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Research report

Electrophysiological correlates of biological motion permanence in humans

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HIGHLIGHTS

- The temporal dynamics of biological motion occlusion was addressed by means of EEG.
- Centro-parietal regions were recruited within the occlusion period.
- The results suggest that the brain enacts the occluded movement.

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ABSTRACT

Spatiotemporal discontinuity of visual input is a common occurrence in daily life. For example, when a walking person disappears temporarily behind a wall, observers have a clear sense of his physical presence despite the absence of any visual information (movement permanence). To investigate the neural substrates of biological motion permanence, we recorded scalp EEG activity of sixteen subjects while they passively observed either biological or scrambled motion disappearing behind an occluder and reappearing. The moment of the occluder's appearance was either fixed or randomized. The statistical comparison between the biological and scrambled motion ERP waveforms revealed a modulation of activity in centro-parietal and right occipito-temporal regions during the occlusion phase when the biological motion disappearance was time-locked, possibly reflecting the recall of sensorimotor representations. These representations might allow the prediction of moving organisms in occlusion conditions. When the appearance of the occluder was unpredictable there was no difference between biological and scrambled motion either before or during occlusion, indicating that temporal prediction is relevant to the processing of biological motion permanence.

1. Introduction

In our daily lives we observe actions that can be temporarily hidden, for instance when a person disappears behind a wall. Despite the absence of sensory information from the moving stimulus, we have the capacity to estimate the current physical position of the hidden walker. The neural basis of this phenomenon, coined as biological motion permanence, remains an open field of research.

Neural substrates for motion permanence were first described by Assad and Maunsell [1], who recorded cortical responses of posterior parietal neurons in non-human primates that reflected the target motion representation in the absence of visual information. Similar results were obtained in humans in a more recent hemodynamic imaging study [2] showing the participation of the intraparietal sulcus (IPS) in the maintenance of the target representation in absence of sensory input. In addition, cells in the anterior superior temporal sulcus area (STSa) of non-human primates also activate when the monkey observes an experimenter disappearing behind an obstacle and reappearing [3]. In humans, many neurophysiological and clinical investigations have shown an involvement of the superior temporal sulcus (STS) in biological motion discrimination [4] using point-light displays (PLD) as visual stimuli [5].

Event related potentials (ERP) recorded from humans viewing PLD portraying human activities reveal a larger negative component for whole-body motion (WbM), when compared to scrambled

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motion (SM), in the 200–350 ms latency range after the stimulation onset, mainly in the right occipito-temporal region supposedly reflecting activity in the STS [6–8]. A series of studies have also demonstrated the participation of the parietal lobe [9–11] and the premotor cortex [12], in addition to the STS, in the recognition of human motion PLD. Classically, the premotor area, the parietal lobule and the STS are considered the cortical core of an action-perception network [13], suggesting that action observation is implicitly mapped into a motor vocabulary [14].

The primate premotor cortex has been shown to contain neurons that fire during the observation of an action whose final part is occluded [15]. Recently, psychophysical studies proposed the recruitment of such an action-perception network to reconstruct the hidden part of a biological motion trajectory [16,17] or to estimate whether a static test posture matched the expected one following a brief hidden period in a biological motion display [18]. One proposal to explain those results was by means of internal models of action [19] which would predict the future spatial position of the observed movement even in absence of visual information [16–18]. Little is known, however, about the neurophysiological basis of biological motion permanence and the temporal course of the cortical activation underlying motion occlusion in human beings.

In order to unveil the cortical network that associates with the biological motion permanence, we compared the electroencephalographic (EEG) activity of volunteers while they observed PLD of either whole body motion or scrambled motion disappearing behind an occluder and reappearing. Two occlusion paradigms were employed. In the first, the occluder's appearance was fixed in time, occurring 1600 ms after stimulus onset and lasting 2300 ms. Cortical activity recorded just before the occlusion and reappearance phases might correspond to predictive processes preventing the cancellation of visual processing during the occlusion and at its reappearance, respectively. Thus, a control experiment was designed to test the effect of predictability of the occlusion onset on the EEG activity by varying the onset of the occluder by 500 ms within a temporal window of 1350–1850 ms after the visual animation onset. In order to allow a direct comparison between the two experiments, three analysis windows were defined: visible, occlusion and reappearance. Based on previous literature [6–8], a difference between whole body and scrambled motion conditions was expected to occur in the early visible phase for both experiments. Furthermore, a pronounced difference between conditions during the occlusion period in the centro-parietal electrodes was predicted. This difference could represent a sensorimotor simulation process involved in motion permanence. Finally, we expected that between-condition differences would disappear when the occlusion onset was unpredictable indicating that temporal prediction is relevant to biological motion permanence processes.

2. Methods

2.1. Participants

A total of twenty four healthy subjects with normal or corrected to normal vision and with no known neurological abnormalities participated in this study. In each experiment we tested twelve volunteers (1: 7 men, 27.33 ± 7.34 years; 2: 9 men, 27 ± 5.44 years). They were unaware of the experiments' purpose and gave their informed consent before the experiment. The study was conducted in accordance with the declaration of Helsinki (1964).

2.2. Stimuli and procedure

Point-light display (PLD) animation was obtained after a session of walker motion capture (sampling rate of 100 Hz, Elite System, BTS Bioengineering, Italy). The whole body motion (WbM) depicted ten markers (head, shoulder, elbow, hand, hip, knee and ankle) indicating walker joint coordinates (x, y positions) displayed as white dots against a black background using Presentation software (Neurobehavioral Systems, Inc.). The animation permitted a vivid percept of a walker's movement

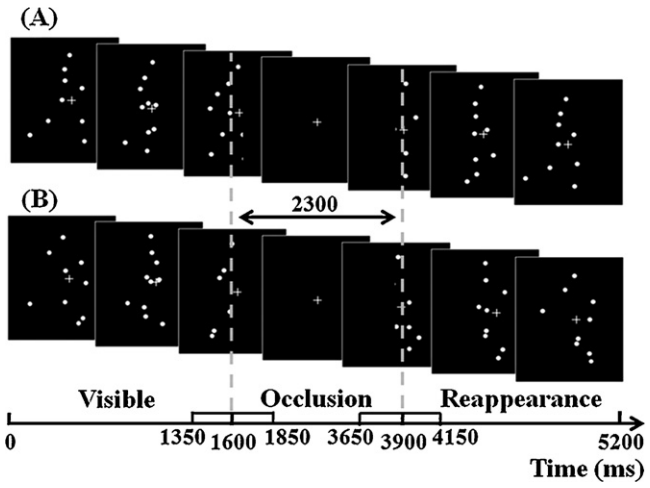

Fig. 1. Examples of experimental stimuli. Seven frames of the whole-body motion (A) and scrambled motion (B) displays across time for each of phases (i.e. visible, occlusion and reappearance). In the first experiment the appearance of occlusion was fixed in the time (i.e. 1600 ms) whereas in the second experiment the appearance of occlusion was randomized (i.e. between 1350 and 1850 ms). The duration of occlusion was the same for the both experiments. A fixation cross remained visible in the center of the screen throughout the visual stimuli presentation.

[5] over a treadmill, achieving a complete gait cycle at a frequency of 1 Hz. A single actor's movement repetition was used to create the biological animation and a few scrambled versions which prevented the recognition of human locomotion pattern. The non-biological motion control, scrambled motion (SM), was created by randomizing the initial position of the dots, destroying the body shape while the biological kinematic of each WbM dot was preserved. A white cross (0.27° × 0.28°) remained at the center of visual field to facilitate gaze fixation and to minimize eye movement contamination in the EEG signal.

All animations were exhibited at 25 frames/s depicting smooth natural movements, in a profile view, on a 17" color flat screen (resolution of 1024 horizontal and 768 vertical pixels, refresh rate of 75 Hz). All target figures subtended approximately 5.7° × 5.7° of a maximal visual angle aperture. The design for both experiments comprised two blocks with a 5 min inter-block interval. Each block consisted of 25 WbM and 25 SM stimuli randomly presented and displayed for 5.2 s followed by a 5 s inter stimulus interval (ISI). A total of 100 point-light animations were displayed (2 blocks × 2 conditions [WbM and SM] × 25 repetitions). Both experiments comprised 3 phases: visible, occlusion and reappearance. In experiment 1 the occluder appearance was fixed at 1600 ms after the stimulus onset (Fig. 1). This period allowed the observation of predictive effects before the occlusion onset, in addition to those of occlusion.

To investigate if cortical activity recorded before the occlusion and reappearance phases related to predictive processes preventing the cancellation of visual input and its reappearance, a control experiment 2 was designed to test the effect of predictability of the onset of the occlusion phase by varying the appearance of the occluder by 500 ms, between 1350 and 1850 ms after the visual animation onset (Fig. 1). In both experiments the gait cycle of WbM was repeated five times without any manipulation of the walker's speed during the trial. The gait cycle before and after occlusion in the experiment 1 differed but the difference between gait cycles was identical in all trials. In contrast to experiment 1, the temporal randomization of occlusion in experiment 2 led to differences in gait cycle before and after occlusion between trials. However, in both experiments the relation between the gait cycle's disappearance and reappearance remained constant because the occlusion duration was kept constant (2300 ms).

Each participant sat at a comfortable viewing distance from the screen (about 70 cm) in a darkened room. The following instructions were given to the participant: "you will see various point-light animations displayed on the center of the screen, which will gradually disappear and then reappear. Please maintain your attention on the fixation spot during the whole trial".

2.3. EEG recording and data analysis

The EEG activity was recorded using a BrainNet BNT 36 (EMSA) consisting of eighteen Ag–AgCl electrodes at the following scalp positions according to the 10–20 system: F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, T6, O1, Oz, O2. The impedance of each electrode was kept below 5 kΩ. The electrical potential was amplified, bandpass filtered (0.1–35 Hz), digitized at a 600 Hz sampling rate with the mastoid electrodes serving as a reference. The recording was stored on a computer for off-line analysis (Matlab – MathWorks, Natick, MA). Raw data was segmented into epochs spanning from 100 ms before to 5200 ms after stimulus onset. The prestimulus period (100 ms) served as baseline. Within each epoch, 4 triggers were

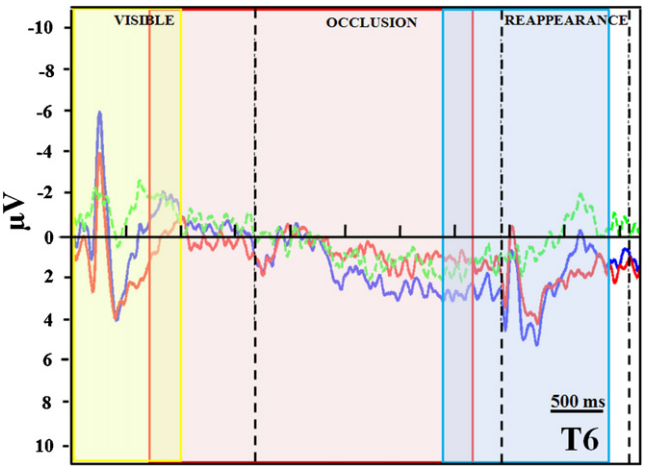

Fig. 2. Grand-averaged event-related potentials (ERP) collected in experiment 1. Data from T6 electrode is displayed. Blue trace indicates the ERP response to the whole-body motion (WbM); red trace represents the ERP response to the scrambled motion (SM); green dashed trace represents the difference between WbM and SM. The yellow area represents the analysis window of the visible period. The red area represents the analysis window of the occlusion period. The blue area represents the analysis window of the reappearance period. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article).

incorporated in order to segment and analyze the different phases of the visual stimulation: stimulus onset (0–1000 ms), occlusion (1000 ms before to 2000 ms after the stimuli disappearance), reappearance (500 ms before to 1000 ms after the stimulus reappearance) and stimulus offset (Fig. 2). The temporal randomization of stimuli disappearance in the second experiment constrained us to analyze the ERPs' responses through three distinct temporal windows. The signal was cut into specific time windows (as described above) and the beginning of each resulting segment was reset to zero.

Accordingly, analysis was done in 3 temporal epochs (visible, occlusion and reappearance), which contained both predictive and stimulation effects in the analysis. The first epoch, encompassing the visible phase, was 1000 ms long, starting at stimulus onset, is the time window most commonly used in the biological motion literature. This duration was comparable to the epochs used in previously published experiments; for example, Hirai et al. [6] used a temporal epoch of 0–1000 ms and Krakowski et al. [8] used 0–500 ms. For the second epoch, the occlusion phase, a temporal interval of 3000 ms (i.e., 1000 ms before and 2000 ms after the stimulus disappearance) was adopted. For the third epoch, the reappearance period, a temporal window analysis of 1500 ms was chosen (i.e., 500 ms before and 1000 ms after the stimulus reappearance) to allow detection of any predictive component before the stimulus reappearance and also to obtain a similar post-onset time window comparable to that of the visible phase (see Fig. 2).

All trials were submitted to an artifact criterion of ±50 μV to reject those with oculomotor or muscle activity. Inclusion criterion per participant consisted of at least 70% valid trials per condition (35 out of 50) for the channels of interest: T6, T5, O2, C3, Cz and Pz. Four participants from each experiment were excluded from further analyses due to insufficient number of trials, and thus the statistical analysis refers to results from eight subjects for each experiment. Thereafter, the grand-averaged ERP of all channels were calculated for both conditions (WbM and SM).

2.4. Statistical analysis

The main objective of the present report was to compare the spatial-temporal properties of the ERP waveforms elicited during WbM vs. SM within three successive periods (i.e. visible, occlusion and reappearance). Therefore, we calculated point-wise paired *t*-tests between-conditions for each period [see Ref. [20] for more details].

The first time point at each electrode site exceeding a 0.05 alpha *t*-tests criterion for at least twelve consecutive data points (20 ms at a 600 Hz digitization rate) was labeled as onset of differential ERP between-conditions. The results of the point-wise *t*-tests from the eighteen electrodes are displayed as an intensity plot to summarize the spatial-temporal comparison of the activity at multiple electrode sites (Fig. 3). The *x*, *y* and *z* axes of the plots represent, respectively, the time scale, the electrode location and the alpha value of the *t*-test results at each data point. We displayed channels ordered from left to right, starting in the back of the head (inion) and sequentially, up to the nasion.

3. Results

The statistical cluster plot analysis (Fig. 3) provides a comprehensive picture of the spatial-temporal comparison of the waveforms for WbM and SM for each phase: visible, occlusion and reappearance. Significant differences between the conditions are described below for the two experiments.

3.1. Visible period

Differential negativities at electrode site T6 were observed shortly after the stimulus onset for both experiments (Fig. 3). ERP waveforms obtained for WbM and SM (Fig. 4) differed significantly at T6 within the temporal ranges of [167–245 ms] in experiment 1 and [170–270 ms] in experiment 2. A stimulus-induced change in electric activity at this electrode site is commonly accepted as reflecting modulation within the right STS area [6], which has been shown to be involved in biological motion perception [4]. Moreover, strong similarities between the two experiments were observed for the centro-parietal regions (i.e. C3, Cz and Pz electrodes) with significant between-condition differences between 430 ms and 950 ms after the stimulus onset for experiment 1 and between 470 ms and 691 ms for experiment 2 (Fig. 4). Interestingly, no distinction between WbM and SM was found for T5 (left STS) in either experiment, revealing a major contribution of the right temporal hemisphere in the WbM recognition process [21,22].

3.2. Occlusion period

In experiment 1 we found significant differences between WbM and SM preceding the occlusion period in the centro-parietal region (i.e. C3, Cz and Pz electrodes) around 540 ms before the stimulus disappearance (Fig. 5), and during occlusion for the following electrodes: C3, Cz, T5, Pz, T6, O2 (Fig. 5). For C3, Cz, Pz and O2 these effects were found within two periods: 15–550 ms and 895–1985 ms. For the T6 site the between-condition differences were present in the periods [581–935 ms] and [960–2000 ms], and for T5, within [740–1355 ms] (see Fig. 5).

Only T5 showed a similar activation in the two experiments, starting around 1080 ms after the beginning of the occlusion (Fig. 3).

3.3. Reappearance period

In experiment 1 the reappearance phase was characterized by a WbM vs. SM waveform difference at four electrode sites: C4, Pz, T6 and O2 (Fig. 6). The statistical cluster plot analysis showed a significant modulation at the T6 and O2 electrodes for this period ([42–165 ms] and [28–93 ms] respectively). Moreover a between-condition difference for T6, O2 and Pz was observed around 500 ms after the stimulus reappearance. For C4, this between-condition difference appeared at around 250 ms before reappearance and remained constant throughout this period (Fig. 3). None of these between-condition differences were found for the reappearance period in experiment 2 (Fig. 3).

4. Discussion

The present study addressed the temporal dynamics of the neural network recruited during the gradual disappearance of a moving visual stimulus behind an occluder. We recorded ERPs during the passive observation of whole-body movement or scrambled point-light displays during three different successive periods: visible, occlusion and reappearance. The moment of the occluder's appearance was either fixed (experiment 1) or randomized (experiment 2). For both experiments, we found a significant difference in activity in WbM vs. SM during the visible phase. In experiment 1 the

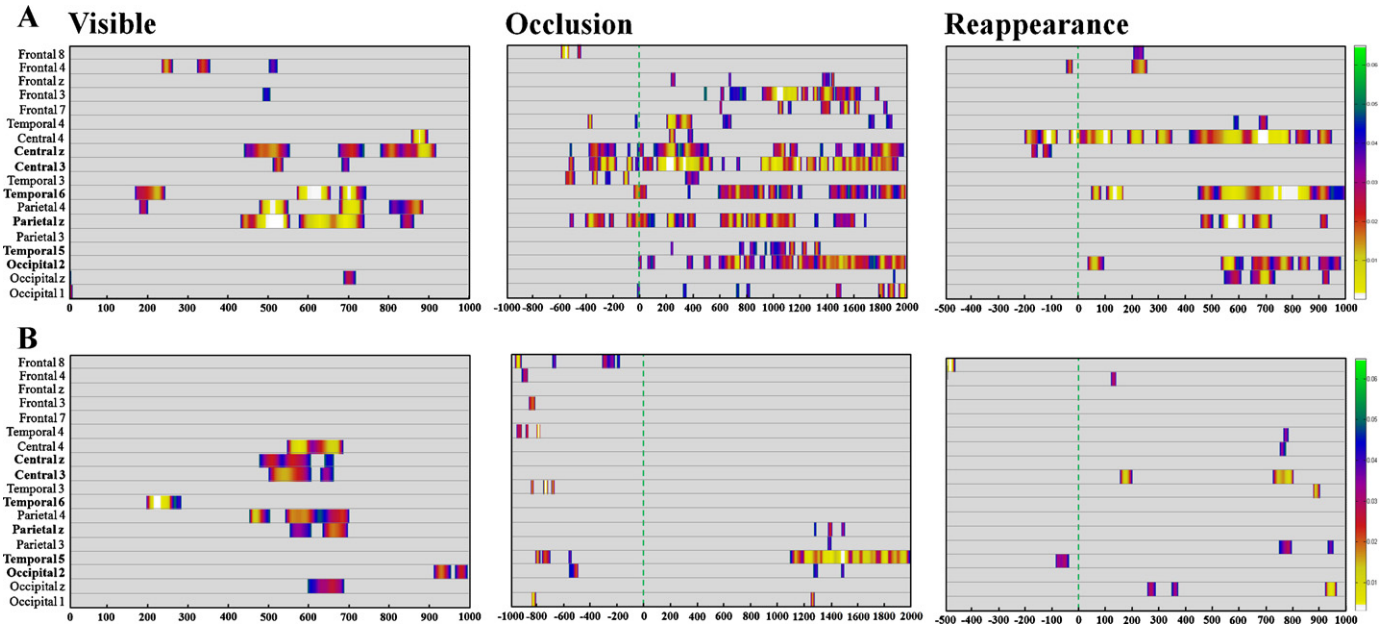

Fig. 3. Statistical cluster plots analysis. ERP waveforms of the two conditions (WbM and SM) were compared throughout the period with running *t*-tests for each phase and for each experiment. The color scale indicates *p*-values ranging from 0.001 up to 0.05. Gray indicates an absence of between-condition difference. Channels are plotted along the vertical axis arranged from left to right, from the inion, at the bottom, to the nasion, at the top of the plot. Dashed lines represent the onset of the occlusion (Occlusion panel) and the reappearance of the PLD (Reappearance panel).

difference between WbM and SM preceding the occlusion phase in the centro-parietal region suggested processes predictive of the upcoming occlusion. A condition difference in the right temporal hemisphere similar to that found in the visible phase was recorded during the reappearance phase. Randomization of the moment of occlusion, in experiment 2, eliminated the condition difference between WbM and SM both preceding and during the occlusion phase, as well as upon stimulus reappearance, suggesting that this activity may correspond to the prediction of an upcoming biological motion disappearance. Consequently, the between-condition cortical activity found before and during the occlusion period in the fixed occlusion paradigm could be specifically linked to the temporal prediction of the disappearance of an upcoming human body movement. These results are discussed in more detail for each period in the following sections.

4.1. Whole-body motion and scrambled motion ERP during the visible phase

As expected, we found a clear between-condition difference at electrode site T6 [6–8], supporting the involvement of the right temporal hemisphere in WbM processing [21,22]. The event-related response associated to the detection of biological motion, N2, occurs classically between 180 and 250 ms after the stimulus presentation in temporal regions [6,7]. A second negative component described as occurring right after the N2 response [6–8] was not identified herein. One possible explanation for this difference is the lower number of electrodes in this study as compared to those in previous studies. Furthermore, the long trial duration (5200 ms) constrained the number of repetitions, possibly affecting the degree of discrimination of these two negative components.

The statistical cluster plot analysis also highlighted a larger negativity for the WbM as compared to the SM from 500 to 800 ms after stimulus presentation within the centro-parietal region (C3, Cz and Pz electrode sites). This central region activation during WbM as compared to SM confirms earlier EEG and MEG frequency analysis studies that showed an involvement of the sensorimotor regions during the visualization of biological PLD [23,24], as characterized by mu rhythm suppression at the central electrodes. Moreover, previous studies [25,26] have reported a modulation of the late ERP component (500–800 ms) during the observation of incongruent vs. congruent actions. Thus one plausible explanation for our results is that the violation of PLD spatial relationship (i.e. in the scrambled condition) might elicit this difference in activity for the SM as compared to WbM within this temporal window.

Taken together these results are consistent with the hypothesis of a wide complex neural network devoted to the processing of biological visual flow within which the motor system can modulate the STS activity [27,28], rather than just a specific cortical region such as STS [22]. Finally, there was no difference in the visible phase between the experiments (i.e., between a context where there is the possibility to predict or not the upcoming occlusion onset, Fig. 3). The strong similarities between the results of both experiments during the visible phase can be taken as a control for the difference in the results in the occlusion and reappearance phases.

4.2. Cortical dynamics preceding and during the occlusion

When the stimulus disappearance was fixed in time we observed a between-condition difference (WbM vs. SM) within the fronto-parietal regions (C3, Cz and Pz) just before and during the occlusion period. Differently from the visible phase, where a negative between-conditions difference was observed, the occlusion period was characterized by a polarity inversion with a clear positive between-conditions difference. The meaning of this polarity inversion during occlusion remains unclear.

In the phase preceding the occlusion, the fronto-parietal activity may reflect preparatory mechanisms anticipating visual cancellation. Such activity might prepare the subject to maintain the continuity of the current action in absence of any visual information. This prediction would allow the motoric counterpart, recorded with the central electrodes, to substitute the gradual lack of visual information for a point-light walker's movement. Moreover, the fixed onset of the temporal occlusion window allowed the subject to predict the onset of visual disappearance and consequently to anticipate the loss of sensory input and may have shifted their brain

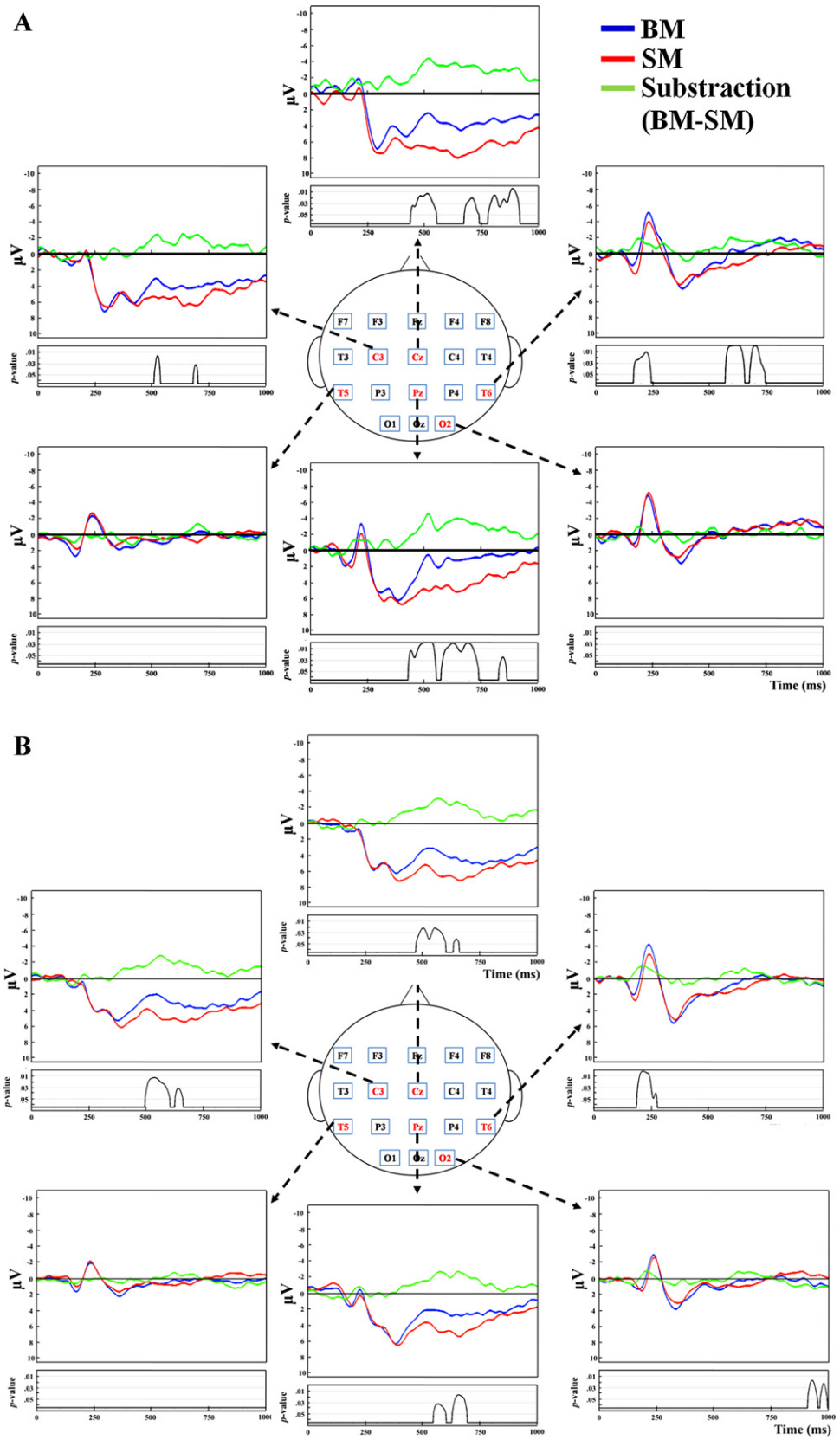

Fig. 4. Grand-averaged event-related potentials (ERP) of the visible period in experiment 1 (A) and 2 (B). Data from central (C3, Cz), temporal (T5, T6), parietal (Pz) and occipital (O2) electrodes sites are displayed. Their locations on the scalp are indicated by the red characters within the schematic view of the 10–20 international system. Blue traces indicate the ERP response to the whole-body motion (WbM); red curves represent the ERP response to the scrambled motion (SM); green lines represent the difference between WbM and SM ERP. Black lines in the bottom inset illustrate the *p*-value of point wise *t*-test between the WbM and SM conditions across the ERP epoch. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article).

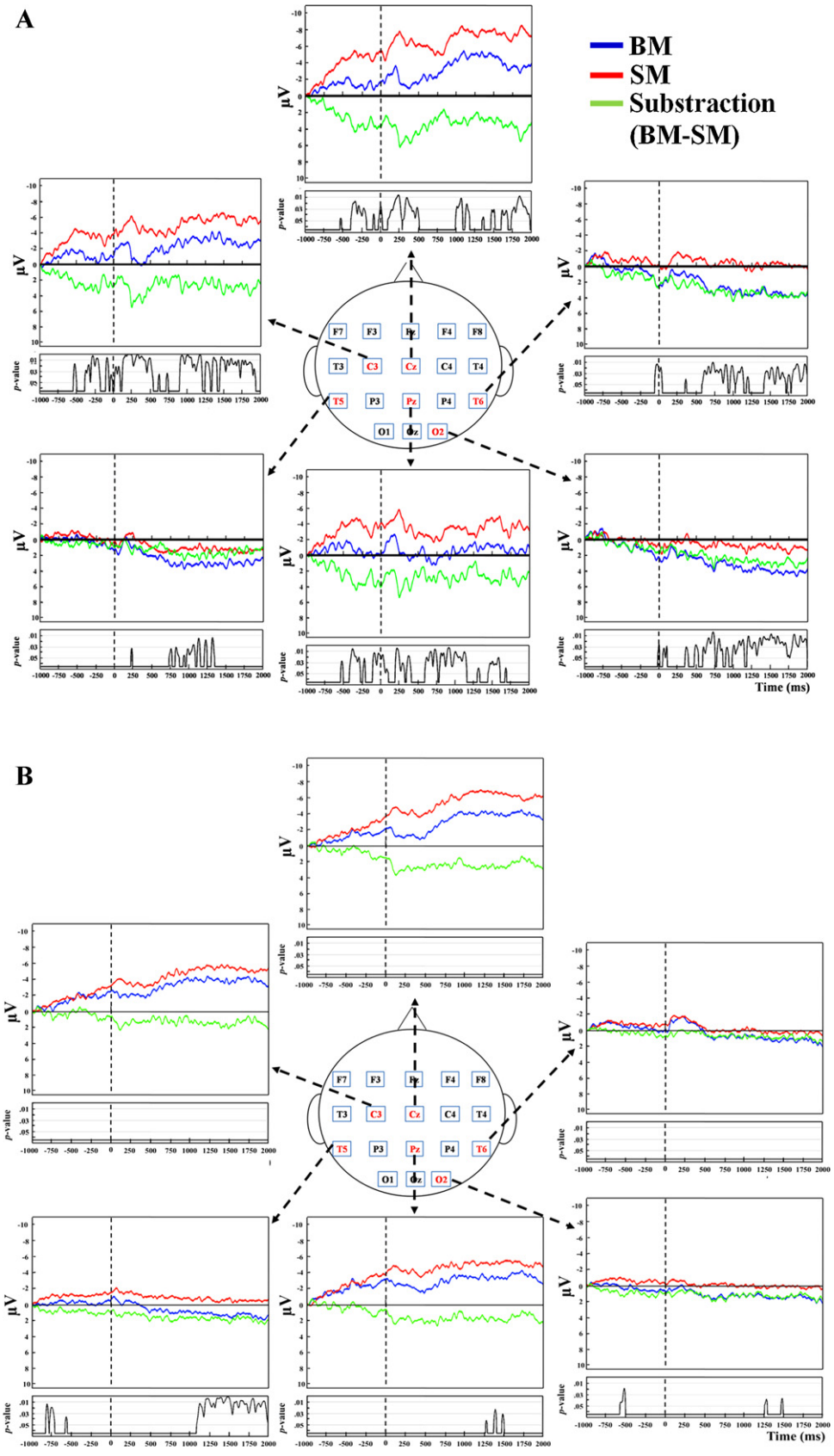

Fig. 5. Grand-averaged event-related potentials (ERP) of the occlusion period in experiment 1 (A) and 2 (B). Conventions are the same as in Fig. 4.

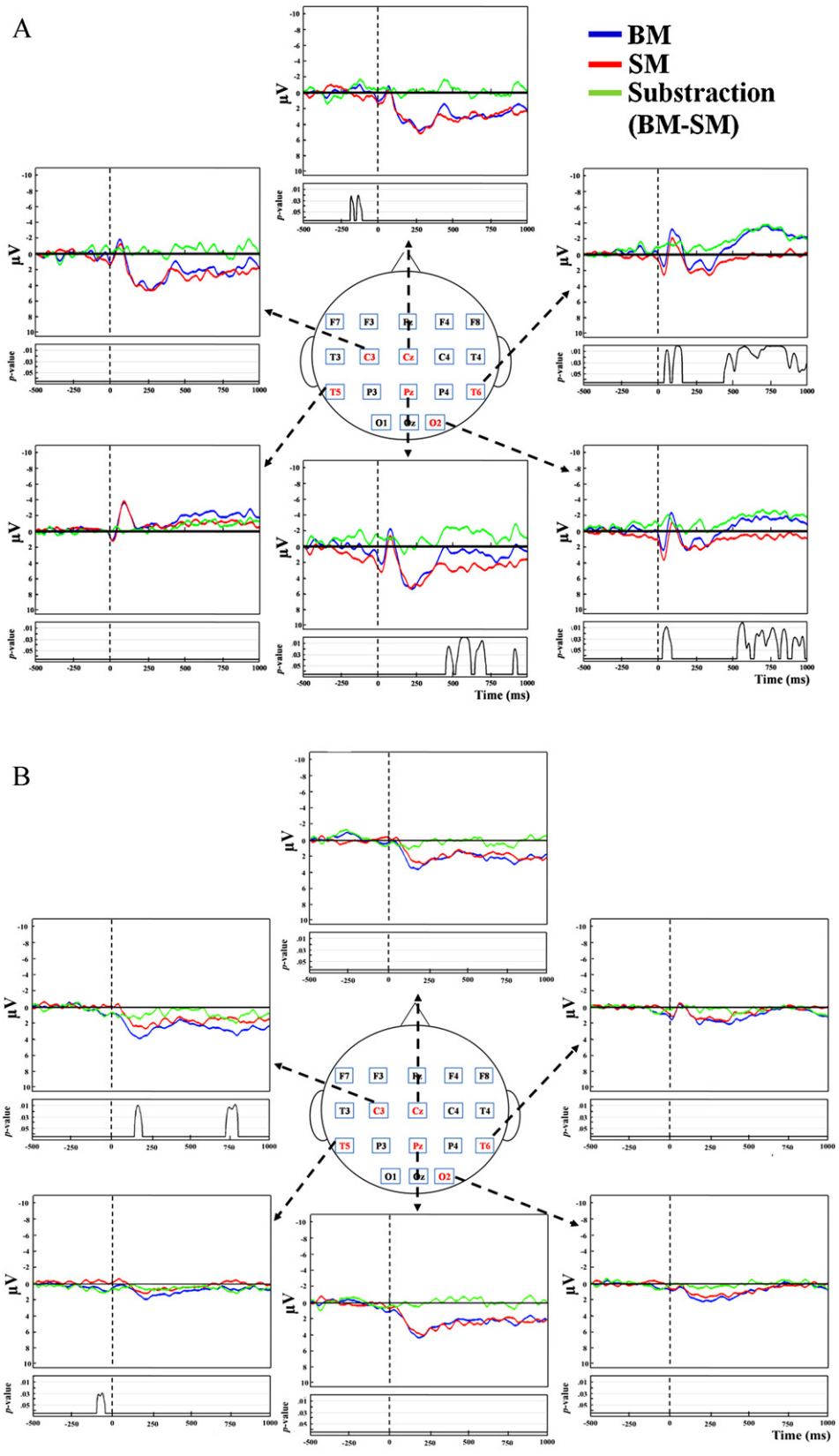

Fig. 6. Grand-averaged event-related potentials (ERP) of the reappearance period for experiment 1 (A) and 2 (B). Conventions are the same as in Fig. 4.

activity into a predictive mode by recruiting networks involved in anticipating others' actions ahead of their realization [29–31]. In contrast, the randomization of the occlusion onset did not allow this prediction, eliminating the between-condition difference. In addition, previous reports [32] proposed that the beta power coupling over central midline sites serves as a central mechanism of timing expectation coding. Similarly, the recorded activity modulation within the centro-parietal region prior to the occlusion period may participate in triggering predictive mechanisms.

During the occlusion period, there was a contrast dependent (WbM vs. SM) brain activation in the centro-parietal sites (C3, Cz and Pz), which may reflect an implicit process of action simulation [33]. This proposal is consistent with a recent psychophysical study [18] in which volunteers were asked to decide whether a test static posture was the continuation of occluded actions. The observers' error in the prediction of the static posture judgment decreased when the static posture matched the time of occlusion, leading the authors to suggest that observers were performing a real-time simulation process. Results obtained with fMRI [34] support this assumption of a real-time simulation process. The present report broadens these previous observations [18,34] for a task that does not require an explicit judgment of the future state of the visual display.

An offset response might have been expected as a consequence of the stimulus disappearance in experiment 1, but such response was not clearly observable. The fact that the occlusion was gradual and not sudden might explain the absence of the offset response. Most studies employing occlusion paradigms have used fMRI [2,34,35] or single unit recording [1,4], precluding inferences about the neurophysiological correlates of the offset response. EEG studies testing the neural consequences of occlusion of a single dot, for example, Doherty et al. [36] and Correa and Nobre [37], focused their analysis on the reappearance period, making a comparison between these experiments and the present results difficult. Anyhow, the question of how the nature of occlusion's appearance (gradual vs. sudden) might affect the offset response in the context of biological motion remains unanswered.

Although the sole difference between the two experiments was the timing of the occlusion onset, results showed a clear between-conditions difference in experiment 1 which was absent in experiment 2. One possible explanation for these different results is an attentional load change induced by the randomization of the occlusion onset. The question of how the temporal unpredictability of an occluder's appearance might affect the attentional processing in the context of coding of biological motion permanence is an interesting matter for future experiments.

Considering the theoretical framework of internal models of action [19], the implicit prediction of sensorimotor movement consequences would ensure the biological motion permanence. This may be reflected in the recruitment of the centro-parietal regions recorded in this study. In this scenario, the lack of visual input would require the observer to recall endogenously the corresponding motor repertoires. However, the exact manner by which motion permanence is processed and whether this circuit is specific to human motion occlusion [3] requires further neurophysiological and psychophysical investigations. For instance, one cannot rule out the possibility of a fairly simple mechanism like a direct mapping of the observed movement kinematics into its corresponding sensorimotor representations [13] rather than a simulation associated with the predictive process based on internal model loops [38].

4.3. Reappearance of visual motion information

The reappearance period emphasizes the difference between the two experiments. When the occlusion onset was fixed in time, ERP waveforms to the reappearance of the stimulus were very similar to those of the visible period (see Figs. 4 and 6). In contrast, the between-conditions difference was eliminated in this period when the timing of occlusion window was randomized in Experiment 2. This result partially supports the idea that the randomization of occlusion onset and the associated predictive mechanisms limit the substitution of visual input by their corresponding motoric representations.

Moreover, the temporal length of the occlusion phase was equal for both experiments. Thus, one could expect similar results during the reappearance phase since a simple temporal estimation of the occlusion duration could be used to predict the reappearance onset. The finding that the between-condition contrast in the reappearance phase was dependent on the predictability of the occlusion onset indicates that reappearance processing does not rely exclusively on temporal estimation but also on covert sensorimotor activity.

5. Conclusion

This is the first study to describe the temporal dynamics of the cortical processing of biological movement occlusion. We propose that the gradual occlusion of whole body motion leads to an implicit sensorimotor prediction of the occluded movement, allowing motion permanence. Such implicit mechanism may be present even in the early stages of infant development as reported in a recent study [39], suggesting a strong phylogenetic advantage.

Acknowledgments

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