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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

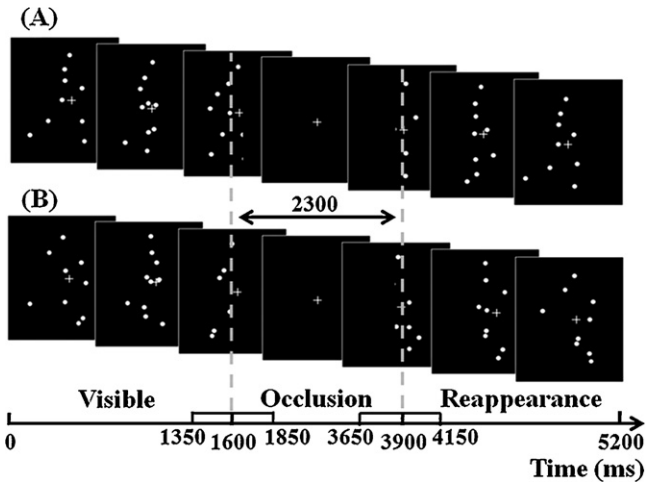

Fig. 1. Examples of experimental stimuli. Seven frames of the whole-body motion (A) and scrambled motion (B) displays across time for each of phases (i.e. visible, occlusion and reappearance). In the first experiment the appearance of occlusion was fixed in the time (i.e. 1600 ms) whereas in the second 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