

Contents lists available at [ScienceDirect](https://www.sciencedirect.com)

Consciousness and Cognition

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

Feeling but not seeing the hand: Occluded hand position reduces the hand proximity effect in ERPs

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ARTICLE INFO

Keywords:

Multisensory integration
 Event related potentials
 Electrophysiology
 Vision
 Proprioception
 Hand proximity effect

ABSTRACT

The hand proximity effect (nearby hands influence visual processing) reflects the integration of vision and proprioception for upcoming action; it is reduced when hand position is occluded. In an ERP study, we investigate whether hand proximity, without vision of the hand, accentuates the processing of stimuli requiring actions (targets) early (N1) and later (P3) in processing. In a go/no-go paradigm, participants viewed stimuli between two panels with hands placed near or far from stimuli. Occlusion of the hand eliminated near-hand target vs. non-target differentiation of the N1; amplification of near-hand target amplitudes emerged at the P3. Visual hand location appears necessary to draw visual attention to intended-action objects to integrate body and visual information early in processing. The integration of visual stimulus information and hand position from proprioception appears later in processing, indicating greater reliance on cognitive systems for discriminating the task-relevance of a stimulus.

1. Introduction

To understand everyday actions, we need to understand how the sensorimotor system supports actions (Bridgeman, Perry, & Anand, 1997). Perception is modulated by the possibility of action and one's intention to act. In other words, perception changes when vision's job changes from describing the world to acting on it (Bridgeman, 2005). From our experiences, we form expectations about how visual inputs should be coordinated and integrated with information from the body to help us navigate the world. Integrating information from our different senses helps to distribute attention in nearby, peripersonal space (Previc, 1998) and attention selects that information most salient to the goals of our intended actions (Tipper, 2004). Despite our reliance on visual information, physical barriers often obstruct the view of objects we want to grasp. For example, an athlete may need to reach around another player to catch a ball. In such scenarios, vision cannot code the hand's position in relation to the object; instead, action performance must rely on proprioceptive and haptic inputs to integrate hand position and object location to perform the intended action. This study investigated the extent to which neural mechanisms that integrate visual information with body position for potential actions depend on vision of the hand. In an event-related potential (ERP) study, we blocked the view of the hand to examine whether proprioceptive cues still facilitate attention to near-hand objects and multisensory integration at early and later stages of visual processing.

Recently, researchers have begun to investigate how body position might direct attention to items within our reach, i.e., items that are candidates for upcoming action, and affect their visual processing (see Reed, Garza, & Roberts, 2007; Tseng, Bridgeman, & Juan, 2012 for reviews). Reed, Grubb and Steele (2006) and Abrams, Davoli, Du, Knapp, and Paull (2008) demonstrated that the

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<https://doi.org/10.1016/j.concog.2018.04.012>

Received 8 February 2018; Received in revised form 14 April 2018; Accepted 18 April 2018

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presence of nearby-hands altered performance in visual tasks. Reed et al. (2006) asked participants to perform a covert-orienting task while resting a hand either on the computer monitor near visual target locations or in their laps, far from those locations. They documented the hand proximity effect—faster response times (RTs) were found for targets appearing near the hand, regardless of cue validity. Importantly, this facilitation effect was specific to the hand (i.e., input from the body); a visual anchor of equivalent shape and size did not change performance when placed near or far from the stimulus. Abrams et al. (2008) showed that hand proximity affected attentional disengagement, the speed of visual search, inhibition of return, and attentional blink. Subsequently studies have documented hand-vision interactions at multiple stages of perceptual and cognitive processing: nearby hand placement and configuration influences figure-ground segmentation (Cosman & Vecera, 2010), local-global attention changes (Davoli, Brockmole, Du, & Abrams, 2012), affordances (Reed, Betz, Garza & Roberts, 2010; Thomas, 2015), change detection (Tseng & Bridgeman, 2011), and contextual learning (Davoli, Brockmole & Goujon, 2012) (c.f., Brockmole, Davoli, Abrams & Witt, 2013 for a review). Across studies, the hand proximity effect is modulated by the distance of the hand from the visual stimulus. As the distance between the hand and the visual stimulus is systematically increased, a corresponding decrease in the magnitude of the hand proximity effect is observed (Reed et al., 2006, 2010; Tseng & Bridgeman, 2011). In terms of proprioception and action, Brown, Morrissey, and Goodale (2009) showed more accurate pointing movements to visual stimuli presented directly onto the palm than further away. Together these studies suggest the neural system codes for spatial relations between the hand and objects to influence subsequent action and cognition.

What neural mechanisms integrate visual information with body position for interacting with the world? Properties of the hand proximity effect can be linked to neural functions largely subserved by the parietal lobe. Neuroimaging, physiological, and patient data point to its role in multisensory integration, spatial attention in peripersonal space, and action. One neural mechanism that integrates visual and tactile inputs comes from non-human primate studies of visuotactile bimodal neurons located in parietal and premotor cortices (Graziano, Yap, & Gross, 1994). Bimodal neurons respond to both tactile and visual stimuli. Their response to visual stimuli decreases as the visual stimulus moves away from the hand (Graziano & Gross, 1998). Further, when the hand moves to a different position, the receptive fields of the cells move with the hand, but not with the eyes, suggesting that these cells encode space in hand-centered coordinates (Graziano et al., 1994). Bimodal neurons are thought to facilitate the grasping of objects and processing of visual information near the hands (Làdavas, di Pellegrino, Farnè, & Zeloni, 1998). Evidence for bimodal neurons in humans comes, in part, from an fMRI study indicating selective BOLD responses for stimuli within 100 cm of the hand in both parietal and motor cortices, (Brozzoli, Gentile, Petkova, & Ehrsson, 2011). Behaviorally, Reed et al. (2006) demonstrated that the hand proximity effect is influenced by similar manipulations that affect bimodal neuron responses.

In addition, the hand's ability to capture attention and influence visual processing has also provided by human neuropsychological studies. A patient with parietal damage subsequent optic ataxia (i.e., an inability to reach for an object) had difficulty fixating on locations other than to where he was reaching because his gaze was captured by his hand location (Buxbaum & Coslett, 1998). Moreover, a patient with a right hemianopsia (i.e., blindness in his left visual hemifield due to occipital lobe damage) demonstrated that his vision loss was attenuated when he held his left hand up near a display screen of targets (Schendel & Robertson, 2004). When he held his hand proximal to the targets, his ability to detect targets in the previously blind hemifield increased significantly. Thus, hand position can alleviate certain neuropsychological visual deficits, perhaps by recruiting body-related neural systems to contribute to visual processing.

More recently, researchers have used electroencephalography and event-related potentials (EEG/ERPs) to reveal the timing and relative contributions of hand proximity to sensory and cognitive processes (Qian, Al-Aidroos West, Abrams, & Pratt, 2012; Reed, Clay, Kramer, Leland, & Hartley, 2017; Reed, Leland, Brekke, & Hartley, 2013; Simon-Dack et al., 2009). To identify whether hand proximity effects were associated with early, sensory-related ERPs or later, task-related ERPs, Reed et al. (2013) manipulated hand proximity in a go/no-go target detection task where targets and non-targets were equally probable. They found that hand proximity selectively distinguished targets, or stimuli requiring actions, from non-targets in terms of ERP amplitudes. Specifically, hands proximal to the stimuli differentiated target from non-target processing at both N1 and P3 ERPs.

The N1 is an early (120–190 ms) negative deflection over posterior sites thought to reflect sensory-related attention discrimination, selective attention to basic stimulus characteristics, initial selection for later pattern recognition, and intentional discrimination processing. With paradigms designed to indicate the relative contributions of visual and tactile inputs, it has also been shown to indicate visuotactile multisensory integration (e.g., Kennett, Eimer, Spence, & Driver, 2001; Vogel & Luck, 2000; Simon-Dack et al., 2009). For example, Kennet et al. (2001) used a cross-modal cuing paradigm and found larger N1 amplitudes in response to visual stimuli presented on the same side as the preceding tactile cue. In addition, this early influence of hand position on visual processing is consistent with the results of Simon-Dack et al. (2009) who found greater N1 amplitudes for lights projected onto the hand compared to off the hand, as well as the results from Qian, et al. (2012) who found a reduced occipital P2 amplitude when two hands were held near a flickering checkerboard stimulus. Further evidence that the N1 represents an integration of hand position with the visual stimulus information comes from Reed et al. (2013). They examined N1 amplitudes for target and non-target stimuli when the hand was placed either near or far from the visual stimulus. A general attention-related effect was expected for target amplitudes over non-target amplitudes, but multisensory integration was indicated by differences produced by hand proximity. Placing a hand near the visual stimuli, not only increased the N1 amplitudes, but selectively increased the amplitudes of target stimuli for which action was required.

The P3 is a later (350–450 ms) positive deflection that is typically maximal over centroparietal regions. Depending on the task it can reflect the allocation of attention resources, working memory, and the discrimination of stimulus categories at a more abstract, task or motivationally relevant level (Kok, 2001). It is considered to be an endogenous potential that is linked to a person's reaction to a stimulus rather than the stimulus' physical attributes. The P3 response to stimuli can vary by category at a very high level, such as on the basis of different motivational values (e.g., Leland & Pineda, 2006; Pineda & Leland, 2011). From the hand proximity effect at

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