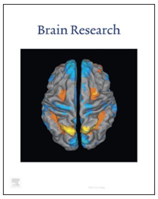
Brain Research 1642 (2016) 353–363

Contents lists available at ScienceDirect

Brain Research

journal homepage: www.elsevier.com/locate/brainres



Research Report

Neural activity associated with attention orienting triggered by implied action cues

Kaiyun Li [a,b], Yong-Jin Liu [c], Fangbing Qu [a,b], Xiaolan Fu [a,*]

[a] State Key Laboratory of Brain and Cognitive Science, Institute of Psychology, Chinese Academy of Sciences, Beijing 100101, China
[b] University of Chinese Academy of Sciences, Beijing 100049, China
[c] Tsinghua National Laboratory for Information Science and Technology, Department of Computer Science and Technology, Tsinghua University, Beijing 100084, China

ARTICLE INFO

Article history:
Received 15 September 2015
Received in revised form
31 March 2016
Accepted 7 April 2016
Available online 8 April 2016

Keywords:
Implied action
Attentional shift
Implied motion perception
ADAN
P2
P3a

ABSTRACT

Spatial attention can be directed by the actions of others. We used ERPs method to investigate the neural underpins 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.

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 underpins 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

---

* Corresponding author.
E-mail address: fuxl@psych.ac.cn (X. Fu).

http://dx.doi.org/10.1016/j.brainres.2016.04.018
0006-8993/© 2016 Elsevier B.V. All rights reserved.

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 humans 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 ERPs 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 defection 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