

# The feet have it: Local biological motion cues trigger reflexive attentional orienting in the brain



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## ARTICLE INFO

### Article history:

Accepted 18 August 2013

Available online 28 August 2013

### Keywords:

Reflexive attention  
Biological motion  
Local  
ERP

## ABSTRACT

Most vertebrates, humans included, have a primitive visual system extremely sensitive to the motion of biological entities. Most previous studies have examined the global aspects of biological motion perception, but local motion processing has received much less attention. Here we provide direct psychophysical and electrophysiological evidence that human observers are intrinsically tuned to the characteristics of local biological motion cues independent of global configuration. Using a modified central cueing paradigm, we show that observers involuntarily orient their attention towards the walking direction of feet motion sequences, which triggers an early directing attention negativity (EDAN) in the occipito-parietal region 100–160 ms after the stimulus onset. Notably, such effects are sensitive to the orientation of the local cues and are independent of whether the observers are aware of the biological nature of the motion. Our findings unambiguously demonstrate the automatic processing of local biological motion without explicit recognition. More importantly, with the discovery that local biological motion signals modulate attention, we highlight the functional importance of such processing in the brain.

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## Introduction

Humans are highly adept at detecting and encoding the motions of other biological entities in the environment, even when they are portrayed by just a small number of point lights attached to the head and major joints (i.e., a point-light walker; Johansson, 1973). Many characteristics such as gender, identity, action, mental state and intention can be readily retrieved from the point-light walker (Barclay et al., 1978; Blakemore and Decety, 2001; Dittrich, 1993; Dittrich et al., 1996; Mather and Murdoch, 1994; Troje, 2002; Troje et al., 2005). Among them, walking direction is a particularly important attribute of biological motion, as it plays a major role in assessing another living creature's disposition and intention. Indeed, numerous studies have indicated that the vertebrate visual system has primitive biases for detecting the direction of biological motion. For example, the walking direction of a point-light walker can be discriminated even when it is embedded in dynamic visual noise (Aaen-Stockdale et al., 2008; Bertenthal and Pinto, 1994; Neri et al., 1998; Thurman and Grossman, 2008). Peripheral walking direction information can be fully extracted (Thompson et al., 2007) and influence the processing of a centrally presented point-light walker (Thornton and Vuong, 2004). Intriguingly, a recent study has shown that the perceived walking direction of a bistable point-light walker (walking toward or walking away from the

observer) can be influenced by the observer's own actions, which has been suggested to be crucial for joint action and social interaction (Manera et al., 2012). Moreover, the ability to detect the direction of biological motion arises at a very early age. Six-month-old infants have been able to discriminate the walking direction of an upright point-light walker (Kuhlmeier et al., 2010). Even newly hatched chicks, lacking any visual experience, have a spontaneous sensitivity to the walking direction conveyed by the point-light animations (Vallortigara and Regolin, 2006; Vallortigara et al., 2005).

Most previous studies have emphasized the contribution of global form to the specialized processing of biological motion (Beintema and Lappe, 2002; Bertenthal and Pinto, 1994; Lange and Lappe, 2006; Lange et al., 2006), whereas the importance of local motion signals in biological motion perception has long been overlooked. Until recently, some studies have shown that human observers can retrieve the walking direction even when all of the point lights are spatially scrambled and the global configural information is entirely disrupted (Troje and Westhoff, 2006). Moreover, such directional information is mainly carried by the motion of the feet (Troje and Westhoff, 2006) and can be successfully extracted as short as 100 ms (Saunders et al., 2009) or in the visual periphery (Gurnsey et al., 2010). Further investigations have revealed that the characteristic vertical acceleration pattern contained in feet motion, which is constrained by gravity, inertia, and the general kinetics of moving bodies, plays a vital role in local biological motion processing (e.g., direction extraction) (Chang and Troje, 2009). Chang and Troje (2009) have hence suggested that the vertical acceleration pattern contained in the motion of the feet may be crucial for the visual

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system to identify the presence of articulated terrestrial animals in the visual environment, and there might exist an evolutionarily old and possibly innate brain mechanism that is extremely sensitive to local biological motion cues, potentially acting as a “life detector” (Troje, 2008; Troje and Westhoff, 2006). However, the idea would remain speculative unless we are clear about the functional importance of such processing in the brain. In other words, such mechanism should provide a measurable benefit to human processing of sensory information. Since walking direction provides important cues for other people’s mental states (e.g., current focus of attention, interests and goals), particularly when viewing them from a distance, it would be of obvious adaptive advantage for humans to pay more attention to their walking direction and enhance related information processing, allowing more resources for the extraction of others’ intentions as well as the execution of appropriate reactions.

It is only recently that a few studies have shown that the processing of walking direction can further affect human behavioral responses (Hirai et al., 2011; Shi et al., 2010). For example, following a brief presentation of a central point-light walker walking toward either the left or right direction, observers’ performance on a subsequent probe (i.e., Gabor patch) task was significantly better when the probe was presented in the walking direction (congruent condition) than in the opposite direction (incongruent condition) even when observers were explicitly told that walking direction was not predictive of target location (Shi et al., 2010). This finding suggests that the walking direction of a point-light walker, like eye gaze (Friesen and Kingstone, 1998; Langton et al., 2000), acts as an important social cue and induces a reflexive attentional orienting effect. However, it remains unknown whether such attentional effect can be triggered by local biological motion cues (i.e., the motion of the feet) and whether it depends on observers’ explicit knowledge of the cues.

Here, we adopted the same central cueing paradigm from mainstream attention research to test the attentional orienting in the motion direction of the feet. This paradigm involved aspects from both standard central cueing and peripheral cueing techniques (Jonides, 1981; Posner, 1980). Feet motion sequences, with the walking direction either towards the left or right of fixation, were presented as central cues (Fig. 1). However, unlike traditional central arrow cues, the motion direction of the feet was not predictive of the probable location of the subsequent target. In this respect, it followed previous peripheral cueing studies that used spatially uninformative cues to investigate the reflexive response of attention (see Frischen et al., 2007 for a review). We also included inverted feet motion cues to disentangle the potential effect elicited by the translatory motion from the feet (see Materials and methods for details). Further, we recorded the event-related brain potentials (ERP) to investigate the electrophysiological correlates of the attentional shift triggered by local biological motion cues. Previous ERP studies have shown that the early directing attention negativity (EDAN), a more negative occipito-parietal component induced by contralateral cues than ipsilateral cues, reflects the encoding of spatial

information provided by the cues and the initialization of attentional orienting (Harter et al., 1989; Hopf and Mangun, 2000; Jongen et al., 2006; Yamaguchi et al., 1994). In the current study, we focused on the EDAN component and aimed to examine both the time course and neural underpinning of reflexive attentional orienting to local biological motion cues. In addition, given that walking direction can be inferred from the motion of the two feet when observers were not informed of the nature of the stimuli (Chang and Troje, 2009; Troje and Westhoff, 2006), we also examined whether behavioral and electrophysiological effects were preserved even when observers were naïve to the biological nature of local motion cues.

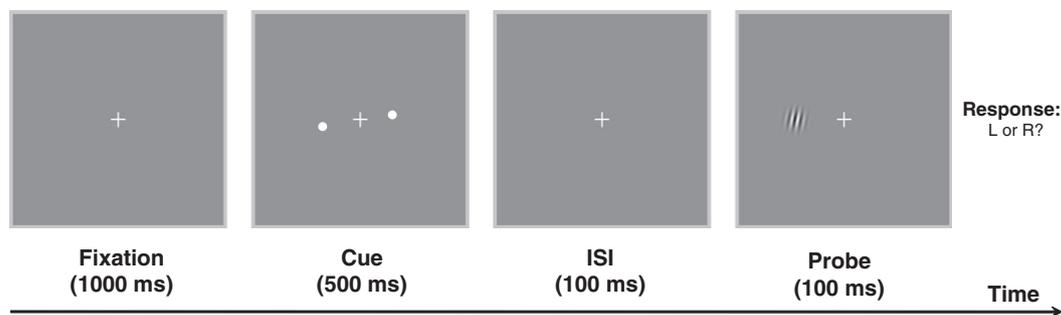
## Materials and methods

### Participants

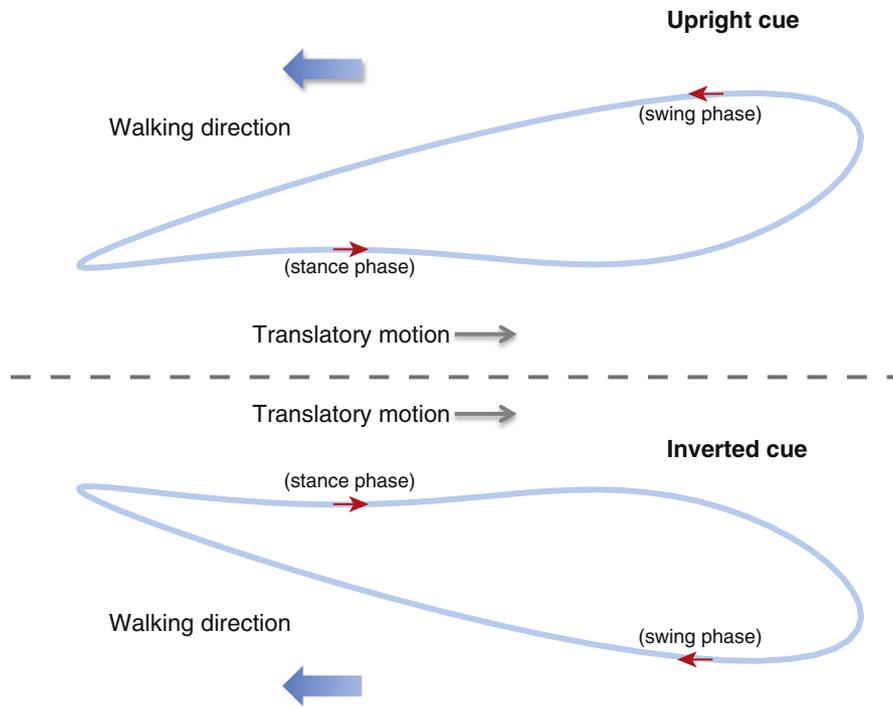
Thirty-six observers (21 female) whose ages ranged from 19 to 28 took part in the study. Ten observers participated in the main psychophysical experiment, ten in the control experiment, and sixteen took part in the event-related potential (ERP) experiment. All had normal or corrected-to-normal vision and gave written, informed consent in accordance with procedures and protocols approved by the institutional review board of the Institute of Psychology, Chinese Academy of Sciences. All observers were naïve to the purpose of the experiments. Two observers were excluded from further ERP data analysis due to poor EEG data quality.

### Stimuli and procedure

Stimuli were generated and displayed using MATLAB (MathWorks, Inc.) together with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). Biological motion stimuli, which were created by capturing the motion of a walking actor, were adopted from Vanrie and Verfaillie (2004). Each biological motion sequence comprised 13 dots depicting the motions of markers attached to the head and the major joints (shoulders, elbows, wrists, hips, knees, and ankles). The two ankle markers were used to specify the motion of the feet in previous studies (Chang and Troje, 2009; Troje and Westhoff, 2006). In the current study, the feet motion sequences were created by isolating the two point lights of ankles from the original biological motion sequences with leftward or rightward walking direction. Each cycle was 1 s and contained 30 frames. The initial frame of the point-light display was randomized for each trial to avoid observers’ prediction. The feet motion sequences consist of two fragments that represent the foot trajectory’s stance and swing phases, respectively. During the stance phase, the corresponding dot moves in the opposite direction of the walking direction at an approximately constant velocity (Fig. 2, gray arrows). During the swing phase, the dot accelerates along both the horizontal and vertical dimensions due to muscle activity and gravitational acceleration. If observers can reliably recognize these two fragments, they will be able



**Fig. 1.** Schematic representation of the experimental paradigm. After a cue (the upright or inverted feet motion) was presented for 500 ms in each trial, there was a 100 ms inter-stimulus interval (ISI) in which only the fixation was displayed, followed by a small Gabor patch that was presented briefly (100 ms) as a probe on the left or right side of the fixation. Observers were then required to press one of two buttons to indicate whether the probe appeared on the left or right side as quickly as possible while minimizing errors. At the beginning of each experiment, observers were explicitly told that the feet motion was not predictive of target location.



**Fig. 2.** Schematic trajectories of the upright (top row) and inverted (bottom row) feet motion cues across a full gait cycle (including the swing phase and the stance phase). The blue arrows indicate the walking direction of the feet and the gray arrows indicate the direction of the translatory motion.

to correctly perceive the walking direction of the feet motion (Fig. 2, blue arrows). It should be noted that the walking direction is essentially opposite to the motion direction indicated by the stance phase (Chang and Troje, 2009). Inverted counterparts were created by mirror flipping the feet motion sequences vertically such that the walking direction (leftward or rightward) was kept the same for the upright and inverted versions. The inversion disrupted all of the meaningful biological signatures (e.g., the vertical acceleration due to muscle activity and gravity), but the linear, horizontal motion in the stance phase fragments was almost unaffected by inversion. In the control experiment, the stimuli were derived from the fragments identical to the feet motion sequences but with critical biological characteristics removed. Specifically, each individual dot moved along a path identical to that of the feet motion sequences but with a constant speed equal to the average speed of the dot. Such manipulation disrupted the natural velocity profile of the feet motion signals but retained the motion trajectories of the individual dots.

Stimuli were displayed on a 22-inch LCD monitor ( $1280 \times 1024$  at 60 Hz), and the viewing distance was 70 cm. Each trial began with fixation on a central cross ( $0.6^\circ \times 0.6^\circ$ ) within a frame ( $18.1^\circ \times 18.1^\circ$ ) that extended beyond the outer border of the stimuli. A cue (an upright or inverted feet motion sequence, subtended approximately  $3.3^\circ \times 0.7^\circ$  in visual angle) was then superimposed on the central cross and was presented for 500 ms. The contrast between the cue and the background was 58% (cue luminance:  $110.20 \text{ cd/m}^2$  and background luminance:  $29.42 \text{ cd/m}^2$ ). After the cue presentation, there was a 100 ms inter-stimulus interval (ISI) in which only the fixation was displayed, followed by a small Gabor patch that was presented briefly (100 ms) as a probe on the left or right side of the fixation. The horizontal distance between the center of the Gabor patch and the fixation was  $4.5^\circ$ . Observers were required to press one of two keys on a standard keyboard to indicate whether the probe appeared on the left or right side as quickly as possible while minimizing errors (see Fig. 1 for a schematic experimental procedure). Throughout the experiment, a central cross was always displayed in the center of the screen, and observers were asked to fixate on the central cross from the beginning of each trial.

The main psychophysical experiment comprised two blocks, the upright feet motion block and the inverted feet motion block. Each block

consisted of 40 trials with 20 congruent trials and 20 incongruent trials. At the beginning of the experiment, observers were explicitly told that the point-light motion sequences were either from the upright or inverted feet motion and that the cue direction did not predict target location. Test trials were presented in a new random order for each observer. The order of the blocks (upright and inverted) was also counter-balanced across observers. The control experiment followed the same procedure as in the main experiment except that the central cues were replaced with the control stimuli devoid of the critical biological characteristics (i.e., the motion acceleration).

In order to test whether the reflexive attentional effect observed in the psychophysical experiment is dependent upon the explicit recognition of biological information and further investigate the specific electrophysiological correlates of the attentional shift induced by the motion of the feet, the ERP experiment was conducted in two sessions. In the first session, observers were naïve to the feet motion sequences (which was further confirmed after this session of the experiment), and they were instructed that the motion of the two dots was irrelevant to the task and not predictive of target location. In the second session, observers were informed of the biological nature of upright and inverted feet motion sequences and that the walking direction did not predict target location, as in the psychophysical experiment. The task employed in the ERP experiment was identical to the psychophysical experiment. There were four blocks for each session, with two blocks for the upright feet motion cues and two blocks for the inverted feet motion cues. There were 100 trials in each block. The order of the upright and inverted blocks was counter-balanced across observers.

#### EEG recordings and data analysis

The electroencephalographic (EEG) activity was recorded using 64 electrodes mounted in an elastic cap with a common vertex reference (CZ reference). Vertical (VEOG) and horizontal (HEOG) electro-oculograms were recorded with bipolar channels from sites above and below the midpoint of the left eye and beside the outer canthi of each eye. Mild skin abrasion was used to reduce the electrode impedances below 5 k $\Omega$ . The EEG signals were band-pass filtered from 0.05

to 50 Hz, amplified with a gain of 500, and stored on a computer disk at the sample rate of 500 Hz (Syn-Amps 4.3, Neuroscan, Inc.).

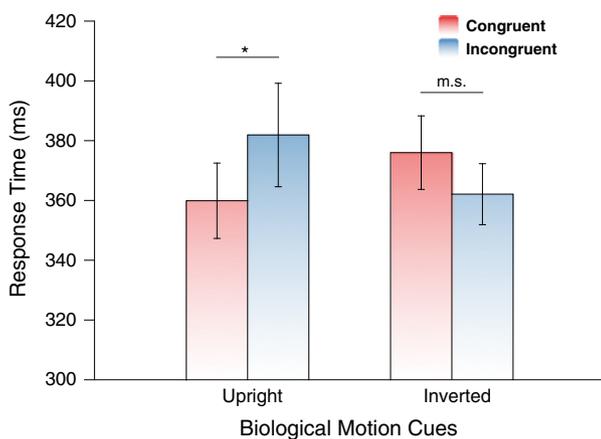
The continuous EEG signal was corrected for blink artifact and digitally filtered (low pass = 30 Hz, high pass = 0.05 Hz). It was then segmented to 700 ms epochs for each cue direction (right or left) starting 100 ms prior to the cue stimuli and ending 600 ms after stimulus presentation. Epochs were baseline-corrected against the mean voltage during the 100 ms pre-stimulus period, and trials were automatically eliminated if the voltage in the epoch exceeded 70  $\mu$ V. All channels were then re-referenced to the average of the mastoids (M1 and M2).

The presence of the attentional lateralized ERP component (i.e., EDAN) sensitive to the direction of an attentional shift is indexed by a significant Cue Direction  $\times$  Hemisphere interaction over occipitoparietal brain areas (Harter et al., 1989; Hopf and Mangun, 2000; Jongen et al., 2006). Therefore, mean amplitudes obtained at posterior recording sites were analyzed to reveal the attentional lateralized EDAN component. In order to disentangle the effect elicited by the translatory motion and highlight the electrophysiological activities specifically related to attentional effect of the processes of local biological motion signals, difference waves were obtained by subtracting ERPs to the inverted cues from ERPs to the upright cues. To further localize the neural sources of the EDAN component, current source density was estimated using standardized low-resolution brain electromagnetic tomography (sLORETA) (Fuchs et al., 2002; Jurcak et al., 2007; Pascual-Marqui, 2002).

## Results

### Psychophysical experiments

The data of response times were entered into a  $2 \times 2$  repeated measures analysis of variance (ANOVA) with two within-subjects factors of Cue-Target Congruency (congruent vs. incongruent) and Cue Orientation (upright vs. inverted). The interaction between Cue-Target Congruency and Cue Orientation was significant in the main experiment ( $F_{1,9} = 14.97, p < .01$ ). Specifically, when upright feet motion sequences were presented as the central cues, results consistently showed that observers' performance on a subsequent probe location discrimination task was significantly better when the probe was presented in the walking direction of the feet (congruent condition) than in the opposite direction (incongruent condition) (Fig. 3; 360 ms vs. 382 ms,  $t_9 = 2.85, p < .02$ ). This result suggests that observers' spatial attention was involuntarily oriented to the walking direction of the feet even though all of



**Fig. 3.** Results from the psychophysical experiment. When the upright feet motion sequence was presented as attentional cues, observers' performance on a subsequent probe location discrimination task was significantly better when the probe was presented in the walking direction of the feet (congruent condition) compared to when the probe was presented in the opposite direction (incongruent condition). However, an inverse pattern was found in the inverted condition. Error bars show standard errors. \* $p < .05$ ; m.s., marginally significant.

the observers were explicitly told prior to the experiment that the walking direction was not predictive of target location. Intriguingly, in the inverted condition, the attentional effect was marginally significant, but showed an inverse pattern (Fig. 3; 376 ms vs. 362 ms,  $t_9 = -2.08, p = .068$ ) compared with that in the upright condition: observers' performance was worse when the probe was presented in the motion direction of the inverted feet signals (congruent condition) than in the opposite direction (incongruent condition). This effect seems to arise from the translatory (extrinsic) motion in the stance phase that essentially points to the opposite direction of the walking direction (see Methods for more detail). It should be noted that the inversion of the feet motion disrupts only the intrinsic biological information contained in the upright feet motion (e.g., the vertical acceleration due to muscle activity and gravity) and the horizontal, translatory motion in the stance phase was unchanged (Fig. 2). In other words, if the motion of the two feet is not integrated, explicitly or implicitly, into a coherent percept of walking direction, the upright feet motion sequence should also have shown a similar effect of the translatory motion (opposite to that induced by the walking direction) (Chang and Troje, 2009).

To test if the observed reflexive attentional orienting effect is indeed triggered by the biological characteristics of the feet motion signals, we conducted a further experiment in which everything was the same as in the main experiment except that the critical biological information (i.e., the motion acceleration) was removed from the feet motion sequences (Chang and Troje, 2009). Results showed that the difference between the congruent and incongruent conditions disappeared when the upright control stimuli were used as central cues (366 ms vs. 369 ms,  $t_9 = 0.63, p > .1$ ), and there was no significant interaction between Cue-Target Congruency and Cue Orientation ( $F_{1,9} = 0.76, p > .1$ ). Therefore, these results suggest that the attentional effect found in the main experiment is largely, if not all, accounted for by the characteristic acceleration pattern contained in the local motion signals.

### ERP experiment

#### Behavioral data

The data of response times of each session were entered into a  $2 \times 2$  repeated measures ANOVA with two within-subjects factors of Cue-Target Congruency (congruent vs. incongruent) and Cue Orientation (upright vs. inverted), respectively. When observers were informed of the nature of the stimuli (i.e., they were told that the stimuli were derived from an intact human walker) in the second session of the experiment, the results were essentially the same as that of the psychophysical experiment. Again, the interaction between Cue-Target Congruency and Cue Orientation was significant ( $F_{1,15} = 17.26, p < .01$ ). That is, observers performed better in the congruent than incongruent condition with the upright biological motion cues (352 ms vs. 367 ms,  $t_{15} = 2.73, p < .01$ ), but a reverse pattern was found when the motion of the feet was shown inverted (361 ms vs. 347 ms,  $t_{15} = -3.46, p < .01$ ). In the first session of the experiment where observers were naïve to the feet motion cues, they simply described the two moving dots as some pattern of random motion and could not even tell the difference between the upright and inverted motions in post-session debriefings. Interestingly, there was still a significant interaction between Cue-Target Congruency and Cue Orientation even without the observers explicitly knowing the walking direction of the feet motion ( $F_{1,15} = 4.56, p < .05$ ). Further analysis showed that when the inverted feet motion sequences were used as the central cues, observers' performance was again significantly better in the incongruent than the congruent cue condition due to the translatory motion in the stance phase (358 ms vs. 347 ms,  $t_{11} = -3.40, p < .01$ ), but this effect was not evident in the upright condition (355 ms vs. 359 ms,  $t_{15} = 1.27, p > .1$ ). This pattern of results likely reflects that the effect from the translatory motion (which is opposite to the walking direction) was offset by the attentional

effect arising from the upright feet walking direction even before observers explicitly recognized the cues.

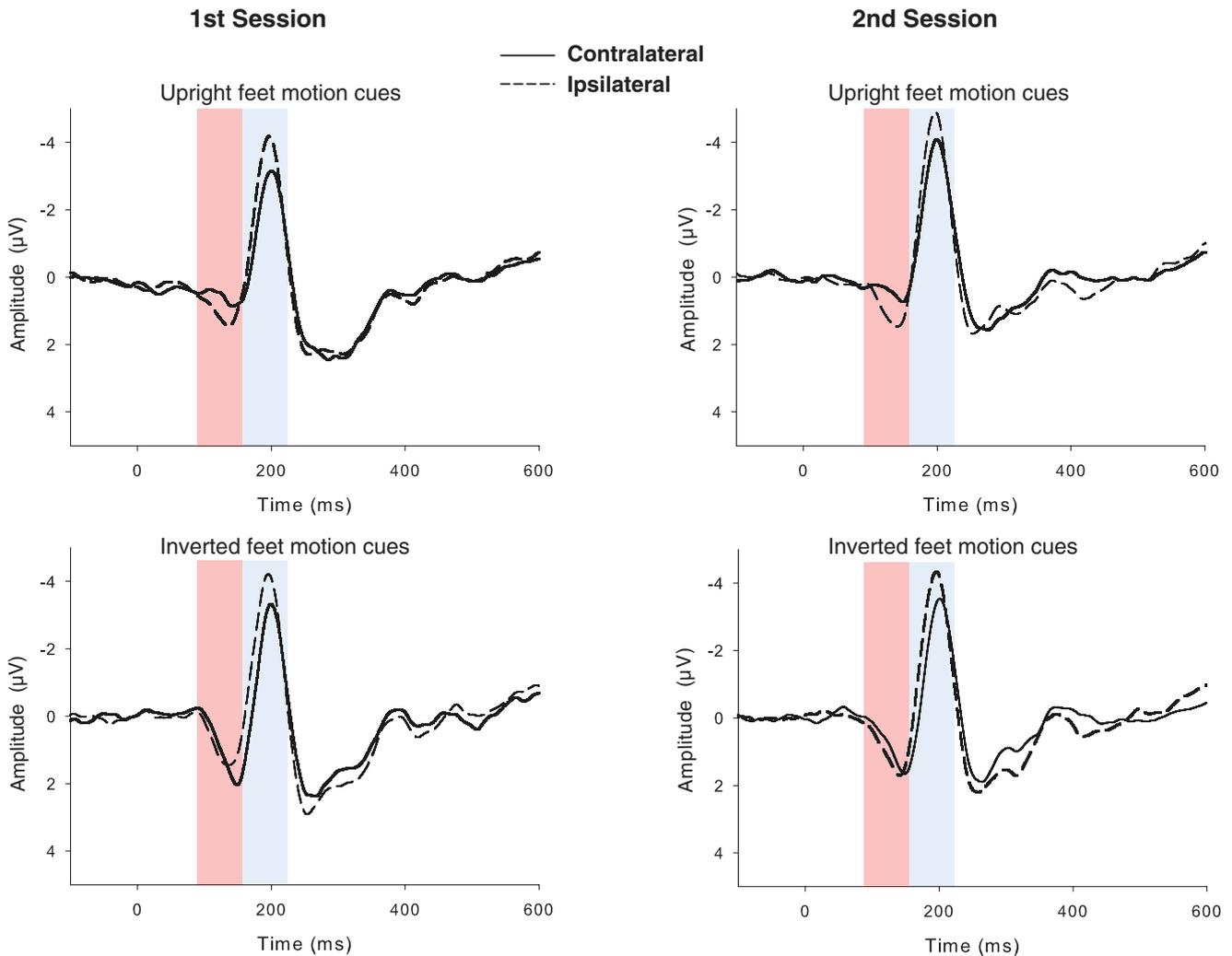
Taken together, the behavioral results replicated those of the psychophysical experiment and provided clear evidence that human observers can involuntarily orient their attention towards the meaningful direction of biological motion even when the motion is carried only by two point lights of the feet.

#### Electrophysiological data

Fig. 4 shows the ERPs in response to the two central cues (upright and inverted feet motion cues) in the first and second sessions, respectively. The ERP data from these two experimental sessions were separately analyzed by three-way repeated measures ANOVAs with Cue direction (left vs. right), Hemisphere (left vs. right), and Cue orientation (upright vs. inverted) as independent variables. When the observers explicitly recognized the feet motion cues in the second session, a significant EDAN effect was found over the posterior electrodes (PO5/6 and PO7/8) during an earlier time window between 100 and 160 ms in the upright condition (Fig. 4, upper right panel;  $F_{1, 13} = 11.3, p < .01$ ). In other words, the upright feet motion cues pointing to the direction contralateral to the recorded hemisphere elicited a larger negative response than those pointing to the ipsilateral direction. This EDAN effect

was evident in both the left and right hemispheres ( $ps < .05$ ). In the inverted cue condition, however, no such EDAN effect was found (Fig. 4, lower right panel;  $F_{1, 13} = 1.41, p > .2$ ), resulting in a significant three-way interaction of Cue direction  $\times$  Hemisphere  $\times$  Cue orientation ( $F_{1, 13} = 9.48, p < .05$ ). Interestingly, this attentional lateralized effect (EDAN) still persisted in the upright feet motion condition (Fig. 4, upper left panel;  $F_{1, 13} = 9.12, p < .05$ ) even when observers were naïve to the biological nature of the stimuli (the first session), but it was not the case in the inverted condition (Fig. 4, lower left panel;  $F_{1, 13} = 0.52, p > .4$ ). The interaction of Cue direction  $\times$  Hemisphere  $\times$  Cue orientation was also significant in the first session ( $F_{1, 13} = 8.07, p < .05$ ). These results provide clear evidence that the EDAN effect was indeed triggered by the upright feet walking direction even without observers' explicit recognition of its biological nature, and this effect was disrupted by inversion of the feet motion cues. The converging evidence from the ERP and psychophysical data suggest that the local biological motion cues can induce robust attentional orienting, which is independent of explicit knowledge of the feet motion cues.

In addition, there was another attentional lateralized ERP component during a relatively later time window between 160 and 220 ms post-cue onset (Fig. 4, blue bars). The Cue direction  $\times$  Hemisphere interaction was significant for both sessions in the upright condition



**Fig. 4.** The grand average ERPs evoked by local biological motion cues. The ERPs are shown at the posterior electrodes contralateral and ipsilateral to the walking direction of the feet, respectively. Significant attentional lateralized EDAN effect (more negative responses for the contralateral than the ipsilateral walking direction) was found 100–160 ms after stimulus onset (red bars) and was evident only from the upright (top row) but not inverted (bottom row) feet motion cues in both the first (left column) and the second sessions (right column). In addition, there was another attentional lateralized effect (more negative responses for the contralateral than the ipsilateral translatory motion direction rather than the walking direction) during a later time window (160–220 ms), which was evident for both the upright and inverted feet motion cues and in both the first and second sessions (blue bars).

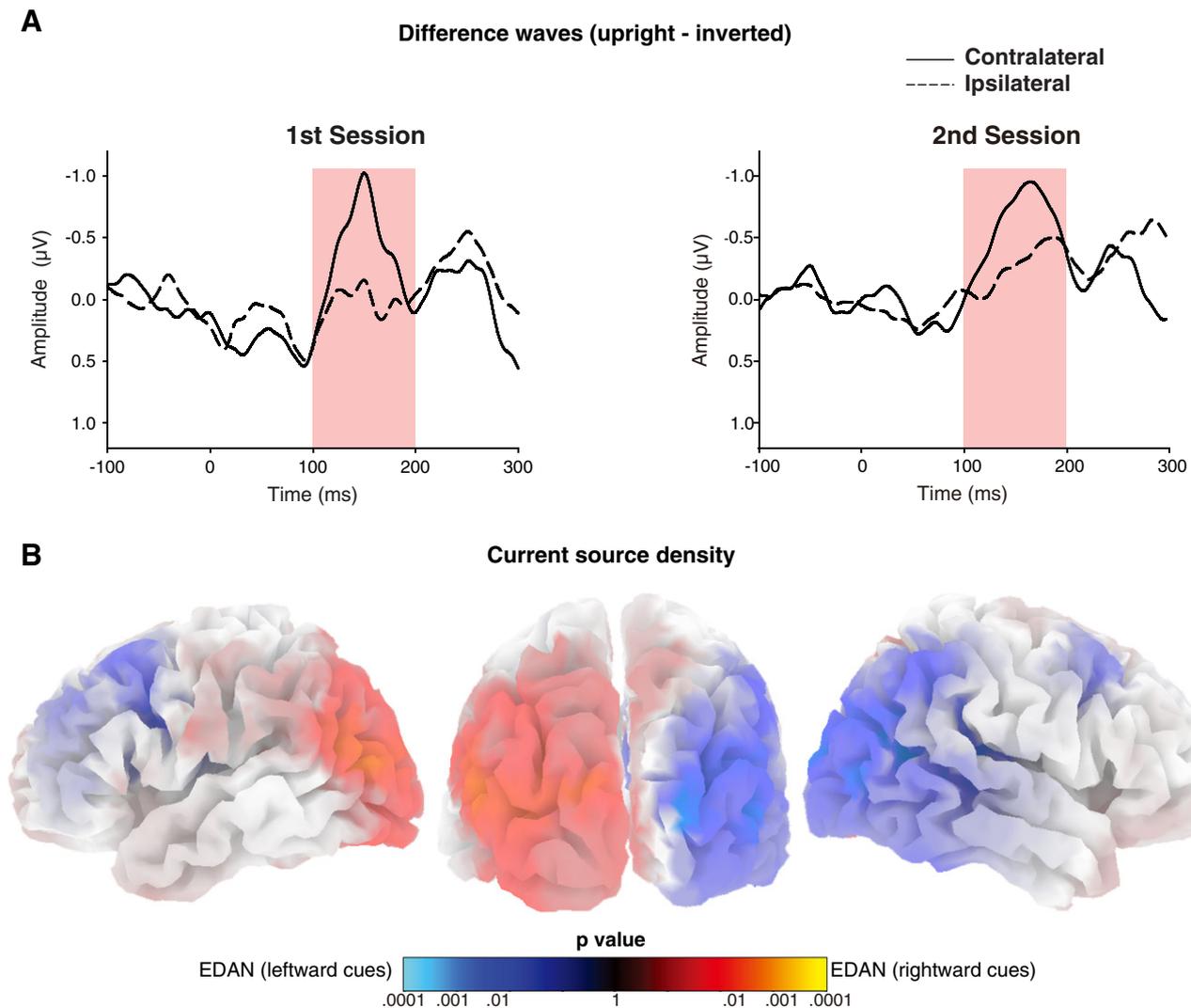
(the first session:  $F_{1, 13} = 40.81, p < .01$ ; the second session:  $F_{1, 13} = 17.75, p < .01$ ). However, different from the earlier EDAN component, this later component was also evident in the inverted condition (the first session:  $F_{1, 13} = 17.77, p < .01$ ; the second session:  $F_{1, 13} = 22.95, p < .01$ ) and did not show a significant interaction of Cue direction  $\times$  Hemisphere  $\times$  Cue orientation (the first session:  $F_{1, 13} = 1.34, p > .05$ ; the second session:  $F_{1, 13} = 3.88, p > .05$ ), suggesting that this ERP component is similar between the upright and inverted orientations and thus is not specific to biological motion signals per se. Moreover, since this later component is consistent with the cueing direction of the translatory motion in the stance phase rather than that of the walking direction (more negative responses for the contralateral than the ipsilateral direction of the translatory motion in the stance phase), it is likely that this component reflects the potential effect induced by the translatory motion signals.

To further localize the neural sources of the attentional shift-related EDAN component, current source density was estimated using standardized low-resolution brain electromagnetic tomography (sLORETA). In order to disentangle the effect elicited by the translatory motion and highlight the electrophysiological activities specifically related to the processes of local biological motion signals, difference waves were first obtained by subtracting ERPs to the inverted cues from ERPs to

the upright cues. The EDAN effects specific to local biological signals were quite similar between the first and the second sessions (Fig. 5, upper panel; 100–200 ms post-cue onset over the posterior occipito-parietal sites). This component was then subject to the source localization analysis. The current sources for the EDAN component (averaged across these two sessions) were primarily localized to the bilateral occipital and occipito-parietal brain areas (Fig. 5, lower panel). Note that the activation maps represent *t*-test statistics computed on each search array comparing between the left and right feet motion cues. Consistent with the ERP amplitude results, current sources showed that feet motion cues evoked a larger negative response in the contralateral than ipsilateral hemisphere (the brain areas that were associated enlarged negativities by the rightward cues are shown in red color, while the brain areas with enlarged negativities related to the leftward cues are shown in blue color).

## Discussion

In the current study, we demonstrated for the first time that feet motion cues could induce a fast and robust reflexive attentional orienting effect, which could serve as a type of detection or alert system to help us quickly assess others' intentions. Notably, such an attentional



**Fig. 5.** Difference waves and current source density. (A) Difference waves were obtained by subtracting ERPs to the inverted cues from that to the upright cues. The EDAN effect specific to local biological motion cues was observed 100–200 ms post-cue onset over the posterior occipito-parietal sites. (B) The current source density related to the EDAN effect. Brain regions with enlarged negativities related to the rightward cues are shown in red color, while brain regions with enlarged negativities related to the leftward cues are shown in blue color.

orienting effect is essentially independent of observers' explicit awareness of the biological nature of the feet motion cues. Walking is arguably the most frequent movement in bipeds (e.g., humans) and quadrupeds. It is thus not surprising that we are extremely sensitive to the walking direction information conveyed by biological motion (Aen-Stockdale et al., 2008; Bertenthal and Pinto, 1994; Neri et al., 1998; Sweeny et al., 2012; Thompson et al., 2007; Thornton and Vuong, 2004; Thurman and Grossman, 2008), and this sensitivity develops very early in life (Kuhlmeier et al., 2010; Vallortigara and Regolin, 2006). Recent studies have emphasized the special role of the motion of the feet in the perception of biological motion walking direction (Chang and Troje, 2009; Gurnsey et al., 2010; Johnson, 2006; Saunders et al., 2009; Troje and Westhoff, 2006), and it has hence been suggested that there might exist an innate brain mechanism sensitive to the direction of the limbs of another creature in locomotion (i.e., a "life detector"). Although this notion is supported by several findings on the processing of local biological motion cues (Chang and Troje, 2009; Saunders et al., 2009; Troje and Westhoff, 2006; Wang and Jiang, 2012; Wang et al., 2010), there still lacks clear empirical evidence as to the functional importance of processing such biological cues in the brain. In what way does such intrinsic sensitivity to local biological motion signals affect human behaviors? The current study provides new insight into this issue and demonstrates that local biological motion cues not only can be processed independent of global configuration, but also can induce robust reflexive attentional orienting even without observers' subjective awareness of its biological nature. Crucially, such an effect disappeared when the motion acceleration was disrupted from the feet motion sequences, suggesting that the observed reflexive attentional orienting effect is triggered by the specific characteristics of local motion signals. A similar phenomenon has been observed with newly hatched domestic chicks that were reared in the dark. It was found that these visually inexperienced chicks tended to align their bodies in the apparent direction of point-light animations, a spontaneous response related to filial imprinting (Vallortigara and Regolin, 2006). Combined with previous evidence obtained from newborn infants (i.e., 2-day-old babies) whose visual experience was reduced to minimum (Bardi et al., 2011; Simion et al., 2008), the effect observed here might conceivably involve some kind of innate and possibly evolutionarily endowed brain mechanism that is sensitive to local biological motion signals and likely shared by humans and other animals.

The reflexive attentional effect was confirmed by electrophysiological data from the ERP experiment. The cue-triggered electrophysiological activities revealed an attentional lateralized effect (EDAN) in response to the upright but not inverted feet motion cues in the occipitoparietal region 100–160 ms after the stimulus onset. That is, the ERP responses were more negative when the feet motion cue pointed to the direction contralateral to the recorded hemisphere as compared to the ipsilateral direction. Importantly, this effect was still evident even when observers were unaware of the biological nature of the feet motion cues. This pattern of results is further confirmed by the difference waves and the source localization analysis, and the EDAN was primarily localized to the bilateral occipital and occipito-parietal brain areas. It should be noted that the EDAN effect induced by biological motion cues in the current study is earlier than the conventional temporal interval (200–300 ms) reported in literature (Harter et al., 1989; Hopf and Mangun, 2000; Jongen et al., 2006). This is because the EDAN effect reflects the encoding of the spatial information provided by the cues and the initialization of attentional orienting, and the processing of the biological motion cues is likely faster and more automatic compared with other nonsocial cues. Indeed, such EDAN effect has been observed in another social cue (i.e., eye gaze) within a similar time window of 100–170 ms (Brignani et al., 2009). Moreover, the EDAN effect has been found to occur earlier in an involuntary peripheral cueing paradigm than in a voluntary central cueing paradigm (Yamaguchi et al., 1994). Taken together, the attentional lateralized effect provides strong evidence that the upright but not inverted feet motion cues can trigger

robust involuntary attentional orienting independent of explicit recognition of the biological cues.

Recent studies have shown that other biological signals (e.g., eye gaze, head direction and body direction) can also elicit similar attentional orienting effects (Driver et al., 1999; Friesen and Kingstone, 1998; Langton and Bruce, 1999; Nummenmaa and Calder, 2009). It is possible that the reflexive attentional effect from the motion of the feet shares a common underlying mechanism with that triggered by other biological cues. Baron-Cohen (1995) proposed the existence of an innate module in support of an "eye-direction detector," identifying where eye-gaze is directed in the environment (Baron-Cohen, 1995; Batki et al., 2000). Other researchers have suggested a more general "direction of attention detector," which combines information from separate detectors analyzing body, head and gaze direction (Perrett and Emery, 1994; Perrett et al., 1992). Moreover, recent brain imaging studies have demonstrated that the neural circuitry subserving the reflexive orienting responses involves complex cortical connections between the temporal and parietal areas including the superior temporal sulcus (STS) (Kingstone et al., 2000, 2004), the neural site where biological motion walking direction is likely encoded (Jackson and Blake, 2010). The STS is heavily connected with the parietal cortex, which is shown to play a key role in overt and covert orienting of attention (Harries and Perrett, 1991; Rafal, 1996). Given all these functional and cortical overlaps of the different types of biological information processing and the reciprocal connections between the STS and the key regions involved in attentional orienting, it is possible that the reflexive attentional mechanism is supported by a specialized neural network that is intrinsically sensitive to various types of biological signals in the environment. This remains an important question worthy of further investigations.

## Conclusions

Humans are social creatures and have evolved mechanisms to efficiently process the biological cues that are meaningful and important for social interactions. From another individual's eye gaze, head orientation and body posture, we can readily detect his focus of attention and orient our own attention towards the same location. The current study provides new insight into this issue and demonstrates that local biological motion cues (in the absence of any global configuration) can induce a robust reflexive attentional orienting effect, which is independent of observers' explicit recognition of the cues. Together our findings provide strong evidence for the automatic processing of local biological motion cues, and highlight the functional importance of such processing in the brain.

## Acknowledgments

This research was supported by grants from the National Basic Research Program of China (No. 2011CB711000), the National Key Technology R&D Program of China (No. 2012BAI36B00), and the Strategic Priority Research Program of the Chinese Academy of Sciences (No. XDB02010003), the National Natural Science Foundation of China (No. 31070903 and No. 31200767) and the Scientific Foundation of Institute of Psychology, Chinese Academy of Sciences (No. Y1CX302005). We thank the anonymous reviewers for their constructive comments and suggestions.

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