



Is automatic imitation a specialized form of stimulus–response compatibility? Dissociating imitative and spatial compatibilities

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ABSTRACT

In recent years research on automatic imitation has received considerable attention because it represents an experimental platform for investigating a number of interrelated theories suggesting that the perception of action automatically activates corresponding motor programs. A key debate within this research centers on whether automatic imitation is any different than other long-term S–R associations, such as spatial stimulus–response compatibility. One approach to resolving this issue is to examine whether automatic imitation shows similar response characteristics as other classes of stimulus–response compatibility. This hypothesis was tested by comparing imitative and spatial compatibility effects with a two alternative forced-choice stimulus–response compatibility paradigm. The stimulus on each trial was a left or right hand with either the index or middle finger tapping down. Speeded responses were performed with the index or middle finger of the right hand in response to the identity or the left–right spatial position of the stimulus finger. Two different tasks were administered: one that involved responding to the stimulus (S–R) and one that involved responding to the opposite stimulus (OS–R; i.e., the one not presented on that trial). Based on previous research and a connectionist model, we predicted standard compatibility effects for both spatial and imitative compatibility in the S–R task, and a reverse compatibility effect for spatial compatibility, but not for imitative compatibility, in the OS–R task. The results from the mean response times, mean percentage of errors, and response time distributions all converged to support these predictions. A second noteworthy result was that the recoding of the finger identity in the OS–R task required significantly more time than the recoding of the left–right spatial position, but the encoding time for the two stimuli in the S–R task was equivalent. In sum, this evidence suggests that the processing of spatial and imitative compatibility is dissociable with regard to two different processes in dual processing models of stimulus–response compatibility.

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1. Introduction

The ability to represent and understand the behaviors of others is crucial for interacting effectively in our social world. Much of this understanding takes place with little awareness of the perceived actions or responses that are involved. When observing others' behaviors (e.g., facial expressions, gestures, postures), we sometimes implicitly know their wants, desires, and intentions (Blakemore & Decety, 2001). In various situations, we tend to involuntarily mimic the actions performed by others (Bertenthal, Longo, & Kosobud, 2006). This automatic tendency contributes to the 'social glue' by which humans coordinate their behaviors, cooperate, and develop affiliative tendencies toward each other (Chartrand & Bargh, 1999; Lakin, Jefferis, Cheng, & Chartrand, 2003).

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In recent years, research on spontaneous mimicry or automatic imitation has received considerable attention because it is an experimental platform for investigating a number of interrelated theories suggesting that the perception of action automatically activates corresponding motor programs in the observer (e.g., Brass & Heyes, 2005; Decety et al., 1997; Dromard, 1906; Greenwald, 1970; Hommel, Müssler, Aschersleben, & Prinz, 2001; Iacoboni et al., 2001; James, 1890; Jeannerod, 1994; Keysers & Perrett, 2004; Prinz, 1997; Rizzolatti, Fogassi, & Gallese, 2001). There are now more than 75 experimental studies investigating automatic imitation (also referred to as imitative compatibility, visuomotor priming, motor mimicry, motor priming, movement compatibility; see Heyes, 2011 for a review). Most of the evidence is based on stimulus–response compatibility paradigms, in which both stimuli and responses involve human movements. For example, in a paradigm introduced by Brass, Bekkering, Wohlschläger, and Prinz (2000), participants respond to the observation of a finger movement by moving either the same or a different finger of their own hand. If the movements of the stimulus and response fingers match, responses are typically faster than when they do not match the same finger

movements. Similar findings are reported with responses to observed hand grasps (Brass & Heyes, 2005), finger movements (Bertenthal et al., 2006; Brass, Bekkering, & Prinz, 2001), and arm, leg, and head movements (Gillmeister, Catmur, Liepelt, Brass, & Heyes, 2008; Heyes & Ray, 2004).

1.1. Is automatic imitation reducible to spatial S–R compatibility?

The finding of faster responding when stimuli and responses correspond along some dimension than when they do not is referred to as a compatibility effect. Although the most common interpretation for this effect when human movements are involved is that automatic imitation facilitates responding, two objections have been raised. One set of objections centers on claims that response times are confounded by stimulus salience and spatial correspondence between stimulus and response (Jansson, Wilson, Williams, & Mon-Williams, 2007). For example, Brass et al. (2000) compared participants' compatible and incompatible responses to a tapping finger (i.e., an imitative cue) and to a static finger with an 'X' appearing on the fingernail (i.e., a spatial cue). The results revealed that participants responded faster to the compatible than to the incompatible tapping finger, and that these responses were faster than the responses to the compatible and incompatible spatial cue. Although these results suggest that automatic imitation is responsible for the differences, the interpretation is problematic because the spatial cue was less salient than the imitative cue. Moreover, imitative compatibility was confounded with spatial compatibility because the response finger matched the stimulus finger not only in terms of anatomical identity, but also in terms of left–right spatial correspondence. Similar problems were present in many of the other earlier studies testing automatic imitation, but more recent studies corrected these problems and confirmed that automatic imitation was independent of stimulus salience or spatial compatibility (e.g., Bertenthal et al., 2006; Catmur & Heyes, 2011; Heyes, Bird, Johnson, & Haggard, 2005).

A second set of challenges to the interpretation of the research on automatic imitation is that the facilitation of response times following the observation of compatible movements is not unique to automatic imitation. According to Kornblum, Hasbroucq, and Osman (1990), S–R compatibility is determined by the perceptual, structural, or conceptual similarity between a stimulus and response. A few recent studies report evidence suggesting that automatic imitation is reducible to S–R compatibility (Aicken, Wilson, Williams, & Mon-Williams, 2007; Jansson et al., 2007). Jansson et al. (2007), for example, reported that participants' finger movement responses to a tapping or lifting pen showed exactly the same compatibility effects as their responses to a tapping or lifting finger. Likewise, participants responding with the opening and closing of their hands showed the same compatibility effects to a pair of dots expanding or contracting as they did to a hand opening or closing. These results imply that automatic imitation is not privileged and that similar S–R compatibility effects can be achieved whenever the salience of the stimuli and other S–R compatibility effects are controlled.

Although the preceding criticism does not necessarily refute the claim that S–R compatibility effects involving human movements are a function of automatic imitation, it raises a legitimate question that must be addressed: Is automatic imitation mediated by different processes than other forms of S–R compatibility? The difficulty in resolving this issue is that the pattern of results for automatic imitation and all other S–R compatibility effects is exactly the same (i.e., faster response times for the compatible than for the incompatible stimulus–response). In order to refute this claim, it is necessary to find a paradigm where the results are predicted to be different.

1.2. Dissociating imitative and spatial compatibilities

One possibility is to consider a paradigm comparing responses to movements produced by human and non-human agents. A number of studies report attenuated or no response facilitation to the

observation of movements performed by non-human as opposed to human agents (Kilner, Paulignan, & Blakemore, 2003; Liepelt & Brass, 2010; Longo & Bertenthal, 2009; Press, Gillmeister, & Heyes, 2006; Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004; Tsai & Brass, 2007). The problem with these studies is that it is virtually impossible to control for differences in stimulus salience which could account for most of the differences in response priming. Moreover, there is some neuroimaging evidence revealing no difference in levels of activation when observing human and non-human movements (Jansson et al., 2007; Stanley, Gowen, & Miall, 2007).

A second possibility was recently suggested by Sauser and Billard (2006) who proposed two different connectionist models to explain the differences between spatial compatibility and imitative compatibility. One model involved a single-route pathway in which all the stimulus cues interacted within a decision layer before mapping to the selected motor response. The second was a direct matching model that involved two distinct pathways and two selection processes that only converged in the final motor selection stage. One of these pathways was designed to integrate spatial and motion cues, whereas the other pathway was exclusively concerned with integrating the representation of the motor plans together with the representation of the observed movements. In other words, this latter model posited an independent and direct pathway for the joint perception and execution of actions consistent with recent theories suggesting a shared representation for these two processes (e.g. Jeannerod, 1994; Prinz, 1997; Rizzolatti et al., 2001).

Even though the architectures for the two models were different, both showed faster responding to compatible than to incompatible spatial and imitative cues. As such, these models are consistent with the research literature suggesting that the standard stimulus–response compatibility task (S–R) is not capable of distinguishing between the two models. By contrast, the models were able to distinguish between imitative and spatial compatibilities when simulating the results from a stimulus–response compatibility task with opposite stimulus–response (OS–R) instructions. In this task, the mapping was reversed and responses were activated to the opposite stimulus cue (e.g., respond to the left cue with the right finger or respond to the index finger with the middle finger). Switching instructions from an S–R to an OS–R task in a stimulus response compatibility paradigm was first investigated by Hedge and Marsh (1975), who reported a reversal of the Simon effect (Simon, 1969; Simon, Sly, & Vilapakkam, 1981). Several explanations of this effect have been proposed (Hasbroucq & Guiard, 1991; Hedge & Marsh, 1975; Proctor & Pick, 2003; Simon & Berbaum, 1990). Although there is no consensus concerning the underlying mechanism, most hypotheses suggest that the reversal effect is produced by a cognitive process involved in the recoding of the stimulus that generalizes to the task irrelevant stimulus involved in the automatic stimulus–response mapping process (i.e., spatial compatibility).

Sauser and Billard's (2006) simulation results from the single route model revealed a reverse compatibility effect (i.e., faster responding to incompatible stimuli) in the OS–R task, whereas the results from the direct matching model failed to show this reverse effect. Given that a reverse compatibility effect is consistently reported when testing spatial compatibility with this task (e.g., Hedge & Marsh, 1975), it appears that the single route model is the better predictor of spatial compatibility. By contrast, it is not yet possible to evaluate which of the two models best fits imitative compatibility, because the necessary experiments have yet to be conducted.

1.3. The present study

The purpose of this study was to empirically test whether spatial and imitative compatibility can be predicted by the same model or whether imitative compatibility is better predicted by a model that includes a direct connection between the perception and execution of actions. Specifically, we investigated whether participants would

show a reverse compatibility effect for both spatial and imitative compatibility when tested with an OS-R task, or whether participants tested for imitative compatibility would not show a reverse compatibility effect. For the purpose of completeness, we also assessed whether participants tested with a S-R task would show faster responding to both the spatially and imitatively compatible stimulus as has been reported previously.

Spatial and imitative compatibilities were tested with a stimulus–response compatibility paradigm developed by Bertenthal et al. (2006), and modified for the current experiments. This paradigm is designed to avoid spatial and stimulus salience confounds by independently testing for spatial and imitative compatibilities while holding the stimuli constant across conditions. Two experiments were conducted. The first tested for spatial compatibility with an imitative cue as the imperative stimulus, and the second tested for imitative compatibility with a spatial cue as the imperative stimulus. The stimulus display consisted of a hand with fingers spread apart appearing on a computer screen from a third person perspective (see Fig. 1). Participants were instructed to respond to either the left–right spatial location or the anatomical identity of the index or middle finger tapping downward. Responses were always performed by the index or middle finger on the right hand. In the S-R task, the responses were compatible with a task-irrelevant stimulus when the stimulus corresponded to a left hand (see Fig. 2). For example, participants instructed to respond to the spatial cue would press a key with their index finger when responding to the left tapping finger. In this condition, both the stimulus and response are index fingers, and thus the response is facilitated via automatic imitation. Likewise, participants instructed to respond to the imitative cue would, for example, press a key with their middle finger when responding to the middle finger tapping. In this condition, both the stimulus and response correspond to the right side, and thus the response is facilitated via spatial compatibility. When the stimulus corresponded to a right hand, the responses were not compatible with a task-irrelevant stimulus. In the OS-R task, the responses were compatible with a task-irrelevant stimulus when the stimulus corresponded to the right hand (see Fig. 2).

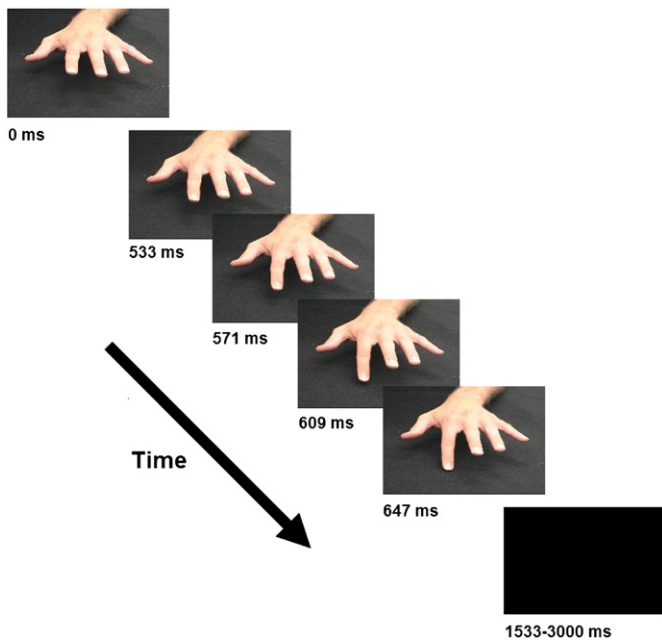


Fig. 1. Each trial consisted of a sequence of six frames. Frame 1 was a hand with fingers spread apart resting above a flat surface. In this example, the index finger begins moving with the second frame at 533 ms and continues moving down on the next three frames shown for 38 ms each. The fifth frame remains visible for 886 ms, and it is followed by a black screen for 1467 ms.

		S-R Task		OS-R Task	
		Compatible (LH)	Incompatible (RH)	Compatible (RH)	Incompatible (LH)
Experiment 1: Spatial Compatibility	Stimulus Hand				
	Response Hand				
Experiment 2: Imitative Compatibility	Stimulus Hand				
	Response Hand				

Fig. 2. The four panels depict the relation between the stimulus and response for compatible and incompatible trials in the S-R and OS-R tasks. *Solid lines* connecting the stimulus and response fingers depict the S-R mapping specified by the imperative stimulus. *Dashed lines* connecting the stimulus and response fingers depict the automatic S-R mapping of the stimulus. The *upper two panels* correspond to the *spatial compatibility* condition: the task is to imitate the tapping finger (e.g., index finger) with the same finger of the right hand and the task irrelevant stimulus is the left–right position of the fingers. In the *left panel* (S-R Task), the left hand stimulus corresponds to the compatible condition – participants respond to the tapping of the left index finger with their index finger (i.e., stimulus and response are spatially congruent). The right hand stimulus corresponds to the incompatible condition (i.e., stimulus and response are spatially incongruent). In the *right panel* (OS-R Task), the right hand stimulus corresponds to the spatially compatible condition and the left hand stimulus corresponds to the spatially incompatible condition. The *lower two panels* correspond to the *imitative compatibility* condition: the task is to respond to the left or right tapping finger with the corresponding left or right index or middle finger, respectively, and the task irrelevant stimulus is the anatomical identity of the fingers. In the *left panel* (S-R Task) the left hand stimulus corresponds to the compatible condition – participants respond to the tapping of the left index finger with their left index finger (i.e., stimulus and response correspond to the same anatomical finger). The right hand stimulus corresponds to the incompatible condition – participants respond to the tapping index finger with their middle finger (i.e., stimulus and response correspond to different fingers). In the *right panel* (OS-R Task), the right hand stimulus corresponds to the compatible condition and the left hand stimulus corresponds to the incompatible condition.

Based on the simulation results reported by Sauser and Billard (2006), it was hypothesized that participants would show faster responding to the compatible than to the incompatible stimulus when tested for spatial or imitative compatibility with a S-R task. By contrast, participants tested for spatial compatibility with an OS-R task would show a reverse compatibility effect, whereas participants tested for imitative compatibility would not show this effect. This predicted dissociation in the results for spatial and imitative compatibilities would counter recent claims that the mechanisms responsible for automatic imitation are no different than those responsible for other forms of stimulus–response compatibility.

2. Experiment 1: spatial compatibility

In this experiment, participants were instructed to respond to the tapping of either the index or middle finger of a hand seen on a computer screen by pressing a key with their index or middle finger of their right

hand. The imperative stimulus was the anatomical identity of the finger, and the task irrelevant stimulus was the left–right spatial position of the finger. Based on previous research (e.g., Hedge & Marsh, 1975) and the Sauser and Billard (2006) model, we predicted a standard spatial compatibility effect in the S–R task, but a reverse compatibility effect in the OS–R task.

2.1. Participants

Twenty-four undergraduate students (13 female; 11 male) between the ages of 18- and 28-years ($M = 19.8$ -years) participated. Participants were naive to the purpose of the study and were awarded course credit for participating.

2.2. Stimuli

The stimuli consisted of six-frame animation sequences of a left or right human hand with either the index or middle finger tapping downward. The sequence began with the fingers spread apart and the hand at rest for 533 ms, and continued over the next three 38 ms frames to depict the finger tapping down incrementally, followed by a frame with the finger in its final position for 886 ms; the last frame showed a black screen for 1467 ms which corresponded to the inter-stimulus-interval (see Fig. 1). Each trial lasted a total of 3 s. Participants responded by pressing the '1' or the '3' key on the keyboard number pad with the index or middle finger of their right hand. E-Prime software (Psychology Software Tools, Pittsburgh, PA) was used for stimulus presentation and data collection.

Participants were seated at a comfortable distance approximately 60 cm from the computer screen. The hand displayed on the screen measured a visual angle of approximately 15° horizontally and 8° vertically, and it was embedded in a black rectangle measuring approximately 20° × 13°. Over the course of five frames, the index or middle finger was displaced downward by approximately 2.5° of visual angle.

2.3. Procedure and design

Participants were instructed to respond as soon as they detected the finger moving. They responded to the anatomical identity of the tapping index or middle finger stimulus with the index or middle finger of their right hand. In the S–R task, participants responded with the same finger they observed tapping. The left hand stimulus was spatially compatible with the response, whereas the right hand stimulus was spatially incompatible (see Fig. 2). In the OS–R task, participants responded with the opposite finger (e.g., participants responded to a tapping index finger with their middle finger). The right hand stimulus was spatially compatible with the response, whereas the left hand stimulus was spatially incompatible (see Fig. 2). Participants were evenly assigned to S–R and OS–R conditions.

Participants completed 20 blocks of 20 trials. The order of the stimuli was random within each block, as long as the number of left and right hand trials crossed with the number of index and middle finger trials remained equal. Before the experiment, participants completed 12 practice trials; three each with the index and middle fingers on both hands, in random order, with feedback regarding accuracy and response time (RT).

3. Results and discussion

3.1. Mean response times

Practice trials, error trials, and trials with RTs less than 200 ms or greater than 1200 ms (0.5% and 0.9%, respectively) were excluded from all RT analyses. A 2 × 2 mixed model Analysis of Variance (ANOVA) with mean RT as the dependent variable was conducted. Task (S–R vs. OS–R) was the between-subject variable, and spatial

compatibility (compatible vs. incompatible) was the within-subjects variable. As can be seen in Fig. 3, response times in the S–R task were significantly faster than in the OS–R task, $F(1, 22) = 22.06$, $p < .001$, $\eta_p^2 = .501$. Crucially, there was also a significant task by compatibility interaction, $F(1, 22) = 23.12$, $p < .001$, $\eta_p^2 = .512$. An analysis of the simple main effects indicated that response times in the S–R task were faster on compatible than on incompatible trials, $F(1, 22) = 14.56$, $p < .001$, $\eta_p^2 = .398$, whereas response times in the OS–R task showed a reverse compatibility effect (i.e., response times were faster in the incompatible than in the compatible condition), $F(1, 22) = 8.91$, $p = .007$, $\eta_p^2 = .288$. The main effect of compatibility was non-significant, $F(1, 22) = .35$, $p = .563$, $\eta_p^2 = .015$, primarily because the effect of spatial compatibility was reversed in the OS–R task.

3.2. Error rates

A second 2 × 2 mixed model ANOVA was conducted with mean percentage of errors as the dependent variable. Errors in the OS–R task were significantly higher than in the S–R task ($M_s = 8.9\%$ and 4.2% for OS–R and S–R tasks, respectively), $F(1, 22) = 6.56$, $p = .018$, $\eta_p^2 = .230$. There was also a significant task by compatibility interaction, $F(1, 22) = 23.36$, $p < .0001$, $\eta_p^2 = .515$. In the S–R task, errors on incompatible trials were higher than on compatible trials ($M_s = 0.8\%$ and 7.6% for compatible and incompatible, respectively), $F(1, 22) = 9.54$, $p = .005$, $\eta_p^2 = .302$, whereas, in the OS–R task, errors on compatible trials were higher than on incompatible trials ($M_s = 13.2\%$ and 4.7% for compatible and incompatible, respectively), $F(1, 22) = 14.04$, $p = .001$, $\eta_p^2 = .390$. The main effect of compatibility was non-significant, $F(1, 22) = .22$, $p = .646$, $\eta_p^2 = .010$. In sum, the pattern of errors across conditions was similar to that of RTs, thus confirming that the results were not attributable to a speed–accuracy trade-off.

3.3. Response time distributions

A quantile analysis (Ratcliff, 1979) was performed to examine the time course of the spatial compatibility effects within trials. For both S–R and OS–R tasks, each participant's RTs on compatible and incompatible trials were ordered from fastest to slowest and evenly divided into quintiles or five proportional bins. Spatial compatibility was calculated for each quintile as the mean difference in response times between compatible and incompatible trials. A 2 × 5 mixed model ANOVA was conducted with spatial compatibility as the dependent variable, task (S–R vs. OS–R) as the between-subjects variable, and quintile (bins 1–5) as the within-subjects variable. As Fig. 4 illustrates, the difference in spatial compatibility increased with each quintile, $F(4, 88) = 2.49$, $p = .049$, $\eta_p^2 = .102$, but the direction of this difference differed for the two tasks, $F(1, 22) = 19.89$, $p < .001$, $\eta_p^2 = .475$. As a consequence, there was also a task by quintile interaction, $F(4, 88) = 12.28$, $p < .001$, $\eta_p^2 = .358$.

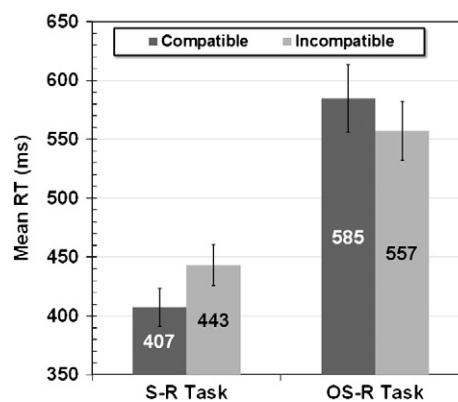


Fig. 3. Mean response times (ms) to spatially compatible and incompatible stimuli as a function of task in Experiment 1. (Error bars represent \pm standard error of the mean.)

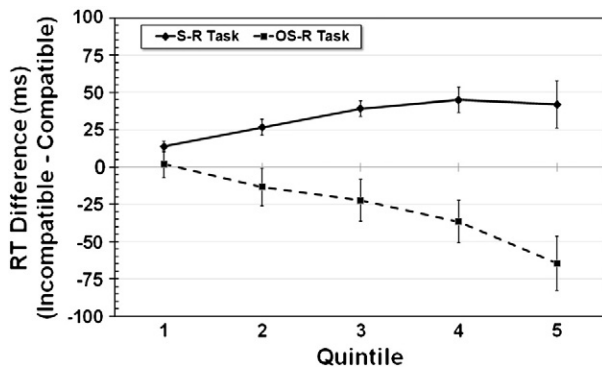


Fig. 4. Mean response times (ms) of the spatial compatibility effect (Incompatible RT – Compatible RT) across quintiles ranging from fastest to slowest RTs in Experiment 1. (Error bars represent \pm standard error of the mean).

Follow-up analyses revealed a significant positive linear trend for quintiles in the S–R task, $F(1, 11) = 4.96, p = .048, \eta_p^2 = .311$, and a significant negative linear trend in the OS–R task, $F(1, 11) = 14.54, p = .003, \eta_p^2 = .569$.

3.4. Discussion

The results from the S–R task replicate previous findings showing that participants instructed to imitate a tapping finger respond faster when the position of the imperative stimulus and the response spatially correspond than when they do not (e.g., Bertenthal et al., 2006). In this experiment, the spatial position of the stimulus was task irrelevant and yet it still interacted with response times, which is exactly what is predicted by the Simon effect (Simon, 1969; Simon & Rudell, 1967). The results from the OS–R task were somewhat novel in that participants had not been previously tested in this paradigm with the specific stimuli and responses that were used. Nevertheless, the pattern of performance was completely consistent with previous OS–R studies reporting a reverse compatibility effect (e.g. Hedge & Marsh, 1975). Moreover, the response times in the OS–R task were significantly longer than in the S–R task, which is consistent with the hypothesis that this task involves additional processing time to recode the stimulus. It is noteworthy that the increase in processing times ranged between 114 and 182 ms which represents between 26 and 45% more processing time needed for responding than in the S–R task. This difference represents a substantial increase in processing time suggesting that the recoding of the imperative stimulus is extremely demanding (which we return to in the General discussion).

The findings from the RT distributions suggest that the compatibility and reverse compatibility effects increase as RTs slow down. The direction of this effect may seem surprising since it is typically reported that the Simon effect and its reversal will decrease with slower response times, presumably because the priming becomes effective very soon after stimulus onset and then dissipates quickly. Evidence for these transient characteristics was first reported by Simon, Acosta, Mewaldt, and Speidel (1976) who showed that the effect disappears when the response is delayed by as little as 350 ms. In spite of this evidence, a recent review of RT distribution analyses of spatial correspondence effects suggests that the direction of the effect is not as consistent as once presumed (Proctor, Miles, & Baroni, 2011). Although the compatibility effect typically decreases with increasing response times for the standard left–right Simon effect, it remains stable or increases across the RT distribution for the vertical Simon effect, object-based or word-based Simon effects, and when responses are made with crossed hands.

According to Proctor et al. (2011), our current understanding of changes in the Simon effect across RT distributions is incomplete, and it is therefore difficult to predict when and why the compatibility

effect will increase or decrease. Nevertheless, they state that “the results for variants of the spatial Simon task are reliable and likely representative of the temporal properties of response activation” (p.263). Given that the difference in RT distributions across the two tasks in the current experiment continued to increase across quintiles (albeit in opposite directions), these results offer further evidence that the compatibility effects persist through the slowest response times in both tasks (S–R task last quintile $M_s = 533.4$ and 595.5 ms for compatible and incompatible response times, respectively; OS–R task last quintile $M_s = 826.8$ and 762.3 ms for compatible and incompatible response times, respectively).

4. Experiment 2: imitative compatibility

The first experiment confirmed that a reverse compatibility effect occurs with the OS–R task. A similar finding in this experiment would suggest little or no difference between spatial and imitative compatibility. Alternatively, no evidence of a reverse compatibility effect would suggest that the two stimulus–response compatibility effects are dissociable and would thus provide empirical support for the hypothesis that automatic imitation and spatial compatibility are mediated by different processes.

4.1. Participants

Twenty-four undergraduates (15 female; 9 male) between 18- and 26-years ($M = 19.7$ -years) participated. Four additional participants, all of whom were assigned to the OS–R task, were excluded because they made errors on 30% or more of the trials, suggesting they misunderstood the task or became confused during testing. None of the participants were tested in the previous experiment.

4.2. Stimuli

The stimuli were the same used in the previous experiment.

4.3. Procedure and design

Participants were instructed to respond to the left–right position of the tapping index or middle finger with the index or middle finger of their right hand. In the S–R condition, participants responded with the spatially corresponding finger (e.g., participants responded to a tapping finger on the left with their index finger). The left hand stimulus was imitatively compatible with the response, whereas the right hand stimulus was imitatively incompatible with the response (see Fig. 2). In the OS–R condition, participants responded with the opposite finger (e.g., participants responded to a tapping finger on the left with their right middle finger). The right hand stimulus was imitatively compatible with the response, whereas the left hand stimulus was imitatively incompatible with the response (see Fig. 2). Participants were assigned evenly to S–R and OS–R conditions. All other procedural and design details were the same as described for Experiment 1.

5. Results and discussion

5.1. Mean response times

Practice trials, error trials and trials with RTs less than 200 ms and greater than 1200 ms (0.6% and 0.7%, respectively) were excluded. A 2×2 mixed design ANOVA revealed a significant effect for compatibility, $F(1, 22) = 9.00, p = .007, \eta_p^2 = .290$ (see Fig. 5). RTs were faster when participants responded to the imitatively compatible than to the imitatively incompatible tapping finger. The effect of task was not significant, $F(1, 22) = .366, p = .551, \eta_p^2 = .016$, nor was the task by compatibility interaction, $F(1, 22) = 2.27, p = .146, \eta_p^2 = .094$. Nevertheless, the compatibility effect was significant in the S–R condition, $F(1, 22) = 10.15, p = .004, \eta_p^2 = .316$, but not in the OS–R condition, $F(1, 22) =$

1.12, $p = .302$, $\eta_p^2 = .048$. Taken together, these results indicate that there was no reverse compatibility effect in the OS–R condition.

5.2. Error rates

Mean percentage of errors was lower when the stimulus was imitatively compatible than when the stimulus was not ($M_s = 3.2\%$ and 5.6% for compatible and incompatible stimuli, respectively), $F(1, 22) = 4.70$, $p = .04$, $\eta_p^2 = .176$. The effect of task was not significant, $F(1, 22) = .197$, $p = .661$, $\eta_p^2 = .009$, nor was the task by compatibility interaction, $F(1, 22) = .001$, $p = .981$, $\eta_p^2 < .001$. In spite of this non-significant interaction, the simple effect for compatibility was significant in the S–R condition ($M_s = 2.8\%$ and 5.2% for compatible and incompatible stimuli, respectively), $F(1, 22) = 6.04$, $p = .022$, $\eta_p^2 = .215$, but was not in the OS–R condition ($M_s = 3.6\%$ and 5.9% for compatible and incompatible, respectively), $F(1, 22) = 1.38$, $p = .25$, $\eta_p^2 = .059$. As in the previous experiment, these results mirror the response time results and confirm that they were not attributable to a speed–accuracy trade-off.

5.3. Response time distributions

A 2×5 mixed model ANOVA with compatibility effect as the dependent variable revealed a significant effect for quintile, $F(4, 88) = 4.47$, $p = .002$, $\eta_p^2 = .169$ (see Fig. 6). Unlike the previous experiment, the compatibility effect did not differ by task, $F(1, 22) = 1.73$, $p = .202$, $\eta_p^2 = .073$, although the task by quintile interaction was significant, $F(4, 88) = 3.33$, $p = .014$, $\eta_p^2 = .131$. As can be observed in Fig. 6, there was a significant linear trend across quintiles for the S–R task, $F(1, 11) = 12.04$, $p = .005$, $\eta_p^2 = .522$, but not for the OS–R task, $F(1, 11) = .04$, $p = .838$, $\eta_p^2 = .004$.

5.4. Comparison of RTs in Experiment 1 vs. Experiment 2

The results from the current and preceding experiment were compared in a $2 \times 2 \times 2$ mixed design ANOVA with mean response time as the dependent variable. Compatibility (compatible vs. incompatible) was the within-subject variable, and task (S–R vs OS–R) and Experiment (1 vs. 2) were the between-subject variables. Response times were faster on compatible than on incompatible trials, $F(1, 44) = 6.75$, $p = .013$, $\eta_p^2 = .133$, faster in Experiment 2 than in Experiment 1, $F(1, 44) = 5.26$, $p = .027$, $\eta_p^2 = .107$, and faster in the S–R than in the OS–R task $F(1, 44) = 13.47$, $p = .001$, $\eta_p^2 = .234$. There was also an experiment \times task interaction, $F(1, 44) = 7.79$, $p = .008$, $\eta_p^2 = .150$, due to significantly slower RTs in the OS–R condition of Experiment 1 relative to the other three conditions (all $F_s \geq 12.93$, all $p_s \leq .001$), and no other differences between conditions (all $F_s \leq 1.09$, all $p_s \geq .31$). This analysis also revealed a task by compatibility interaction, $F(1, 44) = 19.15$, $p < .001$, $\eta_p^2 = .303$, and a task by compatibility by experiment

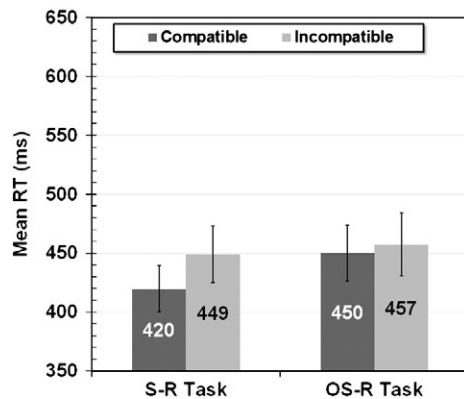


Fig. 5. Mean response times (ms) to imitatively compatible and incompatible stimuli as a function of task in Experiment 2. (Error bars represent \pm standard error of the mean.).

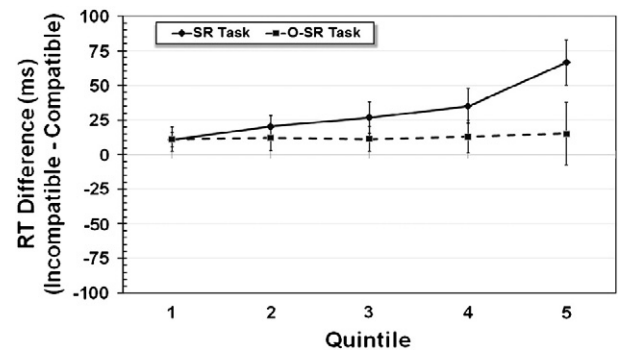


Fig. 6. Mean response times (ms) of the imitative compatibility effect (Incompatible RT–Compatible RT) across quintiles ranging from fastest to slowest RTs in Experiment 2. (Error bars represent \pm standard error of the mean.).

interaction, $F(1, 44) = 4.70$, $p = .036$, $\eta_p^2 = .096$. These interactions were due to the reversed spatial compatibility effect in the OS–R condition of Experiment 1, and either no effect or a compatibility effect in each of the other three conditions.

5.5. Discussion

The results from this second experiment differ in one significant way from those of the first experiment. In the S–R task, participants responded faster to the spatial location of the tapping finger when it was imitatively compatible than when it was not. This result was expected given that it is consistent with previous studies of automatic imitation. In the OS–R task, participants also responded faster to the imitatively compatible than to the imitatively incompatible finger, although this difference was non-significant. Nevertheless, this latter result contrasts sharply with the analogous result from the first experiment in which participants showed a reverse compatibility effect when tested for the effects of spatial compatibility. The results from the RT distribution analysis converge in showing that there is no evidence of a reverse compatibility effect in this experiment, even at the slowest response times; thus, it does not appear that the failure to observe this effect was attributable to the need for additional processing time.

In spite of these results, we do not want to suggest that it is impossible to observe a reverse compatibility effect in response to human movements. In fact, a reversal has been reported when the context of the task shifts participants' attentional or intentional set from imitation to communication or some other complementary action (Liepelt, Prinz, & Brass, 2010; van Schie, van Waterschoot, & Bekkering, 2008). For example, observing a photograph of a hand in a typical handshake gesture is more likely to prime a complementary action with the opposite hand than an imitative action with the same hand (Liepelt et al., 2010). By contrast, the context in the current experiment was completely neutral since participants observed a hand at rest and were instructed to respond with their index or middle finger based on the left–right position of the tapping finger. Nothing was mentioned about an imitative, communicative, or complementary action. Nevertheless, participants responded faster to the task irrelevant, but compatible matching finger movement in the S–R task suggesting that imitation was automatically activated. By contrast, participants did not show a reverse compatibility effect in the OS–R task which would have suggested that a complementary action was also automatically activated.

The failure to find a reverse compatibility effect for automatic imitation in the OS–R task suggests that the single route model proposed by Sausser and Billard (2006) for explaining spatial compatibility does not generalize to imitative compatibility. Instead, it appears that their direct matching model is needed to explain these results. As previously discussed, this model predicted no reverse compatibility effect for automatic imitation, and the current results confirm this prediction. The main

difference between this model and the single route model is the inclusion of a direct pathway between the observation of actions and a motor plan, as suggested by the neurophysiological evidence for a direct matching system (e.g., Rizzolatti & Craighero, 2004; Rizzolatti et al., 2001). This finding of the need for two different models to explain the results for spatial and imitative compatibilities is the type of evidence that we claimed was necessary for establishing a dissociation between spatial and imitative compatibilities.

6. General discussion

The findings from these two experiments converge to show that imitative compatibility and spatial compatibility are not mediated by the same domain-general process. Two specific results are especially noteworthy.

6.1. One vs. two pathways

Whereas spatial compatibility reversed in the OS–R condition of Experiment 1, imitative compatibility did not reverse in the comparable condition of Experiment 2. In the case of spatial compatibility, the empirical results support the single route model proposed by Sauser and Billard (2006). It seems reasonable to conclude that the relevant (finger identity) and irrelevant (spatial position) stimulus information were decoded separately and simultaneously during a first stage, and then were processed by a cognitive recoding and decision stage in preparation for executing a motor response. Consistent with previous interpretations (e.g., DeJong, Liang, & Lauber, 1994; Wühr & Biebl, 2009), we surmise that responding to the stimulus cue opposite to the one that appears on the screen requires a logical recoding of the relevant stimulus and that this recoding carries-over to the irrelevant stimulus as well. This carry-over effect explains why spatial compatibility is reversed in the OS–R condition.

In the case of imitative compatibility, the results are consistent with the second model proposed by Sauser and Billard (2006), which suggests that there are two separate pathways activating the response. The first pathway corresponds to the regime already described for the spatial compatibility condition. The second pathway corresponds to a direct route between the observation of a finger movement and the preparation of a response by the same finger, presumably because the observation and execution of the action share a common representation (e.g., Craighero, Metta, Sandini, & Fadiga, 2007; Hurley, 2008; Prinz, 1997). In the OS–R condition, the excitation by this second pathway will offset the reversal of the compatibility effect that occurs in the first pathway. As a consequence, the reverse compatibility effect is eliminated in the automatic imitation condition. Given that the results from these two sets of experiments necessitate different processing models, they clearly challenge the claim that the same underlying processes are responsible for automatic imitation as well as other stimulus–response compatibility effects.

6.2. Response time differences associated with logical recoding

The second noteworthy result is that the response times for testing spatial compatibility were between 110 and 180 ms longer in the OS–R condition than in S–R condition. We hypothesize that this increase is due primarily to the differences associated with the recoding of the two imperative stimuli. It appears that the recoding of the anatomical identity of the stimulus finger requires significantly more time than the recoding of the left–right spatial position. Although differential encoding of the two stimuli might have also contributed to this difference, the results revealed that there was no significant difference in responding to the imitative and spatial cues in the S–R condition where no recoding was necessary (407 vs. 420 ms in the compatible condition, $t(22) = .51, p = .616$; 443 vs. 449 ms in the incompatible condition, $t(22) = .32, p = .753$). It thus appears that it is specifically

the cognitive recoding of the anatomical identity of the stimulus finger that is responsible for the additional processing time.

Logically, this increase could also be attributed to recoding at the response level, but participants were explicitly instructed to respond to the opposite stimulus. As such, we assume that most, if not all, participants recoded the stimulus first and then responded, as opposed to first selecting the response and then recoding it before responding. If participants had selected a response first and then recoded it, there would not be any reason to expect longer response times in the OS–R than in the S–R task, because recoding in both tasks would be identical (i.e., responding by pressing the opposite key). Contrary to this finding, responding to the opposite finger required significantly more time than responding to the opposite spatial position.

This finding suggests a second dissociation in the processing of spatial and imitative stimuli, but this dissociation is qualitatively different from the previous one. Whereas the predicted dissociation concerned the response time differences resulting from the task irrelevant and automatic stimulus effects, these latter differences involved the intentional response to the relevant stimuli. Given that the RT differences in recoding the stimulus cues are not attributable to differences in stimulus encoding, they provide additional evidence that the underlying processes responsible for the S–R mapping by spatial and imitative cues are dissociable. In this case, however, the findings suggest differences associated with the logical recoding of the imperative stimulus. It seems likely that the time required for this recoding is at least partly attributable to the strength of the association between the stimulus and the response. If the observation of the finger in the imitative cue condition automatically activates a matching response, then the recoding of the stimulus also requires inhibition of the initial prepotent response as well as activation of a new response. For example, the observation of an index finger automatically activates the index finger in the participant, but this stimulus will need to be recoded as the middle finger which will also require inhibiting the index finger before executing a middle finger response. By comparison, the automatic spatial S–R association elicited in the spatial cue condition is presumably not as strong, and thus the time necessary to recode the stimulus and execute the response is significantly less.

In sum, the evidence from these two experiments suggests that the processing of spatial compatibility and automatic imitation is dissociable at two different levels in dual processing models of S–R compatibility (e.g., DeJong et al., 1994; Tagliabue, Zorzi, Umiltà, & Bassignani, 2000). These models include both short-term or conditional S–R connections which are associated with an intentional response as well as long-term or unconditional S–R connections which are either compatible or incompatible with the controlled response. It has proved difficult to show any differences in the processing of spatial vs. imitative compatibility when testing with the standard S–R task in a stimulus–response compatibility paradigm because both stimuli show analogous compatibility effects. By contrast, testing spatial and imitative compatibilities with an OS–R task reveals differences at the level of both automatic as well as controlled processes.

6.3. Converging evidence for a dissociation between spatial and imitative compatibilities

The current findings thus represent compelling evidence for a dissociation between spatial and imitative compatibilities. This result was foreshadowed by previous findings in our lab revealing that imitative compatibility effects were attenuated or eliminated by perturbing the naturalness of the stimulus, whereas spatial compatibility was not affected by these perturbations (Longo & Bertenthal, 2009; Longo, Kosobud, & Bertenthal, 2008). For example, the facilitating effects of observing a task irrelevant moving finger were eliminated when the finger appeared to move in a biomechanically impossible manner, yet the response was still facilitated by this same finger when it was spatially compatible (Longo et al., 2008). In addition, we previously reported differences in the time course over trials for spatial and imitative compatibilities

(Bertenthal et al., 2006). In these previous studies, these results were incidental and thus did not receive much attention; nevertheless, they are clearly consistent with the current findings. Likewise, a recent study by Wiggett, Hudson, Tipper, and Downing (2011) reveals a dissociation between the ability to learn incompatible associations between actions and human movements and the inability to learn incompatible associations between actions and spatial relations.

One last source of evidence suggesting a dissociation between imitative and spatial compatibilities concerns recent findings showing that imitative compatibility is modulated by the inferred goals and intentions associated with perceived movements (e.g., Liepelt, von Cramon, & Brass, 2008). By contrast, it is difficult to imagine how this sort of mental state attribution would affect spatial compatibility since this process applies equally to both human and non-human movements. Furthermore, inferred intentions modulate the likelihood of infants as young as 7 months of age imitating an observed reach (Hamlin, Hallinana, & Woodward, 2008), whereas we know of no evidence of spatial correspondence modulating reaching performance at such a young age. This sort of evidence was recently reviewed by Teufel, Fletcher, and Davis (2010) who concluded that the perception of others' movements is influenced by a bidirectional process involving bottom-up processing of sensory information as well as top-down processing of mental states. The authors argue that this interactive process is important for ensuring that the percept encapsulates socially relevant information that is not directly perceived, but rather depends on the observers' beliefs about the intentionality and animacy of the observed movements. Whereas this interactive process should modulate automatic imitation (Teufel et al., 2010), there is no obvious reason why it would modulate the effects of spatial compatibility.

6.3. Can associative learning explain differences in spatial and imitative compatibilities?

One final issue concerns how best to interpret the differences between spatial and imitative compatibilities that were reported in this paper. Our view is that these differences suggest that automatic imitation and spatial compatibility are mediated by different processes. Yet, Catmur and Heyes (2011) argue otherwise based on results from the time course for both imitative and spatial compatibilities measured with a S–R compatibility paradigm involving an abduction of the little or index finger. This conclusion is somewhat surprising given that the results from this study reveal within trial differences for spatial and imitative compatibilities. More specifically, the effects of spatial compatibility emerge earlier than the effects of imitative compatibility, but these latter effects continue to increase for a longer period of time.

In spite of these differences, Catmur and Heyes (2011) suggest that the same process of associative learning between sensory representations (movement or spatial location) and motor representations (same movement or response in same location) could result in the imitative and spatial compatibility effects. Their explanation for why the two compatibility effects are processed at different rates is because the inputs are different and it takes longer to encode a body part than a position in space. Although this hypothesis is plausible, it lacks empirical support; moreover, the findings from the current study showing no difference in response times for encoding spatial vs. imitative cues are inconsistent with this prediction. More importantly, this proposal for a general mechanism seems to confuse how these S–R associations are initially learned with how these long-term S–R connections are assembled with other processes and contribute to response selection in a stimulus–response compatibility paradigm. As we've demonstrated in this paper, the effect of spatial compatibility on response times is consistent with a single route model, whereas the effect of imitative compatibility is consistent with a dual route model.

Although we question whether associative learning represents a general mechanism that can explain the differences between imitative and spatial compatibilities, we agree with Catmur and Heyes (2011) that this mechanism is very likely responsible for the development of S–R connections. It does not necessarily follow, however, that all S–R associations share the same connection strength, are modified equally by learning and experience, or interact with the response in the same way (Wiggett et al., 2011). Sauser and Billard (2006) specifically proposed that spatial compatibility could be modeled by integrating long-term spatial correspondence connections with other short-term or controlled connections to select the response, whereas imitative compatibility could be modeled by not integrating long-term imitative connections with other short-term S–R connections; instead these two processes proceed independently and converge at the final output. In contrast to the proposal by Catmur and Heyes (2011), this model was able to make specific predictions which we have now validated.

One limitation of the Sauser and Billard (2006) is that it is essentially qualitative and lacks sufficient specificity to make any novel predictions. For example, this model is not capable of predicting the effects of the RT distribution analyses revealing that both spatial and imitative compatibilities increase as a function of response time. We recently developed a preliminary version of a connectionist model capable of making more quantitative predictions for spatial and imitative compatibilities in S–R and OS–R tasks (Boyer, Scheutz, & Bertenthal, 2009), but a complete model capable of predicting compatibility effects for RT distributions as well as making novel predictions is still being developed.

6.4. Conclusion

In sum, automatic imitation or imitative compatibility measured in a stimulus–response compatibility paradigm provides unequivocal evidence that action observation automatically activates corresponding motor programs. Some critics have cautioned that the mechanisms responsible for imitative compatibility are no different than those responsible for other forms of stimulus–response compatibility. Contrary to this criticism, the current findings reveal significant differences between spatial and imitative compatibilities that were predicted by two distinct processing models. It is therefore concluded that automatic imitation is not reducible to other forms of stimulus–response compatibility, and instead is mediated by a specialized network of processes consistent with those theories advocating a shared representation between the observation and execution of actions.

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