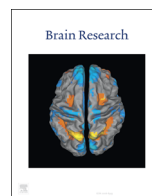




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Research Report

Neural activity associated with attention orienting triggered by implied action cues

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ABSTRACT

Spatial attention can be directed by the actions of others. We used ERPs method to investigate the neural underpinnings associated with attention orienting which is induced by implied body action. Participants performed a standard non-predictive cuing task, in which a directional implied action (throwing and running) or non-action (standing) cue was randomly presented and then followed by a target to the left or right of the central cue, despite cue direction. The cue-triggered ERPs results demonstrated that implied action cues, rather than the non-action cue, could shift the observers' spatial attention as demonstrated by the robust anterior directing attention negativity (ADAN) effects in throwing and running cues. Further, earlier N1 (100–170 ms) and P2 (170–260 ms) waveform differences occurred between implied action and non-action cues over posterior electrodes. The P2 component might reflect implied motion signal perception of implied action cues, and this implied motion perception might play an important role in facilitating the attentional shifts induced by implied action cues. Target-triggered ERPs data (mainly P3a component) indicated that implied action cues (throwing and running) speeded and enhanced the responses to valid targets compared to invalid targets. Furthermore, P3a might imply that implied action orienting may share similar mechanisms of action with voluntary attention, especially at the novel stimuli processing decision-level. These results further support previous behavioral findings that implied body actions direct spatial attention and extend our understanding about the nature of the attentional shifts that are elicited by implied action cues.

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1. Introduction

Spatial attention can be voluntarily or reflexively shifted by the actions of others (e.g., Langton and Bruce, 2000; Gervais et al., 2010; Shi et al., 2010). The actions of others are important indicators in daily life, because these actions convey crucial information that can provide a “window into the other's mind” (Loula et al., 2005).

Normally, local body actions/postures such as gaze, head turn, and hand pointing are important directional action components that are critical for attentional shift (Driver et al., 1999; Hietanen et al., 2008; Langton and Bruce, 2000). Recently, the application of a covert attention paradigm has revealed that spatial attention can also be directed by global body action (e.g., biological motion) (Bardi et al., 2015; Grubb et al., 2008; Shi et al., 2010; Wang et al., 2014; Zhao et al., 2014). Even when global body actions are

portrayed by static pictures only, i.e., “implied body action” – also known as body with implied motion (*implied motion* broadly refers to the dynamic information extracted from static stimuli (Kourtzi and Kanwisher, 2000), could shift the viewers' attention (Gervais et al., 2010; Reed et al., 2007; Shirai and Imura, 2014). Gervais et al. (2010) first investigated the viewer's attention directed by implied body action (static images of people throwing or running) and non-action cue (static images of the same person standing in a neutral pose with hands at sides and facing the lateral side). These authors found that only implied body action cues produced cuing effects, suggesting that implied action, not just directional information (e.g., trunk or head orientation), shifts attention. In addition, action cues produced faster responses than the non-action cue, implying that action may prime and facilitate responses. Previous psychophysical studies have provided a completely convergent measure of how the implied actions of others direct attention. However, until now, the neural underpinnings by which implied body action shifts spatial attention remains unclear. Furthermore, what might facilitate attentional shifts that are induced by implied body action cues with respect to non-action cues

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remains unknown.

The ERP method permits the analysis of spatiotemporal dynamics of neural activity, and these temporal dynamics provide sufficient insight into the sequential psychological processes that are involved in attentional shift (Luck et al., 2000). With regard to ERP components that reflect attentional shift, three lateralized components emerge with a relative positive or negative deflection in the hemisphere that is contralateral to the location indicated by the central cues. The first component is known as the early directing attentional negativity (EDAN), a posterior (occipital-parietal) negativity between 200–400 ms post-cue onset (e.g., Hopf and Mangun, 2000). The EDAN was initially interpreted as revealing an initial attentional orienting bias to the cued location (e.g., Nobre et al., 2000). However, if the central stimulus is not symmetrical with respect to the fixation, the EDAN may reflect the selection of task-relevant aspects of the cue stimuli but not the orienting of attention (van Velzen and Eimer, 2003). The second component is the anterior directing attention negativity (ADAN), an enhanced negativity in anterior scalp locations that are contralateral to the location indicated by the cue between approximately 300 and 500 ms post-cue onset (Eimer et al., 2002; Nobre et al., 2000). The ADAN has been conclusively shown to reflect the activity of executive control and the initiation of attentional shifts (Jongen et al., 2006, 2007), and is presumed to be generated in the fronto-parietal attentional control network (Coull et al., 2000; Green et al., 2008; Nobre et al., 2000). A late directing attention positivity (LDAP) occasionally follows the EDAN and ADAN after 500–700 ms cue onset at posterior electrodes and may reflect a modulation of target presentation anticipation (e.g., Nosek et al., 2005). These lateralized components are sensitive to attention shifts that are triggered by local body postures, such as local feet motion-elicited EDAN (Wang et al., 2014) or eye gaze-elicited ADAN (Holmes et al., 2010). No study has investigated attentional lateralized ERP responses to global implied action cued attentional shift. Thus, using the ERP method, the aim of the present study was to verify whether implied body action induces attentional shift, as reflected by attentional lateralized ERP components, as well as RT cuing effects.

Detecting visual motion is an important ability, and visual motion areas, such as the medial temporal/medial superior temporal (MT/MST or hMT+) complex, play a vital role in the analysis of the direction and motion of objects in the visual world (Bisley and Pasternak, 2000; Blake and Shiffrar, 2007). Visual motion areas can be activated not only by perceiving actual motion (e.g., motion of the human body, Wheaton et al., 2004), but also in the absence of any real visual motion experience; that is, by the processing of the implied motion of objects (David and Senior, 2000; Fawcett and Singh, 2006; Kourtzi and Kanwisher, 2000; Krekelberg et al., 2005; Senior et al., 2002). Neuroimaging studies in healthy participants have indicated that hMT+(MT/MST in human) was involved in the processing of implied motion of the human body. For example, when participants passively view photographs of human bodies with or without implied motion, either actual human figures (Kourtzi and Kanwisher, 2000), artistic depictions of humans (Kim and Blake, 2007) or line-drawn cartoons of humans (e.g., Hokusai Manga) (Osaka et al., 2010), stronger activation was found within hMT+ during the viewing of static photographs with implied motion than during the viewing of photographs without implied motion. ERPs and magnetoencephalography studies have also revealed that implied motion evokes a delayed response in an area overlapping the motion sensitive cortex (hMT+) (Fawcett and Singh, 2006; Lorteije et al., 2006; Proverbio et al., 2009). Lorteije et al. (2006) found that when participants passively viewed (500 ms individually) still photographs of a person with (running) or without (standing) implied motion, two enhanced ERP components occurred in response to

photographs with implied motion over posterior electrodes after stimulus onset, maximally at PO4 and POz. The earlier divergence between the two conditions was a negative component from 60 to 100 ms (similar to the N1 component), which is assumed to reflect low-level stimulus differences between the running and standing pictures, such as differences in luminosity. The later divergence was a positive component from 260–400 ms (similar to the P2 component), which is considered to reflect implied motion processing of the running photograph, because the second difference was much more pronounced, and the source location was in concordance with an extrastriate source, possibly hMT+. Therefore, following the line of these findings, when the central stimuli was implied action cues in a covert-orienting task, it is reasonable to speculate that implied motion processing at visual motion sensitivity areas might also be involved in implied action cues. Further, we are tempted to speculate that this implied motion processing in implied body action cues might help to facilitate attentional shifts that are induced by implied body action cues, contrast to the non-action cue (standing).

Even though the present investigation was mainly focused on the ERPs evoked by the directional implied action and non-action cue, we also analyzed ERPs components evoked by the cued (valid) and un-cued (invalid) targets to assess the consequences of the attentional shifts that are triggered by these cues on target processing. We focused on three components that reflect distinct stages of target processing, the perceptual sensory-level processing as indexed by the P1 (approximately 100 ms latency) and N1 (approximately 180 ms latency) components, and the higher-order semantic/decision-level processing as indexed by the P3 (approximately 300 ms latency) component. The P1 component is a positive deflection at posterior sites and reflects a mechanism that suppresses information from invalid (un-cued) locations (Hopfinger and West, 2006). The N1 component is a negative component at posterior sites and is considered to reflect benefit of paying attention to valid locations and the starting of discrimination processing (Eimer and Schröger, 1998; Mangun, 1995). A late P3 has been suggested to reflect preparation for responses or subjective expectancy violations of unexpected stimuli (Griffin et al., 2002; Digiacomo et al., 2008). Two subcomponents (P3a and P3b) are associated with different decision levels. A larger P3a in invalid target trials at anterior electrodes would reflect the processing of the invalidly cued target as a novel and unexpected stimulus, whereas the larger P3b at posterior electrodes would reflect the context updating of the working memory (Digiacomo et al., 2008; Polich, 2007). Recent ERP studies have provided strong evidence that the early sensory-evoked P1 and N1 components mainly reflect reflexive attention, whereas modulations of the P3 plays important roles in social orienting (e.g., gazing orienting) and voluntary orienting (Chanon and Hopfinger, 2011).

In summary, in the current study, we employed ERP measurement to measure neural activity that is evoked by two implied body action cues (throwing and running) and one non-action cue (standing). The participants performed a standard non-predictive cuing task in which a single left- or right- directional-implied action or non-action cue was randomly presented at each trial, followed by presentation of a target to the left or right of the cue, despite cue direction (Fig. 1 left). The stimuli used (Fig. 1 right) were identical to those used by Gervais et al. (2010). Regarding the ERP responses to directional implied body cues, only ADAN was of interest due to the use of asymmetrical stimuli and a relatively short cue-target interval (600 ms) in the current experiment. We assumed that if an implied action rather than body direction alone (standing without any other implied action) is necessary to shift an observer's attention, then a lateralized ADAN effect should be observed for implied action cues (throwing and running), but not for the non-action cue. More importantly, we focused on the

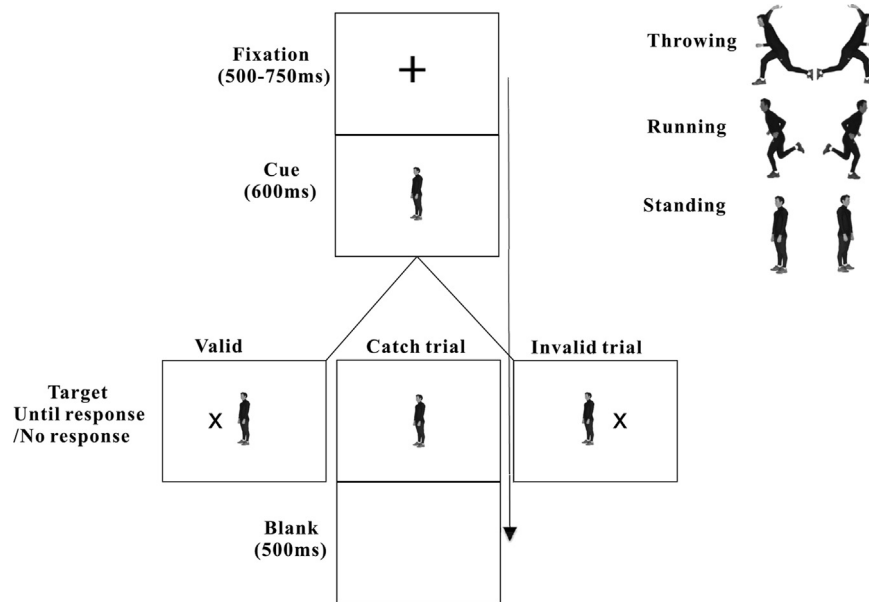


Fig. 1. Left: Schematic representation of the sequence of stimuli presented in each trial (valid, invalid and catch trials). Right: Illustration of the stimuli used as centrally presented cues: throwing, running, and standing which were directed either to the left or to the right.

potential differences between implied body action and non-action cue. Before lateralized attentional components (ADAN) emerged, we would expect to observe a positive difference between the implied action and non-action cue conditions at approximately 200 ms over the posterior electrodes. Finally, we expected that the early and late ERPs to target following the implied action cues would be different when preceded by valid and invalid cues.

2. Results

2.1. Behavioral data

The mean response time was calculated for each participant and each condition, excluding catch trials, anticipation errors (RTs less than 150 ms), and inattention errors (3SDs above the overall mean). On average, participants performed the task with high accuracy ($M=99.7\%$), confirming that the instructions were effective at inducing participants to pay attention to the cues, even though the participants were informed that the cues were not informative about the location of the upcoming target.

To determine whether body action cues shifted the participants' attention, a repeated 3 (cue type: throwing, running, standing) \times 2 (cue validity: invalid, valid) ANOVA was conducted, and the Greenhouse–Geisser correction was applied to compensate for possible effects of non-sphericity in the measurements. The statistical analysis yielded a significant cue type effect ($F(2, 46)=29.07, p<.001, \eta_p^2=.56$), in which the RTs for the throwing cue ($M=319$ ms) were significantly shorter than those for the running ($M=326$ ms) ($p<.001$) and standing ($M=330$ ms) cues ($p<.001$). RTs for the running cue was also significantly shorter than that for the standing cue ($p<.05$). There was also a significant cue validity effect ($F(1, 23)=5.44, p<.05, \eta_p^2=.19$), with faster responses in valid trials ($M=323$ ms) compared to invalid trials ($M=327$ ms). Cue type significantly interacted with cue validity ($F(2, 46)=3.92, p<.05, \eta_p^2=.15$), and a cue validity effect occurred only in the throwing cue condition ($M_{\text{valid}}=315$ ms vs. $M_{\text{invalid}}=323$ ms, $p<.05$). No cue validity effects were found under running and standing cue conditions.

2.2. Cue triggered ERP components

2.2.1. Cue induced lateralized shift-related ERP components

For the ADAN effect (averaging at F5/F6, F7/F8, FC5/FC6, and FT7/FT8), a 3-way repeated ANOVA with cue type (throwing vs. running vs. standing), cue direction (left vs. right) and hemisphere (left vs. right) was conducted. In the analyses, the effect of major interest was the cue type \times cue direction \times hemisphere interaction as previous study used (Eimer et al., 2002).

An apparent ADAN effect was revealed for the implied action cues (throwing and running) but not for the non-action cue (standing) based on the significant effect of the cue type \times cue direction \times hemisphere interaction ($F(2, 46)=7.19, p<.01, \eta_p^2=.24$) (Fig. 2, top). Further simple comparisons showed that for the throwing cues, the responses were less positive for the contralateral cues compared to ipsilateral cues in both the left and right hemispheres (all $ps<.05$). For the running cues, less positive activities were found for the contralateral cues than the ipsilateral cues in the two hemispheres, but only in the right hemisphere approaching significant ($p<.05$). For the standing cue, although the response in the left hemisphere was significantly different ($p<.05$), it was more positive for the contralateral cue than for the ipsilateral cue, contrary to the defined ADAN effect. There was no difference in the right hemisphere between the contralateral and ipsilateral cue ($p>.05$). In addition, when considering the ADAN effect over different hemispheres, it should be noted that for the throwing and running cues, these ADAN effects were more pronounced in the right hemisphere than in the left hemisphere (see Fig. 2, top). Topographic maps of left direction cue minus right direction cue further reflected the ADAN effect under throwing and running cue conditions (Fig. 2, bottom). These results suggest that the ADAN effect might be specifically unique to characteristic of implied body action rather than purely body direction.

2.2.2. Cue induced early ERP components

The earlier N1 and P2 components over the posterior electrodes reflected differences between the three centrally presented cues (Fig. 3, top). The peak amplitude and latency of N1 and P2 were determined in separate 3-way repeated ANOVA measures with cue type (throwing vs. running vs. standing), cue direction (left vs. right) and electrodes (measured at P1/P2, P3/P4, P5/P6, P7/

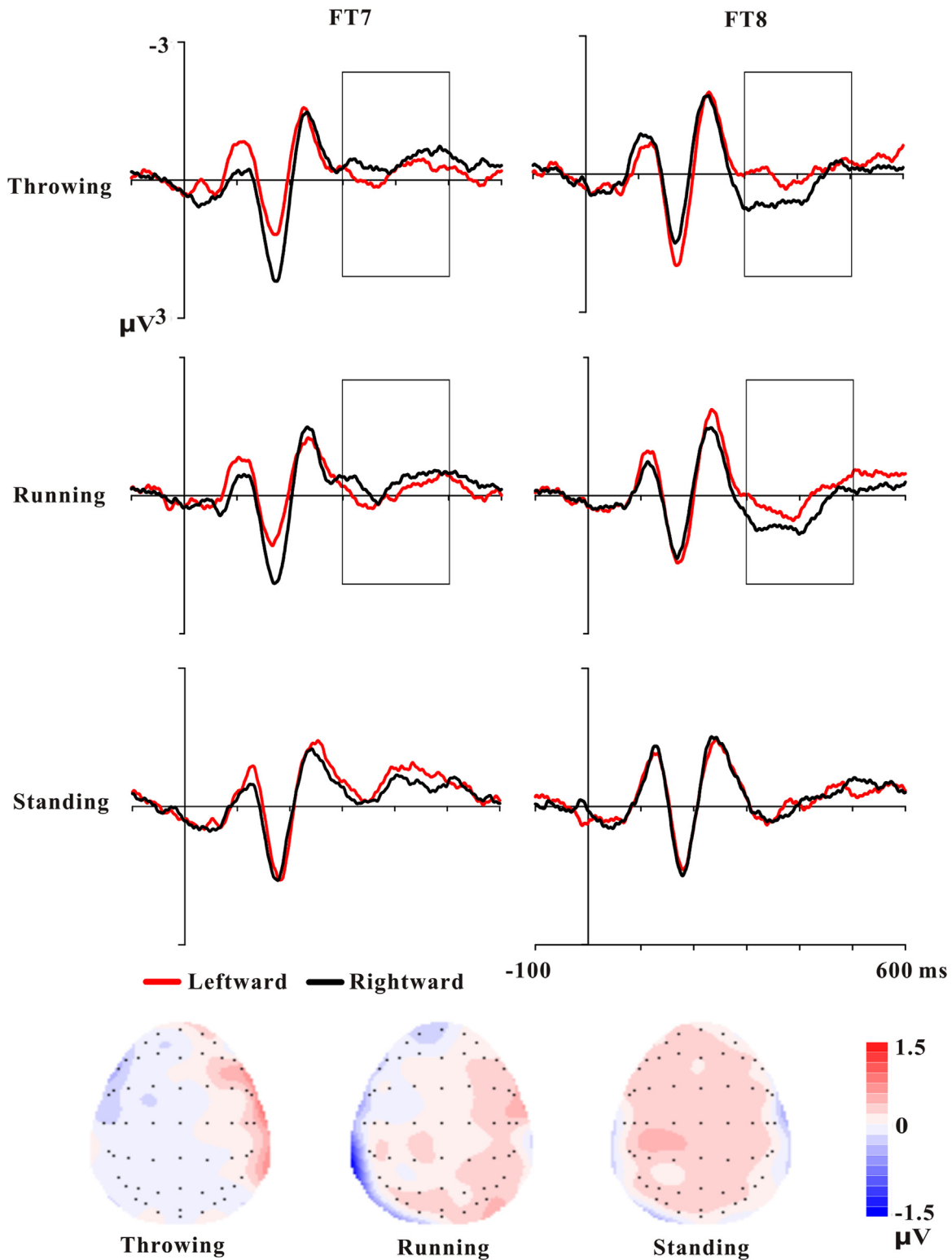


Fig. 2. Top: Average ERPs waveforms at the frontal FT7 and FT8 electrodes elicited by centrally presented cues (throwing, running and standing) pointing to the left (red line) and right (black line). The ADAN effect is indicated by the gray rectangle. Time = 0 ms indicates cue onset. Bottom: Topographic maps of the mean voltage amplitudes for the difference waveforms (right minus left) in the time windows of 300–500 ms after cue onset. Notice the frontal distribution of the three topographies. Enlarged negativity related to rightward attentional shift is shown in blue, whereas enlarged positivity to leftward attentional shift is shown in red.

P8, PO3/PO4, PO5/PO6, PO7/PO8, O1/O2, CB1/CB2, Pz, POz and Oz). In the analyses, the effects of major interest were cue type and the cue type \times electrodes interaction.

N1. The analysis of N1 (latency range of 100–170 ms) peak amplitude revealed a highly significant cue type effect ($F(2, 46) =$

38.13, $p < .001$, $\eta_p^2 = .62$), with significant peak amplitude differences across all three cues (throwing vs. standing, $p < .001$; running vs. standing, $p < .001$; throwing vs. running, $p < .01$). The throwing cue induced the largest N1 ($-3.42 \mu\text{V}$), followed by the running ($-2.97 \mu\text{V}$) and standing ($-2.14 \mu\text{V}$) cues. There was a

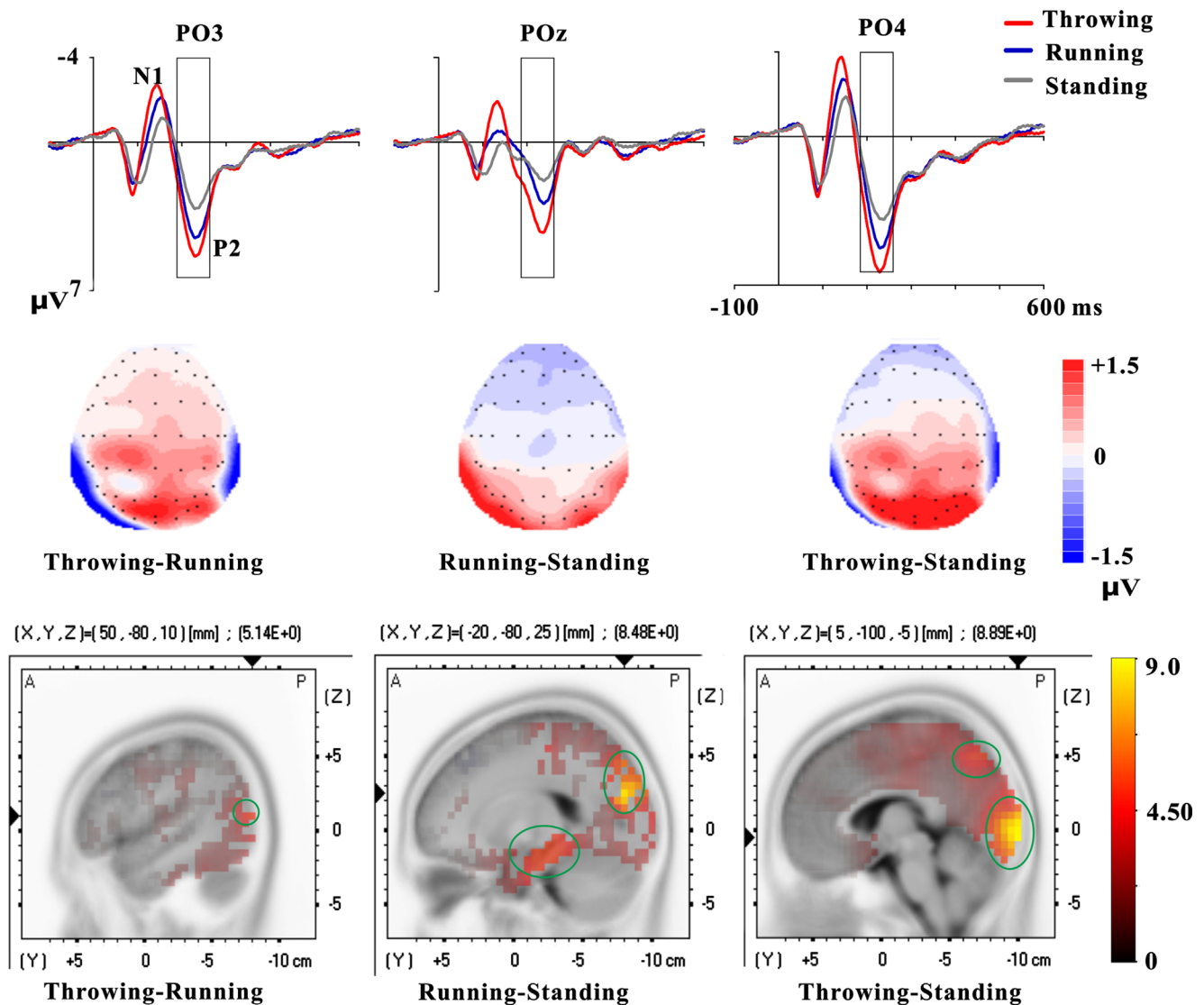


Fig. 3. Top: Average ERP waveforms elicited by throwing, running and standing cues at PO3, POz and PO4 electrodes after cue onset. The P2 component (170–260 ms) indicated in the gray rectangles was more pronounced. The N1 component should also be noted. Time=0 ms indicates cue onset. Middle: Topographic maps of the mean voltage amplitudes for the differences waveforms (throwing minus running, running minus standing and throwing minus standing) in the time windows of 170–260 ms. Notice the posterior distribution of P2. Bottom: sLORETA source localization maps representing current density for the differences 'throwing minus running, running minus standing and throwing minus standing' for the P2 component. These maps represent t -statistics of log-transformed data computed on P2. Red to yellow colors indicate areas of stronger activations among the three cues and the green circles signs the significant areas ($p < .05$).

significant cue type by electrode interaction ($F(40, 920)=3.38$, $p < .001$, $\eta_p^2=.13$). Further simple comparisons indicated that the voltage differences between the throwing and standing cues were significant at all posterior electrodes (all $ps < .05$) and was most pronounced over PO6 ($p < .001$); when comparing the running and standing cues, the voltage differences were significant at all posterior electrodes (all $ps < .05$) except at P4 ($p=.054$) and was largest at PO7 ($p < .001$). In addition, the difference between the throwing and running cues was greatest at PO4 ($p < .001$) and were significant at all electrodes except PO7, POz and CB1 ($ps > .05$). For N1 latency, there was also a significant cue type effect ($F(2, 46)=13.14$, $p < .001$, $\eta_p^2=.36$), because the peak of N1 appeared significantly earlier for the throwing cue (145 ms) than for the running (150 ms, $p < .01$) or standing cues (156 ms, $p < .001$). No cue type by electrode interaction effect was found.

P2. Peak amplitude analysis of P2 (latency range of 170–260 ms) revealed a highly significant cue type effect ($F(2, 46)=55.76$, $p < .001$, $\eta_p^2=.71$), because the throwing cue induced the largest P2 (5.04 μV), followed by the running (4.34 μV) and

standing (3.38 μV) cues (throwing vs. standing, $p < .001$; running vs. standing, $p < .001$; throwing vs. running, $p < .01$). A significant cue type by electrode interaction was also observed, $F(40, 920)=6.34$, $p < .001$, $\eta_p^2=.22$. Further simple comparisons revealed that the voltage differences between throwing and standing cues were all significant at the posterior electrodes (all $ps < .01$) and was most significant at PO4 ($p < .001$). When running and standing cues was compared, the voltage differences were also significant at all electrodes and was largest at PO5 ($p < .001$). In addition, the differences between throwing and running cues were significant nearly all all electrodes (all $ps < .05$) except the lateralized parietal electrodes (P5/P6, P7/P8), and was pronounced at the POz ($p < .001$). Non-significant cue type effect ($M_{\text{throwing}}=224$ ms, $M_{\text{running}}=228$ ms, $M_{\text{standing}}=228$ ms) and cue type by electrode interaction effects were observed for P2 latency (all $ps > .20$). The topographic distributions for the grand average difference 'throwing cue minus running cue, running cue minus standing cue, and throwing cue minus standing cue' around P2 (170–260 ms) further illustrated the differences between these three

cues (see Fig. 3, middle). The P2 positive enhancement was characterized by a more posterior scalp distribution.

To gain some insight into the source of P2 waveform differences, sLORETA statistical nonparametric maps were used to compare the current density for the grand average difference 'throwing cue minus running cue, running cue minus standing cue, and throwing cue minus standing cue', as seen in the bottom of Fig. 3. The results correspond to maps of the t -statistics of log-transformed data for each voxel, for corrected $p < .05$. The t -values threshold for the one tailed test was 4.59, 4.57, 4.50 for 'throwing minus running cues, running minus standing cues, and throwing minus standing cues', separately. We observed that the sources of the P2 waveform differences were mainly localized at the occipital, temporal and parietal lobes. Specifically, the significantly stronger activations for throwing cue compared to running cue were mainly localized at the medial temporal cortex (MT), and medial occipital cortex; the significantly stronger activations for running cue compared to standing cue were mainly localized at structures including medial temporal cortex (MT), superior temporal cortex, superior/inferior parietal lobule, cuneus, precuneus, angular gyrus, parahippocampal gyrus and fusiform gyrus; and the significantly stronger activations for throwing cue compared to standing cue were also mainly localized at structures including superior temporal cortex, cuneus, precuneus, lingual gyrus, medial occipital cortex, postcentral gyrus and medial temporal cortex (MT). For a detailed list of the regions involved, see Appendix Table 1.

2.3. Target triggered ERP components

2.3.1. The early P1 and N1 components

The amplitudes and latencies for target-locked P1 and N1 components were inspected at the posterior parietal (P5/P6, P7/P8) and occipital-parietal (PO5/PO6, PO7/PO8) electrodes. As P1 and N1 are maximal on the contralateral hemisphere to stimulus presentation, and to avoid unnecessarily complicated results, only electrodes that were contralateral to the target side were analyzed, as described previously (e.g., Lassalle and Itier, 2013). For the P1 and N1 peak amplitude and latency, 2-way repeated ANOVAs with cue type (throwing vs. running vs. standing) and cue validity (invalid vs. valid) were separately conducted.

Separately repeated ANOVA analysis of P1 peak amplitude and latency revealed neither cue type and validity effects nor an interaction effect (all $ps > .10$). For N1 amplitude analysis, no cue type, cue validity and interaction effects were found. The analysis

of N1 latency revealed a significant cue type effect ($F(2, 46) = 6.34$, $p < .01$, $\eta_p^2 = .21$), and the latency in implied action cues ($M_{\text{throwing}} = 164$ ms, $M_{\text{running}} = 162$ ms) was longer than that in the non-action cue ($M_{\text{standing}} = 161$ ms) ($ps < .05$).

2.3.2. The late P3a and P3b components

For the target triggered P3a and P3b components, separately repeated ANOVAs with cue type (throwing vs. running vs. standing) and cue validity (invalid vs. valid) were conducted. Target-triggered average P3a and P3b waveforms at the FCz, Cz and POz electrodes and topographical maps of difference wave invalid trials versus valid trials are shown in Fig. 4.

For the P3a component (200–280 ms), the ANOVA analysis of the P3a mean amplitude (averaged over Fz, F1/F2, F3/F4, FCz, FC1/FC2, FC3/FC4, Cz, C1/C2, and C3/C4 electrodes) revealed a significant cue validity effect, $F(1, 23) = 4.99$, $p < .05$, $\eta_p^2 = .18$, with a higher voltage triggered by invalid targets than valid targets ($M_{\text{invalid}} = 3.06$ μV vs. $M_{\text{valid}} = 2.71$ μV). There was a trend toward an interaction effect between cue type and cue validity ($F(2, 46) = 2.63$, $p = .08$, $\eta_p^2 = .10$). Further comparisons showed that for implied action cues (throwing and running), the voltages in invalid trials were all significantly more positive than those in valid trials ($ps < .05$); no such larger voltages in invalid trials were observed for non-action (standing) cue. No cue type main effect was found, $F(2, 46) = .70$, $p = .51$.

For the P3b component (280–380 ms), the ANOVA analysis of the P3b mean amplitude (averaged over Pz, P1/P2, P3/P4, POz, PO3/PO4, PO5/PO6 electrodes) showed neither a cue type main effect nor a cue type and validity interaction effect ($ps > .20$). A significant cue validity effect was found, $F(1, 23) = 20.41$, $p < .001$, $\eta_p^2 = .48$, with higher voltage value triggered by invalid targets than by in valid targets ($M_{\text{invalid}} = 3.00$ μV vs. $M_{\text{valid}} = 2.57$ μV).

2.3.3. Correlation between behavioral measures and P3a and P3b amplitudes

To better clarify the functional meaning of P3a and P3b in response to targets, we finally carried out a correlation analysis between behavioral and P3a/P3b data. We subtracted RTs, P3a and P3b waveforms for invalid trials from those for valid trials. More positive values of these indices indicate a stronger cuing effect in RTs, P3a and P3b amplitudes. A significant positive correlation between behavioral index and the corresponding P3a/P3b index would indicate that participants with higher behavioral-implied action-driven orienting show larger amplitudes in the invalid trials

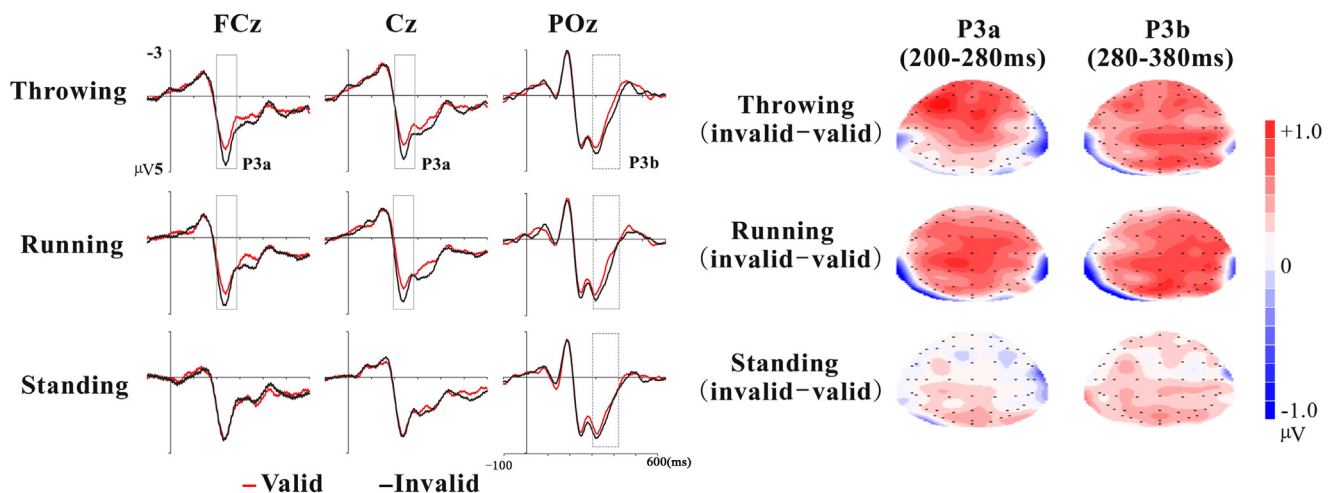


Fig. 4. Left: Average ERPs waveforms elicited by target stimuli at FCz, Cz and POz electrodes for valid (red) and invalid (black) trials. The P3a (200–280 ms) and P3b (280–380 ms) components are indicated using the solid and dotted gray rectangles respectively. Time = 0 ms indicates target onset. Right: Topographic maps of the mean voltage amplitudes for the difference waveforms (invalid minus valid) in the time windows of 200–280 ms and 280–380 ms after target onset.

compared than in the valid trials.

The correlation analysis between behavioral index and P3a index revealed a significant positive correlation only in the throwing cue condition ($\rho=0.55$, $p<.01$, one tailed). In the running cue condition, although the correlation did not reach significance, it was positively correlated ($\rho=.28$, $p=.09$, one tailed). In the standing cue condition, no correlation was observed ($\rho=.098$, $p=.32$, one tailed) between behavioral index and P3a index. The correlation analysis between behavioral index and P3b index, it should be noted that there was a significant positive correlation under the standing cue condition ($\rho=.53$, $p<.01$, one tailed) and a marginally significant correlation under the throwing cue condition ($\rho=.33$, $p=.057$, one tailed). In the running cue condition, non-significant positive correlation was observed ($\rho=.10$, $p=.32$, one tailed).

3. Discussion

In current study, we measured cue-triggered and target-triggered ERP responses and reaction times while participants performed a standard non-predictive spatial cuing task with centrally presented directional implied action (throwing and running) and non-action (standing) cues, followed by laterally presented targets. The cue-triggered ERPs data provided evidences that implied body action rather than non-action could trigger robust attentional shift despite explicit non-informative instruction, as demonstrated by the robust anterior directing attention negativity (ADAN) effects in throwing and running cues. Furthermore, N1 (100–170 ms) and P2 (170–260 ms) waveform differences existed between implied action and non-action cue over posterior electrodes. The P2 component might reflect the implied motion signal perception of implied action cues, and this implied motion perception might play an important role in facilitating the attentional shifts that are induced by implied body action cues. The target triggered ERPs data (mainly P3a component) showed that implied action cues (throwing and running) speeded and enhanced the responses to valid targets compared with invalid targets, generally consistent with previous behavioral study (Gervais et al., 2010). These results provide further support for previous behavioral findings that implied body actions direct spatial attention and extend our understanding about the nature of the attentional shifts that are elicited by implied action cues.

3.1. ADAN reflects attentional shift

Earlier studies have shown that centrally presented attentional-directing social and non-social cues (either asymmetrical or symmetrical) elicit an anterior directing attention negative (ADAN) component, which is observed in anterior frontal electrodes between 300 and 500 ms after cue onset. Compatible with previous findings and our hypothesis, we observed that clear and robust ADAN effects were induced by the throwing and running cues (defined as implied action cues); these effects occurred in the lateral frontal electrodes between 300–500 ms after cue onset. However, no ADAN effect was evident in response to the non-action cue (standing). These patterns were further confirmed by the topographic map of the difference waveforms (right minus left).

In the current study, the right hemisphere attentional orienting bias for implied action cues was reflected by larger ADAN effects in the right hemisphere, which was not initially within the scope of the present experiment (see Fig. 2). Imaging normal participants has revealed a greater role of the right hemisphere in the distribution of attention within the left and right visual hemifields (Corbetta et al., 1993; Shulman et al., 2010). Birmingham and Kingstone (2009) once suggested that the right hemisphere is

activated more intensively by biologically relevant stimuli (e.g., faces and gaze) than by biologically irrelevant stimuli (e.g., arrow). Thus, the results of the ADAN effect in the present experiment might suggest that orienting to implied action cues mainly depends on the right lateralized network.

Previous studies of attention have used non-predictive, but task-relevant, arrow cues to demonstrate that the ADAN component is related to voluntary shifts of visuo-spatial attention (Hopf and Mangun, 2000). Hietanen et al. (2008) have inclined to suggest that voluntary attention rather than reflexive attention results in the ADAN effect, because arrow-triggered shifts of attention activate the voluntary attention shifting mechanisms more than eye gaze-triggered shifts of attention do. Eye gaze-triggered shifts of attention have been considered more reflexive (e.g., Driver et al., 1999). Moreover, some imaging studies found that ADAN was mainly generated in brain areas within the dorsal fronto-parietal attentional network (e.g., Praamstra et al., 2005; Seiss et al., 2007). This dorsal network has mainly been implicated in voluntary controlled attention (Geng and Mangun, 2009). However, Holmes et al. (2010) observed ADAN effects in response to both arrow- and gaze-triggered shifts of attention. Therefore, in the current study, the finding of ADAN effects in response to implied action cues (throwing and running cues) might suggest neurocognitive mechanisms of implied action orienting, possibly mediated by the dorsal fronto-parietal network. Especially, it might be mainly involved in the right dorsal fronto-parietal network. However, based on previous studies and the current results, any suggestion as to whether implied action cues shift observer' attention voluntarily or reflexively should be viewed with caution, and future studies are warranted to investigate this uncertain issue.

3.2. ERPs to implied action cues

The second aim of the present ERP experiment was to measure waveform differences and source localization between implied action and non-action cue, to determine whether implied motion perception contributes to implied action cues in directing attention shifts. We initially observed earlier significant differences in amplitudes (N1) at approximately 100–170 ms after cue onset between throwing, running and standing cues. Previous neuropsychological studies, including a study by Lorteije et al. (2006), have indicated that the timing of the N1 deviation coincides with its spatial frequency and orientation (Arakawa et al., 2000), size and eccentricity (Busch et al., 2004). Here, we also propose that the low-level stimulus differences are responsible for the N1 differences among these three cues, such as the considerable differences in body size and eccentricity among the three cues.

Regarding the the ERP waveform differences among the three cues (throwing minus running, running minus standing, and throwing minus standing), attention should be directed to a more pronounced late P2 (170–260 ms) component over posterior occipital-parietal electrodes. We observed that the amplitude voltage of P2 increased with the cue motion degree heighten (throwing > running > standing). As proposed by Lorteije et al. (2006), the late P2 differences over posterior electrodes in response to implied action versus non-action cue might be caused by the presence versus absence of implied motion in the photographs. Importantly, in the current study, the sLORETA source localization analysis revealed that the P2 differences among the three cues appeared to arise from areas in the occipital and temporal regions, including at the medial temporal(MT) cortex (see Appendix Table 1). This result is in accordance with previous neurophysiological and imaging studies that implied motion evokes a response in an area that overlaps with motion sensitive cortex (hMT+) (David and Senior, 2000; Fawcett and Singh, 2006; Kourtzi and Kanwisher, 2000; Krekelberg et al., 2005; Lorteije

et al., 2006; Proverbio et al., 2009; Senior et al., 2002).

However, beyond our hypothesis, the source localization for implied action vs. no-action extended beyond hMT+ to several contiguous regions including the superior temporal cortex, superior/inferior parietal lobule, medial occipital cortex, cuneus, precuneus, angular gyrus, parahippocampal gyrus, fusiform gyrus and lingual gyrus, detailed in Appendix Table 1. These involved regions are consistent with some previous studies, which proposed that other areas extending posterior, superior and inferior to MT/MST are also involved in motion analysis (e.g., De Jong et al., 1994). For example, Kourtzi and Kanwisher (2000) reported a difference in the BOLD response between implied and non-implied motion conditions in temporal regions, the additional implied motion activation in the superior temporal sulcus (STS). Perrett and colleagues found that the superior temporal cortex played a role in implied articulated action rather than static non-articulated action per se (Jellema and Perrett, 2003, 2006; Puce and Perrett, 2003). The STS is considered to integrate form and motion signals (Oram and Perrett, 1996). The parahippocampal gyrus and fusiform gyrus are also parts of the temporal lobe. In addition, the parietal cortex is part of the dorsal action stream, and Hermsdörfer et al. (2001) found that still hand gestures (with implied action) can activate the inferior parietal cortex (BA40), and that finger gestures induced the right intraparietal sulcus and medial visual association areas (BA18/19). Moreover, one study found that the observation of static postures suggesting a transition to action selectively activates the lateral occipital temporal junction (BA 19/37) (Peigneux et al., 2000). In our study, the throwing and running cues used required that body parts (e.g., a limb, a hand, a finger or the feet) move with respect to the remainder of the body (trunk) which remained static; conversely, non-action cue is required that the equivalent body parts did not move with respect to each other. We cannot rule out the possibility that differences in body part, including form and local motion differences, contaminate the P2 differences due to the poor spatial resolution of the ERP method. Thus, in light of the present results and previous implied motion findings, it is likely that the implied motion perception at the temporal/occipital visual motion sensitivity areas represents a critical processing difference between implied action and non-action cue.

Some researchers have proposed that the extrapolation of dynamic information from static human action pictures engages not only visual motion areas such as the MT/MST cortex, but also a higher-order frontal-parietal network, which is termed the motor mirror system. For example, one transcranial magnetic stimulation (TMS) study observed that the human motor mirror system facilitation that is triggered by implied motion (using a hand picture) occurred when participants observed ongoing but not yet completed hand actions (Urgesi et al., 2006). Proverbio et al. (2009) also found that observing effortful implied action (260 pictures of human actions differing in their degrees of dynamism and muscular exertion) enhanced the activity of movement-related brain areas (mainly mirror neural areas). Regarding spatial attention directed by implied body action, Gervais et al. (2010) speculated that the internal motor simulation of implied body action not only helped the viewer to predict the outcome of that action, but also guided the viewer's spatial attention to action-relevant spatial locations. However, in the current study, no evidence was found to support an internal motor simulation process in the frontal-parietal network that are involved in implied body action cues. Instead, before the attentional lateralized ERP components (ADAN, 300–500 ms) emerged, a more pronounced P2 difference over posterior electrodes (measured at the temporal and occipital-parietal electrodes) occurred between the implied action cues and the non-action cue. The results obtained here might shed light on the implied motion perception that is derived from the temporal/

occipital motion-sensitive areas and that might help to guide the implied body action cues directing spatial attention. Of course, we do not unequivocally exclude the role of an internal motor simulation in implied body action due to the simplicity of the stimuli used in the current experiment. Future investigations are warranted to verify the involvement of internal motor simulation in implied body action that directs spatial attention.

3.3. Behavioral and electrophysiological responses to targets

The behavior results revealed that only the throwing cue induced attentional cuing effects, in either the left or right visual field. However, surprisingly, no quantitative cuing effect was induced by running cues. Wang et al. (2014) recently showed that local biological feet motion could trigger reflexive attentional orienting. Thus, one possible reason for the lack of a cuing effect could be that the local feet opposite motion of the running cue might attenuate or disturb the shift of attention (Fig. 1). Additionally, Bonato et al. (2009) showed that cuing effects with non-predictive arrows were more consistent at shorter SOAs (200–350 ms) than at longer SOAs (550–800 ms). It is therefore possible that by the time the target appeared, the cuing effect induced by the running cue had almost completely decayed. This interpretation might be validated by our ERPs finding that the running cue also elicited attentional-related ADAN component after the cue onset 300–500 ms. Regarding the non-action cue, no cuing effect was observed when the target appeared in both the left and right visual fields. These results are generally in line with a previous study (Gervais et al., 2010), except for the result relating to the running cue, which to some extent confirmed that implied body action appears to shift attention.

Regarding the target-triggered ERPs components, in general, the present results were consistent with recent studies investigating the ERPs to targets preceded by valid and invalid gaze cues (Chanon and Hopfinger, 2011). At an early stage of sensory processing, in each cue type condition, no differences were found between valid and invalid targets, neither in P1 nor in N1 component. This result might suggest that early sensory processing plays little or no role in the behavioral consequences of implied action orienting.

At the late stage (P3a and P3b), implied action cues orienting were differed from non-action cue shifting. Specifically, implied action cues (throwing and running) produced a more pronounced larger P3a amplitude for invalid targets than for valid targets, but no such difference was found when the cue was a no-action (standing). The larger P3a amplitude for invalid targets represents the processing of invalidly cued targets as novel and unexpected stimuli, because the subjective expectance of the target position, which is induced by the central cue, is validated in valid trials and invalidated in invalid trials (as reviewed by Gómez and Flores, 2011). Thus, in current data, a larger P3a under the implied action cues conditions might indicate that the invalidly cued target is processed as a novel and conflicting stimulus and is potentially more important. Further, implied action cue, rather than non-action cue, produces a bias in subjective expectancies for valid targets. The correlation analysis revealed that P3a effects under implied action cue conditions were significantly correlated with the behavior-implied action cuing effects (response time), especially for the throwing cues with a high degree of motion. This pattern further supports the argument that P3a is related to attention shifts during implied action cuing. Thus, these later decision-level effects, which are observed as the P3a modulation, may play a critical role in the behavioral consequences of implied action orienting.

Regarding P3b, we found higher P3b amplitude in invalid trials than in valid trials under both implied action cue and non-action

cue conditions. A higher value of P3b in invalid trials represents a context-updating operation and subsequent memory storage (Polich, 2007). One possible reason for the larger P3b in invalid trials than valid trials under all three cue conditions, is that the uneliminated directional information (trunk orientation) might have triggered attentional shifts that were insensitive to response time but sensitive to ERPs component. Some researchers have suggested that trunk orientation influences sensorimotor planning for many common actions and should therefore affect the distribution of spatial attention (Prinz, 1997). Our findings of the later significant positive correlation between non-action behavioral consequence and P3b might further prove the above point. However, the ability of trunk orientation alone to trigger a bias for spatial attention remains controversial (Grubb and Reed, 2002; Grubb et al., 2008). Some studies have observed that trunk orientation alone (standing cue) is not sufficient to influence a viewer's spatial attention, and that other critical factors that necessitate a trunk orientation bias in everyday life, such as motion activation (throwing, running or walking) or motor load, are needed (Grubb et al., 2008; Westwood et al., 2013). Thus, given the different results and the less reliable results obtained in the current study, more investigations are required to examine the cognitive meaning of P3b component in the attention orienting task.

It is interesting to note that implied action cues were able to produce clear behavioral effects without any enhancement of early perceptual processing. Recent results have provided strong evidence that the modulation of early sensory-evoked components (e.g. P1) is strongly linked to a reflexive shift of attention, whereas social gaze orienting and voluntary attention produces a similar P3 component, at the decision-level processing (Störmer et al., 2009; Chanon and Hopfinger, 2011). Moreover, small or nonexistent effects of voluntary attention during early visual processing are not uncommon when using a localization task (Prime and Ward, 2006). The present results lend further support to the above argument, and suggested that implied action orienting may share similar mechanisms of action with voluntary attention or social orienting, especially at the level of novel stimuli processing (as indexed by the P3a effect).

4. Methods

4.1. Participants

Twenty-eight healthy college students were paid to participate in the experiment. All participants reported normal or corrected normal vision. The experiment was conducted with the informed written consent of each participant and was approved by the Institutional Review Board of the Institute of Psychology at the Chinese Academy of Science. Data from four participants were discarded because the EEG segments comprised less than 30%. The data of the remaining twenty-four participants (13 females, $M=22.6$ years, $SD=1.77$, age range 18–25 years) were used.

4.2. Experimental design and procedure

The stimuli used in current experiment were identical to those used in the experiment 1 of Gervais et al. (2010). The Implied body cues were static, black images of a male actor poised in action with high-implied motion (throwing), mid-implied motion (running) or without implied motion (standing) (Fig. 1, right). The visual angles of the three cues were 5.7–6.0° high and 4.4–4.7° wide. The target “X” (1.3° high and 0.8° wide) appeared 6.0° from the body pose's center of gravity.

Participants sat approximately 65 cm from a computer screen (a 17-inch cathode-ray tube (CRT) monitor: 39.1 cm × 29.3 cm,

1024 × 768 pixels, 100 Hz) and were asked to keep their heads on a head-rest and their eyes focused on the center of the screen during the test session except for rest periods (at least 1 second) between blocks. The experimental stimuli were presented using E-prime 2.0 in a black against a white background.

For the non-predictive covert attention task, each trial began with a central fixation cross (angle 0.8°) for a varied period of 500–750 ms, which was then followed by a directional cue (left or right) at the center of the screen that lasted for 600 ms. A target (“X”) then appeared either to the right or left of the cue; the targets remained until either the participants responded accurately and quickly by pressing the SRBOX buttons with their left and right index fingers (except for catch trials, for which no responses were required) or after 2000 ms had elapsed. After 6 practice trials, the participants completed six blocks of experimental trials (540 trials; 80 catch trials). Each block contained randomly presented equiprobable combinations of cue type, cue direction, and cue validity (invalid or valid). Prior to the task, all participants were clearly instructed that the target locations were not related to the cues' direction.

4.3. ERP recordings and data analysis

Continuous EEG was recorded using 64 electrodes mounted in an elastic cap (Electro-Cap International, Inc.) that was connected to the left mastoid. The data were removed offline and then referenced to the average of the left and right mastoids (M1 and M2). The vertical (VEOG) and horizontal (HEOG) electro-oculograms were recorded with bipolar channels from sites above and below the midpoint of the left eye and next to the outer canthi of each eye. Mild skin abrasion was performed to reduce electrode impedance below 5 kΩ. The EEG was band-pass filtered from 0.05 to 100 Hz, amplified with a gain of 500, and stored on a computer disk at a sample rate of 1000 Hz (Syn-Amps 4.5, Neuroscan, Inc.).

The continuous EEG signal was corrected for blink artifacts using an eye-movement reduction algorithm (Semlitsch et al., 1986) and was segmented into two 700-ms epochs: one starting 100 ms prior to presentation of the cue stimulus and another starting 100ms prior to the target. The cue and target-triggered epochs were digitally filtered (low pass=30 Hz, high pass=1 Hz) and were baseline-corrected against the mean voltage during the 100-ms pre-stimulus period. The trials were automatically eliminated if the voltage in the epoch exceeded $\pm 50 \mu\text{V}$. For the cue-triggered epochs, we first focused on lateralized attentional shift-related anterior directing attention negativity (ADAN) over anterior electrodes. For the ADAN, mean amplitude activity was measured at four pairs of lateralized anterior electrodes (F5/F6, F7/F8, FC5/FC6, and FT7/FT8) for a time interval of 300–500 ms. For the cue-triggered epochs, we also measured the two earlier ERP components (peak amplitude and latency) that were elicited by the three centrally presented cues, N1 (100–170 ms) and P2 (170–260 ms), which were identified over the posterior electrodes (P1/P2, P3/P4, P5/P6, P7/P8, PO3/PO4, PO5/PO6, PO7/PO8, O1/O2, CB1/CB2, Pz, POz and Oz). For the target-triggered epochs, three components of target processing were focused on. The peak amplitude and latency of the P1 and N1 components were inspected from posterior parietal (P5/P6, P7/P8) and occipital-parietal (PO5/PO6, PO7/PO8) electrodes. For the later P3 component, mean amplitude activities of a P3a component (200–280ms) over central anterior electrodes (Fz, F1/F2, F3/F4, FcZ, FC1/FC2, FC3/FC4, Cz, C1/C2, C3/C4) and a P3b component (280–380 ms) over central posterior electrodes (Pz, P1/P2, P3/P4, POz, PO3/PO4, PO5/PO6) were measured. For each ERP component, a separate statistical analysis was conducted, for detail see Section 2.

The sLORETA software was used to perform the voxel-by-voxel within-group comparisons of the P2 current density distribution.

Specifically, to identify possible differences, the sLORETA-built-in voxel-wise randomization tests (5000 permutations), which are based on statistical nonparametric mapping corrected for multiple comparisons were performed for each cue type within the groups. The results correspond to maps of *t*-statistics of log-transformed data for each voxel, for corrected $p < .05$. Anatomical labels are reported using an appropriate correction from MNI to Talairach space.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.brainres.2016.04.018>.

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