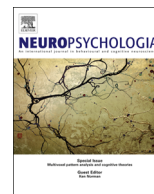




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Heartfelt imitation: High interoceptive awareness is linked to greater automatic imitation [☆]



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ABSTRACT

'Interoceptive awareness', defined as the individual's awareness of internal body signals, modulates self/other distinction under conditions of multisensory integration. We examined here, for the first time, the potential impact of interoceptive awareness on self/other distinction in the motor domain. In automatic imitation, inhibition of imitation is an index of an individual's success in distinguishing internally generated motor representations from those triggered by observing another person's action. This is measured by the 'congruency effect', which is the difference between mean reaction times when the observed action is 'incongruent' with the required action and when it is 'congruent'. The present study compared the congruency effect in a typical finger lifting paradigm, with interoceptive awareness measured by heartbeat perception. Contrary to expectation, interoceptive awareness was positively correlated with the congruency effect and this effect depended on mean reaction times in the incongruent condition, indicating that good heartbeat perceivers had more difficulty inhibiting the tendency to imitate. Potentially, high interoceptive awareness involves stronger interoceptive representations of the consequences of an action, implying higher empathy, greater motor reactivity in response to observed action and hence a greater tendency to imitate. Our results may also tentatively be explained within a predictive coding account of interoception.

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1. Introduction

The ability to distinguish between self and other is crucial to all aspects of self-processing and has relevance for action-awareness (Farrer et al., 2003), body-awareness (Tsakiris, 2013), empathy (Singer et al., 2004) and social cognition (Lamm, Batson, & Decety, 2007). In the motor domain, self/other distinction has been extensively studied using 'automatic imitation' paradigms (Brass, Bekkering, & Prinz, 2001; Catmur, Walsh, & Heyes, 2007), where the ability to resist imitating an action performed by another person is taken to indicate a stronger sense of self (Spengler, Brass, Kühn, & Schütz-Bosbach, 2010). Recent theories propose, however, that the self is grounded in 'interoception', which refers to the signals arising from within the body (Craig, 2010; Damasio, 2010; Seth, 2013). Awareness of such internal signals has been shown to influence the ability to distinguish between self and other in multisensory contexts (Suzuki, Garfinkel, Critchley, & Seth, 2013; Tsakiris, Tajadura-Jiménez, & Costantini, 2011).

Given the inter-connectedness of perception and action (Friston, 2010; Hommel, 2009) the purpose of this study was to investigate whether awareness of interoceptive cues similarly impacts on self/other distinction in the domain of action.

Humans have a tendency to involuntarily imitate actions that they observe. Thus, when an individual is required to perform a given action, observing another person perform an identical action typically facilitates performance, whereas observing a different action generally interferes with it, even when the observed action is entirely task-irrelevant (see Heyes, 2010, for a review). Although the term 'automatic imitation' is commonly used, the phenomenon rarely involves true imitation, in that people actually seldom perform the wrong action. They must, however, resist a tendency to copy the action they observe. The ability to inhibit imitation is measured by 'the congruency effect', which is the difference between the slower mean reaction time (RT) typically found when the required and observed actions are 'incongruent' (i.e. different) and the faster mean RT when the desired and observed actions are 'congruent' (Brass, Bekkering, Wohlschläger, & Prinz, 2000).

According to the Theory of Event Coding, automatic imitation occurs because actions are coded in terms of their goals and thus their sensory consequences. The distinction between perception and action is thus a false dichotomy (Hommel, Müssele, Aschersleben,

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& Prinz, 2001) and seeing an action necessarily primes the motor representation of that action. The Associative Sequence Learning (ASL) theory (Catmur, Walsh, & Heyes, 2009), suggests that visual and motor components of actions are linked by long-term stimulus response (SR) bonds, such that the activation of a visual mental representation necessarily predicts a motor representation (Heyes, 2010). More recently, the theory of predictive coding has linked perception and action within a unified framework that may, in future, elucidate the neural mechanisms behind automatic imitation (Adams, Shipp, & Friston, 2012; Friston, 2010).

Not only does automatic imitation rarely involve imitation but neither is it truly 'automatic', because it is not immune to interference by other processes. According to the ASL model (Catmur et al., 2009) these processes can be divided into 'input modulation', which alters the extent to which the relevant long-term SR bond is activated, and 'output modulation', where social factors potentially inhibit the involuntary imitation (Heyes, 2010). Input modulation is demonstrated by selective attention to one's own actions, which reduces imitation (Bortoletto, Mattingley, & Cunnington, 2013; Chong, Cunnington, Williams, & Mattingley, 2009). Automatic imitation also can be reduced by modest amounts of training (Cook, Press, Dickinson, & Heyes, 2010; Gillmeister, Catmur, Brass, & Heyes, 2008; Heyes & Bird, 2007; Heyes, Bird, Johnson, & Haggard, 2005), which reverses the muscle specificity of the motor-evoked potentials (MEPs) produced by TMS (Catmur et al., 2007).

Output modulation depends on the top-down influence of participants' traits and social attitudes. Eye contact, or priming with pro-social cues, enhances the congruency effect (Leighton, Bird, Orsini, & Heyes, 2010; Wang & Hamilton, 2012; Wang, Newport, & Hamilton, 2011). Similarly, a desire to affiliate to the person observed increases automatic imitation in both experimental settings and social interaction (Lakin & Chartrand, 2003; Wang & Hamilton, 2012). People scoring high in 'self-monitoring' (Snyder, 1974), or who have an interdependent self-construal, have a greater tendency to mimic others, possibly as an unconscious affiliation strategy (Cheng & Chartrand, 2003; Obhi, Hogeveen, & Pascual-Leone, 2011). Interestingly, priming participants with examples of interdependent self-construal increases the amplitude of MEPs elicited by TMS (Obhi et al., 2011), indicating that these top-down influences increase cortical excitability in the motor areas that produce imitation.

Automatic imitation is one of a number of phenomena which involve 'self/other overlap', defined as "any phenomenon whereby an observer engages a state similar to that of the target, via activation of the observer's personal representations for experiencing the observed state, whether through direct perception or simulation" (Preston & Hofelich, 2012). These shared representations occur at a very early, preconscious, processing stage. The ability to inhibit imitation requires that the individual distinguishes between internally generated motor representations and those that are triggered by observing other people's actions (Brass, Ruby, & Spengler, 2009). Successfully inhibiting the tendency to imitate activates cortical areas thought to be involved in discriminating between self and other (Brass, Derrfuss, & von Cramon, 2005; Brass & Heyes, 2005; Brass et al., 2009). The most active of these regions – the temporal parietal junction and anterior fronto-medial cortex (BA10) – are related to perspective taking, feelings of agency and theory of mind (Wang, Ramsey, & Hamilton, 2011). Greater activation in BA10 correlates with smaller congruency effects and thus with better self/other distinction (Spengler, von Cramon, & Brass, 2009). Furthermore, experimentally increasing self-focus reduces the congruency effect, by reducing RTs on incongruent trials (Spengler et al., 2010). Similarly, observing an action increases the amplitude of MEPs if that action is attributed to another individual but reduces cortico-spinal excitability when the action is illusorily attributed to the self (Schutz-Bosbach, Mancini, Aglioti, & Haggard, 2006).

Automatic imitation can therefore be characterised as a tool to measure how effectively the self can be distinguished from others (Spengler et al., 2009). The purpose of the current experiment was to investigate how the congruency effect is linked to 'interoceptive awareness' – a fundamental dimension of self-awareness that has been the focus of recent research in body ownership (Tsakiris et al., 2011), self-recognition (Tajadura-Jiménez & Tsakiris, 2013) and empathy (Fukushima, Terasawa, & Umeda, 2011).

Recent neuroscientific models of the self emphasise the role of 'interoception' (Craig, 2010; Critchley & Harrison, 2013; Hayes & Northoff, 2012; Panksepp & Northoff, 2009) defined as "the afferent information arising from within the body, affecting the cognition, emotion or behaviour of an organism, with or without awareness" (Cameron, 2001). Insular cortex, which is activated by all feelings arising within the body (Craig, 2010; Critchley & Harrison, 2013; Singer, Critchley, & Preusschoff, 2009; Wiebking et al., 2013; Zaki, Davis, & Ochsner, 2012), may underpin this fundamental representation of self (Craig, 2009; Seth, 2013; but see also Philippi et al., 2012). Recent predictive coding accounts of cortical function (Clark, 2013; Friston, 2010) similarly propose interoceptive information as an essential component of the self (Apps & Tsakiris, 2013; Seth, Suzuki, & Critchley, 2011). 'Interoceptive awareness', which is the extent to which internal signals reach consciousness, has been extensively studied in relation to emotion, stemming originally from William James' theory that emotion comprises unconscious bodily responses (Damasio & Carvalho, 2013; James, 1890).

Recent studies have begun to investigate the contribution of interoceptive awareness to self-processing. In the rubber hand illusion, people with low interoceptive awareness are more likely to claim ownership over a prosthetic hand (Tsakiris et al., 2011), and similarly experience a stronger illusory identification with a stranger's face when they observe that face being stroked synchronously with felt touch on their own face (Tajadura-Jiménez & Tsakiris, 2013). Conversely, enhanced self-focus, through mirror self-observation, a self-photograph or self-relevant words, can improve interoceptive awareness in people for whom this is initially low (Ainley, Maister, Brokfeld, Farmer, & Tsakiris, 2013; Ainley, Tajadura-Jiménez, Fotopoulou, & Tsakiris, 2012; Maister, Tsiakkas, & Tsakiris, 2013). Individuals who see a virtual image of their own hand (Suzuki et al., 2013) or of their whole body (Aspell et al., 2013) have a greater sense of self-identification with, and self-location towards, the image under conditions of cardio-visual synchrony.

Despite these investigations into the contribution of interoceptive awareness to self/other distinction in multisensory contexts, little is known about the potential role of interoception in the action system, for example in automatic imitation. This lack of empirical research is striking, given that human actions are thought to be driven by the goal of homeostatic control, which is signalled interoceptively (Craig, 2010; Damasio, 2010; Seth, 2013). Theoretical accounts of the neural basis of perception and action stress their inter-connectedness (Friston, 2010; Schütz-Bosbach & Prinz, 2007). While it has been previously assumed that the sensory consequences of an action are primarily interoceptive, empathy for pain (Avenanti, Buetti, Galati, & Aglioti, 2005; Singer et al., 2004) and overlapping cortical activation during the experience, observation or imagination of disgust (Wicker et al., 2003) can only be explained if actions involve a representation of their interoceptive sensory consequences (Heyes & Bird, 2007).

Given that the ability to inhibit automatic imitation seems to index better self/other distinction, at the level of visual and motor representation, and also that people with high interoceptive awareness appear more reliably able to distinguish their own bodies from those of others, at a multisensory level, we hypothesised that in an automatic imitation paradigm individuals with high interoceptive awareness would successfully inhibit the tendency to imitate, whereas those with low interoceptive awareness

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