



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

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## 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.

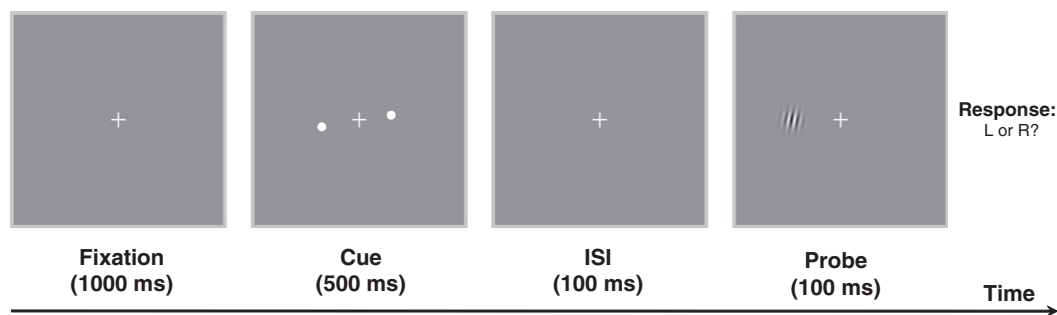
## Materials and methods

### 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.

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