Title: Orthogonal-compatibility effects confound automatic imitation: Implications for measuring self-other distinction.

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Abstract

Accurate distinction between self- and other-representations is fundamental to a range of social cognitive capacities, and understanding individual differences in this capacity is an important aim for psychological research. This demands accurate measures of self-other distinction (SOD). The present study examined an experimental paradigm employed frequently to measure SOD in the action domain; specifically, we evaluated the rotated finger-action stimuli used increasingly to measure automatic imitation (AI). To assess the suitability of these stimuli, we compared AI elicited by different action stimuli to performance on a perspective-taking task believed to measure SOD in the perception domain. In two separate experiments we reveal three important findings: Firstly, we demonstrate a strong confounding influence of orthogonal-compatibility effects on AI elicited by certain rotated stimuli. Second, we demonstrate the potential for this confounding influence to mask important relationships between AI and other measures of SOD; we observed a relationship between AI and perspective-taking performance only when the former is measured in isolation of orthogonality compatibility. Thirdly, we observed a relationship between these two performance measures only in a sub-group of individuals exhibiting the pure form of AI. Furthermore, this relationship revealed a self-bias in SOD – reduced AI was associated with increased egocentric misattributions in perspective taking. Together our findings identify an important methodological consideration for measures of AI, and extend previous research by showing an egocentric style of SOD across action and perception domains.

Keywords: Self-other distinction; automatic imitation; perspective taking; egocentrism; individual differences.

1. Introduction

Self-other distinction (SOD) is the process through which we treat independently and distinguish flexibly between representations of the self and others. This provides an important foundation for various social cognitive faculties; inefficient SOD will result in egocentric misattributions of our own cognitive and affective states onto others, leading us to respond inappropriately during social interactions (for related discussions see Decety & Lamm, 2007; Lamm, Bukowski & Silani, 2016; Steinbeis, 2016). As such, understanding individual differences in this fundamental capacity presents an important challenge for psychological research. This demands accurate measures of SOD, however, with stimuli capable of eliciting this process independently of other unrelated cognitive mechanisms. The present study evaluated the suitability of stimuli employed increasingly in this endeavour.

The finger-lifting stimulus-response compatibility (SRC) procedure (Brass, Bekkering, Wohlschläger, & Prinz, 2000; 2001) is employed frequently by studies of SOD (e.g., Guzman, Bird, Banissy & Catmur, 2016; Hogeveen et al., 2014; Santiesteban et al., 2012; Tomova et al., 2014). On this task, participants are faster and more accurate at executing right-hand finger-lifting movements signalled by an imperative stimulus when they observe simultaneously a task-irrelevant compatible (matching) compared with an incompatible (opposing) finger movement performed by a model's left hand. This compatibility effect is referred to as *automatic imitation* (AI), and is considered an experimental measure of spontaneous mimicry (for a review see Heyes, 2011). Studies have revealed that AI elicited on this SRC task results from a common neural coding of self- and other-action: Observing passively another's finger-lifting actions engages cortical motor systems involved in their execution (e.g., Iacoboni et al., 1999), thereby priming or interfering in the performance of, respectively, compatible or incompatible finger movements. Furthermore, AI elicited by finger-action stimuli is altered by modulating neural activity within these motor systems (e.g., Catmur, Walsh & Heyes, 2009;

Catmur, Mars, Rushworth & Heyes, 2011). This demonstrates that our own and others' actions share a common representational space in the brain, and controlling imitative tendencies requires a mechanism capable of distinguishing between these overlapping self- and other-action representations (for theoretical papers see Brass, Ruby & Spengler, 2009; Guzman et al., 2016; Lamm et al., 2016; Steinbeis, 2016). For this reason, the magnitude of AI elicited on the finger-lifting SRC task is employed increasingly as a measure of SOD, with several studies reporting relationships between performance on this task and other indices of SOD (e.g., perspective taking [Santiesteban et al., 2012, Spengler, Bird & Brass, 2009; 2010], empathy [Guzman et al., 2016; Tomova et al., 2014]).

Importantly, however, the finger-lifting stimuli often employed on this task confound two sources of AI, throwing into question whether performance reflects SOD mechanisms specifically or other domain-general cognitive processes. By presenting a model's *left* hand horizontally, the stimulus comprises a mirror image of the horizontal right response hand; index- and middle-finger movements are both executed and observed towards the left and right of the stimulus display, respectively. As such, AI likely results from both the imitative and *spatial* compatibility between observed and executed actions (Boyer, Longo, & Bertenthal, 2012; Boyer, Scheutz, & Bertenthal, 2009). This spatial confound was demonstrated by Bertenthal, Longo and Kosobud (2006), who report a partial reversal of AI in response to a right stimulus hand for which imitative- and spatial-compatibility effects oppose one another. In response to mirror-like actions, then, AI is driven by both sources of compatibility, making it impossible to dissociate between SOD involved in the control of imitative tendencies and more general response-inhibition mechanisms required to overcome (unspecific) stimulus-response mappings (mapping stimuli onto responses of effectors in corresponding spatial locations; see Marsh, Bird & Catmur, 2016; Snowden & Catmur, 2013). While some researchers have questioned the distinction between spatial- and imitative-compatibility effects

(Catmur & Heyes, 2011; Cooper, Catmur, & Heyes, 2013), empirical studies suggest it is reflected at the neural level; neuroscientific experiments employing the SRC procedure with finger-action stimuli report greater brain function within mirroring systems during the observation of actions that are imitatively compatible with executed actions, relative to those that are spatially compatible (Bien et al., 2009; Cross et al., 2013; Mengotti et al., 2012; Snowden & Catmur, 2013). This implies the degree of overlap between neural self- and other-action representations – and the need for SOD to withhold resulting imitative tendencies – is modulated by imitative rather than spatial compatibility.

Motivated by an increasing awareness of the need to isolate imitative- from spatial-compatibility effects, recent studies employ a counter-clockwise rotation of these left-hand finger-action stimuli that places observed and executed finger movements orthogonal to one-another (e.g. Cook & Bird, 2011; 2012; Guzman et al., 2016; Hogeveen et al., 2014; Hogeveen & Obhi, 2013; Obhi et al. 2014; Santiesteban et al., 2012; Santiesteban, Banissy, Catmur & Bird, 2012). Yet research shows that when a horizontal response set is mapped to a vertical stimulus display, an up-right/down-left advantage emerges (for reviews see Cho & Proctor, 2003; Proctor & Vu, 2012). This *orthogonal*-compatibility effect introduces an alternative spatial confound to measures of AI; in response to this rotation of a left stimulus hand, right-hand finger movements might be facilitated by their orthogonal rather than imitative compatibility with the observed actions. Although Jiménez et al. (2012) observed little influence of orthogonal-compatibility effects on AI elicited with *clockwise*-rotated action stimuli, Cross et al. (2013) report that neural responses differentiate between spatial and imitative compatibility even when behaviour does not. It remains possible, then, that this potentially confounding influence reduces the degree to which AI indexes SOD processes, instead reflecting unspecific and domain-general response-inhibition mechanisms.

One way to assess this is to examine the relationship between AI elicited by these rotated stimuli and other indices of SOD. The Director Task (DT; Keysar, Barr, Balin & Brauner, 2000) provides an experimental measure of SOD with which to perform such an assessment. The DT requires participants to move objects around a grid of shelves according to instructions given by a ‘director’. The grid affords two competing perspectives; the participants’ viewpoint from the front differs from the director’s viewpoints from the rear. To follow the instructions correctly, participants must detach themselves from their own self-perspective and act according to their representation of the director’s perspective. While it remains contentious whether the DT demands mentalising (representing what the director can *see* [e.g., Apperly et al., 2010; Dumontheil et al, 2010; Keysar, Lin, & Barr, 2003]) or sub-mentalising processes (constructing an alternative spatial representation [Heyes, 2014; Santiesteban et al. 2015]), avoiding egocentric errors requires flexible distinction between competing self- and other-representations. In this light, AI and DT performance reflect a unitary SOD process (Steinbeis et al., 2016), and should converge to reveal individual differences. The relationship between these measures should, however, be more evident when AI is driven by imitative rather than spatial compatibility.

The present study evaluated the potential influence of orthogonal-compatibility effects on AI elicited by rotated finger-action stimuli. First, we compared directly AI elicited by a left or a right stimulus hand at clockwise or counter-clockwise rotations. At a given rotation, only one stimulus hand affords both imitative and orthogonal compatibility between observed and executed finger-actions. We expected greater AI in response to that confounded stimulus. We then compared AI in response to these different stimuli with DT performance, assessing the potential for orthogonal compatibility to mask relationships between these two measures of SOD. We predicted that AI would relate to DT performance more when the former was elicited by the stimulus affording only imitative compatibility.

2. Experiment 1.

2.1. Methods

2.1.1. Subjects

We recruited 100 students (38 males) from Farmingdale State College, New York. Due to separate exclusion criteria applied to SRC and DT data (see below), the data from 87 of these individuals (30 males) were analysed. The mean age of this final sample was 21.89 years (standard deviation [SD]=4.98, range=18-52). All participants were right handed with normal or corrected-to-normal vision. The experimental procedure was approved by the Ethical Review Board of Farmingdale State College, and informed consent was obtained beforehand.

2.1.2. Procedure

The experimental procedure was programmed and executed in Cogent (v1.31; www.vislab.ucl.ac.uk/cogent), a MATLAB toolbox (vR2015b; The MathWorks Inc., Natick, MA). Participants performed the finger-lifting SRC and DT procedures in immediate succession, but the order of the two tasks was counterbalanced.

2.1.3. Stimulus-Response Compatibility Procedure

Each trial began with a warning stimulus comprising a model's pronated left or right hand with all fingers resting on a flat surface, but rotated 90° counter-clockwise (-90°) from the participants' perspective. Upon presentation of this warning stimulus, participants depressed the left and right directional arrows on a standard keyboard with the index and middle finger of their right hand, respectively. After a variable period (800, 1600, or 2400 msec, selected randomly) the stimulus changed to the end-point of either an index- or middle-finger extension performed by the same hand, and a dot was presented between the index and middle finger. The colour of the dot served as an imperative stimulus, signalling whether the participant should extend their own index or middle finger. The colour-finger pairing was counterbalanced across participants. In response to the imperative stimulus, participants lifted the corresponding finger as quickly as possible, thereby releasing a key. A blank screen was then presented for 1000 msec, after which the warning stimuli re-appeared to signal the next trial. Intermixed among 148 of these experimental trials were 12 catch trials, on which the warning stimulus changed to the end-point of an index- or middle-finger movement but no imperative stimulus was presented.

The two stimulus elements defined the experimental conditions: Firstly, the change from the warning to end-point stimulus produced apparent motion, resulting in the observation of a finger movement either imitatively compatible (*COM*) or incompatible (*INCOM*) with the response signalled by the imperative stimulus; second, the stimulus display presented either a model's left ($LEFT_{-90°}$) or right hand ($RIGHT_{-90°}$). At a -90° rotation, an orthogonal left-down/up-right relationship existed between executed and observed finger movements only in response to the $LEFT_{-90°}$ stimulus (see Figure 1A). The procedure comprised two blocks of 80 trials, each consisting of one stimulus hand. The block order was counterbalanced. Five practice trials were completed before the first block.

2.1.4. Director Task

The stimulus on each trial of the Director Task (DT) consisted of a grid of shelves forming 16 boxes. Objects were placed within eight of these boxes, and on each trial the participant received a recorded verbal instruction from a female "director" to move one of the objects to a different box. In three of four conditions, the director sat behind the shelves, a location from which she could not see the contents of five boxes; with opaque backs, the contents of these boxes were visible only from the participant's (front) perspective. On *Exp* trials, the instruction referred to an object that created a discrepancy between the director and participants' perspectives (e.g., “move the smallest apple”, when the director could see only the medium-sized apple). To follow the instruction correctly, the participant had to discount any “distractor” objects not visible to the director (e.g., move the medium-sized apple rather than the smallest). In the first and second control conditions (*Cont.1* and *Cont.2*) the director was positioned behind the shelves but there was no conflicting object to discount: In *Cont.1* the distractor was replaced, and in *Cont.2* the director’s instruction changed so as to render the distractor irrelevant. In the third control condition (*Cont.3*), the director was not present in the scene and participants were told to follow the instruction from their own perspective. This is illustrated in Figure 1B.

Each condition comprised 20 trials presented randomly. The audio recordings of instructions were equivalent across all 80 trials (mean=3.26 [SD=.22] sec). Participants responded by indicating with the mouse into which box the object should be moved. Errors involved selection of the wrong object or wrong location, the latter including omission of left-right switching. Any potential difference in perspectives was emphasised on practice trials that included a front and rear view of the shelves.

2.2. Results

For each participant we removed trials on both the SRC and DT procedure with response times (RT) beyond three standard deviations of the subjects’ overall mean. We then excluded data from six individuals achieving zero accuracy (Acc) on any two DT conditions (suggesting a misunderstanding of task instructions), and seven participants with aggregate performance measures (see below) beyond three standard deviations of the sample mean. The analyses of the remaining 87 individuals were performed with SPSS (version 22). Unless stated otherwise, values below represent means (± standard error [SE]) and all probabilities are given after Bonferroni correction for multiple comparisons.

2.2.1. Automatic Imitation

Figure 2A illustrates greater RT and lower Acc on *INCOM* relative to *COM* trials for both stimulus displays. A Spearman test revealed that RT and Acc were correlated when collapsing across these conditions for both stimuli ($\rho > .19$, $p < .040$), so we first calculated inverted efficiency scores (IE; RT/[Acc/100]; see Bruyer & Brysbaert, 2011) on each condition and for both displays separately. This accounted for any speed-accuracy trade-off. Applying a repeated-measures 2x2 ANOVA to these IE scores, with the factors *Hand* ($LEFT_{-90°}$ and $RIGHT_{-90°}$) and *Compatibility* (*COM* and *INCOM*), we observed no main effect of stimulus hand (609.07 [±10.73] vs. 602.20 [±8.58] msec, respectively; $F_{[1,86]}=1.61$, $p=.208$) but a strong Compatibility effect (588.74 [±9.49] vs. 622.53 [±9.77] msec; $F_{[1,86]}=49.66$, $p<.001$; $\eta^2=.37$). Moreover, a significant interaction term revealed that the compatibility effect was greater in response to the $LEFT_{-90°}$ (575.37 [±8.73] vs. 629.02 [±9.43] msec) compared with the $RIGHT_{-90°}$ stimulus (602.12 [±11.36] vs. 616.03 [±11.11] msec; $F_{[1,86]}=21.11$, $p<.001$; $\eta^2=.21$). We then subtracted the IE scores on each *COM* condition from the corresponding *INCOM* condition to produce aggregate performance measures – $AI_{LEFT-90}$ and $AI_{RIGHT-90}$, with positive values representing AI in response to the respective stimulus display. A paired-samples t-test confirmed greater $AI_{LEFT-90°}$ compared with $AI_{RIGHT-90°}$ (53.66 [±5.96] vs. 13.91 [±6.68] msec; $t_{[86]}=4.81$, $p<.001$; $\eta^2=.67$).

Interestingly, paired-sample t-tests revealed that individuals expressing AI in response to $LEFT_{-90}$ (n=74; $AI_{LEFT-90}=67.61$ [±5.40]) showed significantly less AI to $RIGHT_{-90}$ ($AI_{RIGHT-90}=14.87$ [±6.92]; $t_{[73]}=6.28$, $p_{corr}<.001$). In contrast, those expressing AI in response to $RIGHT_{-90}$ (n=52; $AI_{RIGHT-90}=53.52$ [±5.65]) showed equivalent AI to $LEFT_{-90}$ ($AI_{LEFT-90}=58.23$ [±7.13]; $t_{[51]}=.56$, $p_{corr}=.581$). This is presented in Figure 3.

2.2.2. Director Task

Since RT and Acc were uncorrelated in some conditions, we examined RT and Acc separately. A Friedman test revealed differences between the conditions in both RT ($\chi^2_{[3]}$=116.03, p<.001) and Acc ($\chi^2_{[3]}$=18.26, p<.001), and Wilcoxon follow-up comparisons confirmed RT was higher and Acc lower on the *Exp* trials (5.75 [±.14] sec and 72.64 [±2.43] %, respectively) relative to *Cont.2* (5.41 sec [±.14] and 75.69 [±2.22] %) and *Cont.3* (4.73 [±.11] sec and 79.25 [±2.55] %; Z>2.30, p<.021); Acc was also significantly higher in *Cont.1* (77.30 [±2.35] %; Z=4.29, p<.001), while RT was equivalent (5.73 [±.15] sec; Z=.46, p=.324). This is illustrated in Figure 2A. To achieve a single measure of DT performance, we collapsed across *Cont.1*, *Cont.2* and *Cont.3* and regressed average RT in these conditions against that measured on the *Exp.* condition. Greater residuals represent greater RT on the experimental relative to control trials – that is, greater egocentric responding. Distributed normally ($D_{[87]}$=.09, p=.062), this measure of DT performance (DT_{RT}) was entered into subsequent regression models.

2.2.3. AI-DT Association

We explored the AI-DT relationship with linear mixed models (LMMs) applied separately to $AI_{LEFT\text{-}90^{\circ}}$ and $AI_{RIGHT\text{-}90^{\circ}}$. Each model was defined independently in a step-up manner, whereby potential fixed effects were added sequentially and retained only if they resulted in a significant decrease in log-likelihood (West et al., 2007). Mean choice RT appears to influence the Compatibility effect (Butler, Ward & Ramsey, 2015), and may determine the relative contribution of spatial- and imitative-compatibility (Catmur et al., 2011). For this reason we considered mean RT collapsed over *COM* and *INCOM* trials (RT_{mean}) for model inclusion, allowing us to assess the AI-DT relationship independently of this potential covariate. We also included a random *Subject* effect, allowing for high variability in AI. Finally, given this high variability we applied the optimal model separately to individuals who did and did not express

AI to each stimulus display – that is, individuals with positive and negative aggregate values, respectively.

For both $AI_{LEFT\text{-}90}$ and $AI_{RIGHT\text{-}90}$, the optimal model included the fixed effects of RT_{mean} and DT_{RT}. For $AI_{LEFT\text{-}90}$, there was no effect of RT_{mean} or DT_{RT} when applied to the entire sample ($F_{[1,87]}$=.33, p=.566; $F_{[1,87]}$=.17, p=.683) or separately to individuals who did express AI in response to $LEFT_{\text{-}90}$ ($F_{[1,74]}$=1.06, p=.306; $F_{[1,74]}$=.49, p=.489) and those who did not ($F_{[1,13]}$=.88, p=.364; $F_{[1,13]}$=.10, p=.761). A different pattern was observed for $AI_{RIGHT\text{-}90}$. While there was no significant effect of RT_{mean} or DT_{RT} when applied to the whole sample ($F_{[1,87]}$=.05, p=.822; $F_{[1,87]}$=.97, p=.328) or individuals expressing no AI in response to $RIGHT_{\text{-}90}$ ($F_{[1,35]}$=.92, p=.343; $F_{[1,35]}$=2.41, p=.130), those who did show AI to this stimulus display showed a significant effect of RT_{mean} ($F_{[1,52]}$=6.78, p=.012) and a strong trend towards the DT_{RT} effect ($F_{[1,52]}$=3.90, p=.054). In this relationship, lower $AI_{RIGHT\text{-}90}$ was associated with slower responding on experimental relative to control trials on the DT – that is, greater egocentrism. Coefficients are presented in Table 1 and plotted in Figure 2B.

3. Experiment 2.

In Experiment 1 we measured significantly greater AI elicited by the $LEFT_{\text{-}90}$ compared with the $RIGHT_{\text{-}90}$ stimulus. Since orthogonal compatibility between observed and executed finger actions can exist only in response to the former stimulus, this confounding influence appears to inflate AI. We also revealed that individuals expressing AI to $LEFT_{\text{-}90}$ showed a decrease in response to $RIGHT_{\text{-}90}$, while those exhibiting AI to $RIGHT_{\text{-}90}$ showed no such change in response to $LEFT_{\text{-}90}$. These behavioural patterns identified two sub-groups: The first express sensitivity to the confounding influence of orthogonal-compatibility effects; the combination of imitative and spatial compatibility afforded by $LEFT_{\text{-}90}$ exert an additive influence on their compatibility effect. This results in greater AI when compared with the compatibility effect measured in response to *RIGHT*$_{-90}$ – a stimulus for which these two sources of compatibility oppose one another. In contrast, AI exhibited in the second group is driven by isolated imitative-compatibility effects; when elicited by *RIGHT*$_{-90}$, their compatibility effect appears relatively insensitive to the additive influence of orthogonal compatibility introduced by *LEFT*$_{-90}$. Moreover, only for individuals expressing AI in response to *RIGHT*$_{-90}$ showed evidence of a relationship between AI and DT performance – the additive influence of orthogonal compatibility appears to mask any AI-DT relationship.

These stimuli differ not only in the orthogonal relationship between observed and executed finger actions, however, but also the anatomical correspondence between the stimulus and response hand. We performed a second experiment to disentangle the relative influence of anatomical correspondence and orthogonal compatibility. Specifically, by rotating the same left and right stimulus hands 90° *clockwise*, we swapped the hand for which orthogonal compatibility exists between observed and executed finger movements. If anatomical correspondence is the influencing factor, the positive association between AI and DT performance revealed in Experiment 1 would still be present when the former is elicited by a right stimulus hand. Alternatively, if orthogonal compatibility is the confounding influence, the AI-DT relationship should now be observed only in response to the left hand.

3.1. Methods

3.1.1. Subjects

An additional 100 students (36 males) were recruited from Farmingdale State College, New York. After applying the same exclusion criteria used in Experiment 1, the data from 86 of these individuals (30 males) were analysed. The mean age of this final sample was 23.05 (standard deviation=3.14, range=18-37) years. All participants were right handed with normal or corrected-to-normal vision.

3.1.2. Procedure

The same SRC and DT procedures were used, and the task order was counterbalanced between participants. The only difference was the stimuli used for the SRC task; the exact same images of a model's left and right hand were rotated 90° *clockwise* (+90°) from the participants' perspective ($LEFT_{+90°}$ and $RIGHT_{+90°}$, respectively). In this opposing rotation, orthogonal compatibility exists only in response to the $RIGHT_{+90°}$ stimulus (see Figure 1).

3.2. Results

We applied the same within- and between-subject exclusion criteria used in Experiment 1, resulting in the removal of data from eight subjects on the SRC task and six from the DT. The analyses presented below were performed on the remaining 86 participants.

3.2.1. Automatic Imitation

Figure 2A illustrates greater RT and lower Acc on *INCOM* relative to *COM* trials for both stimulus displays. A Spearman correlation confirmed that RT and Acc were correlated for both stimulus hands when collapsing across conditions (ρ=.54, p<.001), so we followed the exact same approach as in Experiment 1 and calculated IE scores for each condition. Applying the same 2x2 repeated-measures ANOVA to these scores, we again observed a strong compatibility effect with faster responding on *COM* relative to *INCOM* trials (539.01 [±8.68] vs. 552.89 [±8.40], respectively; $F_{[1,85]}$=15.63, p<.001) but no difference between the $LEFT_{+90}$ or $RIGHT_{+90}$ stimulus (547.34 [±7.99] vs. 544.55 [±9.21] msec; $F_{[1,85]}$=.58, p=.447) and no interaction ($F_{[1,85]}$=2.15, p=.146). Next we subtracted the *COM* from the *INCOM* scores to arrive at $AI_{LEFT+90}$ and $AI_{RIGHT+90}$. Comparing these aggregated performance measures directly with a paired-samples t-test revealed that $AI_{LEFT+90°}$ and $AI_{RIGHT+90°}$ did not differ significantly from one another (7.58 [±5.07] vs. 20.19 [±5.99] msec, respectively; $t_{[85]}=1.466$, $p=.146$).

In opposition of Experiment 1, paired-samples t-tests showed that individuals expressing AI in response to $LEFT_{+90}$ (n=47; $AI_{LEFT+90}=19.25$ [±7.78]) showed only a non-significant increase in response to $RIGHT_{+90}$ ($AI_{RIGHT+90}=40.83$ [±4.64]; $t_{[46]}=2.046$, $p_{corr}=.092$). In contrast, those expressing AI in response to $RIGHT_{+90}$ (n=55; $AI_{RIGHT+90}=51.79$ [±4.83]) showed a significant decrease in AI when elicited by $LEFT_{+90}$ ($AI_{LEFT+90}=.66$ [±5.33]; $t_{[54]}=7.01$, $p_{corr}<.001$). This is illustrated in Figure 3.

3.2.2. Director Task

Following the same approach used in Experiment 1, a Friedman test revealed differences between the conditions in both RT ($\chi^2_{[3]}=62.67$, $p<.001$) and Acc ($\chi^2_{[3]}=19.64$, $p<.001$). Wilcoxon follow-up comparisons confirmed RT was higher and Acc lower on the *Exp.* trials (5.22 [±.17] sec, 77.27 [±2.48] %) compared with *Cont.1* (5.09 [±.15] sec, 83.26 [±2.34] %) and *Cont.2* (5.02 [±.15] sec, 82.79 [±2.17] %; Z>3.14, p<.012). RT was also greater on *Exp.* compared with *Cont.3* trials (4.65 [±.13] sec; Z=6.80, p=.006), but Acc was not significantly different (75.35 [±3.32] %; Z=.23, p=.816). No differences existed between the control conditions in Acc (Z<2.02, p>.258), but *Cont.3* did differ from *Cont.1* and *Cont.2* on RT (Z>5.24, p<.006). This pattern is illustrated in Figure 2A. We then computed DT_{RT} by regressing RT averaged across the three collapsed control conditions against RT on *Exp.*

3.2.3. AI-DT Association

The same model specified in Experiment 1 outperformed any other models applied to both $AI_{LEFT+90}$ and $AI_{RIGHT+90}$, but these clockwise-rotated stimuli elicited AI with opposing relationships to DT performance. For $AI_{LEFT+90}$ there was no significant effect of RT_{mean} or

DT_{RT} when applied to the entire sample ($F_{[1,86]}$=.06, p=.802; $F_{[1,86]}$=.08, p=.785), and no effect of DT_{RT} in those showing no AI in response $LEFT_{+90}$ ($F_{[1,39]}$=1.31, p=.259); only the effect of RT_{mean} was significant for these individuals ($F_{[1,39]}$=5.99, p=.019). In those showing positive $AI_{LEFT+90}$, however, both RT_{mean} and DT_{RT} effects were significant ($F_{[1,47]}$=4.99, p=.030; $F_{[1,47]}$=5.41, p=.024). Conversely, for $AI_{RIGHT+90}$ there was no effect of RT_{mean} or DT_{RT} in the whole sample ($F_{[1,86]}$=1.61, p=.207; $F_{[1,86]}$=1.74, p=.191) or for those showing no AI to $RIGHT_{+90}$ ($F_{[1,31]}$=.01, p=.914; $F_{[1,31]}$=2.23, p=.146). Furthermore, only the RT_{mean} effect was significant in those showing positive $AI_{RIGHT+90}$ ($F_{[1,55]}$=5.37, p=.024); there was no effect of DT_{RT} for individuals showing AI to this stimulus display ($F_{[1,55]}$=.39, p=.531).

3.2.4. Influence of Orthogonal Compatibility

Together our experiments converge to indicate a AI-DT relationship only in individuals exhibiting AI in response to stimuli for which no confounding orthogonal-compatibility effects exist, regardless of anatomical correspondence. To assess this directly we combined the data from both experiments to compare AI elicited by these $RIGHT_{-90}$ and $LEFT_{+90}$ stimuli ($AI_{non\text{-}orth}$) with AI measured in response to the $LEFT_{-90}$ and $RIGHT_{+90}$ stimuli affording orthogonal compatibility (AI_{orth}). A paired-samples t-test confirmed that $AI_{non\text{-}orth}$ was significantly lower than AI_{orth} (10.76 [±4.19] vs. 37.02 [±4.40] msec, respectively; $t_{[172]}$=4.35, p<.001; η^2=.464). Applying Bonferroni-corrected paired-samples t-tests to the AI data combined over both experiments, we found that individuals exhibiting AI in response to stimuli for which orthogonal compatibility exists ($LEFT_{+90}$ and $RIGHT_{-90}$; n=129; AI_{orth}=60.87 [±3.78]) showed less in response to stimuli for which no such confounding influence is present ($LEFT_{-90}$ and $RIGHT_{+90}$; $AI_{non\text{-}orth}$=8.81 [±4.60]; $t_{[128]}$=9.106, p_{corr}<.001). In contrast, those expressing AI in response to the stimuli affording no orthogonal-compatibility effects (n=99; $AI_{non\text{-}orth}$=47.50 [±3.73]) showed no difference in AI elicited by stimuli for which this confound exists

(AI_{orth}=39.75 [±5.59]; $t_{[128]}$=1.14, p_{corr}=.580). This confirms that the corresponding results from each experiment reflect a differential sensitivity among this sample to orthogonal-compatibility effects.

Furthermore, applying the same LMMs to these collapsed data confirmed pattern of results shown in Experiments 1 and 2. For $AI_{orth.}$, there was no effect of RT_{mean} or DT_{RT} when applied to the entire sample ($F_{[1,173]}$=1.41, p=.237; $F_{[1,173]}$=.01, p=.942), or for those expressing no AI in response to $LEFT_{-90}$ or $RIGHT_{+90}$ ($F_{[1,44]}$=.63, p=.433; $F_{[1,44]}$=.72, p=.400). Further, only the effect of RT_{mean} was significant in those expressing AI_{orth} ($F_{[1,129]}$=8.44, p=.004); there was no effect of DT_{RT} ($F_{[1,129]}$=.62, p=.434). For $AI_{non\text{-}orth.}$, however, a different pattern was observed. There was no effect of RT_{mean} or DT_{RT} for the whole sample ($F_{[1,173]}$=.16, p=.694; $F_{[1,173]}$=1.29, p=.257), and those expressing no AI in response to $LEFT_{+90}$ and $RIGHT_{-90}$ showed an effect of RT_{mean} ($F_{[1,74]}$=8.34, p=.005) but no DT_{RT} effect ($F_{[1,74]}$=3.21, p=.077). Yet individuals expressing $AI_{non\text{-}orth}$ showed strong effects of both RT_{mean} and DT_{RT} ($F_{[1,99]}$=14.06, p<.001; $F_{[1,99]}$=8.28, p=.004). In these individuals, less AI was associated with greater egocentrism on the DT. Coefficients are presented in Table 1, and plotted in Figure 2B.

Finally, by examining AI measured across both stimulus hands and rotations we were able to consider the effects of other potentially confounding influences; namely, anatomical- and spatial-compatibility effects. In Supplementary Figure 1 we illustrate how each of these factors might influence AI in response to the different stimulus displays, and Table 2 presents the pattern of AI measured across each stimulus together with the compatibility effect(s) they afford. If anatomical compatibility contributed to our measures of AI we would expect one of the stimulus hands to elicit greater AI on both experiments. This was not the case, however, with AI differing significantly between stimulus hands only in Experiment 1. Anatomical compatibility, then, exerted no systematic influence on AI. In isolation of other potential compatibility factors, both mirror and 1st-person spatial-compatibility effects also exerted no systematic influence on AI. The selective increase in AI for the *LEFT-90* stimulus appears to reflect an additive influence of orthogonal- and mirror-compatibility effects, however, which we discuss below.

4. Discussion

In this study we conducted two experiments to evaluate an experimental paradigm used increasingly to measure self-other distinction (SOD) in the action domain; namely, the finger-lifting stimulus-response compatibility procedure (SRC; Brass et al., 2000; 2001). First we compared AI measured in response to two types of action stimuli – those for which observed and executed finger movements are both imitatively and orthogonally compatible, and stimuli affording only imitative compatibility. We then assessed the degree to which AI measured in response to these different stimuli are related to a measure of SOD in the perception domain; specifically, perspective-taking performance on the Director Task (DT). Three important results emerged: Firstly, orthogonal-compatibility effects present a strong confounding influence on measures of AI. Second, this confounding influence has the potential to mask important relationships between AI and DT performance. Third, for the sub-group of individuals expressing AI in isolation of confounding orthogonal-compatibility effects, a possible self-bias in SOD processing is observed.

Our observation of a behavioural dissociation between these types of action stimuli is consistent with neuroimaging studies. Brain responses within mirroring systems differentiate between observed actions according to their imitative compatibility with executed actions (e.g., Bien et al., 2009; Cross et al., 2013), and similar differentiations are reported in brain systems implicated in SOD processes (e.g., temporo-parietal junction; e.g., Sowden & Catmur, 2013). On this basis we question whether AI confounded by orthogonal-compatibility truly indexes SOD, or other unspecific cognitive mechanisms involved in stimulus-response mapping. Some researchers argue against such a distinction, contending that both sources are mediated by domain-general associative-learning processes (Catmur & Heyes, 2011; Cooper, Catmur, & Heyes, 2013). In support of this proposition, studies have modified AI after brief periods of stimulus-response training (e.g. Gillmeister, Catmur, Liepelt, Brass, & Heyes, 2008; Heyes, Bird, Johnson, & Haggard, 2005; Press, Gillmeister, & Heyes, 2007; but for a critical review see Shaw & Czekóová, 2013). By demonstrating the specificity of the AI-DT relationship to actions that isolate imitative from orthogonal compatibility, however, the present study suggests that imitative compatibility engages SOD processes more than its spatial counterpart.

Importantly, we observed AI even when orthogonal-compatibility effects are not possible. This argues against the notion that AI is simply an artefact of spatial compatibility (Jansson, Wilson, Willliams & Mon-Williams, 2007), and converges with the findings of previous studies: By comparing finger movements with various control stimuli, studies have shown that the congruency effect cannot be reduced to spatial compatibility alone (Brass et al., 2001; Bertenthal et al., 2006; Cook & Bird, 2011; 2012). Our observation of AI in response to both anatomically congruent and incongruent actions that isolate imitative- from spatial-compatibility are also in line with studies that employ action stimuli less susceptible to confounding influences (for a review see Heyes, 2011); some experiments examine hand-opening/-closing movements for which spatial- and orthogonal-compatibility effects can be eliminated (e.g., Heyes, Bird, Johnson & Haggard, 2005; Leighton, Bird, Orsini, & Heyes, 2010; Press, Bird, Flach, & Heyes, 2005; Press et al., 2007; Press, Bird, Walsh & Heyes, 2008; Shaw et al., 2013; Wang & Hamilton, 2013). Such strong convergence across different SRC paradigms indicates that our results are unlikely to be influenced by subtle differences in protocol (e.g., apparent motion produced by two rather than three frames, or the use of catch [no execution] rather than baseline trials [no observation]). Nevertheless, future studies employing the finger-lifting SRC task should consider the potential influence of these methodological differences.

The clockwise rotation of our action stimuli was relatively unaffected by orthogonal compatibility – AI did not differ between left and right stimulus hands at this rotation. It is possible that this pattern of results reflects differences in the direction of finger-lifting movements between rotations – right to left for clockwise-rotated stimuli, and left to right for a counter-clockwise rotation. Importantly, however, our findings replicate those of Jiménez et al. (2012), rendering this explanation unlikely; these authors employed clockwise rotations of finger-*tapping* movements, such that apparent motion occurred left to right. Instead, the end-state hypothesis proposed by Lippa and Adam (2001) may go some way in explaining this difference between clockwise and counter-clockwise rotations. These authors suggest that orthogonal-compatibility effects emerge because the spatial codes of responses are transformed to match those of the stimulus set, but this remapping is determined by end-state comfort; actions performed towards the body midline are more comfortable than those directed away from the body. In this light, rotating our right wrist inwards (counter-clockwise) is much more comfortable than an outward (clockwise) rotation. If participants mentally rotate their right response hand counter-clockwise to match the stimulus, a left stimulus hand at the same rotation becomes a mirror image. In this situation, mirror spatial compatibility between the observed and executed action will confound imitative compatibility, as demonstrated by Bertenthal et al. (2006). This hypothesis provides a potential explanation for the selective increase in AI for the $LEFT_{-90}$ stimulus, since this confounding mirror-compatibility effect could not exist between a counter-clockwise rotated response hand and a clockwise-rotated left *or* right stimulus hand. Furthermore, this would account for the additive influence of orthogonal- and mirror-compatibility effects suggested by our findings; for mirror compatibility to exist with the *LEFT*$_{-90}$ stimulus, it must be rotated clockwise or the response hand rotated counter-clockwise so that they become mirror images of one another.

It is entirely conceivable that the action observation-execution mapping believed to underlie AI is facilitated when the observed action is a mirror image of the observer's corresponding effector, thereby minimising the correspondence problem (see Brass & Heyes, 2005). With such a mirror image, however, it is impossible to distinguish between action-specific matching and other domain-general cognitive processes involved in (unspecific) stimulus-response mapping (Marsh et al., 2016; see also Sowden & Catmur, 2013). In this sense, when AI is measured in response to mirror-image actions it is impossible to dissociate between SOD mechanisms necessary to control imitative tendencies and more general response-inhibition mechanisms. For this reason, we isolated imitative-compatibility effects by rotating anatomically compatible and incompatible finger-action stimuli. By complicating the observation-execution mapping process, however, these stimuli may recruit additional cognitive mechanisms involved in mental rotation. Since these same cognitive mechanisms might also be involved in perspective taking, further studies are needed before we can be sure that AI-DT relationship revealed in the present study truly reflects unitary a SOD mechanism. This could be explored by comparing the relationship when AI is elicited by stimuli that vary in the degree of spatial- and/or orthogonal-compatibility between observed and executed actions (e.g., see Press et al., 2008).

We found that AI was related to DT performance only when the former was elicited by action stimuli for which imitative compatibility is isolated from other spatial influences. This relationship took the form of an inverse association: reduced sensitivity to imitative-compatibility effects was related to slower responding on DT trials requiring a switch from self- to other-representations. This is consistent with the notion that unitary SOD processes underline both AI and DT performance (e.g., Santiesteban et al., 2012). Imitative-compatibility effects are driven by the activation of overlapping neural motor representations of self- and other-action (Catmur, Walsh & Heyes, 2009), and overcoming imitative tendencies requires SOD to disentangle these competing representations. Conversely, experimental DT trials require us to detach from our own self-perspective and act according to an opposing representation. As such, we interpret this finding as evidence for a self-bias in SOD that serves to discount any competing other-representations – that is, an egocentric style of SOD.

This interpretation is congruent with the findings of Obhi et al. (2014; see also Hogeveen et al., 2013), who report that individuals scoring high on narcissism exhibit less interference than controls on the SRC task. Narcissists have also been shown to express lower affective empathy (Wai & Tiliopoulos, 2012) – a socio-emotional process requiring distinction between simultaneous representations of self and other affective states (Lamm et al., 2016). The nature of the AI-DT relationship we have observed might also point towards a potential mechanism behind the results of other studies. Recently it has been demonstrated that training individuals to inhibit imitative tendencies on the SRC task improves their DT performance (Santiesteban et al., 2012) and empathic expression (Guzman et al., 2016). Our data suggest that such training may help individuals to overcome self-biases in SOD processing by encouraging more flexible distinction ("tagging"; Lamm et al., 2016) between competing self-other representations. Importantly, however, these studies elicited AI with rotated action stimuli affording orthogonal compatibility. We wonder if training to inhibit imitative tendencies has a bigger effect on other socio-cognitive tasks when it focuses specifically on the inhibition of imitative-compatibility effects.

Our homogeneous student sample prevented us from exploring individual differences that might underlie the sub-groups we observed on the basis of AI, but several studies suggest that a more person-centred focus is necessary. Individual differences have been demonstrated in the responsiveness of neural mirroring systems believed to drive AI (e.g., Gazzola, Aziz-

Zadeh & Keysers, 2006), and both choice reaction-time (Der & Deary, 2006) and measures of SOD have been found to vary with age (e.g., Riva et al., 2016). Although Butler, Ward and Ramsey (2015) suggest that AI is not related to personality, these authors employed the non-rotated (horizontal) left stimulus hand for which strong spatial-compatibility effects have been demonstrated (Bertenthal et al., 2006). The present study indicates that these spatial influences have the potential to overshadow such relationships, and egocentrically biased SOD processing manifests only when observed actions are imitatively – not spatially – compatible with executed actions. Future studies should examine these two sub-groups more closely, investigating potential differences between individual members.

Ethical approval

Informed consent was obtained from all subjects prior to their participation. All procedures performed in this study were in accordance with the ethical standards of the Ethical Review Board of Farmingdale State College, and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

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Conflict of Interest

Authors declare that they have no conflicts of interest.

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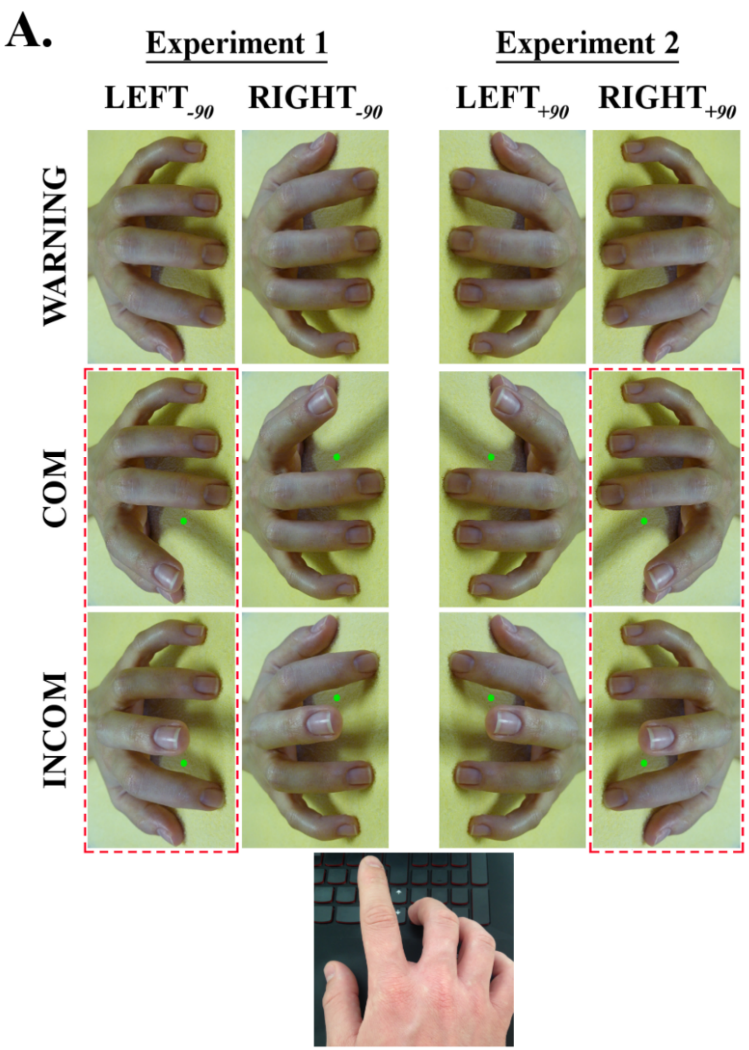
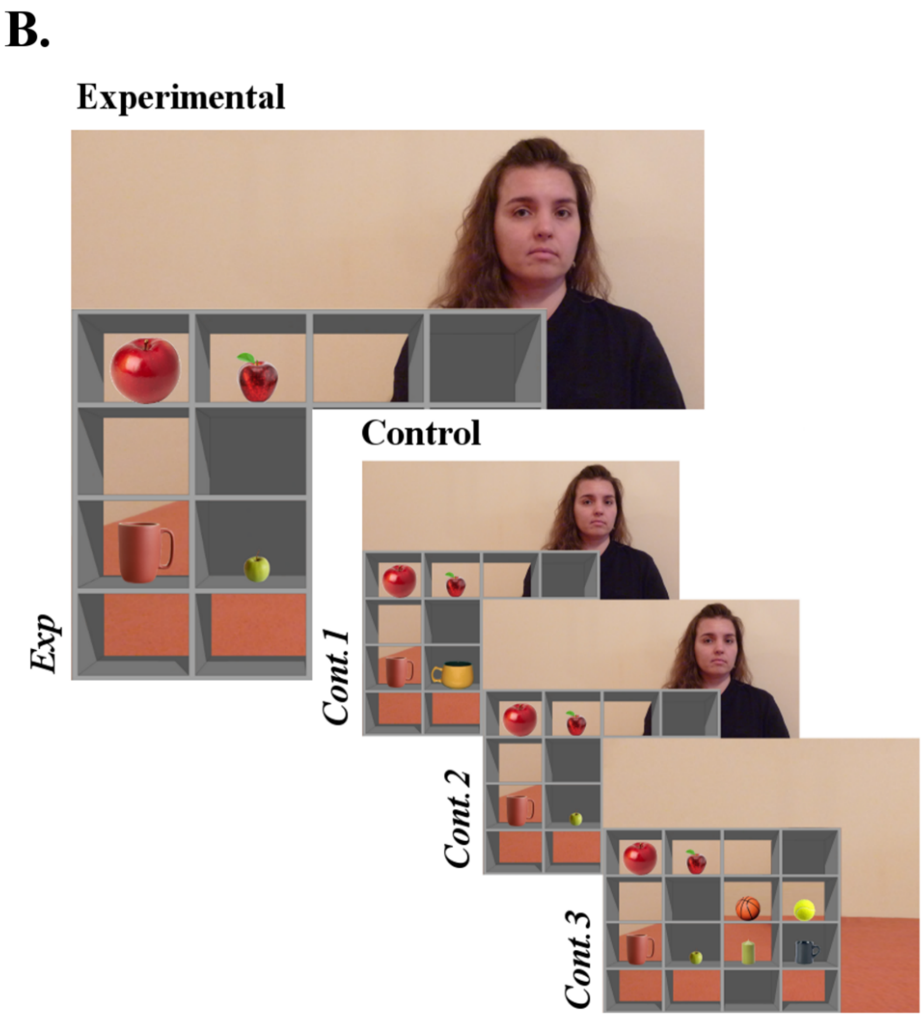
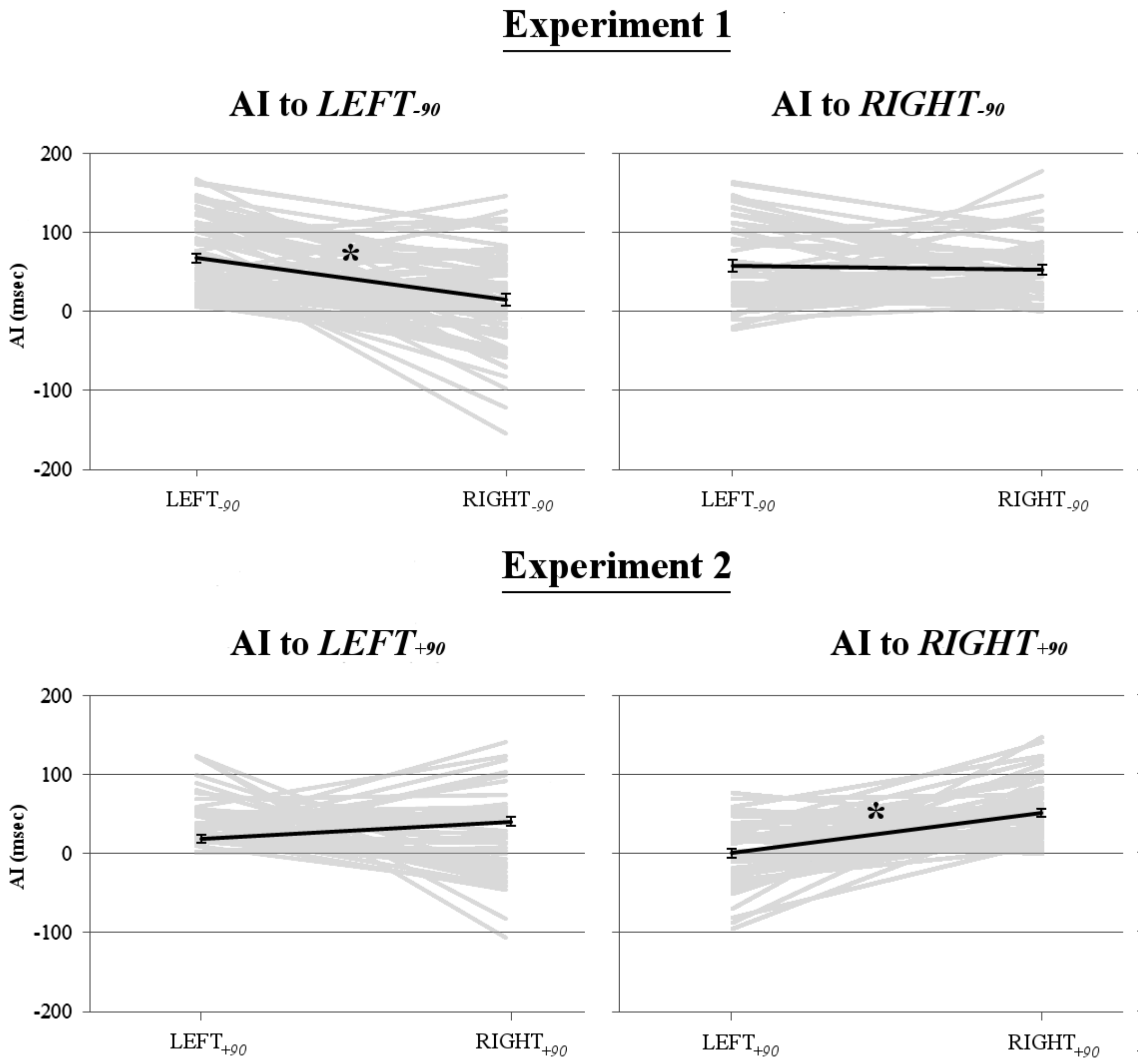
			Intercept	RT_{mean}	DT_{RT}
Experiment #1	*$RIGHT_{-90}$*	*Absent* $_{(35)}$	-37.91 (±11.01)**	-.06 (±.07)	7.50 (±4.83)
		Present $_{(52)}$	29.07 (±10.69)**	.19 (±.07)**	-8.78 (±4.45)^{T}
	$LEFT_{-90}$	*Absent* $_{(13)}$	-39.46 (±16.66)*	.09 (±.10)	-2.83 (±9.10)
		Present $_{(74)}$	58.78 (±10.32)**	.07 (±.07)	-2.99 (±4.30)
Experiment #2	*$RIGHT_{+90}$*	*Absent* $_{(31)}$	-34.19 (±11.11)**	-.01 (±.09)	15.89 (±10.65)
		Present $_{(55)}$	40.75 (±6.88)**	.19 (±.08)*	-5.06 (±8.02)
	$LEFT_{+90}$	*Absent* $_{(39)}$	-20.95 (±6.29)**	-.14 (±.06)*	8.45 (±7.38)
		Present $_{(47)}$	28.70 (±6.74)**	.15 (±.07)*	-15.84 (±6.81)*
Combined	*Orthogonal*	*Absent* $_{(44)}$	-38.74 (±9.22)**	.05 (±.06)	6.30 (±7.42)
		Present $_{(129)}$	48.00 (±5.73)**	.13 (±.04)**	-2.81 (±3.57)
	Non-Orthogonal	*Absent* $_{(74)}$	-26.66 (±5.42)**	-.11 (±.04)**	6.71 (±3.74)
		Present $_{(99)}$	29.59 (±5.81)**	.17 (±.05)**	-10.65 (±3.58)**

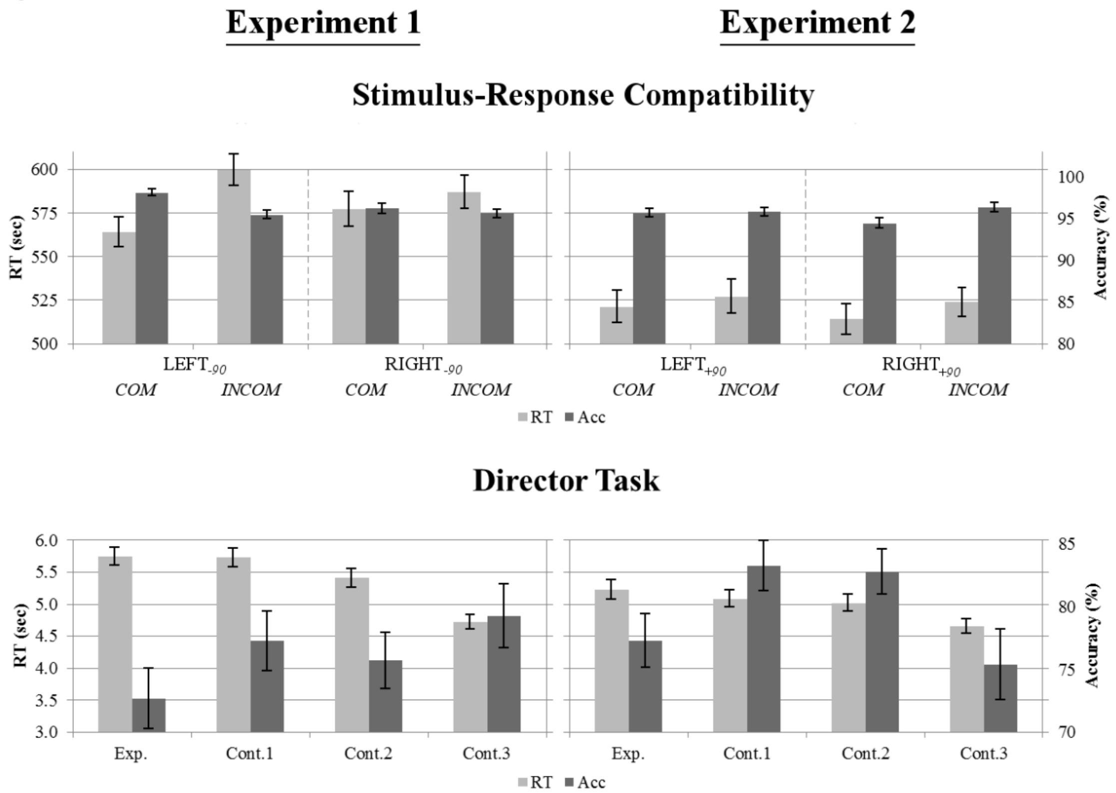
Stimulus				
	LEFT$_{-90}$ [53.66]	*RIGHT*$_{-90}$ [13.91]	*LEFT*$_{+90}$ [7.58]	*RIGHT*$_{+90}$ [20.19]
Congruency Effect	Spatial (mirror) Orthogonal	Anatomical Spatial (1st person)	Spatial (mirror)	Anatomical Spatial (1st person) Orthogonal


A.
Experiment 1
Experiment 2
LEFT-90
RIGHT-90
LEFT+90
RIGHT+90
WARNING
COM
INCOM


B.
Experimental
Control
Exp
Cont.1
Cont.2
Cont.3


Experiment 1
AI to LEFT-90
AI to RIGHT-90
200
100
0
-100
-200
AI (msec)
*
LEFT-90
RIGHT-90
LEFT-90
RIGHT-90
Experiment 2
AI to LEFT+90
AI to RIGHT+90
200
100
0
-100
-200
AI (msec)
*
LEFT+90
RIGHT+90
LEFT+90
RIGHT+90

A.


Experiment 1
Experiment 2
Stimulus-Response Compatibility
RT (sec)
Accuracy (%)
600
575
550
525
500
100
95
90
85
80
$LEFT_{-90}$
$RIGHT_{-90}$
$LEFT_{+90}$
$RIGHT_{+90}$
COM
INCOM
RT
Acc
Director Task
6.0
5.5
5.0
4.5
4.0
3.5
3.0
85
80
75
70
Exp.
Cont.1
Cont.2
Cont.3

B.

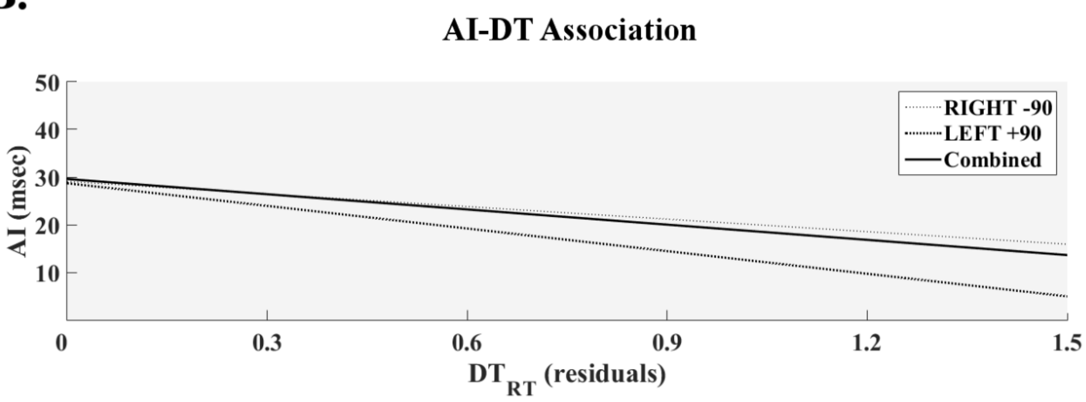

AI-DT Association
AI (msec)
50
40
30
20
10
0
0.3
0.6
0.9
1.2
1.5
DT_{RT} (residuals)
RIGHT -90
LEFT +90
Combined

Table 1. Regression coefficients. Values present estimated coefficients (±SE) emerging from the linear mixed-model regression analyses applied to data from Experiment 1 (*top*) and 2 (*middle*) separately, and the data combined across both experiments (*bottom*). For the combined data, coefficients represent relationships with AI elicited by the $LEFT_{-90}$ and $RIGHT_{+90}$ (*Orthogonal*) or LEFT_{+90} and $RIGHT_{-90}$ (*Non-orthogonal*) stimuli. The coefficients represent the main effect and interactions defining the optimal models applied separately to individuals who did and those who did not express AI to the respective stimulus (*Presence* and *Absence*, respectively; see text for details). Subscripts indicate the number of participants comprising each sub-group. The significant coefficients for the *Presence*-by-DT_{RT} interaction are plotted in Figure 2B. $^{\mathbf{T}}$ = p<.055, * = p<.05, ** = p<.01.

Table 2. Potentially confounding influences on AI. This presents the pattern of AI measured across each stimulus (expressed as *INCOM-COM*, in msec) together with the compatibility effects afforded by that stimulus. Only orthogonal compatibility exerts a systematic influence on AI across stimuli, with a potentially additive effect of orthogonal- and mirror-compatibility effects. See Supplementary Figure 1 for an illustration of how each source of compatibility can emerge with the different stimulus displays, and the distinction between "mirror" and "1st-person" spatial-compatibility effects.

Figure 1. Experimental stimuli. *A:* Example stimuli (*top*) used to elicit AI in both experiments, for one colour-finger pairing (green dot signals the index-finger lift response; *bottom*). In a given block of trials, either a left or right stimulus hand was presented at a 90° counter-clockwise ($LEFT_{-90°}$ and $RIGHT_{-90°}$) or clockwise rotation ($LEFT_{+90°}$ and $RIGHT_{+90°}$). Whether the observed finger extension was the same or different to the response signalled by the imperative stimulus (coloured dot) defined compatible (*COM*) or incompatible (*INCOM*) trials,

respectively. Stimuli affording an orthogonal relationship between observed (*top*) and executed actions (*bottom*) are highlighted in red dashed lines. *B:* Example stimulus set used in the Director Task. On the *Exp*, *Cont.1* and *Cont.3* trials, the instruction is to *"Move the smallest apple down one box"*; on the *Cont.2* trial, the instruction is to *"Move the biggest apple down one box"*. On *Cont.1* trials the potential distractor object (smallest apple) is replaced, but all other objects remain unchanged across the remaining stimulus set. On *Cont.3* the director is removed (see text for detail).

Figure 2. Results of analyses applied to AI and DT performance. *A:* Histograms present mean (±SE) response time (RT) and accuracy (Acc) measured in each condition of the SRC procedure (*top*) and DT (*bottom*), in Experiment 1 (*left*) and 2 (*right*). These values were used to create single aggregate performance measures on each task, which were then entered into mixed-model regression analyses (see text). *B:* The figure plots the significant coefficients emerging from the regression analyses for the AI-DT_{RT} relationship, as presented in Table 1. Lower AI was associated with more egocentric responding on the DT, but only in individuals showing AI to the respective stimuli.

Figure 3. Pairwise comparisons of AI across different stimuli. Comparisons were performed in individuals expressing AI (positive aggregate values) in response to either left or right stimulus hands rotated counter-clockwise (Experiment 1; *top*) or clockwise (Experiment 2; *bottom*). Mean responses (black lines) revealed that individuals expressing AI (positive aggregate values) in response to $LEFT_{-90}$, for which imitative- *and* orthogonal-compatibility effects exist, showed a significant reduction in response to $RIGHT_{-90}$ where these two influences oppose one another. No such change is observed in individuals expressing AI in response to $RIGHT_{-90}$. Likewise, subjects exhibiting AI in response to $RIGHT_{+90}$, the stimulus

affording both imitative and spatial effects, showed less in response to $LEFT_{+90}$. No such change was observed for subjects expressing AI to $LEFT_{+90}$. As such, these pairwise comparisons identify two sub-groups according to AI: one influenced by the confounding influence of orthogonal compatibility, and another driven primarily by isolated imitative-compatibility effects and relatively insensitive to orthogonal compatibility. * = p<.001.