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.

Highlights

- Interoceptive awareness modulates self/other distinctions in body-awareness tasks.
- Automatic imitation also indexes the ability to distinguish ‘self’ from ‘other’.
- In a finger-lifting task, good heartbeat perceivers had larger ‘congruency effects’.
- Interoceptive awareness correlated with difficulty in inhibiting imitation.

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, Müsseler, Aschersleben, & 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, Johnson, & Haggard, 2005; Heyes & Bird, 2007), 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 et al., 2009; Brass & Heyes, 2005). The most active of these regions - the temporal parietal junction and anterior fronto-median 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 et al., 2009). Furthermore, experimentally increasing self-focus reduces the congruency effect, by reducing RTs on incongruent trials (Spengler, Brass, Kühn, & Schütz-Bosbach, 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, von Cramon, & Brass, 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 emphasize 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, & Preuschoff, 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, Garfinkel, Critchley, & Seth, 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 signaled 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 exteroceptive, empathy for pain (Avenanti, Bueti, 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 would exhibit less self/other distinction and would therefore have a greater tendency to automatic imitation.

‘Interoceptive awareness’ is generally assessed using a heartbeat perception task (Schandry, 1981; Whitehead & Drescher, 1980). Such measures correlate with awareness of gastric cues (Herbert, Muth, Pollatos, & Herbert, 2012; Whitehead & Drescher, 1980). We used the Mental Tracking task (Schandry, 1981) which is well-validated (Knoll & Hodapp, 1992), with good test retest reliability (Mussgay, Klinkenberg, & Rüddel, 1999; Werner, Kerschreiter, Kindermann, & Duschek, 2013) and which discriminates well between individuals. The measure we have called ‘interoceptive awareness’ in this study assesses the accuracy of cardiac awareness, by comparing the subjectively reported number of heartbeats experienced with the number (objectively) recorded (Cuenen, Van Diest, & Vlaeyen, 2012; Garfinkel & Critchley, 2013). Gender, body mass index (BMI), and resting heart rate were also recorded, as possible confounds of the heartbeat perception task (Cameron, 2002). Automatic imitation was assessed using an established inhibition imitation paradigm developed by Brass and colleagues (Brass et al., 2005; Spengler et al., 2009). It was anticipated that people who performed accurately in heartbeat perception would also be more accurate during the automatic attention task (show a smaller congruency effect). However, both these variables might be affected by participants’ general willingness and ability to attend to the tests. Attention is a possible source of input modulation in automatic imitation (Davis, 1983; Kaplan & Iacoboni, 2006; Preston & Hofelich, 2012). It has also been reported (Matthias, Schandry, Duschek, & Pollatos, 2009) that interoceptive awareness is linked to scores on the d2 test (Brickenkamp & Zilmer, 1998), which measures individual differences in motivation and attention. We accordingly administered the d2 test as a check for this potential confound.

2. Method

2.1 Ethics statement

The study was approved by the Department of Psychology Ethics Committee, Royal Holloway University of London. All participants gave written informed consent and were free to withdraw from the experiment at will.

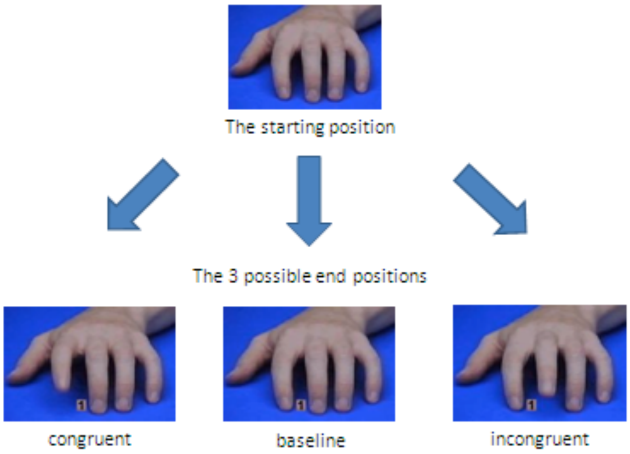
2.2 Participants

Participants were 45 students at Royal Holloway University of London who participated for course credit. All declared themselves right handed and had normal or corrected to normal vision. The data for 2 participants was excluded for excessive numbers of errors (more than 10%, i.e. 3SD above the mean) in the action imitation task, indicating a failure to concentrate and follow the instructions. Of the remaining 43 participants, mean age = 19.6 (SD = 4.9), 9 were male.

2.3 Stimuli

The stimuli consisted of sequences of 5 frames (Brass et al., 2005; Spengler et al., 2009). Each video stared with a frame showing the hand, which mirrored the right hand of the subject, in the starting position, for 2s. The next two frames, each lasting 34ms, presented a number (either 1 or 2) and simultaneously showed the finger movement (if any). The fourth frame showed the finger in the end position for 1.3s, with the number (1 or 2) superimposed. Between trials, the screen turned black for 2.7s. Each video trial was thus 6s duration. The video hand was presented on a blue rectangular background, measuring 22 x 12cm.

Figure 1. Example of the video stimuli for the index finger, from Brass et al., (2005)



There were six possible video sequences, consisting of each of the two fingers (index or middle) in each of three conditions (baseline, congruent or incongruent). Participants were required to lift either the index (1) or middle (2) finger in response to a number appearing on the screen. The three possible conditions (for the index finger) are shown in Figure 1. Thus in the baseline condition, simultaneous with the appearance of the number, the video hand remained static. In the congruent condition the video hand lifted the finger that corresponded to the number shown (i.e. the index finger was lifted when the number 1 appeared). In the incongruent condition the video hand lifted the 'wrong' finger (i.e. the middle finger was lifted when the number 1 appeared).

2.4 Procedure

2.4.1 Interoceptive awareness

After giving informed consent, participants' gender, age, height and weight were recorded. Heartbeat signals were acquired with a piezo-electric pulse transducer, fitted to the participant's left index finger and connected to a physiological data unit (26T PowerLab, AD Instruments) sampling at 1 kHz which recorded the derived electrical signal onto a second PC running LabChart6 software (AD Instruments). Instructions for the Mental Tracking Method (Schandry, 1981) were presented over noise-attenuating headphones. The onset and offset of each heartbeat counting trial were cued by the words "go" and "stop", presented audiovisually. We used a standard instruction (Ehlers, Breuer, Dohn, & Fiegenbaum, 1995) whereby participants were asked to concentrate hard and try to silently count their own heartbeats, simply by "listening" to their bodies, without taking their pulse. The three trials (25s, 35s & 45s) were presented in random order. A criticism of the Mental Tracking Method is that participants may estimate the elapsed interval and then use knowledge of their own heart rate to guess the number of heartbeats. We therefore asked individuals to estimate the length of three, randomly presented, intervals (19s, 37s, 49s) and to provide an estimate of their resting heart rate (Dunn et al., 2010).

2.4.2 Action imitation

The stimuli were viewed on a standard PC, using Presentation software (Neurobehavioral Systems, Albany, CA). Participants were seated about 60 cm in front of the screen and were instructed to execute their movements as quickly and accurately as possible. Participants placed the index and middle fingers of their right hand on a serial response box which was linked to another PC which recorded the times of all finger movements, using Spike2 software (Cambridge Electronic Design, Cambridge UK). This recorded the onset of the visible stimulus on screen (i.e. the number 1 or 2, which coincided with the onset of movement of the video hand) and also recorded whenever the participant lifted an index or middle finger. Following 6 tests trials, 150 trials experimental trials were presented in three blocks of 5mins, with obligatory rests of at least 2mins between blocks. The order of the presentation of the trials was fully randomised and comprised 25 trials in each of the 6 conditions.

2.4.3 The d2 test of attention

Finally, the d2 test was administered (Brickenkamp & Zilmer, 1998). This is a widely used measure of selective visual attention. The test items consist of the letters *d* and *p* with up to four dashes, arranged either individually or in pairs, above and/or below each letter. The subject is given 20s to scan across each of the 14 closely printed test lines, during which they must identify and cross out every letter *d* which has exactly two dashes, while ignoring all other distractor letters. The d2 test produces several norm-referenced scores, of which the most commonly reported are the total number of items processed (TN) regardless of whether these are correct or incorrect (this is a measure of processing speed), the percentage of errors made (E%) and the total number of items processed correctly (TN-E). This final score is designed to provide a measure of the capacity to selectively orient to relevant aspects of the task, while screening out irrelevant ones.

2.5 Data reduction

2.5.1 Interoceptive Awareness

LabChart6 was employed to identify and count the number of R-wave peaks on the heart trace recorded for each participant in each trial, as well as to calculate the average heart rates for each trial (Jennings et al., 1981). Every heart trace was visually inspected for artefacts and the number of R-wave peaks was recounted manually, if necessary. No participant was excluded due to artefacts. Interoceptive awareness was calculated as (1/3Σ (1-(|recorded heartbeats – counted heartbeats|/recorded heartbeats)) (Schandry, 1981). Higher scores indicate higher interoceptive awareness. As a control on guessing, the participant's ability to estimate the length of an elapsed interval was also calculated as (1/3Σ (1-(|estimated elapsed time – actual elapsed time|/actual elapsed time)) which we called the "time modulus" measure (Dunn et al., 2010).

2.5.2 Action imitation

Data was extracted using Matlab (mathworks.com) and analysed with Microsoft Excel. The mean reaction time (RT) was calculated for each of the 6 conditions (congruent, incongruent and baseline, for each of the two fingers). The 'congruency effect' was found by subtracting the mean RT for congruent trials from the mean RT for incongruent trials.

3. Results

3.1 Error analysis

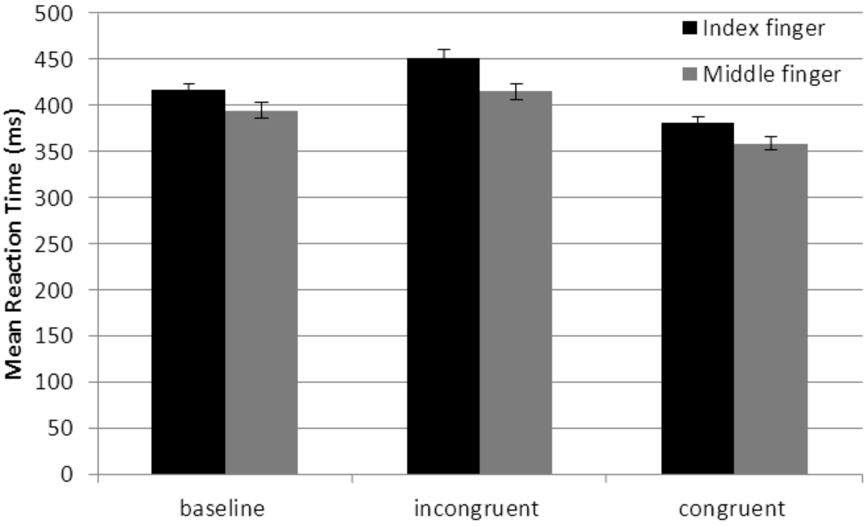
RT errors were removed before analysis. There were 2 possible sources of RT errors. Firstly, participants occasionally lifted the wrong finger. Secondly, in common with most RT analyses, some response times were omitted as outliers (Miller & Diego, 1991). Thus RTs less than 80ms or greater than 800ms were excluded from the RT analysis (Brass, Bekkering, & Prinz, 2001). The rate for all errors was 2.3% of trials. Two participants were excluded for total errors > 10% i.e. 3SD above the mean. The distribution of errors was thereafter approximately Normal, skewness = .64, kurtosis = -.16.

Paired sample *t* tests (with Bonferroni correction for multiple comparisons and a significance level of 0.017) showed that there were significantly more errors in the incongruent condition than in the baseline, *t*(42) = 5.07, *p* < .001, but no significant difference between the numbers of errors in the congruent condition and baseline, *t*(42) = 0.82, *p* = .42, replicating the finding of Brass et al. (2005).

3.2 Reaction Time (RT) Analysis

Repeated measures ANOVA was performed, with both the finger (index or middle) and the condition (congruent, incongruent and baseline) as within-subjects variables. Mauchley's test of Sphericity was significant; therefore Greenhouse Geisser corrections were applied. There was a main effect of condition (RTs in the incongruent conditions were slower), *F*(2, 84) = 186.4, *p* < .001. This indicates significant automatic imitation i.e. slower mean RTs in the incongruent than congruent condition, for both fingers (Brass et al., 2000; Brass, Derrfuss, & von Cramon, 2005). There was a main effect of finger, *F*(1, 42) = 13.2, *p* = .001 (reaction times were generally faster for the middle finger), as shown in Figure 2. The interaction of finger and condition was also significant, *F*(2, 84) = 8.9, *p* < .001. Paired samples *t* tests (with Bonferroni correction and a significance level of 0.008) showed that, compared with RTs in the baseline, RTs in the incongruent condition were significantly longer when participants were required to lift their index finger rather than their middle finger, *t*(42) = 3.32, *p* = .002. However, there was no significant difference between the two fingers for RTs in the congruent condition, compared with the baseline, *t*(42) = .57, *p* = .57. Despite the significantly shorter RTs for the middle finger, particularly in the incongruent condition, the relationships between interoceptive awareness and the various reaction time measures in our study were very similar for the two fingers. For the remaining analysis we therefore used the mean of the data for the index and middle fingers, to give a single measure of average RT in each condition.

Figure 2. Mean reaction times by condition and by finger (Errors bars = SEM)



To investigate the relationship between interoceptive awareness and the congruency effect, we calculated the latter, in the standard way (as the mean RT in the incongruent condition minus the mean RT in the congruent condition), for the average of the two fingers, for each participant. Correlations between interoceptive awareness and differences in RTs between conditions are shown in Table 1. Interoceptive awareness was positively correlated with the congruency effect (Figure 3) and this was wholly accounted for by RTs in the incongruent condition. Interoceptive awareness was significantly correlated with the difference between mean RTs in the incongruent condition and the baseline but not with the difference between mean RTs in the congruent and baseline conditions.

Figure 3. Scatter diagram of the average congruency effect against interoceptive awareness

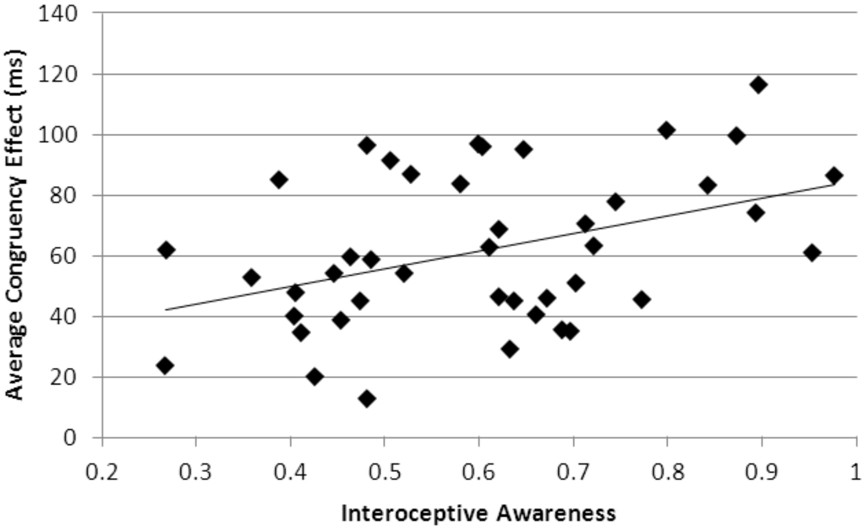


Table 1. Correlations between interoceptive awareness (IA) and RT measures

IA & ‘the congruency effect’ (mean RT in incongruent condition minus the congruent condition)	$r = .41$ $p = .006$**
IA & mean RT in the incongruent condition minus the baseline	$r = .45$ $p = .002$**
IA & mean RT in the congruent condition minus the baseline	$r = -.04$ $p = .73$

*** significant at the 1% level*

The wide range of mean RTs amongst our participants (318ms - 513ms, median 398ms) might have affected our results. We therefore calculated the percentage difference in RTs between the incongruent and congruent conditions using the formula [{(mean RT incongruent - mean RT congruent)/mean RT baseline} x 100]. This statistic was also significantly positively correlated with interoceptive awareness, $r = .40$, $p = .008$.

In this experiment we recorded a number of confounding variables known to impact on interoceptive awareness, namely gender, Body Mass Index (BMI), resting heart rate, and two measures designed to assess possible guessing on the Mental Tracking task (i.e. the ‘time modulus’ measure of the participant’s ability to estimate elapsed time, and the participant’s belief about his/her heart rate). An independent samples t test (with equal variances not assumed) showed no effect of gender on interoceptive awareness, $t(41) = 1.32$, $p = .24$. Likewise the correlation of interoceptive awareness and BMI was not significant, $r = -.20$, $p = .21$. Although people with slower hearts are often better heartbeat perceivers (Ainley et al., 2012; Cameron, 2001; Knapp-Kline & Kline, 2005), in this sample the correlation of interoceptive awareness and average heart rate did not reach significance $r = -.22$, $p = .16$.

The ‘time modulus’ measure (of participants’ ability to estimate the length of an elapsed interval) was correlated with interoceptive awareness, $r = .35$, $p = .02$ but the correlation of interoceptive awareness and participants’ estimates of their own heart rates was not significant, $r = -.08$, $p = .62$.

Table 2. Hierarchical multiple regression with the average congruency effect as the dependent variable

	Step 1	**Step 2**	**Step 3**	**Step 4**	**Step 5**	**Step 6**
Independent variables	***Beta (p)***					
Interoceptive awareness (IA)	1.74 ($p = .36$)	1.96 ($p = .16$)	1.90 ($p =.16$)	.52 ($p = .14$)	0.40 ** ($p = .009$)	0.41** ($p = .006$)
Average heart rate (HR)	0.22 ($p = .82$)	0.26 ($p = .78$)				
‘Time modulus’	-0.76 ($p = .64$)	-0.66 ($p = .66$)	-0.10 ($p = .29$)			

Interaction of IA & 'time modulus'	0.19 (p = .86)					
Interaction of IA & HR	-1.47 (p = .31)	-1.55 (p = .25)	-1.49 (p = .26)	-.15 (p = .69)		
Interaction of 'time modulus' & HR	0.86 (p = .62)	0.85 (p = .62)	1.22 (p = .23)	.15 (p = .40)	.11 (p = .45)	
Adjusted R^2 (p)	**.08 (p = .18)**	**.10 (p = .11)**	**.13 (p = .06)**	**.12* (p = .05)**	**.14** (p = .02)**	**.15** (p = .006)**

** significant at the 5% level*
*** significant at the 1% level*

Given previous correlations in the literature between interoceptive awareness and both participants' average heart rates and the 'time modulus' measure (Cameron, 2002; Dunn et al., 2010), we performed a hierarchical multiple regression analysis with the average congruency effect as the dependent variable and independent variables comprising interoceptive awareness, average heart rate, 'time modulus', and their interactions. Only interoceptive awareness had any significant effect on the congruency effect (see Table 2).

Results of the d2 test of attention were analysed in terms of the total number of items processed (TN), total number correct (TN-E) and percentage of errors (E%). Compared with published norms, d2 scores for our participants (mean TN = 516, mean (TN-E) = 493) were at the 70th percentile for students. Previous research (Matthias et al., 2009) found significant correlation between interoceptive awareness and TN but in this experiment none of the d2 measures were correlated with interoceptive awareness, for TN $r = .03$, $p = .87$, for (TN-E) $r = .04$, $p = .82$ and for (E%) $r = -.02$, $p = .92$. To replicate the analysis of Matthias et al. (2009), we split the data using their cut off at interoceptive awareness = .85 but found no significant difference in any d2 measures between 'good' (interoceptive awareness > .85, $n = 5$) and 'poor' (interoceptive awareness < .85, $n = 38$) heartbeat perceivers (e.g. for TN, $F(1, 41) = .46$, $p = .50$). There were likewise no significant correlations between any of the d2 measures and the average congruency effect, for TN $r = .18$, $p = .24$, for (TN-E) $r = .11$, $p = .47$, and for (E%) $r = .15$, $p = .32$.

4. Discussion

We investigated the relationship between interoceptive awareness and automatic imitation, measuring interoceptive awareness (IA) with a well-validated heartbeat perception task (Schandry, 1981) and automatic imitation by a widely used finger-lifting paradigm (Brass et al., 2005). The expected 'congruency effect' was obtained, i.e. mean reaction times (RTs) were slower when the observed and required actions were incongruent and were faster when they were congruent (compared with the baseline of no observed movement). Interoceptive awareness was significantly positively correlated with the congruency effect. This was fully accounted for by the difference between RTs in the incongruent condition and the baseline. There were no significant effects of interoceptive awareness on RTs difference between the congruent and the baseline. Thus the relationship we observed depended on RTs the incongruent condition and thus on interference between the observed and required action (Blakemore & Frith, 2005), indicating that people with high interoceptive awareness had greater difficulty inhibiting the tendency to automatically imitate. Had there been a motor facilitation effect, it would have taken the form of shorter RTs on congruent trials. RTs in the incongruent condition were significantly slower for the index finger than for the middle finger, probably because lifting an index finger is a more familiar experience than the isolated lifting of a middle finger, with a consequently stronger, learned associative bond.

The result we obtained was contrary to our original hypothesis. Experiments in multisensory integration have suggested that people with high interoceptive awareness are better at making self/other body ownership distinctions (Tajadura-Jiménez & Tsakiris, 2013; Tsakiris et al., 2011). We hypothesized that this effect might translate into the motor domain. The ability to inhibit imitation is assumed to index self/other distinction (Spengler et al., 2009) and we therefore predicted that people with high interoceptive awareness would more successfully inhibit the tendency to imitate. Our results show that, on the contrary, they were *more* inclined to imitate, implying greater self/other overlap.

Despite the findings from body-ownership paradigms, which suggest that high interoceptive awareness is linked to better ability to make self/other distinctions, this is likely to be context dependent. Thus while low interoceptive awareness might predict greater ability to distinguish between self and other in cases of multisensory body-related integration (Tajadura-Jiménez & Tsakiris, 2013; Tsakiris et al., 2011), in other contexts high interoceptive awareness seems to suggest greater self/other overlap. A fundamental difference between self/other distinction in the automatic imitation task and self/other distinction in the rubber hand illusion is that confusion in the automatic imitation task is at a representational level and at a point in time where participants have no sensory information about their own movements. The link between interoceptive awareness and automatic imitation may therefore be indirect and depend on the sensitivity of people with high interoceptive awareness to social influences. Thus the concentration of our effect in incongruent cues indicates that it depended on the action observation aspect of the task and therefore on output modulation, rather than the preparation of the individual's own action (input modulation). The lack of correlation between the congruency effect and the d2 test also supports this conclusion. The d2 test scores are measures of *"the capacity to selectively orient to relevant aspects of the task while screening out irrelevant ones"* (Zimmerman & Frimm, 2002). The d2 was included to counter the criticism that if we had found the hypothesised correlation between high accuracy in both the heartbeat detection and the automatic imitation tasks, this might have reflected the participants' level of motivation and attention. We did not replicate previous reports of a correlation between high interoceptive awareness and selective and divided attention (Matthias et al., 2009), indicating that general differences in individuals' motivation and attention to the tasks were unlikely to have confounded our results.

In terms of the Associative Sequence Learning model of automatic imitation (Catmur et al., 2009) output modulation is occasioned by social factors which influence individuals to suppress or enhance the tendency to imitate. High interoceptive awareness has been linked to anxiety (Domschke et al., 2010) and particularly to social anxiety (Terasawa, Shibata, Moriguchi, & Umeda, 2013). We did not assess trait anxiety in this study but potentially, if our high interoceptive awareness participants were more socially anxious, they might have had a greater desire to affiliate, which could have enhanced their tendency to imitate.

A potential source of output modulation is affective empathy, which is assumed to involve shared representations between one's own emotional state and that of another individual (Decety & Jackson, 2004; Iacoboni, 2009; Preston & Hofelich, 2012; Zaki, Weber, Bolger, & Ochsner, 2009). People with high interoceptive awareness are thought to exhibit greater empathy (Ernst et al., 2013; Terasawa, Shibata, Moriguchi, & Umeda, 2013), perhaps because they have a stronger interoceptive representation of the consequences of an observed action, for example, they are more sensitive to masked fear conditioning (Katkin, Wiens, & Ohman, 2001). Scores on the empathetic concern scale of the Interpersonal Reactivity Index (Davis, 1983) correlate with the amplitude of heartbeat evoked potentials (Fukushima, Terasawa, & Umeda, 2011), which are larger in people with high interoceptive awareness (Pollatos & Schandry, 2004). Empathy has, in turn, been linked to action observation. Kaplan and Iacoboni (2006) found that when participants observed another individual reaching for a cup, inferior frontal mirror activity was greater in those people who had higher scores on the Empathetic Concern subscale. Such motor activity in response to action observation is also linked to a greater tendency to imitate (Catmur et al., 2007; Obhi et al., 2011; Schutz-Bosbach et al., 2006). Empathy is inversely correlated with narcissism and it has recently been shown that individuals who are high in trait narcissism - thus displaying a lack of empathy and concern for others - have a greater ability to inhibit automatic imitation (Obhi, Hogeveen, Giacomin, & Jordan, 2013). Thus high interoceptive awareness may involve stronger interoceptive representation of the consequences of an action, implying higher empathy, greater mirror neuron activity in response to observed action and hence a greater tendency to imitate.

Our results may alternatively depend on some hitherto unexplored aspect of interoceptive awareness and its relationship to the action system. Given that accounts of cortical function, including both the Theory of Event Coding (Hommel, 2009) and predictive coding (Clark, 2013; Friston, 2010) stress that perception and action are reciprocally connected, further research is needed to confirm whether interoceptive awareness impacts not only on action in interoceptive systems but on motor activity as well. The basis of inter-individual differences in interoceptive awareness is not well understood (Verdejo-Garcia, Clark, & Dunn, 2012). Such differences have generally been assumed to depend simply on the strength of interoceptive signals arising within the body, which are conveyed principally by the vagus nerve (Craig, 2003; Cameron, 2002; Critchley et al., 2007). However, interoceptive awareness may perhaps be interpreted in a predictive coding context (Friston, 2010; Seth et al., 2011).

Hypothetically, high interoceptive awareness might relate to the high 'precision' of interoceptive signals, which could, in turn, account for the high levels of autonomic activity that have been observed in people with good interoceptive awareness (Herbert, Pollatos, Flor, Enck, & Schandry, 2010; Pollatos, Füstös, & Critchley, 2012). Although very speculative, it seems possible that interoceptive signals are more reliable and attended (i.e. more precise) in people with high interoceptive awareness, which would account for these individuals' reduced liability to body ownership illusions. Given that interoceptive awareness affects perception of the body, it is also likely to modulate action representations. It has recently been indicated that in order to avoid mirroring another person’s actions it is essential to *reduce* the precision of proprioceptive precision errors (Friston, Mattout, & Kilner, 2011). If people with high interoceptive awareness have initially precise proprioceptive precision errors, then their tendency to imitate others may be accounted for. Potentially, recently observed individual differences in levels of neurotransmitters in the insula (e.g. Wiebking et al., 2013) may provide the means to unravel the links between interoceptive signals and proprioceptive, motor and autonomic reflexes.

5. Conclusion

Interoceptive awareness, measured by the accuracy with which people perceive their own heartbeats, is known to modulate self/other distinction in multisensory contexts. Here we demonstrate for the first time that interoceptive awareness also impacts on shared representations in the motor domain, such that people with high interoceptive awareness have greater difficulty in inhibiting the tendency to imitate, in a standard automatic imitation paradigm.

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