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Letter to the Editor

Left or right? Rapid visuomotor coding of hand laterality during motor decisions

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ARTICLE INFO

Article history:
Received 4 September 2014
Reviewed 10 November 2014
Revised 1 December 2014
Accepted 2 December 2014
Published online 13 December 2014

To interact successfully with a dynamic world, our brain must quickly process incoming visual information regarding objects in our immediate environment, and integrate it with the current position of our hands. In particular, previous research shows that visual information about hand position contributes both to the planning and correction of movements (van Beers, Wolpert, & Haggard, 2002; Reichenbach, Franklin, Zatka-Haas, & Diedrichsen, 2014; Sober & Sabes, 2005). However, visual information provided in these studies is typically underspecified – limb position is represented using a point-light, cursor, or virtual image. The fact that vision of the hand in these paradigms is typically degraded may contribute to sensory uncertainty, with consequences for visuomotor integration (Körding & Wolpert, 2004). This is particularly relevant as the sensorimotor system responds to relatively more detailed visual features of the hand. For example, firing rates of neurons in area 5 of the macaque brain are affected by visual information of static hand identity; Tonic neuronal activity was modulated only when hand laterality was congruent with hand position from an egocentric perspective (Graziano, Cooke, & Taylor, 2000; see also Fadiga et al., 2013). Here, we investigate the contribution of visual information about hand laterality during online response selection.

Fronto-parietal mechanisms in both macaques and humans are known to spatially code visual stimuli approaching near the body (peripersonal space) in hand-centred coordinates (Brozzoli, Ehrsson, & Farnè, 2014). We previously suggested that these mechanisms, generally

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http://dx.doi.org/10.1016/j.cortex.2014.12.004

thought to guide defensive behaviour (Cooke, Taylor, Moore, & Graziano, 2003), play a role in updating limb position (Makin, Holmes, & Ehrsson, 2008). More recently, we argued that these hand-centred mechanisms play a specific role in guiding dynamic hand–object interactions using a specialized anatomical pathway (Makin, Holmes, Brozzoli, & Farnè, 2012). Indeed, previous TMS studies demonstrated that the motor system is visually informed about changes in object properties as early as 70 msec following stimulus presentation (Buch, Mars, Boorman, & Rushworth, 2010; Makin, Holmes, Brozzoli, Rossetti, & Farnè, 2009, see also Serino, Annella, & Avenanti, 2009 for related results for auditory stimuli). Specifically, we showed that when participants were engaged in a reaction time (RT) task, the appearance of a task-irrelevant three-dimensional object approaching the hand suppressed corticospinal excitability in a hand-centred fashion. We interpreted this as proactive suppression of avoidance-related response to the approaching ball.

Here we extended the experimental design of Graziano et al. (2000) to determine whether visual information about hand laterality can guide rapid motor decisions in humans. Ten right-handed participants were recruited, based on an a-priori power calculation (Makin et al., 2009). Participants' right hand rested below a workspace, aligned centrally with their body. Visual information was restricted using computer-controlled LCD goggles, such that only a brightly illuminated LED, placed on the workspace above their hand, could be seen. Participants were instructed to press a button with their right index finger whenever the LED was turned off. Visual hand information was manipulated using artificial (dummy) hands (Fig. S1). Prior to each trial (Fig. 1A) , and unseen by the participants, two dummy-hands were placed on each side of the LED, one in an egocentric orientation (aligned with the subjects' right shoulder, but displaced from the central position of their actual hand), and the other in an allocentric orientation. The angle and laterality of the two dummy-hands was varied across trials, resulting in four configurations (Fig. 1B). The goggles were opened at trial onset for a period of 130 msec, allowing the participants to view directly the LED illumination offset and the dummy-hands configuration (Fig. 1A). Trial onset also coincided with the appearance of an illuminated ping-pong ball (4 cm diameter), rapidly approaching one of the two dummy-hands, resulting in eight experimental conditions. The distractor ball was mounted on a vertically positioned 55 cm rod, and was released to fall under gravity into the workspace in an arced trajectory. The ball traversed ~37 cm in approximately 100 msec after becoming visible to the participant, having a mean velocity when visible of ~370 cm/sec, and stopped with minimal bouncing ~3 cm above the workspace. Participants were instructed to ignore

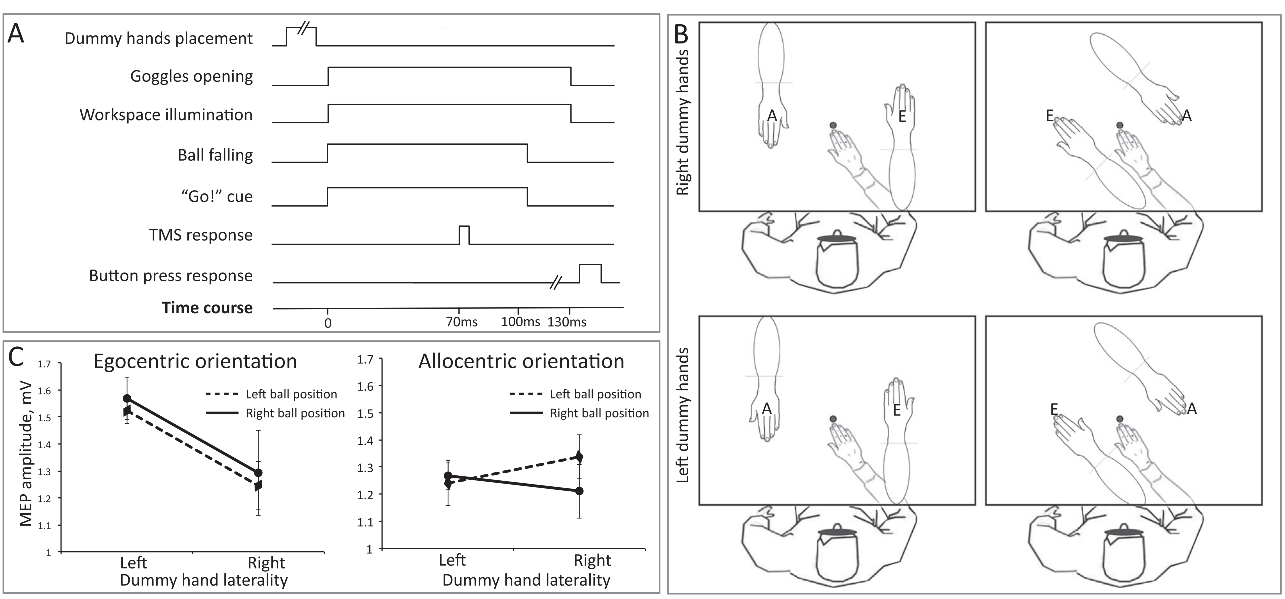

Fig. 1 – Differential motor response for visual hand laterality under egocentric, but not allocentric, configuration. (A) Experimental time-course. Prior to each trial, two dummy-hands were placed one on each side of the workspace. Visual information was restricted to the participant using computer-controlled LCD goggles. At the onset of each trial, the goggles were opened for a period of 130 msec, allowing the participants to view the workspace directly, including the "go" cue. Trial onset coincided with the appearance of a distractor ball, rapidly approaching one of the dummy-hands. (B) Experimental conditions. Participants performed a reaction time task to the "go" cue (at the centre of the workspace) with their occluded right hand, placed underneath it. At each trial onset, two dummy-hands were presented in allocentric or egocentric orientations on both sides of the workspace. In each trial, the position and laterality of the dummy-hands, as well as the ball position, was varied, resulting in 8 experimental conditions. (C) Group mean MEP amplitude in mV [±, SEM, normalised for a within-subject design, (Morey, 2008)], measured 70 msec following trial onset. A significant main effect of laterality was found for the egocentric dummy-hands (top, $p = .003$), but not for the allocentric orientation, resulting in a significant interaction between dummy-hand laterality and orientation ($p = .007$).