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Exploring visuomotor priming following biological and non-biological stimuli

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ABSTRACT

Observation of human actions influences the observer's own motor system, termed visuomotor priming, and is believed to be caused by automatic activation of mirror neurons. Evidence suggests that priming effects are larger for biological (human) as opposed to non-biological (object) stimuli and enhanced when viewing stimuli in mirror compared to anatomical orientation. However, there is conflicting evidence concerning the extent of differences between biological and non-biological stimuli, which may be due to stimulus related confounds. Over three experiments, we compared how visuomotor priming for biological and non-biological stimuli was affected over views, over time and when attention to the moving stimulus was manipulated. The results indicated that the strength of priming for the two stimulus types was dependent on attentional location and load. This highlights that visuomotor priming is not an automatic process and provides a possible explanation for conflicting evidence regarding the differential effects of biological and non-biological stimuli.

1. Introduction

There is evidence for visuomotor priming or automatic imitation, whereby passively observing a human movement influences the observer's own motor system (see Vogt & Thomaschke, 2007 for a recent review of the perception–action system). For example, concurrent observation and execution of a compatible action (e.g. lifting the index finger while observing index finger elevation) results in a facilitation in reaction time (RT), whereas during incompatible observation/action combinations (e.g., lifting the index finger while observing finger depression) interference in movement initiation is indicated by increased RTs, leading to a *compatibility effect* (Brass, Bekkering, & Prinz, 2001; Craighero, Bello, Fadiga, & Rizzolatti, 2002; Sturmer, Aschersleben, & Prinz 2000; Vogt, Taylor, & Hopkins, 2003). In the latter type of priming, the movement *type* or *direction* is compatible or incompatible but the effector remains the same, while another set of studies have investigated the compatibility of the *effector*, for example lifting the index finger versus lifting the little finger (Bertenthal, Longo, & Kosobud, 2006; Brass, Bekkering, Wohlschlager, & Prinz, 2000). The current work focuses on the former type of priming. Although still speculative, it has been suggested that facilitation and interference effects in visuomotor priming may result from co-activation of compatible or incompatible sets of mirror neurons respectively (Blakemore & Frith, 2005). Mirror neurons, originally identified in monkey ventral premotor cortex (BA 44), discharge during both observation and execution of an action (Rizzolatti & Craighero, 2004; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Neuroimaging of human participants suggests that functionally similar brain areas exist in homologous areas of premotor cortex and inferior parietal lobe (Buccino et al., 2001; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Grezes, Armony, Rowe, & Passingham, 2003; Iacoboni et al., 1999; Rizzolatti et al., 1996).

Our overall goal in the current study was to compare the strength of priming for biological stimuli (such as moving hands or limbs) and non-biological stimuli (such as moving objects or robotic limbs) under different conditions. Biological stimuli have been found to produce stronger compatibility effects than symbolic cues and non-biological stimuli (Brass et al., 2001; Jonas et al., 2007; Kilner, Paulignan, & Blakemore, 2003; Press, Bird, Flach, & Heyes, 2005). This biological specificity has been attributed to activation in mirror neuron areas being specific to the observation of human movements (Engel, Burke, Fiehler, Bien, & Rosler, 2008; Perani et al., 2001; Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004). However, it still remains uncertain as to whether these observed behavioural and neural differences reflect a real dissociation in the way that biological and non-biological stimuli are processed. For example, it has been argued that behavioural differences may reflect unevenly matched stimulus characteristics and stimulus–response compatibility effects (Aicken, Wilson, Williams, & Mon-Williams, 2007; Jansson, Wilson, Williams, & Mon-Williams, 2007). In addition, recent work highlights that even observation of non-biological stimuli can cause activation of mirror neuron areas (Cross, Hamilton, Kraemer, Kelley,

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& Grafton, 2009; Engel et al., 2008; Gazzola, Rizzolatti, Wicker, & Keysers, 2007). Therefore, in the current study, we further investigated visuomotor priming by comparing priming during observation of an upward or downward moving finger (biological) with a moving block (non-biological). Importantly, participants responded to the onset of a cross rather than the onset of the movement, reducing the potential confound of unmatched stimulus salience across the biological and non-biological conditions (Aicken et al., 2007).

Our first aim was to examine how priming for biological and non-biological stimuli is modulated by the view of the stimulus. The strength of visuomotor priming can differ according to whether the stimulus is presented in a mirror (specular) or anatomical orientation (Koski, Iacoboni, Dubeau, Woods, & Mazziotta, 2003). In the former, the observer's and actor's fingers are spatially congruent (e.g. index fingers are directly opposite), whereas in the anatomical view, finger positions are not spatially coincident (e.g. the observer's index finger is to the right of the actor's index finger; Fig. 1a). Stronger visuomotor priming in the mirror as opposed to anatomical view has been reported previously (Bertenthal et al., 2006). Such increased priming in the mirror view is at least partly due to stimulus response compatibility effects (Simon, 1990), where responses are faster to spatially aligned stimuli, e.g. stimuli on the left are responded to more rapidly by the left hand. We refer to this as *lateral spatial compatibility*. In the current study, manipulating the stimulus

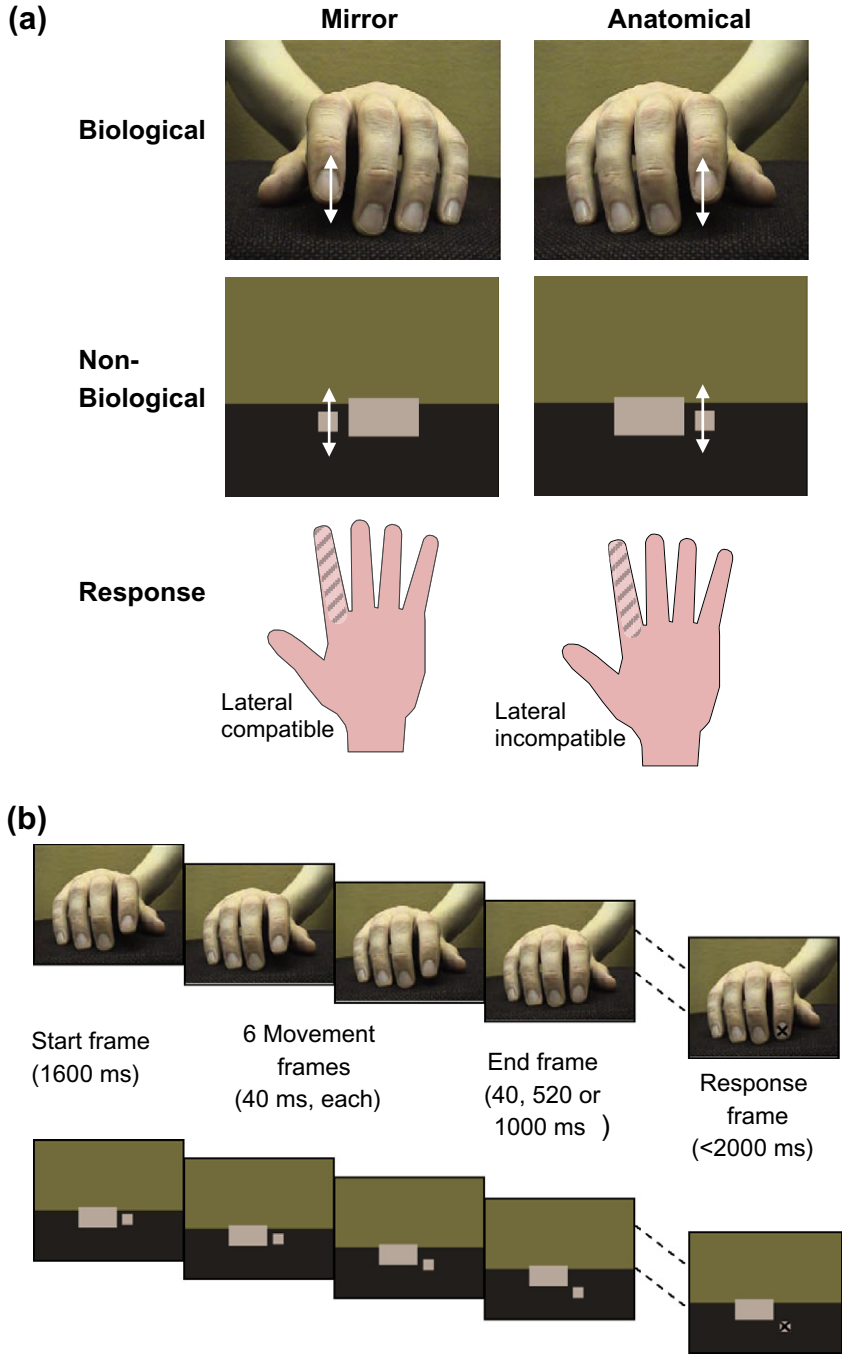

Fig. 1. (a) Example of biological hand (top) and non-biological object (bottom) stimuli in the mirror (left) and anatomical (right) orientations. Both stimuli types are positioned at the start of the movement. The participants response is laterally compatible in the mirror view and laterally incompatible in the anatomical view. (b) Time course of one experimental trial for non-biological (top) and biological (bottom) stimuli. Trial starts at left of picture in neutral position and shows a downward movement for both stimulus types.