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Imitative Response Tendencies Following Observation of Intransitive Actions

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Clear and unequivocal evidence shows that observation of object affordances or transitive actions facilitates the activation of a compatible response. By contrast, the evidence showing response facilitation following observation of intransitive actions is less conclusive because automatic imitation and spatial compatibility have been confounded. Three experiments tested whether observation of a finger movement (i.e., an intransitive action) in a choice reaction-time task facilitates the corresponding finger movement response because of imitation, a common spatial code, or some combination of both factors. The priming effects of a spatial and an imitative stimulus were tested in combination (Experiment 1), in opposition (Experiment 2), and independently (Experiment 3). Contrary to previous findings, the evidence revealed significant contributions from both automatic imitation and spatial compatibility, but the priming effects from an automatic tendency to imitate declined significantly across a block of trials whereas the effects of spatial compatibility remained constant or increased slightly. These differential effects suggest that priming associated with automatic imitation is mediated by a different regime than priming associated with spatial compatibility.

Keywords: imitation, response priming, intransitive actions, common coding, mirror neurons

The human tendency to mimic actions performed by others has long been noted in studies of normal and abnormal behavior. Charles Darwin (1872/1965), for example, commented that at leaping matches spectators would move their own feet as if imitating the athletes. More recently, Dijksterhuis and Bargh (2001) noted that we tend to whisper or speak louder when others do, scratch our head upon seeing someone else scratch, walk slower in the presence of elderly individuals, and cycle faster after seeing a cycling race on TV. Evidence for automatic imitation has also been observed in pathological conditions, such as autism (Fay & Hatch, 1965), schizophrenia, and catatonia (Ford, 1991); certain abnormal startle reactions or hyperekplexias (Beard, 1880; Ford, 1991; Simons, 1980); Tourette's syndrome (Ford, 1991; Gilles de la Tourette, 1884/1996); postepileptic or confusional states (Schneider, 1938; Stengel, 1947); dementia or mental retardation (Dromard, 1905; Stengel, 1947); and following lesions of the frontal lobes (De Renzi, Cavalleri, & Facchini, 1996; Lhermitte, Pillon, & Serdaru, 1986). This automatic tendency may contribute 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).

The prevailing interpretation for these effects is that the perception of action automatically activates corresponding motor programs in the observer. Darwin (1872/1965), for example, argued that in man, there is "a strong tendency to imitation, independently of the conscious will" (p. 355). To account for the occurrence of echopraxia in his patients, Dromard (1905) similarly suggested that "a movement that has been perceived tends to pass from the visual center to the motor center" (p. 389 [our translation]). He went further to propose that this latent imitation was an integral part of the mental representation of movement. In recent years, Prinz and colleagues (e.g., Prinz, 1990, 1997; Hommel, Müsseler, Aschersleben, & Prinz, 2001) proposed that observing the effect of an action facilitates its execution because perception and action planning share a common representational code. More specifically, the perception of an event possessing certain features (e.g., a loud sound) will automatically prime those actions that produce the same features (e.g., speaking in a loud voice). This formulation of a common coding framework for the perception and planning of actions is a direct descendent of the ideomotor theory of James (1890) and Greenwald (1970).

Empirical Evidence for Common Coding

Recent neurophysiological, neuroimaging, and behavioral research offer support for a common coding framework. The remarkable discovery of mirror neurons in monkeys provided the first direct evidence that action observation and action execution shared a common neural representation. Mirror neurons, located in ventral premotor area F5, discharge both when the monkey performs specific goal-directed actions and when the monkey observes a human or conspecific perform the same or a similar action (di

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Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Similar properties were observed in inferior parietal area PF, which shares direct connections with F5 (Gallese, Fadiga, Fogassi, & Rizzolatti, 2002). It is important to emphasize that mirror neurons are selective only for goal-directed actions, such as grasping, holding, or manipulating objects, and not for observation of a moving hand or object alone (Rizzolatti, Fogassi, & Gallese, 2001). In other words, mirror neurons in monkeys code for the goals of an observed action but do not code for the means of these actions (Rizzolatti, Fadiga, Fogassi, & Gallese, 2002). Consistent with this finding is that monkeys are capable of emulating observed behaviors but not explicitly imitating them via the same means (Byrne, 2002; Tomasello & Call, 1997; Whiten, 2002). (For a recent exception to this generalization with a nonmotor task, see Subiaul, Cantlon, Holloway, & Terrace, 2004.) Thus, these neurons provide monkeys with a mechanism for action understanding via the observation and simulation of goal-directed actions, but they are apparently insufficient for enabling monkeys to imitate (see Rizzolatti & Craighero, 2004, for a review).

Indirect evidence for a mirror system in humans is provided by a number of electrophysiological and neuroimaging studies revealing that observation of human actions activates a complex network formed by occipital, temporal, and parietal visual areas, as well as two motor regions (e.g., Decety, Chaminade, Grèzes, & Meltzoff, 2002; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Grèzes, Costes, & Decety, 1998; Nishitani & Hari, 2000, 2002; Rizzolatti, Fadiga, Matelli, et al., 1996). These motor regions are the rostral part of the inferior parietal lobule and a frontal region including the lower part of the precentral gyrus (ventral premotor cortex) and the pars opercularis of the inferior frontal gyrus (area 44), part of Broca's area. In conjunction with the superior temporal sulcus (STS), these latter two regions form the neural circuit comprising the mirror system in humans.

Unlike the monkey mirror system, the human analogue also enables imitation because it codes the specific movements that represent the means for achieving goals (Chaminade, Meltzoff, & Decety, 2002; Grèzes, Costes, & Decety, 1999; Iacoboni et al., 1999; Koski, Iacoboni, Dubeau, Woods, & Mazziotta, 2003; Koski et al., 2002). Although the basic circuit underlying imitation coincides with that which is active during action observation, the superior parietal lobule also shows strong activation when the task is to observe an action to repeat it immediately or later (Grèzes et al., 1999; Iacoboni et al., 1999). This division of labor is consistent with the notion that observation of actions activates cortical regions involved in their planning and understanding, but observation of actions for the purpose of imitation is more likely to also activate regions that are directly involved in preparing a specific motor response (Iacoboni, 2005; Rizzolatti & Craighero, 2004). Thus, the neural circuit responsible for imitation appears somewhat more extensive than the circuit involved in the observation and understanding of actions (cf. Arbib, 2005).

Additional evidence for common coding is observed in response to the observation of object affordances. Canonical neurons, also found in macaque ventral premotor area F5, respond selectively to the execution of an object-directed action as well as to an object affording that action (Murata et al., 1997). Neurons with similar properties are observed in inferior parietal area AIP (Sakata, Taira, Murata, & Mine, 1995), which is heavily connected with area F5 (Murata et al., 1997). Neuroimaging studies provide evidence for a homologous canonical system in humans (e.g., Chao & Martin, 2000; Grèzes, Armony, Rowe, & Passingham, 2003; Grèzes & Decety, 2002). Together, these mirror and canonical circuits provide a system for the common coding of goal-directed actions and the observation of these actions or object affordances.

One of the principal sources of behavioral evidence for common coding is based on showing that object affordances or action observation influence the subsequent execution of the relevant action (i.e., visuomotor priming).[1] Tucker and Ellis (1998), for example, measured stimulus–response compatibility from object affordances by instructing participants to respond as quickly as possible to the orientation of a displayed object by pressing a key with their right or left hand. When objects were presented in a horizontal orientation, they afforded a right- or left-hand grasp and response times were faster when the hand responding was compatible with the hand that would grasp the object. Similar object-based visuomotor priming effects were reported by Craighero and colleagues (Craighero, Fadiga, Rizzolatti, & Umiltà, 1998; Craighero, Fadiga, Umiltà, & Rizzolatti, 1996). Visuomotor priming was also observed when grasping a bar in a horizontal or vertical orientation was preceded by a picture of a hand or the observation of an action that was congruent or incongruent with the required grasping action (Castiello, Lusher, Mari, Edwards, & Humphreys, 2002; Edwards, Humphreys, & Castiello, 2003; Vogt, Taylor, & Hopkins, 2003).[2] Collectively, these studies reveal that object affordances or object-directed actions prime the selection and/or execution of a compatible response.

Transitive Versus Intransitive Actions

Whereas priming of a compatible response from the observation of object affordances or transitive actions is supported by both behavioral and neural evidence, the status of response priming following the observation of an intransitive action is more tenuous.[3] As previously discussed, one of the defining characteristics of an observation–execution matching system in monkeys is that mirror neurons in the ventral premotor cortex are not activated unless an action is directed toward a visible or occluded object that was previously seen (Umiltà et al., 2001). If the human mirror system is homologous to the primate system, then we would not

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[1] In this article, *visuomotor priming* refers to the presentation of any visual stimulus that precedes the presentation of an imperative stimulus (signaling the initiation of a response) and also to the presentation of any visual stimulus presented simultaneously with the imperative stimulus. In the latter case, it is assumed that the priming stimulus will activate the planning of a response prior to explicit response selection.

[2] One limitation of these studies is that they lack a baseline and thus it is unclear whether priming is a function of facilitation from compatible responses, inhibition from incompatible responses, or some combination of both processes. Our own findings show that separate assessments of facilitation and inhibition offer valuable insights into how action observation is related to action execution.

[3] There is some confusion in the literature over the meaning of intransitive actions. An *intransitive action* refers to an act that is completed without any accompanying object, regardless of whether the object is real or virtual. Accordingly, most pantomimes involve transitive actions even though no real object is present.

expect to find mirror regions showing increased activation following the observation of gestures or actions that are not object directed. The evidence, however, is inconsistent on this issue. Rizzolatti and Craighero (2004) reported in their recent review of the human mirror system that observation of intransitive actions, such as finger tapping and lifting, do not activate inferior parietal mirror regions but do activate frontal mirror regions (e.g., Buccino et al., 2001; Iacoboni et al., 1999, 2001; Koski et al., 2002, 2003). The ventral premotor mirror region receives visual input for biological movements from the STS, but these regions are connected only indirectly via the inferior parietal lobule. Thus, it is surprising that the perception of intransitive actions would activate frontal mirror regions without correspondingly activating the inferior parietal lobule. Rizzolatti and Craighero suggested that the lack of activation in the inferior parietal lobule may be due to the absence of an object, reducing activation below statistical threshold. Nevertheless, this explanation remains highly speculative and appears inconsistent with the evidence for significant activation in the inferior frontal cortex following observation of intransitive actions. Thus, the finding that the inferior parietal lobule is not activated by intransitive actions represents a conundrum.

A few behavioral studies claim to provide evidence for response priming following the observation of intransitive actions, such as hand opening and closing or finger tapping and lifting (Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschläger, & Prinz, 2000; Stürmer, Aschersleben, & Prinz, 2000). In these experiments, participants were instructed to respond to an imperative stimulus (such as a color or a number) while primed by an irrelevant action in the stimulus display. Brass et al. (2000), for example, instructed participants to lift their index or middle fingers in response to a short video clip of a hand showing the index or middle finger lifting up or a number (*1* or *2*) appearing between the index and middle fingers. Participants were instructed to respond as quickly as possible by matching their response to the lifting finger (imitative cue condition) or to the symbolic cue (*1* = index finger, *2* = middle finger; symbolic cue condition). In addition, on some trials, the irrelevant cue appeared simultaneously with the imperative stimulus, with which it was either congruent or incongruent. The results revealed (a) that in the baseline condition, participants responded faster to the imitative than to the symbolic cue and (b) that irrelevant finger movements facilitated reaction times (RTs) when congruent with the symbolic cue and interfered with RTs when incongruent with the symbolic cue.

Although this experiment has been interpreted as providing evidence for automatic imitation of meaningless actions, this interpretation is somewhat premature because the results were confounded by spatial compatibility. Participants responded with their right hand to a stimulus depicting a left hand that appeared as if it were a mirror image of their own hand (see Figure 1). Thus, the index finger always appeared on the left side and the middle finger always appeared on the right side of the screen, which meant that the stimulus and the index and/or middle response fingers were always spatially compatible.[4] Similar confounds with spatial compatibility appear in other experiments testing visuomotor priming following the observation of meaningless actions (cf. Heyes, Bird, Johnson, & Haggard, 2005).

In sum, the behavioral and neuroimaging evidence supporting the common coding of intransitive actions remains inconclusive. This is not to say that response priming to the observation of intransitive actions is an epiphenomenon. Indeed, there is some indirect evidence for behavioral mimicry or contagion involving meaningless actions or gestures (Blakemore & Frith, 2005; Chartrand & Bargh, 1999). What is currently missing is clear and unequivocal experimental evidence showing that automatic imitation contributes to visuomotor priming following the observation of intransitive actions.

The goal of the current research was to provide a definitive test for evaluating the status of response priming following observation of an intransitive action and also to clarify the relative contributions of a common spatial code and imitation to response priming. To address this question, we adapted the paradigm developed by Brass et al. (2000) to test whether observation of a finger movement primes the finger movement response because of a shared representation for the observation and execution of the action (indexed by imitation), a common spatial code (indexed by spatial compatibility), or some combination of both factors. Three experiments were conducted to assess this relation between imitation and spatial compatibility. Experiment 1 was a replication of Brass et al.'s (2000) paradigm to provide a baseline for the combined effects of imitation and spatial compatibility. Experiment 2 was designed to place spatial compatibility in opposition to imitation as the priming stimulus. Experiment 3 was designed to directly assess the independent contributions of spatial compatibility and imitation to RTs by assessing the priming effects of spatial compatibility with an imitative cue and the priming effects of imitation with a spatial cue. If the strength of the stimulus–response mapping is primarily a function of either imitation or spatial compatibility, then placing them in opposition in Experiment 2 should lead to results showing levels of visuomotor priming comparable to those observed in Experiment 1. If, however, the strength of the stimulus–response mapping is a function of both stimulus cues, then the priming from both stimuli would tend to cancel each other. In this case, the relative contributions of imitation and spatial compatibility would be revealed by the results of Experiment 3, in which imitation and spatial compatibility are assessed separately.

Experiment 1

This first experiment was a replication of Brass et al.'s (2000) Experiment 1 to establish that the effects could be reproduced in our lab and to provide a baseline for the subsequent experiments. We introduced four minor methodological changes to the paradigm. First, the response consisted of finger tapping as opposed to finger lifting. Finger tapping is more common than finger lifting, as it is observed in many activities, such as typing on a keyboard, tapping on a desk, and so forth. Previous studies suggest that familiarity of gestures influences imitation in normal and brain-damaged patients (Goldenberg & Hagmann, 1997; Rumiati & Tessari, 2002). Thus, we considered it valuable to test the generalizability of the previous findings when a more familiar imitative stimulus was used. Second, whereas in the original study responses were measured with a motion tracking system, in this experiment

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[4] This confound was noted by Brass et al. (2000), and they claimed to control for it in Experiment 2; however, as we discuss later in the article, the control for spatial compatibility was insufficient.

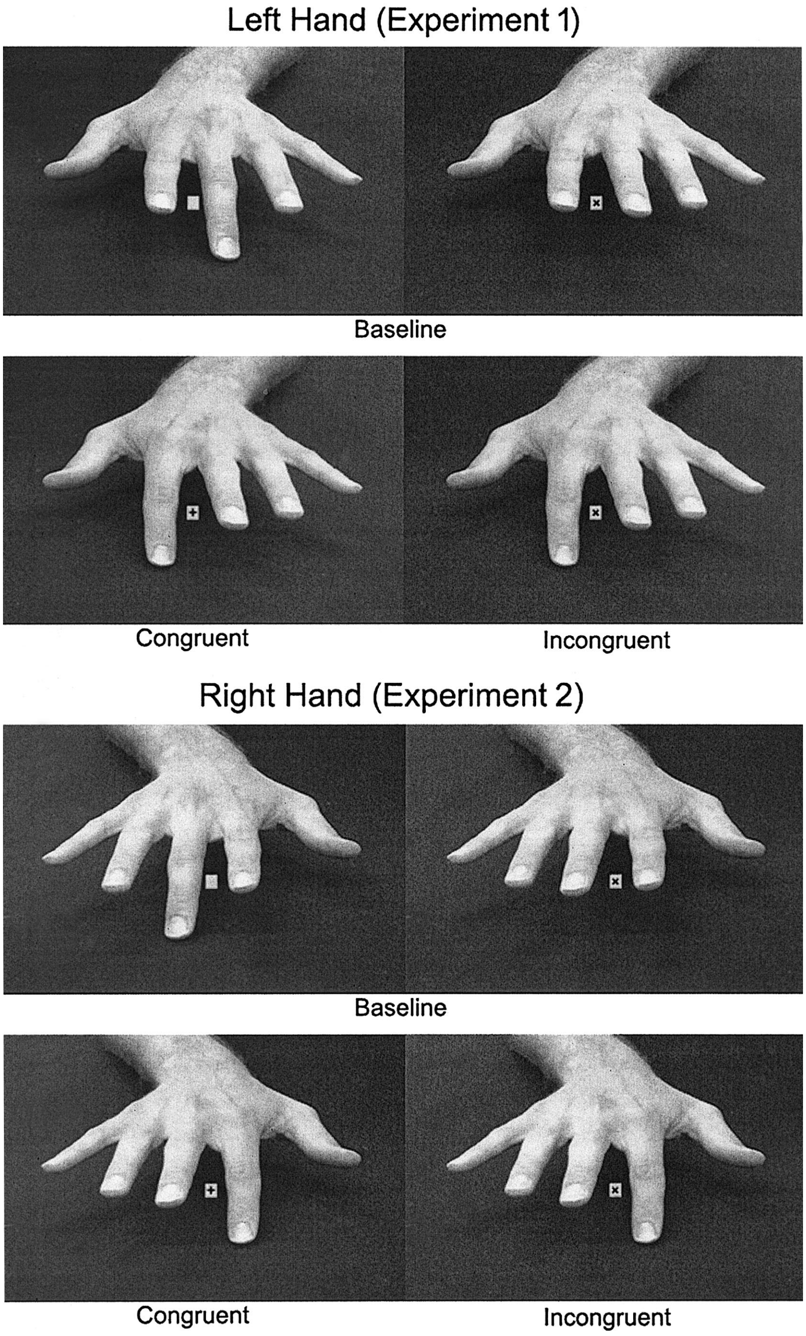

Figure 1. Sample stimulus events for Experiments 1 (top two panels) and 2 (bottom two panels). First row: Stimulus events that appeared as baseline stimuli (only the last frame of the video sequence is shown). The left panel shows one of the two moving finger stimuli, and the right panel shows one of the two symbolic cue stimuli. Second row: Stimulus events in the congruent and incongruent conditions. The left panel shows a congruent stimulus for finger or symbolic cue, and the right panel shows an incongruent stimulus for finger or symbolic cue. Third row: Stimulus events that appeared as baseline stimuli. Fourth row: Stimulus events in the congruent and incongruent conditions. The left panel shows a congruent stimulus that is spatially incompatible with the response, and the right panel shows an incongruent stimulus that is spatially compatible with response.

participants responded by pressing different keys with their index and middle fingers.

The last two changes involved the symbolic cue. First, a box surrounding the symbolic cue was introduced at the onset of the trial instead of approximately 500 ms later when the symbolic cue first appeared. This change was designed to minimize the interfering effect of a visual transient (i.e., the box) appearing with the stimulus cue. The last change was to substitute completely arbitrary symbols for the *1* and *2* used in the original study. Dehaene, Bossini, and Giraux (1993) showed that choice RTs involving numerical magnitudes are faster when the lower magnitude is compatible with the left hand and the higher magnitude is compatible with the right hand—the so-called "SNARC effect." To avoid this potential confound, we substituted + and × for the previously used numbers. Although all of these changes were relatively subtle, there was no empirical or theoretical basis for predicting their effects on the results and thus this replication also served to test the effects of some minor, yet significant, variations in the stimuli as well as responses.

Method

Participants

Twelve students at the University of Chicago between 18 and 25 years of age participated. All were right-handed, naive as to the purpose of the study, and paid for their participation.

Apparatus and Materials

Five-frame video sequences of a hand were displayed on a 43.2-cm computer monitor. Participants were seated at a comfortable distance approximately 60 cm from the monitor. 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° × 13.3°. On those trials involving finger movement, the index or middle finger was displaced downward by approximately 2.5° of visual angle. E-Prime software (Psychology Software Tools, Pittsburgh, PA) was used for stimulus presentation and data collection.

Design and Procedure

The index and middle fingers of the right hand rested on the first two keys of a response box. Responses were executed to two types of stimulus events (see Figure 1). In the finger condition, participants responded by imitating the tapping movement of the index or middle finger of the hand, pressing the first key on the response box with their index finger if the index finger moved down and the second key with their middle finger if the middle finger moved down. In the symbol condition, participants responded to a symbolic cue that appeared in a box (measuring 0.56° × 0.60° of visual angle) between the index and middle fingers of the hand. Participants were required to press the first key with their index finger if a + appeared and the second key with their middle finger if an × appeared. Participants were instructed to respond as quickly and as accurately as possible. On baseline trials, only the relevant stimulus (finger movement or symbol) cue appeared. On congruent and incongruent trials, both the relevant and the irrelevant stimulus cues appeared simultaneously. Congruent and incongruent trials differed only by whether the irrelevant cue indicated the same or a different response as the relevant cue.

The experiment was divided into 24 blocks of 24 trials each. Blocks alternated between finger and symbol conditions. The initial condition was counterbalanced between participants. Each block consisted of 8 baseline, 8 congruent, and 8 incongruent trials, which were randomly ordered. Thus, there were a total of 576 trials, 96 in each of the 6 conditions. Each block was preceded by instructions on the screen reminding participants as to which cue they should respond. The experimental blocks of trials were preceded by two practice blocks (one each for the finger and symbol cues) of 24 trials each. Like experimental blocks, each practice block consisted of 8 baseline, 8 congruent, and 8 incongruent trials, ordered randomly. Practice blocks were not included in the analysis.

The video clips began with a frame showing the hand at rest with the small box midway between the index and middle fingers (see Figure 2). This frame lasted for 533 ms. The next three frames presented the finger moving, the symbol, or both, depending on the condition. Each of these frames lasted 38 ms. A fifth frame showing the finger resting on a surface, the symbol, or both lasted for 886 ms. The video sequence was followed by a blue screen that lasted 1,467 ms. Thus, each trial lasted a total of 3 s.

Results

A repeated measures analysis of variance (ANOVA) was conducted on participant median RT with stimulus cue (finger, symbol) and condition (congruent, baseline, incongruent) as variables. Error trials and trials in which RT was greater than 800 ms were excluded from analysis. There was a significant main effect of stimulus cue, $F(1, 11) = 217.99$, $p < .0001$, indicating that participants responded faster to the finger cue than to the symbolic cue (285 ms vs. 385 ms). There was also a main effect of condition, $F(2, 22) = 21.60$, $p < .0001$. Responses were faster in the congruent (325 ms) than in the baseline (335 ms) or incongruent (345 ms) conditions. Most important, there was a significant interaction between stimulus cue and condition, $F(2, 22) = 17.32$, $p < .0001$, suggesting that facilitation and interference from the irrelevant stimulus differed as a function of stimulus cue (see Figure 3).

When participants responded to the symbolic cue, planned contrasts revealed a significant facilitation effect for the congruent trials relative to the baseline trials (19.42 ms), $F(1, 66) = 36.48$, $p < .0001$, and a significant interference effect for the incongruent trials relative to the baseline trials (19.88 ms), $F(1, 66) = 38.19$, $p < .0001$. Neither a facilitation (0.67 ms), $F(1, 66) = 0.04$, *ns*, nor an interference effect (0.79 ms), $F(1, 66) = 0.06$, *ns*, was observed when participants responded to the imitative cue. Thus, when the relevant cue was the symbol, task-irrelevant finger movements significantly influenced RT. No such effect was found from task-irrelevant symbolic cues.

Overall, errors were made on 3.9% of trials, and data from 0.4% of trials were excluded because of RTs over 800 ms. A repeated measures ANOVA on the percentage of errors revealed main effects of stimulus cue, $F(1, 11) = 12.19$, $p < .01$, and condition, $F(2, 22) = 10.79$, $p < .001$, as well as a significant interaction between cue and condition, $F(2, 22) = 6.38$, $p < .01$. The pattern of errors across conditions was similar to that of the RTs, thus confirming that the results were not attributable to a speed–accuracy trade-off.

Discussion

These findings replicate the results of Brass et al. (2000, Experiment 1), demonstrating priming effects from a task-irrelevant imitative stimulus. Overall, the differences in RTs between the imitative and symbolic cues were very similar between experiments (approximately 100 ms), as was the magnitude of the facilitation and interference effects (approximately 20–30 ms). Thus, neither the change in the response nor the changes in the symbolic and imitative cues significantly influenced the results, confirming that the effect of the imitative cue in this paradigm is neither stimulus nor response specific.

More important, these results confirm that priming is bidirectional, involving both facilitation and interference. In the congru-

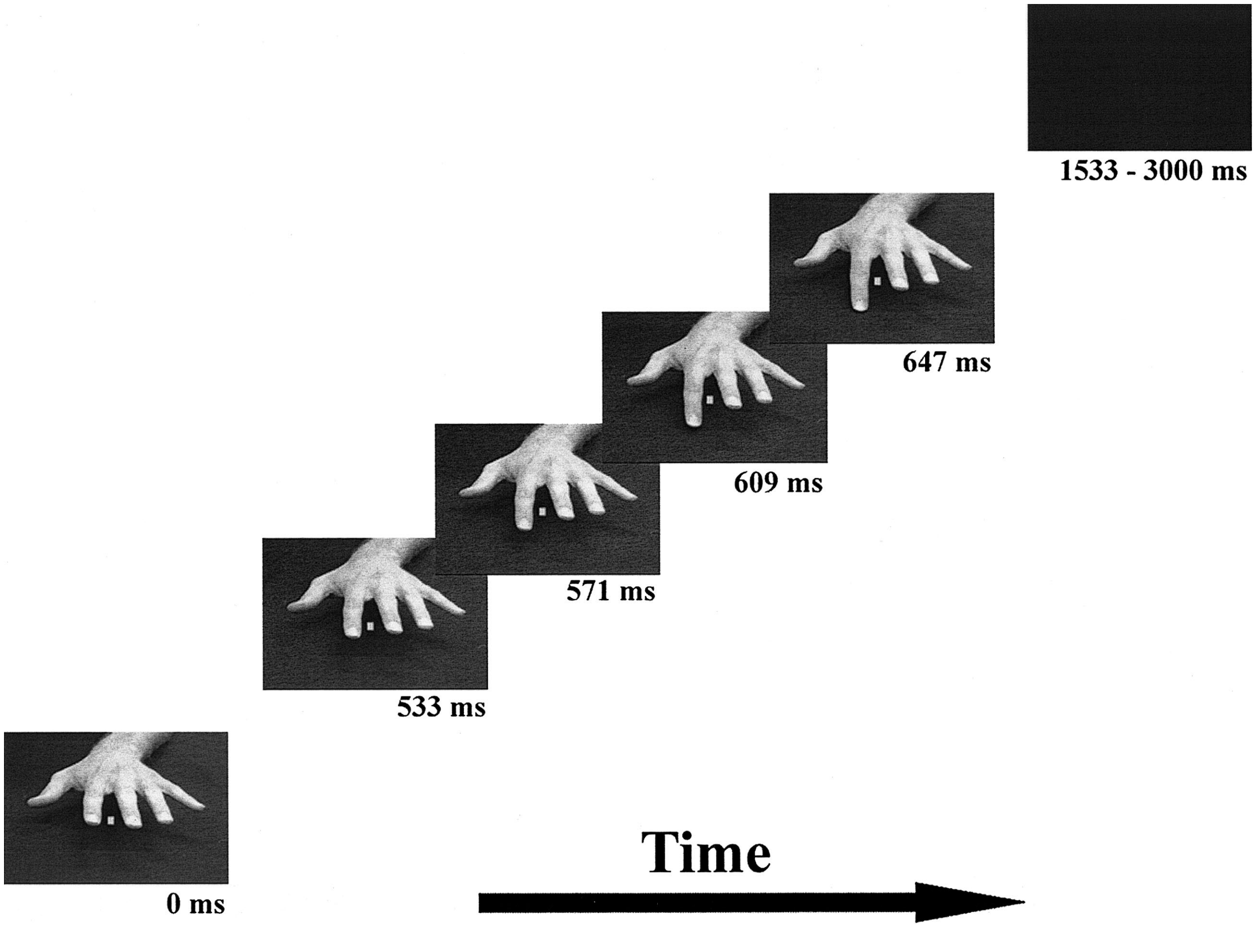

Figure 2. Stimulus sequence for each baseline trial depicting a finger movement. The finger begins moving on the presentation of the second frame at 533 ms and moves incrementally down on the next three frames. The fifth frame is replaced by a blue screen at 1,533 ms into the trial. In the symbolic cue condition, the symbol appears at 533 ms and remains visible until the blue screen appears at 1,533 ms. In congruent and incongruent trials, symbolic and moving finger stimuli appear together at 533 ms.

ent condition, this priming automatically prepares the correct response and results in response facilitation, whereas in the incongruent condition, this priming prepares the incorrect response and results in response interference. The interpretation offered by Brass et al. (2000) for these priming effects is that the finger cue was highly ideomotor compatible with the response because it was mediated via imitation, whereas the symbolic cue did not share any dimensions with the response. A competing interpretation is that the RT advantage for the imitative cue results from spatial compatibility.

As mentioned in the introduction, Brass et al. (2000) acknowledged this confound with spatial compatibility and conducted a second experiment as a control. In this experiment, they substituted a spatial cue, consisting of a black × on the index or middle finger, for the symbolic cue. In essence, the spatial × shares the same spatial compatibility confound as does the imitative cue. If differential responding to the congruent and incongruent stimuli was equivalent in the spatial × and moving finger conditions, then it would seem reasonable to conclude that spatial compatibility was responsible for the results. If, however, the pattern of results were similar to those reported in the first experiment, then spatial compatibility could not account for the effects of the imitative cue. In general, the results were consistent with those from the first experiment, with the exception that the presence of an irrelevant spatial cue did produce significant interference effects in the moving finger condition. Still, an unequivocal interpretation for these results is difficult. Brass et al. matched their cues in terms of spatial similarity, assuming that similarity was the sole determinant of the stimulus–response compatibility effects. The spatial × and moving finger conditions, however, were still markedly different in perceptual salience, and, thus, it is possible that the results were primarily a function of the differential salience of the two stimulus cues (i.e., moving finger vs. ×).

In a related simple RT study, Brass, Bekkering, and Prinz (2001) instructed participants to respond in one block by lifting their finger and to respond in a second block by tapping their finger to the onset of an index finger moving randomly up or down. Thus, the response was directionally compatible or incompatible on each trial, and the results revealed an RT advantage for the spatially compatible responses. In a follow-up experiment, the stimulus

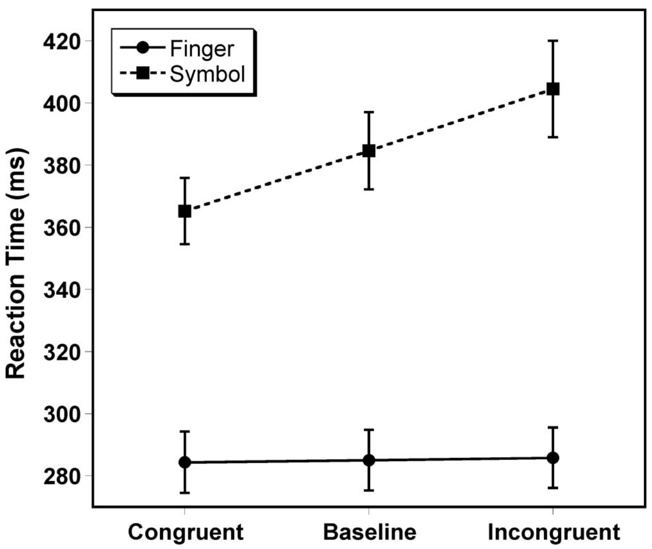

Figure 3. Mean reaction times (in milliseconds) in Experiment 1 as a function of stimulus cue (finger movement or symbol) and condition (congruent, baseline, or incongruent). Error bars represent standard errors of the mean.

hand was flipped upside down to investigate whether the response was a function of the movement type (lifting or tapping) or movement direction. The findings revealed that compatibility of the response with movement type (or imitation) shows a greater effect on RT than does direction, suggesting that automatic imitation primes a response above and beyond the effect of directional compatibility. It remains an empirical question, however, whether these results would generalize to left–right spatial compatibility in a choice RT experiment. Moreover, the interpretation is based on movement direction assuming an environmental frame of reference, whereas movement direction specified by a body-centered frame of reference would lead to the same results reported for movement type. Thus, it is unclear whether participants responded to the direction of movement or to the specified action. The next two experiments were designed to avoid the aforementioned problems and to systematically evaluate the relative contributions of imitation and spatial compatibility to the facilitation and interference of the RT responses.

Experiment 2

The purpose of Experiment 2 was to investigate the contributions of spatial compatibility to the imitative cue while keeping stimulus salience constant. A right hand was substituted for the left-hand stimulus in Experiment 1. In Experiment 1, participants responded with their right hands while a left-hand stimulus was presented, as if they were seeing their own hands in a mirror. Koski et al. (2003) referred to this condition as *specular imitation* and the opposite condition in which a right hand imitates another right hand as *anatomic imitation*. In the specular condition, the relative spatial orientation of the index and middle fingers of the stimulus match those of the observer. In the anatomical condition, the relative spatial position is reversed (see Figure 1, bottom two panels). In Experiment 2, a right- (rather than a left-) hand stimulus was presented, reversing the relative spatial location of the index and middle fingers. As such, the effects of imitation and spatial compatibility were placed in opposition to each other. If the facilitation and interference effects observed in Experiment 1 were due entirely to spatial compatibility, then the facilitation and interference effects in this experiment should be completely reversed relative to Experiment 1. If, however, the effects were due entirely to imitation, then the results should mirror those from Experiment 1.

Method

Participants

Twelve students at the University of Chicago between 18 and 25 years of age participated; none had participated in the previous experiment. All were right-handed, naive as to the purpose of the study, and paid for their participation.

Apparatus and Materials

All materials were identical to those used in Experiment 1.

Design and Procedure

The design and procedure were identical to those of Experiment 1 except that the hand in the video clips was a right hand rather than a left hand.

Results

As in Experiment 1, error trials and trials in which RTs were greater than 800 ms were excluded from analysis. A repeated measures ANOVA was run on participant median RT with stimulus cue (finger, symbol) and condition (congruent, baseline, incongruent) as factors. There was a significant main effect of stimulus cue, $F(1, 11) = 69.99$, $p < .0001$, and a significant main effect of condition, $F(2, 22) = 3.36$, $p = .05$. There was also a significant interaction of cue and condition, $F(2, 22) = 6.46$, $p < .01$, again revealing that the finger cue influenced RTs to the symbolic cue but not vice versa (see Figure 4). It is important to note, however, that the direction of the effects is reversed from those found in Experiment 1. Planned comparisons for the symbolic cue revealed a significant facilitation effect when the irrelevant finger movement was spatially congruent (11.2 ms), $F(1, 66) = 28.09$, $p < .01$, but no interference effect when the irrelevant finger movement was spatially incongruent (2.71 ms), $F(1, 66) = 1.64$, *ns*.

Errors were made on 5.18% of trials, and no trials were excluded for having RTs over 800 ms. An ANOVA on error scores revealed no significant effects of stimulus cue, $F(1, 11) = 0.09$, *ns*; condition, $F(2, 22) = 1.13$, *ns*; or the interaction between these two factors, $F(2, 22) = 0.84$, *ns*.

Baseline RTs to the finger cue were significantly shorter to the left hand (Experiment 1) than to the right hand (Experiment 2), $t(22) = 4.24$, $p < .001$, demonstrating a clear advantage for spatially compatible stimuli. If, however, the effects involving the symbolic cue observed in this experiment and in the study of Brass et al. (2000) were due entirely to spatial compatibility, then the effect size for spatial congruence should have been equivalent for the left and right hands. Comparing the size of the spatial congruence effect (incongruent – congruent) between Experiments 1 and

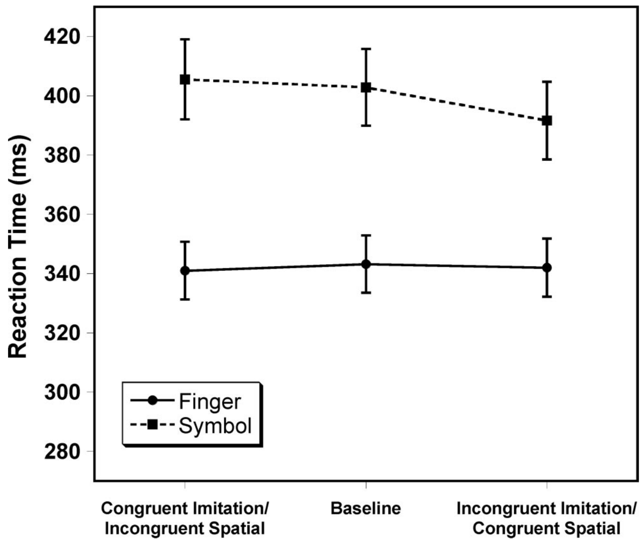

Figure 4. Mean reaction times (in milliseconds) in Experiment 2 as a function of stimulus cue (finger movement or symbol) and condition (congruent, baseline, or incongruent). It is important to note that the imitatively congruent condition is spatially incompatible and that the imitatively incongruent condition is spatially compatible. Error bars represent standard errors of the mean.

2 revealed a significantly larger spatial compatibility effect from the left hand than from the right hand (39 ms vs. 14 ms), $t(22) = 3.84$, $p < .001$. This difference suggests that spatial compatibility between the stimuli and responses cannot account for the entirety of the effect.

Discussion

The results from this experiment confirm that the priming effect of the imitative cue in Experiment 1 was partly a function of spatial compatibility. In Experiment 1, RT to the imitative cue in the baseline condition was 30 ms faster than the RT to the imitative cue in Experiment 2, in which spatial compatibility was eliminated. Still, the results from the current experiment also show that the priming effects observed in Experiment 1 are not entirely attributable to spatial compatibility. In Experiment 2, the overall effect of the irrelevant spatial compatibility stimulus on responses to the symbolic cue (i.e., incongruent – congruent RTs) was only about one third the size of the effect of the imitative stimulus in Experiment 1. Furthermore, the irrelevant imitative stimulus in the symbolic cue condition in Experiment 1 was responsible for both facilitation and interference of RT responses, whereas the irrelevant spatial compatibility stimulus in Experiment 2 was responsible only for facilitation effects.

These results are consistent with a recent functional MRI (fMRI) study by Koski et al. (2003) in which participants were instructed to imitate left- (specular imitation) and right- (anatomical imitation) hand finger movements with their right hands. Koski et al. predicted differential responsiveness to the two stimuli because previous research shows a preference, strongest in childhood, to imitate the actions of others from the perspective of a mirror image (Bekkering, Wohlschläger, & Gattis, 2000; Wapner & Cirillo, 1968). Their results revealed that bilateral inferior frontal and right posterior parietal cortex (areas corresponding to the human mirror system) were more active during imitation with the left hand than with the right hand. Thus, these neuroimaging results confirm that we are biased toward specular imitation. Our findings showing faster RTs to imitation of the left versus right hand are consistent with this evidence but also show that this conclusion extends to automatically stimulated imitation as well. Moreover, our findings offer a more specific reason for participants showing a preference for specular imitation: This form of imitation includes both direct mapping of observed and executed movements as well as spatial compatibility, whereas anatomical imitation does not involve spatial compatibility.

In recent years, a number of fMRI studies were designed to investigate the human mirror system with a finger imitation task similar to our baseline condition showing a tapping finger (e.g., Iacoboni et al., 1999; Koski et al., 2002, 2003). These studies consistently report activation in Broca's area and also in the superior parietal cortex. On the basis of the current findings showing that imitation and spatial compatibility are confounded in a finger imitation task, it would be advisable for researchers to consider whether the activation in these brain regions reflects exclusively an observation–execution matching system or whether these regions reflect the contribution of spatial compatibility as well.

Experiment 3

The first two experiments assessed the priming effects of an imitative cue and a spatial cue together (Experiment 1) and in opposition (Experiment 2). The results provided indirect evidence that both spatial compatibility and imitation contributed to the priming effects, but the interpretation of these findings is limited because participants were instructed to produce an imitative response to the finger cue (i.e., respond with the same finger presented as the stimulus). It is unclear how the intention to imitate when presented with the finger movement cue might carry over and facilitate the automatic tendency to imitate or execute a spatially compatible response when presented with an irrelevant finger movement cue in the symbolic cue condition. To address this question, we designed Experiment 3 to compare the priming effects of a spatial cue and an imitative cue when the explicit goal of the study was either to only imitate or only match the left–right spatial relations of the moving stimulus finger. Experiment 3a investigated the priming effects of spatial compatibility when the imperative stimulus was an imitative cue; Experiment 3b investigated the priming effects of imitation when the imperative stimulus was a spatial cue. In both experiments, participants were shown the left and right animated hands, but they were instructed to respond with the identical finger in Experiment 3a and with the spatially compatible finger in Experiment 3b. The left-hand stimulus required a response that was always compatible with the irrelevant stimulus cue (spatial cue in Experiment 3a, imitative cue in Experiment 3b), whereas the right-hand stimulus required a response that was always incompatible with the irrelevant stimulus cue.

Experiment 3a

Method

Participants. Twelve students at the University of Chicago between 18 and 25 years of age participated; none had participated in the previous experiments. All were right-handed, naive as to the purpose of the study, and paid for their participation.

Apparatus and materials. All materials were identical to those used in Experiments 1 and 2.

Design and procedure. Participants responded by imitating with their right hand the movements of the index or middle finger of a left or right hand. The hand stimuli were the same as in Experiments 1 and 2 except that the box in which the symbol had appeared in the earlier experiments was removed. The experiment was divided into 10 blocks of 20 trials each. On each block, either the left or the right hand was presented. Blocks alternated between the left and the right hand. The hand presented on the initial block was counterbalanced between participants. Two practice blocks (each showing one of the two hands for 12 trials) preceded the experimental blocks but were not included in the analyses.

Results

Error trials and trials in which RT exceeded 800 ms were excluded from analysis. As can be seen in Figure 5, median RTs were significantly faster when the spatial mapping between stimulus and response was compatible (left hand) rather than incompatible (right hand), $t(11) = 7.09$, $p < .001$.

Errors were made on 4.38% of trials, and 0.08% of trials were excluded because of RTs over 800 ms. Similar to the RT analyses, more errors were made on incompatible (6.83%) than on compatible trials (1.92%), $t(11) = 3.84$, $p < .001$.

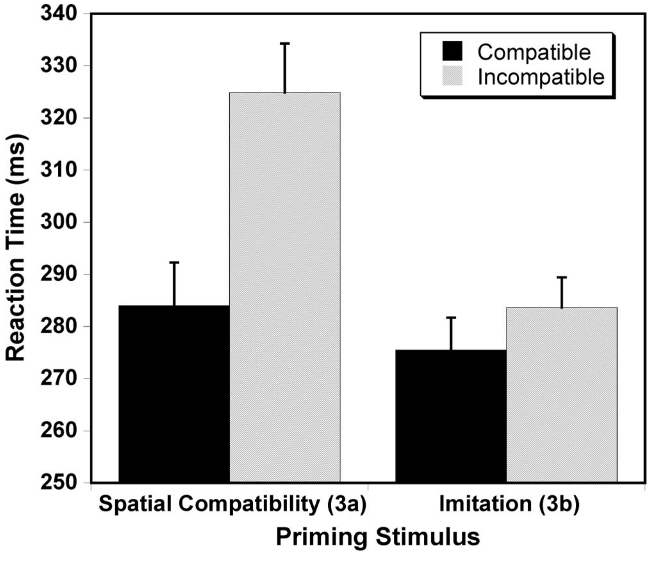

Figure 5. Mean reaction times (in milliseconds) to identical finger movement (with spatially compatible and incompatible stimuli) in Experiment 3a and mean reaction times (in milliseconds) to spatial cue (with imitatively compatible and incompatible stimuli) in Experiment 3b. Error bars represent standard errors of the mean.

Experiment 3b

Method

Participants. Twelve students at the University of Chicago between 18 and 25 years of age participated; none had participated in the previous experiments. All were right-handed, naive as to the purpose of the study, and paid for their participation.

Apparatus and materials. All materials were identical to those used in the previous experiments.

Design and procedure. All procedures were identical to those of Experiment 3a except that participants were instructed to respond with a spatially congruent finger to the moving index or middle finger shown as the stimulus.

Results

Error trials and trials in which RT exceeded 800 ms were excluded from analysis. Responses were significantly faster when compatible with imitation of the identical finger (275 ms) than when incompatible with imitation of the identical finger (284 ms), $t(11) = 2.90$, $p < .05$ (see Figure 5).

Errors were made on 2.88% of trials, and 0.21% of trials were excluded because of RTs over 800 ms. Errors did not significantly differ between conditions, $t(11) = 0.08$, *ns*.

Comparison Between Experiments 3a and 3b

The priming effect of spatial compatibility in Experiment 3a was significantly larger (41 ms) than the effect of automatic imitation in Experiment 3b (9 ms), $F(1, 22) = 19.35$, $p < .001$ (see Figure 6). To evaluate whether this difference was constant or changed across trials, we divided the trials in each block into quartiles. A repeated measures ANOVA revealed a significant interaction between experiment and quartile, $F(3, 66) = 5.21$, $p < .005$. As can be seen in Figure 6, the priming effect of spatial compatibility in Experiment 3a showed a positively sloped linear trend over quartiles, $F(1, 66) = 3.03$, $p = .086$, whereas the priming effect of automatic imitation in Experiment 3b showed a negatively sloped linear trend over quartiles, $F(1, 66) = 11.61$, $p < .002$. This difference between linear trends as a function of quartiles was significant, $F(1, 66) = 13.25$, $p < .001$. In Experiment 3b, the compatibility effect was significantly greater in the first quartile than in the second, $F(1, 66) = 8.58$, $p < .005$; third, $F(1, 66) = 11.22$, $p < .002$; and fourth, $F(1, 66) = 11.90$, $p < .002$. In the first quartile, the compatibility effects of the two experiments did not differ significantly, $F(1, 66) = 0.00$, *ns*. By contrast, compatibility effects were significantly larger for Experiment 3a than Experiment 3b in the second, $F(1, 66) = 11.02$, $p < .002$; third, $F(1, 66) = 21.81$, $p < .0001$; and fourth, $F(1, 66) = 24.40$, $p < .0001$, quartiles.

An ANOVA on mean RTs for Experiment 3a revealed significant main effects of spatial compatibility (compatible vs. incompatible trials), $F(1, 11) = 46.50$, $p < .0001$, and quartile, $F(3, 33) = 10.01$, $p < .0001$. The interaction of compatibility and quartile was not significant, $F(3, 33) = 1.09$, *ns*. As can be observed in Figure 7, RTs declined relative to the first quartile for both compatible, $F(1, 33) = 28.59$, $p < .0001$, and incompatible conditions, $F(1, 33) = 8.19$, $p < .01$. Still, a comparison between the linear trends for both conditions showed that they declined more for the compatible than for the incompatible stimulus, F(1,

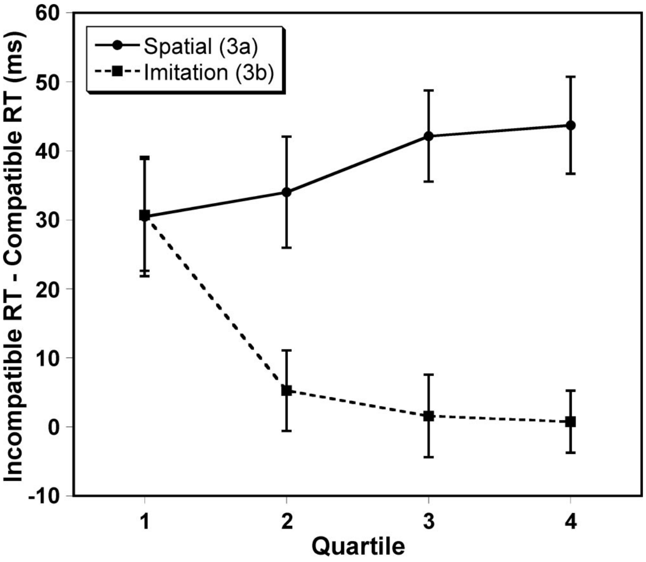

Figure 6. Mean reaction time difference between incompatible and compatible priming stimuli as a function of quartile for Experiment 3a (testing priming effects of spatial compatibility) and Experiment 3b (testing priming effects of imitative compatibility). Error bars represent standard errors of the mean.

33) = 20.40, $p < .0001$, explaining the overall increase in spatial compatibility effect across quartiles seen in Figure 6.

An ANOVA on mean RTs for Experiment 3b revealed significant main effects of imitative compatibility, $F(1, 11) = 9.07$, $p < .02$, and quartile, $F(3, 33) = 8.84$, $p < .001$. There was also a significant interaction of compatibility and quartile, $F(3, 33) = 5.27$, $p < .005$. As can be observed in Figure 7, RTs declined across the first and second quartile in the incompatible condition, $t(66) = 2.93$, $p < .005$, but remained flat in the compatible condition. A trend analysis revealed a significant linear decrease in the incompatible condition, $F(1, 33) = 31.71$, $p < .0001$, but no comparable decrease in the compatible condition, $F(1, 33) = 0.73$, *ns*. The difference between linear trends was significant, $F(1, 33) = 30.98$, $p < .0001$. This differential decline in RTs explains why the compatibility effect in Figure 6 showed such a significant decline between the first and second quartiles.

Discussion

The results from Experiment 3a are consistent with many previous studies showing that spatial compatibility provides an RT advantage (e.g., Hommel, 1993; Lu & Proctor, 1995). This same conclusion was suggested by findings from Experiments 1 and 2, but the design of these experiments did not allow for an independent test of the effects of spatial compatibility. The current results confirm that spatial compatibility primes responding even when the imperative stimulus is an imitative cue.

Similarly, the results from Experiment 3b showing a significant effect of an automatic tendency to imitate, independent of spatial compatibility, provide more conclusive evidence for the priming effect of imitation than had heretofore been reported. Whereas previous studies confounded imitation and spatial compatibility, this study assessed the priming effects of each stimulus independently. Although both imitation and spatial compatibility prime responses, response priming is significantly greater as a function of spatial compatibility than of imitation.

How can we account for this differential effect? One possibility is that the similarity between the stimulus and response predicts the strength of the priming effect. Indeed, "perception of an action," according to Knoblich and Flach (2003), "should activate representations to the degree that the perceived and represented actions are similar" (p. 622). This interpretation is problematic, however, because the results revealed that spatial compatibility was a stronger priming stimulus than was imitation, which is at

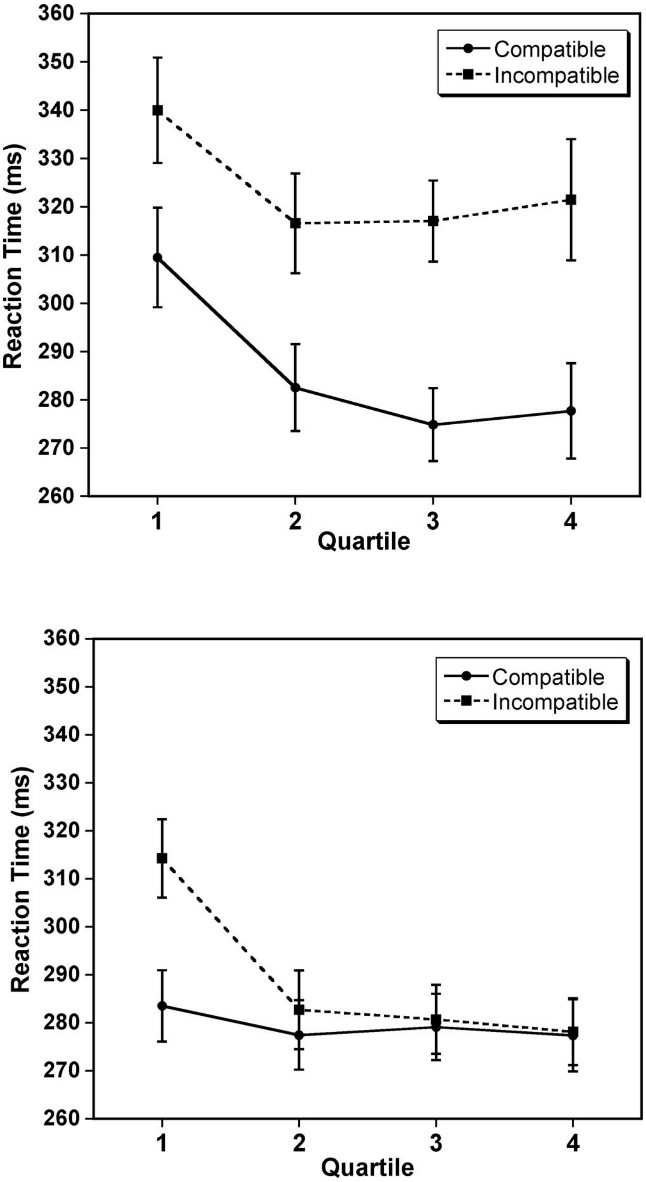

Figure 7. Top: Mean reaction times (in milliseconds) as a function of quartile for spatially compatible and incompatible stimuli (Experiment 3a). Bottom: Mean reaction times (in milliseconds) as a function of quartile for imitatively compatible and incompatible stimuli (Experiment 3b). Error bars represent standard errors of the mean.

odds with the suggestion that imitative cues should be more, not less, similar to responses than spatial cues (e.g., Brass et al., 2000). Still, not all models of stimulus–response compatibility define similarity in the same way. Similarity can be defined in terms of dimensional overlap (Kornblum, Hasbroucq, & Osman, 1990) or alignment (Goldstone, 1996; Medin, Goldstone, & Gentner, 1993) or, for that matter, any number of other metrics. These different definitions do not necessarily make the same predictions about the relation between a stimulus and a response, and indeed some suggest that features differ in their salience (Weeks & Proctor, 1990) or are differentially weighted depending on their task relevance (Hommel, 1993). In the current experiment, some measure of similarity is likely contributing to the priming of the response, but the differential priming effects associated with spatial compatibility and imitation are also a function of differences in how priming changed across trials.

In Experiment 3a, the difference between spatially compatible and spatially incompatible stimuli remained fairly constant across trials. In Experiment 3b, however, the difference between compatible and incompatible imitative responses decreased dramatically following the first quartile of trials. During the first quartile of trials, differences between compatible and incompatible trials were very similar in both experiments. By the second quartile, the differences between compatible and incompatible imitative responses had declined abruptly, suggesting a nonlinear change in the priming mechanism.

Additional information about the time course of priming was revealed by examining separately the changes in RTs in the compatible and incompatible conditions. In Experiment 3a, RTs within blocks decreased for both compatible and incompatible conditions, suggesting either an increase in RTs at the beginning of the block as a function of stimulus set switching (Monsell, 2003), a decrease in RTs as a function of responding continuously to the same stimulus within the block, or perhaps some combination of both processes. By contrast, in Experiment 3b, RTs decreased only between the first and second quartile for the incompatible condition.

One interpretation for these findings is that the RT function in Experiment 3b was artifactually flattened by a floor effect. As can be observed in Figure 7, the fastest RTs in this study were fixed at around 280 ms. This could explain why the RTs in the compatible condition did not decrease between the first and subsequent quartiles. As a consequence of this function not decreasing, it appears that the compatibility effect (difference between compatible and incompatible trials) was limited to the first quartile because the RTs for the incompatible condition did decline across quartiles. By contrast, the RTs for both conditions in the first quartile of Experiment 3a were well above 280 ms, which explains why the RTs in both compatible and incompatible conditions declined over quartiles.

Is a floor effect interpretation correct? When the differences between the compatible and incompatible conditions are analyzed for each of the five blocks separately, it becomes apparent that 280 ms does not represent an absolute floor. First, the compatible condition remains flat whether RTs averaged 285 ms or 270 ms in the first quartile. Second, the mean RTs are as low as 270 ms in some quartiles, suggesting that 280 ms does not represent a floor. Furthermore, we recently replicated this time course difference in responding to the priming effects of imitation and spatial compatibility in a new study using the same procedure except for a subtle change in the stimuli (Longo, Kosobud, & Bertenthal, 2006). Whereas the current experiments used a real hand that was videotaped, the new study used a computer-generated three-dimensional model of a human hand. It is interesting to note that the RTs in this study were elevated by 25 ms to 40 ms, and the RTs for the compatible condition corresponding to Experiment 3b averaged 306 ms. Nevertheless, the RTs across quartiles were still flat, suggesting that the results from the current experiment were not a function of a floor effect. It thus appears that the temporal dynamics of the responses to the two priming stimuli were quite different. (See the General Discussion for an interpretation of this finding.)

General Discussion

The goal of these experiments was to test whether the observation of an intransitive action facilitated a response because of a tendency to automatically imitate an intransitive action (as mediated via the human mirror system) or because of a common spatial code between the stimulus and the response. In Experiment 1, imitation and spatial compatibility were confounded, but the results were consistent with previous findings that revealed significant response priming (both facilitation and interference) by the irrelevant imitative stimulus when the imperative stimulus was a symbolic cue. By contrast, when the imperative stimulus was an imitative cue, there was no evidence of priming by the irrelevant symbolic cue. Furthermore, participants' intentional RT responses to the imitative cue were significantly faster than to the symbolic cue, suggesting that an imitative stimulus conferred a processing advantage on the stimulus–response translation process. Although this processing advantage could have been a function of differences in the salience of the moving finger and symbolic stimulus, a recent high-density event-related potential (ERP) study revealed that the N100 latency (measured at frontal, central, and parietal sites) associated with detection of the imperative stimulus showed no difference as a function of whether the symbol or the finger stimulus was presented (Bertenthal, Norris, Longo, & Cacioppo, 2006).[5] Conceivably, RT differences could have still been attributable to differential difficulty in the decoding of the two stimuli, but the ERP evidence for this effect was equivocal. Thus, RT differences between the two stimulus conditions are most likely a function of differences in the stimulus–response translation process.

In Experiment 2, imitation and spatial compatibility were placed in opposition to each other and the results suggested that the priming observed in Experiment 1 could not be explained entirely by either process. RTs to the moving finger were still significantly faster than to the symbolic stimulus. Nevertheless, the priming effects in the symbolic cue condition were significantly reduced relative to Experiment 1 and were limited to spatial compatibility

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[5] Although these results may seem surprising because motion perception often shows a processing advantage relative to shape perception, it is important to remember that decoding of the symbolic stimulus could begin as soon as it appeared but decoding of the moving finger might have required more time because the apparent movement might not have been consistently detected following its onset. Given the small displacement of the finger from Frame 1 to Frame 2, participants may have required more frames (and hence more time) to begin decoding which finger moved.

showing a modest facilitation effect and no interference effect. The most parsimonious interpretation for these findings is that both factors contribute to priming and, when placed in opposition, tend to interfere with each other. Still, spatial compatibility appeared to be a stronger priming stimulus than imitation.

In Experiment 3, imitation of a spatially compatible finger movement was significantly faster than imitation of a spatially incompatible finger movement. Likewise, RTs to a spatial cue consistent with imitation of the identical finger were significantly faster than RTs to a spatial cue inconsistent with imitation of the identical finger. Nevertheless, the difference between the priming by spatially compatible and spatially incompatible stimuli was markedly greater than the difference between the priming by compatible and incompatible imitative stimuli.

Automatic Imitation Versus Spatial Compatibility

The above pattern of results suggests that not all stimulus–response mappings are based on the same processes. Unlike imitative and spatial cues, the stimulus–response translation for the symbolic cue involves an arbitrary mapping that must be stored in working memory to control the selection of the correct response. As such, this translation is neither automatic nor unintentional.[6] By contrast, the stimulus–response translations for the imitative and spatial cues involve a direct mapping between the stimulus and the response such that the response is automatically triggered by the appearance of the stimulus. These stimulus–response translations are able to bypass working memory because the mappings are intrinsic to the execution of the relevant sensory–motor responses (Jeannerod, 1997; Rizzolatti et al., 2001). In a related positron emission tomography (PET) study measuring brain activity during a spatially congruent response and during an arbitrary stimulus–response mapping, Toni, Rushworth, and Passingham (2001) found that visual information can influence the motor system through different task-dependent pathways consistent with the preceding discussion.

Although both imitation and spatial compatibility involve a direct mapping between stimulus and response, the evidence suggests that attentional mechanisms may differentially contribute to the priming effects of these two factors. In Experiment 3a, both compatible and incompatible priming conditions led to an increase in RTs following a switch from one condition to the other. One interpretation for this effect follows from evidence suggesting that the direction and extent of the Simon effect is determined by stimulus–goal correspondence (Hommel, 1993). In this case, the goal changes from specular to anatomic imitation, and, correspondingly, the stimulus–response mapping becomes more attentionally weighted to the spatial location of the moving finger in the compatible as opposed to the incompatible conditions. As the task switches from one condition to the other, a few trials are required to recalibrate the weightings before RTs become stable again. Thus, changes in the salience of the spatial location explain why RTs decline within blocks, but these changes cannot explain the RT differences between compatible and incompatible conditions. This latter difference is explained by the priming of the incorrect finger movement in the incompatible condition and the additional time required inhibiting this response before executing the correct response.

It is conceivable that a similar interpretation could explain the decline in response times during the first quartile of the incompatible condition of Experiment 3b. The problem with this interpretation is that it cannot account for why RTs do not decline during the first quartile of the compatible condition. Although a floor effect in RTs constitutes one explanation, we previously explained when discussing the results of Experiment 3 why this interpretation is not entirely consistent with the data. An alternative interpretation is that the tendency for imitation following a priming stimulus is completely automatic, and its attentional salience or weighting does not change from the compatible to the incompatible condition. This constant weighting would explain why there is no set switching and why there is no decrease in RTs during the first quartile of the compatible condition. The reason for the decline in RTs in the incompatible condition is that inhibition of this automatic response is cumulative during the block of trials. When participants switch to the incompatible condition, the automatic tendency to imitate the movement of the anatomically matching finger interferes with the execution of the correct response. To minimize this interference, the inhibition of the incorrect imitative response increases over trials until this tendency is reduced to a null effect.

One issue that is not completely resolved by this interpretation is why the dynamic changes in priming converge differently in the two conditions. In the automatic imitation condition, the priming effect became nonsignificant by the second quartile, suggesting almost complete inhibition of the interfering imitative response after as few as only five trials. By contrast, the priming effect in the spatial compatibility condition continued to persist throughout the experiment, consistent with prior research showing no attenuation of spatial compatibility effects over as long as 5 consecutive days of testing (Simon, Craft, & Webster, 1973).

Although the preceding interpretation for the differences in the time course of priming is currently incomplete and somewhat speculative, it is consistent with the findings of Lhermitte et al. (1986), who observed patients with lesions in the prefrontal cortex. These patients exhibited exaggerated dependence on environmental cues and showed utilization behavior and compulsive imitation. The authors suggested that lesions in the prefrontal cortex impair these patients from inhibiting automatic actions assembled in the parietal cortex. On the basis of this inhibitory function associated with the prefrontal cortex, we would predict that our participants should show greater activation in this part of the frontal cortex when engaged in tasks involving automatic imitation as opposed to spatial compatibility.

These differences in priming as a function of imitation versus spatial compatibility complement recent findings suggesting that overlearned stimulus–response mappings and imitative mappings are mediated by different mechanisms. Recently, Brass, Derrfuss,

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[6] Although arbitrary stimulus–response mappings will initially involve working memory, the empirical evidence suggests that some of these mappings become automatic quite quickly and bypass working memory (Hommel & Eghau, 2002; Logan, 1980). We suspect that this transformation did not occur over the time course of the current experiments because there was no evidence of a practice effect in the baseline condition for the symbolic cue nor was there any evidence of an increase in facilitation or interference by the symbolic cue in responding to the moving finger over blocks.

Matthes-von Cramon, and von Cramon (2003) compared participants' performance on a Stroop task and an imitation task similar to that used in Experiment 1. Patients with frontal and nonfrontal lesions and normal control participants were tested. Given that patients with frontal lobe lesions show difficulties in inhibiting automatic response tendencies, these patients were predicted to show increased difficulty inhibiting the prepotent response in both tasks. As predicted, frontal lesion patients showed significantly greater interference (incongruent – congruent conditions) on the imitation task than did the other participants, but the differences between frontal lesion patients and the other two groups on the Stroop task were less clear cut. In addition, a very low correlation between the interference scores on the two tasks for the frontal patients suggested that these tasks were unrelated. In related fMRI studies, differences in the neural networks mediating Stroop performance and automatic imitation performance were reported (Brass, Derrfuss, & von Cramon, 2005; Brass, Zysset, & von Cramon, 2001). These findings converge with those from the current experiments to emphasize that all automatic response tendencies are not mediated by identical neural circuits.

Imitation of Movements Versus Goal-Directed Responses

The current study included conditions in which imitation was intentional and other conditions in which imitation was primed by an irrelevant stimulus cue. In all experiments except Experiment 3b, participants were explicitly instructed to imitate in one of the conditions (i.e., the moving finger condition). In the other conditions, participants were instructed to respond to a symbolic or spatial cue by pressing a key with their index or middle fingers; a tendency to imitate was primed when an irrelevant finger movement stimulus was also presented. When the instruction was to explicitly imitate a finger movement, the imitative response was goal-directed because the participant intended to match his or her action to the observed finger movement. By contrast, the primed tendency to imitate a finger movement was unintentional, automatic, and somewhat obligatory. This automatic tendency to imitate was extrinsically stimulated by the observation of a finger movement performed by someone else. Thus, it does not appear that this response was goal directed.

Strictly speaking, this conclusion is correct with regard to the execution of the action but leaves open the possibility that the observed action is perceived as goal directed. Some theorists (e.g., Wohlschläger, Gattis, & Bekkering, 2003) hypothesize that all forms of imitation rely on reproducing a goal-directed action. If this hypothesis is correct, then how can we account for perceiving the automatic tendency to imitate as goal directed? One possibility is that the observed finger movement was viewed as a goal-directed response because it was implicitly perceived as corresponding to a voluntary and intentional movement by another agent. If the finger movement is perceived as goal-directed, then presumably its reproduction would involve simulating this goal-directed action as would be predicted by the functioning of the human mirror system (Blakemore & Decety, 2001; Rizzolatti et al., 2002).

An alternative interpretation for explaining the observation of an irrelevant finger movement as goal directed is that the finger movement corresponds to a goal-directed response (i.e., response to imitate the imperative stimulus) in other conditions of the experiment. This correspondence might influence participants to build up an association between an observed finger movement and a more specific goal to imitate during the course of the experiment. Although this interpretation is plausible, it falls short of explaining automatic imitation in Experiment 3b. Whereas Experiments 1, 2, and 3a included conditions involving intentional imitation, Experiment 3b did not include an intentional imitation condition to bias the perception of the moving finger as goal directed. Thus, this interpretation of perceiving a goal-directed finger movement by means of association with an intentional finger response cannot explain the priming of imitation observed in Experiment 3b.

Additional evidence consistent with this interpretation of simulating a goal-directed response following observation of a finger movement derives from differences in the neuroimaging of familiar versus unfamiliar actions. A series of PET studies (Decety et al., 1997; Grèzes, Costes, & Decety, 1998) reveal that observation of familiar actions activates Broca's area, whereas observation of unfamiliar actions activates only the upper part of the inferior parietal lobule and the superior parietal lobule. This finding thus suggests that familiar actions are coded by the human mirror system, whereas unfamiliar actions are coded primarily in terms of their kinematic properties. Given that the mirror system codes actions as goal directed, it is reasonable to conclude that familiar actions are coded as goal directed whereas unfamiliar actions are not coded in terms of goals.

Taken together, these considerations lead us to conclude that the irrelevant finger tapping stimuli are perceived implicitly as familiar and goal directed. This conclusion thus begs the question as to what would happen if the irrelevant stimuli were not familiar and goal directed. For example, the presentation of an anatomically impossible finger movement would not be predicted to show the same degree of response priming as that produced by the finger tapping stimulus in the current experiments. Although there is currently insufficient empirical evidence to fully evaluate whether automatic imitation relies on perceiving an action as goal directed, it nevertheless highlights the importance of specifying what is meant by a goal-directed imitative stimulus and response when discussing both voluntary and automatic imitation.

Functional Significance of Automatic Imitation

Before concluding, we would like to offer a few brief comments on the functional significance of automatic imitation. Early authors, such as James Mark Baldwin (1895) and Clark Hull (1933), suggested that unconscious imitation was analogous to suggestibility in hypnosis. Other authors (e.g., O'Toole & Dubin, 1968) have interpreted such behavior as a manifestation of empathy following from George Herbert Mead's (1934) principle of *taking the role of the other*. Another possibility is that automatic imitation, per se, does not have any function at all. If simulated action is an integral part of the representation of a perceived action, imitative behavior may leak out without serving any particular purpose (Dromard, 1905; Prinz, 1997; Rizzolatti et al., 2001).

Currently, the most intriguing interpretation is that mimicry communicates social affiliation and rapport. This view emerged originally from studies of psychiatric sessions in which it was found that postural congruence between patient and therapist was associated with rapport (Charny, 1966; Scheflen, 1964). Subsequently, researchers such as Kendon (1970) and LaFrance (1979) observed similar mimicry in normal conversational situations, the latter author finding a significant relation between mimicry and rapport. Bavelas, Black, Lemery, and Mullett (1986) observed that mimicry is affected by the visual availability of the model, arguing on this basis that it must serve a communicative function. More recently, Chartrand and colleagues (e.g., Chartrand & Bargh, 1999; Lakin & Chartrand, 2003) demonstrated in a series of studies a relation between mimicry and liking and rapport. Lakin and Chartrand (2003), for example, found that participants who enter an interaction with the goal of affiliating with an interlocutor were more likely to imitate movements by that person than participants without such a goal. Conversely, van Baaren, Holland, Kawakami, and van Knippenberg (2004) found that participants who were imitated during a face-to-face interaction were subsequently friendlier than those who were not imitated. Lakin et al. (2003) argued, on the basis of these and similar results, that automatic mimicry evolved specifically to facilitate human communication.

These findings thus suggest that automatic imitation may sometimes be socially desirable. In such cases, we would predict that the imitative tendency would be less likely to be inhibited, as we reported in Experiment 3b. This possibility could be tested by repeating Experiment 3b after manipulating whether participants would or would not be motivated to develop rapport with the person whose hand would then be used as the stimulus in the experiment. In this way, studying the function of automatic imitation will help us to better understand the mechanisms responsible for its occurrence.

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