.* 65 (3-A) (2007) 623–627.
- [44] B. Wauschkuhn, R. Verleger, E. Wascher, W. Klostermann, M. Burk, W. Heide, et al., Lateralized human cortical activity for shifting visuospatial attention and initiating saccades, *J. Neurophysiol.* 80 (1998) 2900–2910.
- [45] A. Sanfim, B. Velasques, S. Machado, O. Arias-Carrión, F. Paes, S. Teixeira, et al., Analysis of slow- and fast-alpha band asymmetry during performance of a saccadic eye movement task: Dissociation between memory- and attention-driven systems, *J. Neurol. Sci.* (2011) [Epub ahead of print].