

Research report

# Active processing of biological motion perception: an ERP study

Masahiro Hirai<sup>\*</sup>, Atsushi Senju, Hirokata Fukushima, Kazuo Hiraki

*Department of Multi-disciplinary Sciences, Course of General Systems Studies, Graduate School of Arts and Sciences, The University of Tokyo,  
3-4-1 Komaba, Meguro-ku, Tokyo, 153-8902, Japan*

Accepted 15 November 2004

Available online 21 January 2005

## Abstract

The purpose of this study was to measure event-related potentials (ERPs) to clarify how attention affects neural activity during the visual perception of biological motion (BM). Thirteen healthy subjects observed BM or scrambled motion (SM). For SM, each point had the same velocity vector as in BM, but the initial starting positions were randomized. Each BM and SM was overlaid with ten noise dots and four rectangles. For the rectangles, one was or was not rotated 90° relative to the others. Subjects were required to undertake two kinds of visual tasks. For the attention-to-motion condition, subjects directed their attention to the type of motion. For the attention-to-rectangle condition, subjects directed their attention to the rotational angle of the overlaid rectangles. As in our earlier study, the ERP response to the perception of BM had two negative components at ~200 ms (N200) and ~330 ms (N330) in both attentional conditions. Our analysis focused on the amplitude of the second negative component, which was sensitive to BM. There was a significant interaction between attention and the type of motion regarding the amplitude of N330. Specifically, the amplitude of N330 in response to BM was greater in the attention-to-motion condition than in the attention-to-rectangle condition, and was greater than the amplitude of the response to SM in the attention-to-motion condition. These results suggest that in this experimental design, processing of BM is modulated by attention.

© 2004 Elsevier B.V. All rights reserved.

*Theme:* Neural basis of behavior

*Topic:* Cognition

*Keywords:* Biological motion; Event-related potentials; Visual stimuli; Visual processing; Attention; Motion perception

## 1. Introduction

The human visual system can reconstruct complex visual images based on astonishingly little information. For example, we can vividly perceive the movement of a human figure from just a dozen moving points of light, and this phenomenon is well known as an example of biological motion (BM) perception [29]. In addition, based only on moving points of light, individuals can discriminate various kinds of information, such as gender [5,12,32,35], personal identity [14], action categorization [16], and emotion [6,9,17,55].

Recent neuroimaging studies have revealed the locations of the neural substrates that subservise perception of BM. In macaques, the superior temporal polysensory area plays an important role in the perception of BM [42,43], whereas in humans, the superior temporal sulcus (STS) appears to be involved in BM perception [7,8,20–23,28,45,47,53]. In addition to the STS, a portion of the lingual gyrus [50], as well as the amygdala [8], fusiform face area [22], and frontal region [49], is activated during the perception of BM. The dynamics of neural activation during BM perception have also been investigated. A recent MEG study revealed the time course of brain activation for BM perception [44]. Pavlova et al. found that oscillatory gamma brain activity was only observed over the parietal and right temporal lobes within 200 ms for BM perception. In a previous study, we measured

<sup>\*</sup> Corresponding author. Fax: +81 3 5454 4513.

E-mail address: [hirai@ardbeg.c.u-tokyo.ac.jp](mailto:hirai@ardbeg.c.u-tokyo.ac.jp) (M. Hirai).

event-related potentials (ERPs) and found perception of both BM and scrambled motion (SM; in which each point had the same velocity vector as in BM, but the initial starting positions were randomized so that the subjects could not perceive a walking person) elicited negative ERP responses over the bilateral occipitotemporal region at ~200 and ~240 ms (designated N200 and N240, respectively) [24]. Moreover, the amplitude of the second negative peak was significantly greater in response to BM than in response to SM. We assumed that the first negative component reflected general (nonspecific) motion processing, whereas the second negative component reflected the processing of BM [24]. Recently, another group [30] also reported two negative peaks during the perception of three kinds of visual stimuli (BM, inverted BM and SM). For the first negative component (N170), the amplitude of the BM condition was greater than that of the inverted BM and SM conditions, and the authors speculated that the first negative component reflected the pop-out effect of a moving dot pattern representing the highly familiar form of a human figure. For the second negative component (N300), the amplitudes of the BM and inverted BM conditions were larger than that of the SM condition, and the authors interpreted that the second negative component may be associated with the specific analysis of motion patterns providing biologically relevant information.

These neuroimaging studies have revealed the responsible area and time course of BM processing, and the STS appears to be the primary center for processing BM. However, the functional properties of the neural responses to BM have not been investigated. Several early psychophysical studies suggested that BM perception is a bottom-up or low-level process, since BM can be perceived spontaneously (i.e., automatically) [29,36]. For example, Johansson noted that a mathematically lawful spatiotemporal relationship determined the perceptual responses, and suggested that the perception of BM was a spontaneous, automatic phenomenon [29]. Other studies have also found aspects of low-level processing during the perception of BM (e.g., [36]) and several computational models have been based on these findings [25,58]. These observations suggest that the attentional effect for BM perception is very low. On the other hand, recent psychophysical studies have suggested that BM processing involves a top-down [10,16] or attentional [11,51,52] process.

In this study, we focused on how attention affects the processing of BM. We measured ERPs, as in our previous study [24], and used the second negative component of the ERP response (which is likely to be associated with BM perception) as an index of neural activation. We hypothesized that if the process of BM perception does not involve attention, the amplitude of the second negative component would remain unaffected by attention, whereas if BM perception does involve attention, the

second component would be affected by attention. We conducted the following experiments based on this hypothesis.

## 2. Materials and methods

### 2.1. Subjects

We studied 13 subjects (range/mean age: 18–30/23.7 ± 3.9 years; 9 males, 4 females). All subjects were right-handed and had normal or corrected-to-normal vision. All subjects provided informed consent for a protocol that was approved by the Ethics Committee of the University of Tokyo. Each subject participated in four trial blocks.

### 2.2. Visual stimuli

Our stimuli were modified from the dual-task paradigm used by Thornton et al. [52] (Fig. 1). Each stimulus comprised 11 moving points of light that were masked by 10 randomly moving (noisy) points and 4 rectangles, that is, the stimuli had 3 features: motion type; noise velocity; and a rectangle configuration. The motion type was either BM or SM (Fig. 1a). For BM, points were attached to 11 joints of a walking person; this produced an animation that made the walking motion immediately obvious to the subject. For SM, each point had the same velocity vector as for BM, but the initial starting positions were randomized so that the subjects could not perceive a walking person. The rectangle configuration was either changing (RC) or unchanging (RNC) (Fig. 1b). For RC, one of four rectangles was rotated 90° after 272 ms. For RNC, the positions of the rectangles were fixed throughout the trial. For both the RC and RNC conditions, four rectangles were displayed spatially randomly within 3 × 3° area. To regulate the difficulty of distinguishing between BM and SM, the noise velocity was either fast (FN) or slow (SN) (Fig. 1c). For FN, the velocity of the noisy points was approximately equal to that of the target points (4.3° per second). For SN, the velocity of the noisy points was 1/10 the velocity for FN. We assumed that SN would interfere with motion detection to a lesser degree than FN because the velocity of SN noisy points differed from that of the target points.

Animations were generated using Cutting's algorithm [13] to calculate the coordinates of each point for a walking speed of 2.0 gait-cycles per second. Animations were displayed on a 17-in. monitor using E-Prime (Psychological Software Tools, Pittsburgh, PA) on a personal computer. Each subject was seated 115 cm from the display in a dimly lit room. All the points were white against a black background (5.8 cd/m<sup>2</sup>). Each point subtended an angle of 9.0 arcmin. The rectangles were 0.40 × 0.15°. The entire visual stimulus was approximately 3 × 3°. Each animation comprised 15 frames,

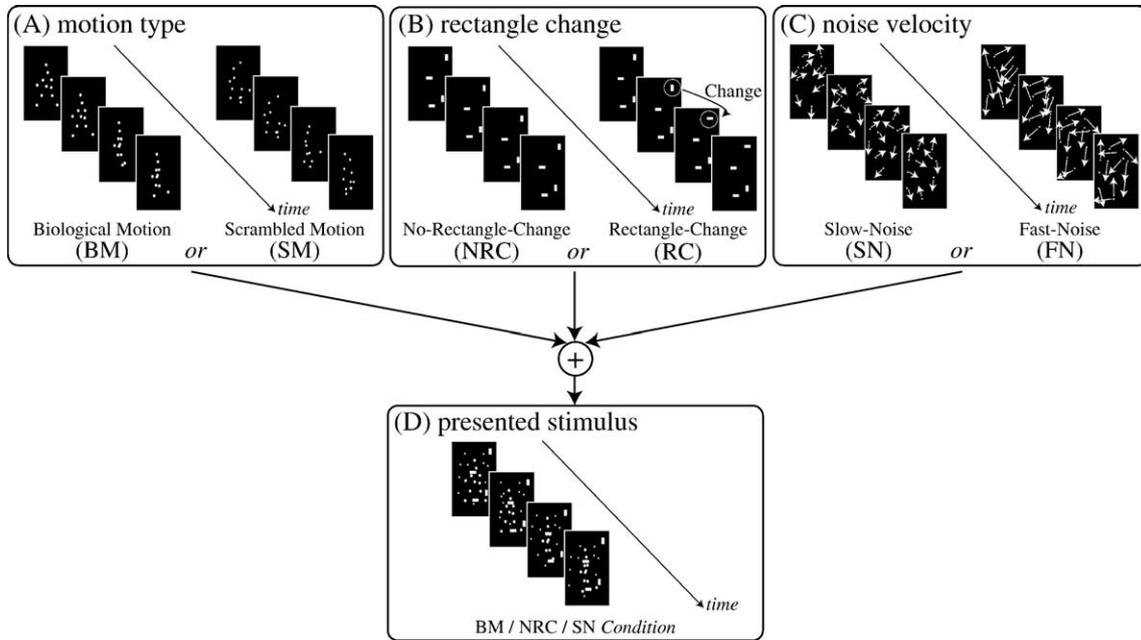


Fig. 1. Components of the visual stimulus used in the present study. (a) Motion type: biological motion (BM) and scrambled motion (SM). (b) Rectangle configuration: no change (NRC) and rotated (RC). (c) Noise velocity: slow (SN) and fast (FN). (d) Example of a stimulus (BM, NRC, SN condition). Though the size of target dots were different from noise dots in this panel, both size of dots were same in the actual experiment.

which was displayed for 510 ms, and the interframe interval was approximately 34 ms; these parameter values produced smooth animated motion.

### 2.3. Behavioral task

Two factors, namely motion type (BM or SM) and rectangle configuration (RC or RNC), were allocated to each trial block. To control the attention of each subject, two kinds of task (attention-to-motion or attention-to-rectangle) were allocated to different blocks. In half of the blocks (attention-to-motion condition), subjects were required to discriminate BM from SM. In the other half of the blocks (attention-to-rectangle condition), subjects were instructed to determine whether or not the rectangle rotated. An

additional factor, namely noise velocity (FN or SN), was also allocated between blocks, which yielded four blocks for each subject.

Each trial block consisted of three sessions. The inter-block interval was 1 min and the order of the blocks was randomized across subjects. One session consisted of 144 trials (four different stimuli presented 36 times in random order). Accordingly, both BM and SM were presented 72 times per session and 216 times per block. The intersession interval was 30 s. In each trial, the stimulus (BM or SM) was presented for 510 ms, and was followed by the presentation of a white fixation point ( $0.3 \times 0.3^\circ$  cross) for 500 ms. Subsequently, a yellow fixation point ( $0.3 \times 0.3^\circ$  cross) was displayed, and the subjects responded. The fixation point then disappeared (Fig. 2). The response of the

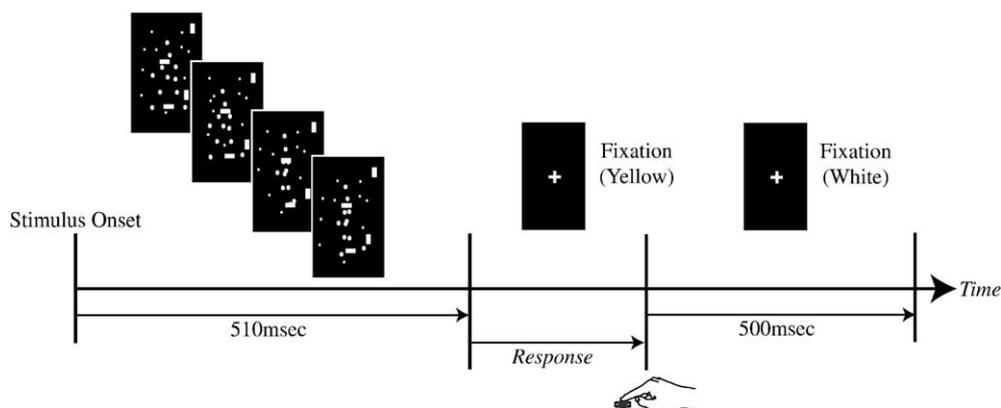


Fig. 2. An example of a trial sequence. The response was the period between the disappearance of the stimulus and the response of the subject (pressing the appropriate response key).

viewer in each trial involved pressing the appropriate response key. Subjects were instructed before each block as to which key to press, as follows. For the attention-to-motion condition, subjects who perceived BM were required to press the left key with their left index finger; subjects who perceived SM were required to press the right button with their right index finger. For the attention-to-rectangle condition, subjects who perceived rotation of a rectangle were required to press the left key with their left index finger; if the rectangles were perceived not to rotate, subjects were required to press the right button with their right index finger. The order of each condition was assigned randomly among subjects. To avoid confounding motor artifacts arising from the response, and to keep subjects focused on the target stimulus, subjects were required to press the appropriate key with their index finger as soon as the stimulus disappeared. This task was very different from conventional RT tasks.

#### 2.4. EEG and EOG recordings

Electroencephalograms (EEGs) were recorded from 64 sites on the scalp using a 64-channel Geodesic Sensor Net (Electrical Geodesics, Eugene, OR). All recordings were referenced initially to the vertex and were later re-referenced to the average potential over the scalp. A 0.1- to 100.0-Hz bandpass filter was applied to the EEG recordings. The electrical potential was digitized at a 250-Hz sampling rate and data were stored on a computer disk for offline analysis. Vertical and horizontal electro-oculograms (EOG) were recorded to monitor eye movements.

In the off-line analysis of the EEG recordings, a 0.1- to 30.0-Hz bandpass filter was applied to the data. Trials in which the EEG or EOG signal variation exceeded 50  $\mu$ V were discarded. The analysis window extended for 500 ms following the onset of each stimulus. A prestimulus period of 100 ms was used as the baseline. The grand mean of the waveform for each condition was calculated.

#### 2.5. Statistical analyses

Performance accuracy was measured for behavioral data. The frequencies of correct behavioral responses

were analyzed in a four-way analysis of variance (ANOVA) with the following factors: task type (attention-to-motion or attention-to-rectangle), noise velocity (FN or SN), motion type (BM or SM), and rectangle configuration (RC or RNC). We considered  $p < 0.05$  as significant.

ERP data were treated as follows. First, behaviorally incorrect trials were eliminated for further analyses. We then analyzed sites T5 and T6 of the International 10–20 System, which relate to left middle temporal gyrus and right STS region, respectively [27,57]. This is based on the observation that the right STS is activated during perception of BM and that there is a significant difference in the amplitude of the response to BM and SM perception in the occipitotemporal region [24]. To avoid a loss of statistical power [41], we collapsed the three electrodes that surrounded each of these sites into two sites. We calculated the peak latencies and amplitudes of each component and carried out a four-way ANOVA using the following as factors: laterality (left or right hemisphere), task type (attention-to-motion or attention-to-rectangle), noise velocity (FN or SN), and motion type (BM or SM).

### 3. Results

#### 3.1. Behavior (performance accuracy)

The frequencies of correct responses are summarized in Table 1. The subjects performed the behavioral task with a high degree of accuracy (>90%) in both the attention-to-motion and attention-to-rectangle condition. This indicates that the subjects paid close attention to the visual attribute of the stimulus, according to instructions.

In a four-way ANOVA of the ratio of correct to incorrect responses with task type, noise velocity, motion type, and rectangle configuration as factors, the task type  $\times$  rectangle configuration interaction was significant [ $F(1,12) = 5.4, p < 0.05$ ]. Specifically, the performance of the behavioral task in the attention-to-motion condition was better than in the attention-to-rectangle condition when the rectangle was rotated (RC) [ $F(1,24) = 6.4, p < 0.05$ ]. In addition, the performance when the rectangle was rotated (RC) was better

Table 1  
Ratio of correct to incorrect responses in the attention-to-motion condition (A) and attention-to-rectangle condition (B)

Noise velocity	Motion type	BM		SM	
		RC	NRC	RC	NRC
<i>(A) Attention-to-motion condition<sup>a</sup></i>					
FN	Correct performance [%]	97.9 $\pm$ 2.8	98.1 $\pm$ 2.0	98.3 $\pm$ 1.5	98.1 $\pm$ 1.4
SN	Correct performance [%]	98.3 $\pm$ 2.3	98.8 $\pm$ 1.3	99.4 $\pm$ 0.7	98.4 $\pm$ 1.0
<i>(B) Attention-to-rectangle condition<sup>b</sup></i>					
FN	Correct performance [%]	95.2 $\pm$ 4.6	95.9 $\pm$ 3.3	96.9 $\pm$ 3.4	96.7 $\pm$ 4.3
SN	Correct performance [%]	92.0 $\pm$ 12.4	92.0 $\pm$ 11.2	98.3 $\pm$ 2.4	97.0 $\pm$ 3.0

<sup>a</sup> mean  $\pm$  SD.

<sup>b</sup> mean  $\pm$  SD.

than when the rectangles were fixed (NRC) in the attention-to-motion condition [ $F(1,24) = 5.2, p < 0.05$ ].

3.2. ERP data

Fig. 3 shows the grand mean waveforms of the ERP responses. We found two negative peaks at ~200 ms (N200) and ~330 ms (N330), which were recorded near the occipitotemporal areas.

In a four-way ANOVA of the latency of the N200 and N330 responses, laterality  $\times$  noise velocity  $\times$  motion type was significant for N200 [ $F(1,12) = 13.1, p < 0.01$ ]. Specifically, the latency of the N200 response in the left hemisphere to SM with SN was significantly shorter than the response in the right hemisphere [ $F(1,48) = 4.6, p < 0.05$ ]. Further, in the left hemisphere with SN, the latency of BM was significantly greater than that of SM [ $F(1,48) = 8.3, p < 0.01$ ]. For the N330, no significant differences were established.

In the ANOVA for the amplitude of N200, the interaction of laterality  $\times$  task type  $\times$  motion type was significant [ $F(1,12) = 5.2, p < 0.05$ ; Fig. 4]. We conducted a subsequent analysis of the simple main effect. For attention-to-motion condition, the negative amplitude of the left

hemisphere is greater than that of the right in SM [ $F(1,48) = 9.9, p < 0.01$ ]. For SM, the negative amplitude in the attention-to-rectangle condition was greater than that in attention-to-motion one in the right hemisphere [ $F(1,48) = 5.9, p < 0.05$ ].

In the ANOVA for the amplitude of N330, the interaction of task type  $\times$  motion type was significant [ $F(1,12) = 34.6, p < 0.01$ ; Fig. 4]. Analysis of the simple main effect revealed that the amplitude of the response to BM in the attention-to-motion condition was greater than that in the attention-to-rectangle condition [ $F(1,24) = 30.3, p < 0.01$ ], whereas the effect of attention was not significant for SM. In addition, the amplitude of the response to BM was greater than for SM in the attention-to-motion condition [ $F(1,24) = 33.6, p < 0.01$ ]; however, the amplitude of N330 was not significantly different for BM and SM in the attention-to-rectangle condition.

3.3. Scalp topography

Fig. 5 depicts the time course of the scalp distributions of the difference amplitudes between BM and SM stimuli for each attentional task. For attention-to-motion tasks, regardless of the noise velocity, negative differences were observed

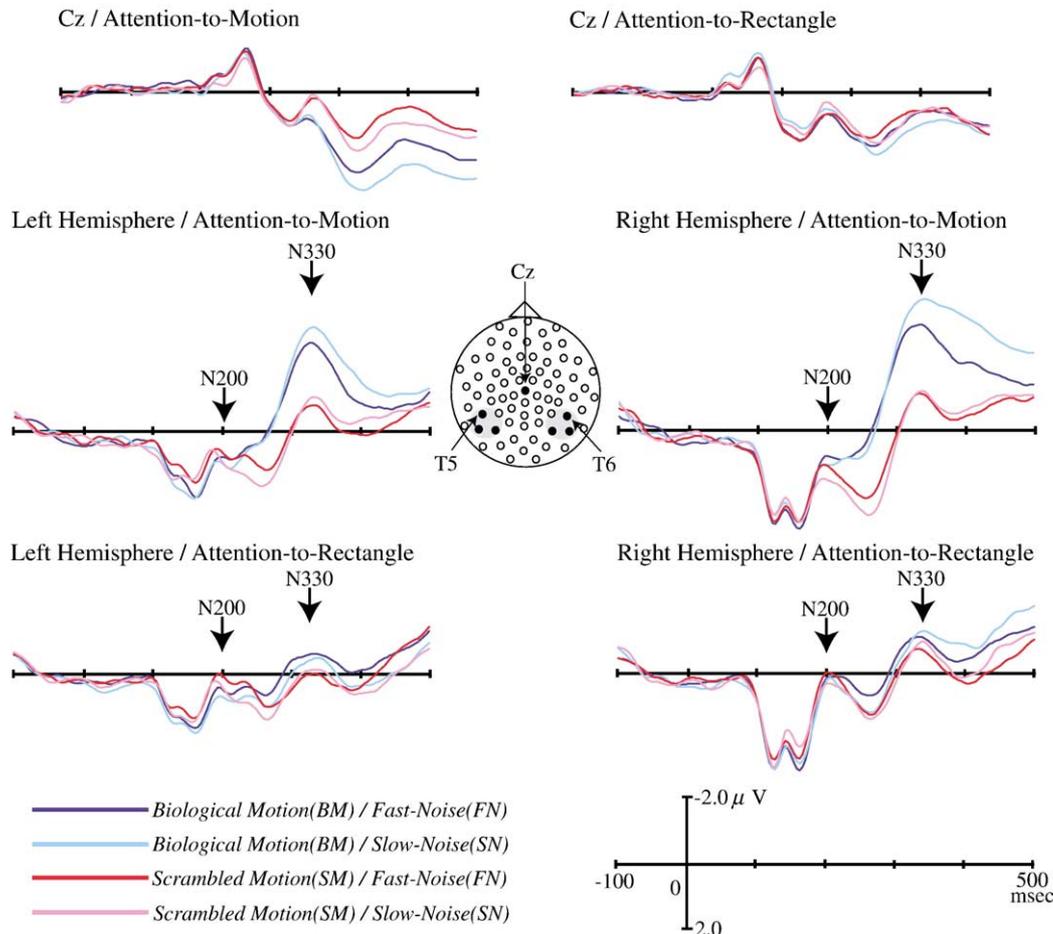


Fig. 3. Average event-related potentials for 13 subjects that were elicited in both hemispheres in the attention-to-motion and attention-to-rectangle condition.

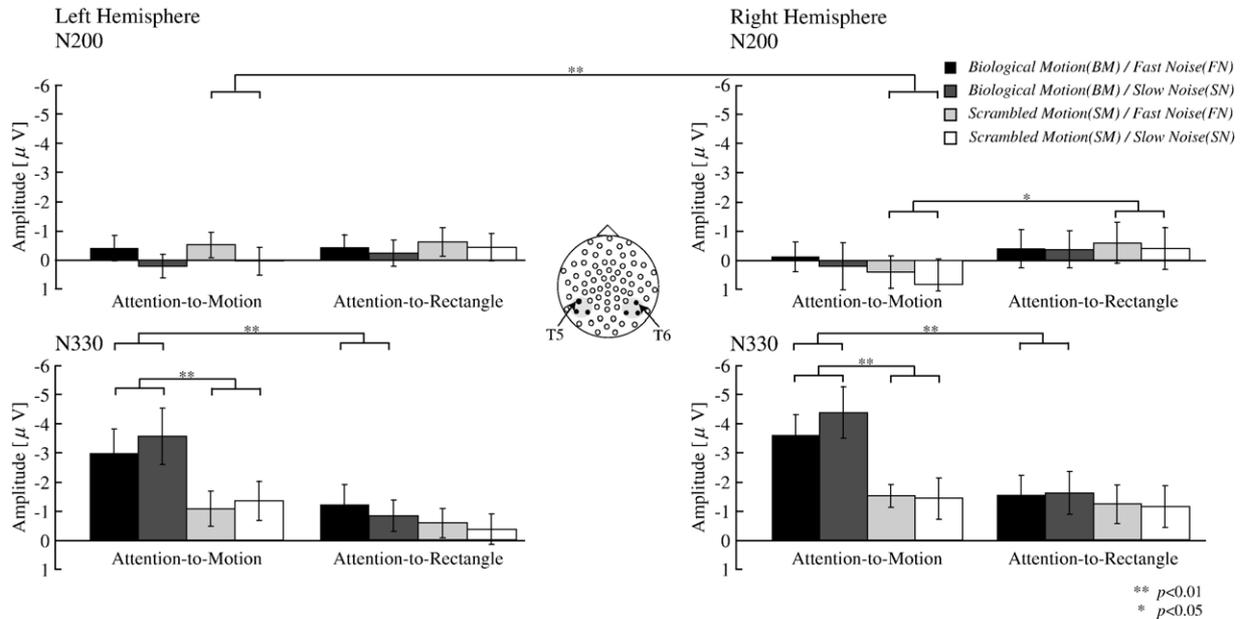


Fig. 4. Mean ( $\pm$ SE) amplitude for 13 subjects for the N200 and N330 components of the ERP for each attentional condition in both hemispheres.

in both occipitotemporal regions at around 200–400 ms; whereas, for the attention-to-rectangle task, we could not find any clear differences between the BM and SM stimuli. In the N200 component, clear differences were not found in any of the conditions whereas a clear difference was observed for the N330 component in the attention-to-motion task.

#### 4. Discussion

The goal of this study was to elucidate the neural mechanism as to whether an attentional process was involved in BM processing. To date, the mechanism of BM processing has remained under debate. Some studies have suggested that BM processing is a bottom-up or low-level process [29,36], while others have indicated that BM processing involves a top-down [10,16] or attentional process [11,51,52]. In this study, to investigate how attention affects BM processing, we measured ERPs when subjects performed an attentional task while viewing Johansson's point-light motion [29] overlaid by random dots and rectangles. In both attentional tasks, the presented stimuli were identical. We used the second negative component as an index that would be related to BM processing. As a result, two negative peaks were recorded at  $\sim$ 200 ms (N200) and  $\sim$ 330 ms (N330) at the bilateral occipitotemporal region. For the N330, two characteristics were clarified: (1) in the attention-to-motion condition, but not the attention-to-rectangle condition, the amplitude of the N330 with the BM stimulus was greater than that with the SM stimulus, and (2) for the BM stimulus, but not the SM stimulus, the amplitude in the attention-to-motion condition was greater than that in the attention-to-rectangle condition. These findings suggest that the N330 reflects the processing

of Johansson's point-light motion and was modulated by the attentional task used in this study.

Our pilot studies revealed that an attentional process would be necessary for BM processing in the present experimental paradigm. When subjects were required to attend to the rectangles, they performed detection of rotation with high accuracy ( $>97\%$ ) and also noticed that dots were moving in the back of the rectangles, but could not ascertain the structure of the dot motion. This result was not consistent with the study by Thornton et al. [52]. In that study, subjects detected both the direction of the walk and rectangle changes with high accuracy. The duration of our stimuli was 510 ms, while their stimuli (the rectangle structure) were presented for 400 ms. Thus, one may consider that the task in our study should be easier for BM detection than that in their study. We could think of two reasons why our subjects were not aware of the dot structure. The first is that our experimental instruction was only to focus on the change in the rectangles for the attention-to-rectangle condition. Thus, the subjects did not need to switch their attention from the rectangles to the structure of the dot motion. The second is that the task in the study by Thornton et al. was easier than that in the present study, since (1) the BM animation was presented for 3200 ms in their 0 ms ISI condition, (2) the size of their visual stimulus was larger ( $9.3 \times 9.3^\circ$ ) than ours ( $3 \times 3^\circ$ ), and (3) the size of the rectangle in their study was also larger ( $0.31 \times 0.93^\circ$ ) than ours ( $0.40 \times 0.15^\circ$ ). In Thornton et al., the duration of the dot motion was longer than in our study, and thus the subjects would easily detect the dot pattern despite the dual-task condition. Furthermore, with such large visual stimuli, the subjects would be able to detect the dot pattern more easily than in our experimental condition. Thus, the effect of "switching attention" (i.e.,

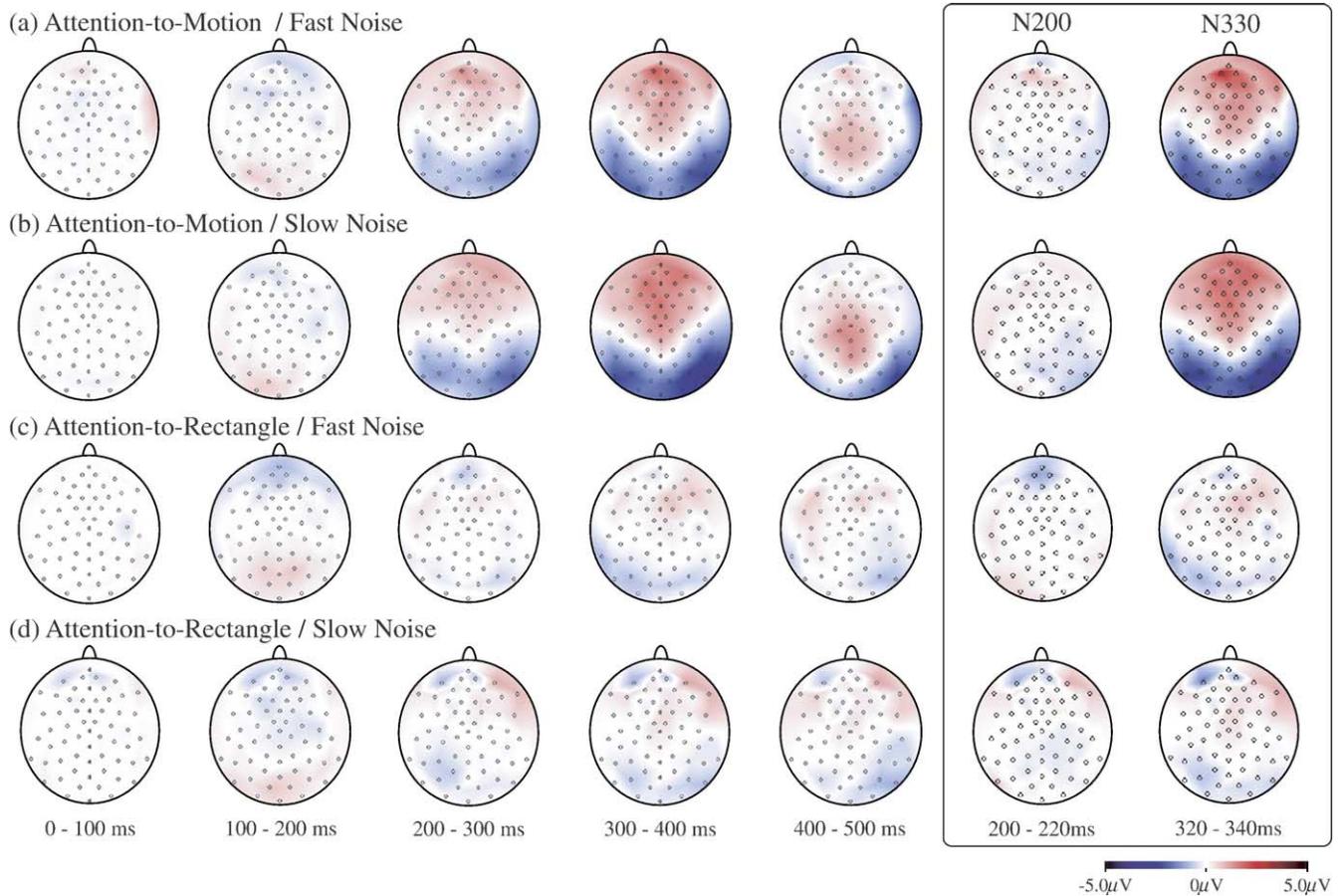


Fig. 5. Scalp distribution of the ERP difference amplitude (ERP amplitude in the BM condition minus SM condition) for each attentional task and noise velocity. The scalp distribution was averaged each 100 ms time window; additionally, scalp distribution for each negative component (N200 and N330) is drawn. (a) attention-to-motion condition with fast noise (b) attention-to-rectangle with slow noise (c) attention-to-rectangle with fast noise (d) attention-to-rectangle with slow noise. The results were interpolated between the electrodes using a triangulation and linear interpolation method. Between 200 ms and 400 ms, clear differences are observed for the attention-to-motion condition at around the bilateral occipitotemporal region. Circles indicate the electrode positions.

subjects repeatedly switching their attention from the rectangle to the target motion) mentioned in their study was hardly estimated in our present experimental paradigm. We speculate that overt attention is needed to detect BM.

In addition to the attentional process, another neural mechanism, such as a feedback mechanism (i.e. projection from higher order areas), may be involved in BM processing in this experimental condition. The second negative component (N330) latency in the present study was delayed compared with that in our previous study, because we superimposed masks (noisy points and rectangles) over the motion stimulus. Through this masking, coherent motion such as BM became more difficult to detect, which increased the response time compared to the situation when the stimulus was not masked. Reports that detection difficulty increases with the number of noise masks support this conclusion [15]. A recent ERP study showed that the negative component (Nc1) related to object recognition was recorded from 230 ms to 290 ms around the bilateral occipitotemporal region [18]. Accounting for such delayed latency, the authors speculated on the existence of such projections from higher order areas as being feedback–

feedforward recursive mechanisms [46]. Another MEG study also revealed analogous latency for object recognition [54]. Due to the possible involvement of a feedback–feedforward mechanism for BM ‘recognition’ of masked dots, the latency of the N330 peak ( $336 \pm 25.0$  ms and  $337.0 \pm 23.5$  ms for BM and SM, respectively) in the current study may be greater than the analogous peak (N240) described in our earlier study ( $268.6 \pm 34.3$  ms and  $267.8 \pm 41.3$  ms for BM and SM, respectively) [24].

As mentioned above, adding noise would delay the second negative component. However, noise velocity itself had no significant effect on the amplitude of N330, contrary to our initial expectations that noise velocity would alter the amplitude. Since the velocity of the masks in FN was approximately the same as in BM and SM, we assumed that separating target motion from noise masks in FN was more difficult than in SN. However, there are several studies that support our present result. Cutting et al. [15] demonstrated that linear masks did not affect the performance of detection of BM direction, whereas circular, dynamic and scrambled-walker masks yielded reliably worse performance under similar conditions to ours. Thornton et al. [52] also showed

that behavioral performance with regard to BM that had been masked by random noise was better than that when BM was masked by scrambled noise that had the same velocity vector as the BM. These findings suggest that the difficulty in detecting a target motion depends on the trajectory rather than the velocity.

Since the conditional difference in the N330 amplitude was observed around the T5/T6 electrode, we assumed that the generator of the N330 might be the occipitotemporal region, particularly that including the STS region [24,57]. Several neuroimaging studies have shown that cortical regions such as the MT/MST [39,40] and STS [26,37] were modulated by attention. These findings are consistent with the results of the present study in terms of the attentional modulation of neural activation at the occipitotemporal region (including the STS region). It has been demonstrated that the orbitofrontal cortex [1,4] and amygdala [2] are interconnected to the STS-complex. Such findings suggest that other cortical regions may modulate the activation of the STS region.

We interpreted that the first negative component would reflect general motion processing and that the second negative component would reflect the BM processing. However, other possibilities can also be considered for each negative component. For N200, we interpreted that the component reflected general motion processing, that is, the latency of the N200 peak ( $207.1 \pm 2.5$  and  $204.4 \pm 22.3$  ms for BM and SM, respectively) in the present study was the same as in our earlier study ( $204.0 \pm 32.6$  and  $200.2 \pm 30.1$  ms for BM and SM, respectively) [24]. In the presented stimuli, the latency did not differ from that in our previous study, despite the addition of noise. Therefore, we consider that the first of the two negative components reflects general motion processing [3,33,38,59]. However, Jokisch et al. [30] reported that the amplitude of N170 in the BM condition was greater than that in the inverted BM and SM conditions, and speculated that the first negative component would reflect the pop-out effect of a moving dot pattern representing the highly familiar form of a human figure.

Several other possible explanations can be considered for the functional properties of the N330 component, including form-from-motion processing [56], object recognition [18] and focusing attention (e.g., [19,34]). Regarding form-from-motion processing, Wang et al. [56] reported that the dN2 component (difference in the waveform between N2 under the attended condition and N2 under the unattended condition) was observed at around 350–450 ms for attentional selection based on kinetic forms. With respect to object recognition, a negative ERP component (Nc1) related to the object recognition was recorded from 230 ms to 290 ms around the bilateral occipitotemporal region [18]. The possibility of focusing attention, that is, this component, could reflect an aspect of the difference in attentional distribution in space. A recent ERPs study [19] revealed a difference in neural activation between an attention search condition and a focused attention condition (the conditional

difference is whether attention is distributed over the whole scene or focused at one location). However, in our experimental paradigm, this probability is hard to contemplate, since the BM or SM stimulus was displayed fully within a  $3 \times 3^\circ$  area. In addition, four rectangles were also displayed randomly within a  $3 \times 3^\circ$  visual field. Thus, we believe that the attentional distribution was approximately the same in both conditions.

However, we believe that the N330 would reflect the BM processing (i.e. Johansson's point-light motion) in this experimental condition for the following reasons: (1) in our pilot studies, the subjects were not aware of the structure of the point-light motion for the attention-to-rectangle condition and the amplitude of N330 was greater in the attention-to-motion condition than in the attention-to-rectangle condition for BM stimulus; and (2) the delayed effect of latency was only found for N330, and not for N200. Another report further supports this interpretation. Jokisch et al. [30] also found two negative components (N170 and N300), similar to our study, during the processing of three kinds of visual stimuli (BM, inverted BM and SM). For the second negative component (N300), the amplitudes of the BM and inverted BM conditions were larger than that of the SM condition, and the authors interpreted that the second negative component may be associated with the specific analysis of motion patterns providing biologically relevant information.

The present finding of modulation of the N330 component could be the output stage of BM processing, rather than a direct part of the processing itself. Several previous studies have reported an attentional effect in such 'low-level' visual processing as a pop-out phenomenon (e.g., [31,48]). Thus, although we cannot reveal at what stages the attentional process intervened, we are able to indicate that attentional modulation is involved in BM processing. Thornton et al. [52] noted that 'top-down' displays should be much more susceptible to the withdrawal of attention than 'bottom-up' displays, and thus we believe that BM processing involves top-down processing.

In conclusion, the amplitude of N330 was affected by attention during the recognition of BM in the present study. This suggests that recognition of BM involves an attentional process under our experimental paradigm. This is the first neurological evidence showing the involvement of attentional processing in the recognition of BM. Further research similar to that conducted by Thornton et al. [52] is now required, namely how the task difficulty affects the neural responses (e.g., how the long ISI is inserted between each stimulus frame) and stricter control of the subjects' attention.

## Acknowledgments

We thank for two anonymous reviewers for helpful comments on a previous version of this manuscript.

## References

- [1] R. Adolphs, The neurobiology of social cognition, *Curr. Opin. Neurobiol.* 11 (2001) 231–239.
- [2] D.G. Amaral, R. Insausti, Retrograde transport of D-[3H]-aspartate injected into the monkey amygdaloid complex, *Exp. Brain Res.* 88 (1992) 375–388.
- [3] M. Bach, D. Ullrich, Motion adaptation governs the shape of motion-evoked cortical potentials, *Vision Res.* 34 (1994) 1541–1547.
- [4] H. Barbas, Anatomic organization of basoventral and mediodorsal visual recipient prefrontal regions in the rhesus monkey, *J. Comp. Neurol.* 276 (1988) 313–342.
- [5] C.D. Barclay, J.E. Cutting, L.T. Kozlowski, Temporal and spatial factors in gait perception that influence gender recognition, *Percept. Psychophys.* 23 (1978) 145–152.
- [6] J.N. Bassili, Facial motion in the perception of faces and of emotional expression, *J. Exp. Psychol. Hum. Percept. Perform.* 4 (1978) 373–379.
- [7] M.S. Beauchamp, K.E. Lee, J.V. Haxby, A. Martin, fMRI responses to video and point-light displays of moving humans and manipulable objects, *J. Cogn. Neurosci.* 15 (2003) 991–1001.
- [8] E. Bonda, M. Petrides, D. Ostry, A. Evans, Specific involvement of human parietal systems and the amygdala in the perception of biological motion, *J. Neurosci.* 16 (1996) 3737–3744.
- [9] S. Brownlow, A.R. Dixon, C.A. Egbert, R.D. Radcliffe, Perception of movement and dancer characteristics from point-light displays of dance, *Psychol. Rec.* 47 (1997) 411–421.
- [10] I. Bulthoff, H. Bulthoff, P. Sinha, Top-down influences on stereoscopic depth-perception, *Nat. Neurosci.* 1 (1998) 254–257.
- [11] P. Cavanagh, A. Labianca, I.M. Thornton, Attention-based visual routines: Sprites, *Cognition* 80 (2001) 47–60.
- [12] R.A. Crawley, J.M.M. Good, A.W. Still, S.S. Valenti, Perception of sex from complex body movement in young children, *Ecol. Psychol.* 12 (2000) 231–240.
- [13] J.E. Cutting, A program to generate synthetic walkers as dynamic point-light displays, *Behav. Res. Methods Instrum.* 10 (1978) 91–94.
- [14] J.E. Cutting, L.T. Kozlowski, Recognizing friends by their walk: gait perception without familiarity cues, *Bull. Psychon. Soc.* 9 (1977) 353–356.
- [15] J.E. Cutting, C. Moore, R. Morrison, Masking the motions of human gait, *Percept. Psychophys.* 44 (1988) 339–347.
- [16] W.H. Dittrich, Action categories and the perception of biological motion, *Perception* 22 (1993) 15–22.
- [17] W.H. Dittrich, T. Troscianko, S.E. Lea, D. Morgan, Perception of emotion from dynamic point-light displays represented in dance, *Perception* 25 (1996) 727–738.
- [18] G.M. Doniger, J.J. Foxe, M.M. Murray, B.A. Higgins, J.G. Snodgrass, C.E. Schroeder, D.C. Javitt, Activation timecourse of ventral visual stream object-recognition areas: high density electrical mapping of perceptual closure processes, *J. Cogn. Neurosci.* 12 (2003) 615–621.
- [19] D. Fernandez-Duque, G. Grossi, I.M. Thornton, H.J. Neville, Representation of change: separate electrophysiological markers of attention, awareness, and implicit processing, *J. Cogn. Neurosci.* 15 (2003) 491–507.
- [20] J. Grezes, P. Fonlupt, B. Bertenthal, C. Delon-Martin, C. Segebarth, J. Decety, Does perception of biological motion rely on specific brain regions? *NeuroImage* 13 (2001) 775–785.
- [21] E.D. Grossman, R. Blake, Brain activity evoked by inverted and imagined biological motion, *Vision Res.* 41 (2001) 1475–1482.
- [22] E.D. Grossman, R. Blake, Brain areas active during visual perception of biological motion, *Neuron* 35 (2002) 1167–1175.
- [23] E.D. Grossman, M. Donnelly, R. Price, D. Pickens, V. Morgan, G. Neighbor, R. Blake, Brain areas involved in perception of biological motion, *J. Cogn. Neurosci.* 12 (2000) 711–720.
- [24] M. Hirai, H. Fukushima, K. Hiraki, An event-related potentials study of biological motion perception in humans, *Neurosci. Lett.* 344 (2003) 41–44.
- [25] D.D. Hoffman, B.E. Flinchbaugh, The interpretation of biological motion, *Biol. Cybern.* 42 (1982) 195–204.
- [26] E.A. Hoffman, J.V. Haxby, Distinct representations of eye gaze and identity in the distributed human neural system for face perception, *Nat. Neurosci.* 3 (2000) 80–84.
- [27] R.W. Homan, J. Herman, P. Purdy, Cerebral location of international 10–20 system electrode placement, *Electroencephalogr. Clin. Neurophysiol.* 66 (1987) 376–382.
- [28] R.J. Howard, M. Brammer, I. Wright, P.W. Woodruff, E.T. Bullmore, S. Zeki, A direct demonstration of functional specialization within motion-related visual and auditory cortex of the human brain, *Curr. Biol.* 6 (1996) 1015–1019.
- [29] G. Johansson, Visual perception of biological motion and a model for its analysis, *Percept. Psychophys.* 14 (1973) 201–211.
- [30] D. Jokisch, I. Daum, B. Suchan, N.F. Troje, Structural encoding and recognition of biological motion: evidence from event-related potentials and source analysis, *Behav. Brain Res.* (in press).
- [31] J.S. Joseph, M.M. Chun, K. Nakayama, Attentional requirements in a ‘preattentive’ feature search task, *Nature* 387 (1997) 805–807.
- [32] L.T. Kozlowski, J.E. Cutting, Recognizing the sex of a walker from a dynamic point-light display, *Percept. Psychophys.* 21 (1977) 575–580.
- [33] Z. Kubova, M. Kuba, H. Spekreijse, C. Blakemore, Contrast dependence of motion-onset and pattern-reversal evoked potentials, *Vision Res.* 35 (1995) 197–205.
- [34] S.J. Luck, S.A. Hillyard, Spatial filtering during visual search: evidence from human electrophysiology, *J. Exp. Psychol. Hum. Percept. Perform.* 20 (1994) 1000–1014.
- [35] G. Mather, L. Murdoch, Gender discrimination in biological motion displays based on dynamic cues, *Proc. R. Soc. Lond., B Biol. Sci.* 258 (1994) 273–279.
- [36] G. Mather, K. Radford, S. West, Low-level visual processing of biological motion, *Proc. R. Soc. Lond., B Biol. Sci.* 249 (1992) 149–155.
- [37] J. Narumoto, T. Okada, N. Sadato, K. Fukui, Y. Yonekura, Attention to emotion modulates fMRI activity in human right superior temporal sulcus, *Cogn. Brain Res.* 12 (2001) 225–231.
- [38] M. Niedeggen, E.R. Wist, Characteristics of visual evoked potentials generated by motion coherence onset, *Cogn. Brain Res.* 8 (1999) 95–105.
- [39] K.M. O’Craven, B.R. Rosen, K.K. Kwong, A. Treisman, R.L. Savoy, Voluntary attention modulates fMRI activity in human MT-MST, *Neuron* 18 (1997) 591–598.
- [40] K.M. O’Craven, P.E. Downing, N. Kanwisher, fMRI evidence for objects as the units of attentional selection, *Nature* 401 (1999) 584–587.
- [41] B.S. Oken, K.H. Chiappa, Statistical issues concerning computerized analysis of brainwave topography, *Ann. Neurol.* 19 (1986) 493–494.
- [42] M.W. Oram, D.I. Perrett, Responses of anterior superior temporal polysensory (STPa) neurons to “biological motion” stimuli, *J. Cogn. Neurosci.* 6 (1994) 99–116.
- [43] M.W. Oram, D.J. Perrett, Integration of form and motion in the anterior superior temporal polysensory area (STPa) of the macaque monkey, *J. Neurophysiol.* 76 (1996) 109–129.
- [44] M. Pavlova, W. Lutzenberger, A. Sokolov, N. Birbaumer, Dissociable cortical processing of recognizable and non-recognizable biological movement: analyzing gamma MEG activity, *Cereb. Cortex* 14 (2004) 181–188.
- [45] K.A. Pelphrey, T.V. Mitchell, M.J. McKeown, J. Goldstein, T. Allison, G. McCarthy, Brain activity evoked by the perception of human walking: controlling for meaningful coherent motion, *J. Neurosci.* 23 (2003) 6819–6825.
- [46] D.A. Pollen, On the neural correlates of visual perception, *Cereb. Cortex* 9 (1999) 4–19.
- [47] M. Ptito, J. Faubert, A. Gjedde, R. Kupers, Separate neural pathways for contour and biological-motion cues in motion-defined animal shapes, *NeuroImage* 19 (2003) 246–252.
- [48] G. Rees, C.D. Frith, N. Lavie, Modulating irrelevant motion

- perception by varying attentional load in an unrelated task, *Science* 278 (1997) 1616–1619.
- [49] A.P. Saygin, S.M. Wilson, D.J. Hagler Jr, E. Bates, M.I. Sereno, Point-light biological motion perception activates human premotor cortex, *J. Neurosci.* 24 (2004) 6181–6188.
- [50] P. Servos, R. Osu, A. Santi, M. Kawato, The neural substrates of biological motion perception: an fMRI study, *Cereb. Cortex* 12 (2002) 772–782.
- [51] I.M. Thornton, J. Pinto, M. Shiffrar, The visual perception of human locomotion, *Cogn. Neuropsychol.* 15 (1998) 535–552.
- [52] I.M. Thornton, R.A. Rensink, M. Shiffrar, Active versus passive processing of biological motion, *Perception* 31 (2002) 837–853.
- [53] L.M. Vaina, J. Solomon, S. Chowdhury, P. Sinha, J.W. Belliveau, Functional neuroanatomy of biological motion perception in humans, *Proc. Natl. Acad. Sci. U. S. A.* 98 (2001) 11656–11661.
- [54] S. Vanni, A. Revonsuo, J. Saarinen, R. Hari, Visual awareness of objects correlates with activity of right occipital cortex, *NeuroReport* 8 (1996) 183–186.
- [55] R.D. Walk, C.P. Homan, Emotion and dance in dynamic light displays, *Bull. Psychon. Soc.* 22 (1984) 437–440.
- [56] J. Wang, Y. Jin, F. Xiao, S. Fan, L. Chen, Attention-sensitive visual event-related potentials elicited by kinetic forms, *Clin. Neurophysiol.* 110 (1999) 329–341.
- [57] S. Watanabe, K. Miki, R. Kakigi, Gaze direction affects face perception in humans, *Neurosci. Lett.* 325 (2002) 163–166.
- [58] J.A. Webb, J.K. Aggarwal, Structure from motion of rigid and jointed objects, *Artif. Intell.* 19 (1982) 107–130.
- [59] E.R. Wist, J.D. Gross, M. Niedeggen, Motion aftereffects with random-dot checkerboard kinematograms: relation between psychophysical and VEP measures, *Perception* 23 (1994) 1155–1162.