

Understanding Action Beyond Imitation: Reversed Compatibility Effects of Action Observation in Imitation and Joint Action

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A robust finding in imitation literature is that people perform their actions more readily if they are congruent with the behavior of another person. These action congruency effects are typically explained by the idea that the observation of someone else acting automatically activates our motor system in a directly matching way. In the present study action congruency effects were investigated between an imitation task and a complementary action task. Subjects imitated or complemented a virtual actor's grasp on a manipulandum. In both tasks, a color-cue could be presented forcing subjects to ignore the task rule and execute a predefined grasp. Reaction times revealed a reversal of congruency effects in the complementary action task, suggesting that subjects were able to circumvent the automatic tendency to copy actions or postures of another person. In 2 additional control experiments, congruency effects were replicated, and a Simon effect was identified to underlie faster responses in the imitation task. These results make a case against current theoretical views on imitation and direct matching in favor of more flexible models of perception-action coupling.

Keywords: imitation, complementary action, stimulus–response congruency, direct matching, perception-action models

An impressive range of evidence over the last 20 years has shown that perceiving the body movements of other people activates motor representations in the observer's brain (e.g. Babiloni et al., 2002; Buccino et al., 2001; Maeda, Kleiner-Fisman, & Pascual-Leone, 2002; Nishitani & Hari, 2002; for review, see Rizzolatti, Fogassi, & Gallese, 2001). Activated motor representations are typically assumed to be of an imitative nature, reflecting the automatic resonance of motor structures with the movement that is observed. Support for the existence of a basic neurophysiological mechanism for imitation has come from different lines of evidence. Of central importance was the discovery of mirror neurons in monkeys (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996) revealing the selective matching of motor neurons in monkey ventral premotor cortex to the observation of specific goal-directed grasping acts. Subsequent neuroimaging studies in humans provided further evidence for direct matching at the level of individual effectors (Buccino et al.,

2001), and Transcranial Magnetic Stimulation studies reported sub-threshold activation of muscles controlling the individual digits of the hand (Maeda et al., 2002) when subjects observed finger movements. Furthermore, behavioral studies have provided evidence for an automatic tendency to imitate, reflected in speeded response times when subjects were presented with task irrelevant actions that are either similar or dissimilar to the executed movement (Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschlagel, & Prinz, 2000; Craighero, Bello, Fadiga, & Rizzolatti, 2002; Sturmer, Aschersleben, & Prinz, 2000). In addition, studies in social psychology have found nonconscious mimicry of gestures, postures, and mannerisms (Chartrand & Bargh, 1999) which are thought to reflect automatic motor activation resulting from perception.

Several social benefits have been associated with the existence of a low level mechanism for imitation. Rizzolatti et al. (2001) stress the importance of direct matching between perception and action to support action understanding of other peoples' actions, whereas nonconscious mimicry between persons has been argued to support social rapport and liking between individuals (Lakin & Chartrand, 2003). Furthermore, neural mechanisms for imitation have been suggested to support imitation learning (Buccino et al., 2004; van Schie, Mars, Coles, & Bekkering, 2004), referring to the capacity to learn novel behaviors from observing the actions of others (see also Schaal, 1999).

Whereas imitation is typically considered to be beneficial for social development of individuals (see e.g. Williams, Whiten, Suddendorf, & Perrett, 2001), in many circumstances an automatic tendency to imitate may actually be an obstacle for successful cooperation between persons. Particularly, in joint action tasks, coactors are often required to select opposite or complementary behaviors instead of imitative actions (Sebanz, Bekkering, & Knoblich, 2006). Consider for example handing

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over of an object (e.g. a pair of scissors, or a cup of coffee) between two persons. Rather than imitate a partner's action, the receiving person must select a grip that is opposite or complementary to the grasp of their partner.

Unfortunately, little is known about the conflict that imitative tendencies may pose for cooperative action and the manner in which such conflicts are resolved. Previous studies have typically focused on imitation and action observation conditions, but have paid little attention to task context, i.e. the relation between actor and observer. Interestingly, a number of recent studies have raised questions about the obligatory and automatic nature of imitation. Heyes, Bird, Johnson, and Haggard (2005) showed automatic effects of imitation may become abolished after incompatible training. Gergely, Bekkering, & Kiraly (2002) showed that imitation of preverbal infants at the age of 14 months is guided by rational inferences about the behavior that is observed (also see Bekkering, Wohlschlagler, & Gattis, 2000). Studies in social psychology furthermore suggest that automatic behavior induced by priming stereotypes (e.g. subjects walking slower after being primed with the category of elderly) may actually reverse (subjects walking faster) when there is a tendency to dissociate from the stereotype (Spears, Gordijn, Dijksterhuis, & Stapel, 2004) or when subjects hold a negative attitude against the primed group (Cesario, Plaks, & Higgins, 2006). These findings suggest that automatic tendencies to imitate may be modulated by a number of factors including previous experience, training, and rational interpretation of behavior and social identification.

In the present experiment we sought to investigate automatic response activation in a cooperative setting. We hypothesized that in tasks requiring cooperative behaviors from two persons, complementary stimulus–response associations may develop that can overcome imitative response tendencies, and that

these associations may manifest as reaction time advantage for complementary actions relative to imitative actions. This prediction is contrary to expectations based on the direct matching hypothesis, which would predict that reaction times should always be speeded by the observation of identical actions.

Three different experiments are presented in which subjects participated in an ‘imitation task’ and a ‘complementary action task’. In both tasks subjects were presented with a manipulandum that that could be grasped in two ways. The top-side of the object allowed a precision grip from above, and the bottom side afforded a full-grip from the side (see Figure 1). In the imitation task subjects imitated the grasping behavior of a virtual coactor displayed on a computer screen, whereas in the complementary action condition, subjects performed the action that is opposite from the coactor (as in taking over the object). In 40% of the trials a color cue indicated that subjects generate a preinstructed grasp of the manipulandum (either full or precision), irrespective of the behavior of the coactor. Reaction times in color trials were compared between congruent (same) and incongruent (opposite) relations between subject and coactor to determine automatic response activation. If the direct matching account is true we should expect reaction times on color trials to be faster when the required action of the subject is congruent (overlapping) with the behavior of the virtual actor, irrespective of the action context. However, if our hypothesis is true that subjects can overcome imitative tendencies and develop task specific stimulus–response couplings, we should expect congruency effects on color trials to reverse between the two tasks. That is, in the complementary action context subjects should be faster to initiate actions that are incongruent (dissimilar) with the behavior of their virtual coactor.

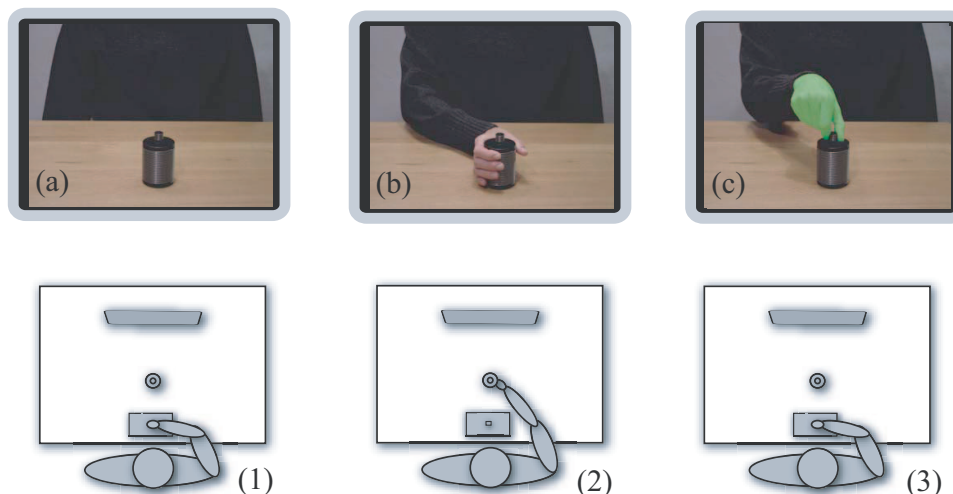


Figure 1. Experimental stimuli and time course. Subjects were presented with an image depicting the coactor in a nonactive posture (a) followed by a second image showing the coactor grasping the manipulandum, using either a full grip (b) or a precision grip (c). In 40% of the trials, the hand of the coactor was colored green (c). As soon as the subjects were sure what movement they were going to make, they (1) released the start button, (2) gripped the manipulandum using the appropriate grip (full grip or precision grip), and (3) returned their index finger to their initial position depressing the start button.

Experiment 1

Method

Subjects. Sixteen subjects, 3 male, 13 female, mainly students from the Radboud University Nijmegen, aged between 18 and 29 ($M = 23$, $SD = 2.9$) participated in the experiment. All subjects were right handed by self-report and were paid 6 euros per hour, or obtained course credits for their studies. Subjects provided informed consent before the experiment and were treated in accordance with international guidelines presented in the Declaration of Helsinki (World Medical Association declaration of Helsinki, 1997).

Apparatus and procedure. Subjects were seated at a table facing a 19 in. (48.26 cm) cathode ray tube computer screen at a distance of approximately 100 cm. A response box, aligned with the subjects' midline was placed directly in front of the subject on the table to serve as a starting position. Midway between response box and the computer screen at a distance of 55 cm from the subject a touch-sensitive manipulandum was fixed to the table (see Figure 1). The manipulandum was custom-made to detect grasping actions of the subject either at the cylinder base ($r = 3$ cm, height = 8 cm), or at the top ($r = .80$ cm, height = 1.80 cm). Both response box and manipulandum were controlled by a PC running Presentation software (Neurobehavioral systems Inc., Albany, CA) to detect release of the response box (reaction time), and grasping of the object (movement time and end-position) at millisecond resolution.

The experiment consisted of four experimental runs of 100 trials each. In two of the four runs subjects were instructed to imitate the grasping behavior of a virtual coactor on the screen. In the other two runs, subjects complemented the behavior of the virtual coactor by performing a grasping action at the opposite end of the manipulandum. Each trial began with subjects pressing the start button with their index finger and the presentation of an image showing the coactor in a nonactive posture (see Figure 1). After 1 s, the image was displaced by a second image¹ (the imperative stimulus) showing the coactor grasping the manipulandum at the top (precision grip) or at the bottom part (full grip). Subjects were instructed to either imitate or complement the behavior of the coactor (depending on the task). Reaction times were measured relative to the onset of the second image showing the virtual actor's grasp, which remained displayed on screen during action execution until subjects returned to press the start button for the next trial. Before the experiment all subjects received explicit instructions and were trained to only initiate their action when they were sure which action to perform and to avoid switching between grasps on the fly. This instruction was given to make sure that reaction times provided a true measure of response selection and to avoid the possibility that subjects postponed their decision to the end of the grasping movement (which was observed in a pilot experiment).

In 60% of the trials subjects responded in the normal manner, either imitating or complementing the behavior of the coactor, depending on the task. However, in 40% of the trials the hand of the coactor was presented in a deviant (greenish) color, and subjects were required to generate a preinstructed grasping action (either full grip or precision grip depending on the instructions), irrespective of the behavior displayed by the virtual actor. Normal

trials and color trials were randomly presented to subjects, except for the first five trials in a block, which were always normal. Task order was counterbalanced over subjects: half of all subjects started first with two imitation blocks, and the other half started with the two complementary action blocks. The order of grip instructions for color trials (full grip or precision grip) were counterbalanced between subjects. Before each block subjects performed 20 practice trials to adapt to the new conditions.

Data analysis. Trials with errors of grip and trials with reaction times (RTs) or movement times (MTs) more than 2.5 SD from the subject mean were excluded from statistical analysis. Reaction and movement times were analyzed with separate statistical designs using repeated measures ANOVA. For normal trials a one-way repeated measures ANOVA with the factor Action context (imitation vs. complementary action) was conducted whereas for color trials a 2 x 2 repeated measures ANOVA with the factors Action context (imitation vs. complementary action) and Congruency (same action vs. opposite action) was conducted.

Results

Preprocessing of behavioral data revealed a small number of errors in grip selection: in 25 trials out of the total of 6400 a wrong grasp of the manipulandum was detected. In 297 trials (4.5%) RTs or MTs were smaller or larger than 2.5 SD from the individual subject mean and excluded from statistical analysis.

Analysis of RTs in normal trials showed a main effect of Action context, $F(1, 15) = 13.14$, $p < .01$, $\eta_p^2 = .47$, reflecting faster RTs for imitative (498ms) than complementary actions (561ms). A comparable main effect of Action Context was found in the RT analysis of color trials, $F(1, 15) = 6.12$, $p < .05$, $\eta_p^2 = .29$, showing shorter RTs for actions in the imitation blocks (544ms) than in the complementary action blocks (597ms). Analysis of color trials furthermore showed a small but significant main effect of Congruency, $F(1, 15) = 8.72$, $p < .01$, $\eta_p^2 = .37$, indicating slightly faster RTs for same (565ms) than for opposite actions (575ms) on average. Critically, there was a highly significant Action Context * Congruency interaction, $F(1, 15) = 29.76$, $p < .001$, $\eta_p^2 = .34$. When subjects responded to color in the context of the imitation block, RTs were facilitated when the required action of the subject overlapped with the action of the virtual actor (relative to the situation where the subject's and coactor's behavior were opposite). In the complementary action context, when subjects responded to color, effects of action congruency were reversed. Nonoverlapping (opposite) actions facilitated subjects' RTs, whereas overlapping actions slowed down RTs. No significant main effects or interactions were found in subjects' movement times.

Discussion

The major result of the present experiment concerns the reversal of congruency effects observed in the complementary context. As expected, in context of the imitation task subjects were faster to initiate a preinstructed action if the action was similar or overlapping with the behavior of the virtual actor, and relatively slowed

¹ Consecutive presentation of the two images caused apparent motion of the coactor's hand moving toward the manipulandum.

down in response to the observation of dissimilar actions. However, in the complementary action blocks the reverse pattern was found. In the latter condition, subjects were faster to respond to the observation of dissimilar actions than to similar actions in line with the task context. These results suggest that the presumed automatic mapping between perceptual and motor representations during action observation can be modulated or circumvented when complementary stimulus–response relations, instead of imitation, are required by the task. This finding is both consistent with and extends the previous work of Heyes et al. (2005), who were able to cancel out automatic imitation effects after incompatible training. Furthermore, the current results indicate that, in addition to training, task context may effectively modify automatic stimulus–response associations in accordance with the task.

Interestingly, although response facilitation was of comparable size in both action blocks (see Figure 2), a general difference in RT was found between imitation and complementary action blocks. In light of the present discussion on the existence of a special mechanism for imitation, this result could be taken to reflect preferential processing of imitative actions over nonimitative ones. In order to investigate the nature of the RT difference between imitation and complementary action a second experiment was conducted. This experiment tested the hypothesis that the faster RTs observed in the imitative block may have been caused by our choice to color cue the hand. Color cueing of the hand may have directed subjects' attention to the manner of grasping and the spatial location (top or bottom part) of the object being grasped. As a consequence, selection of a similar end-posture on the object for imitation may have been facilitated relative to the complementary action condition where subjects needed to select the opposite grasp. For complementary actions, on the other hand, it would seem to be more beneficial to attend to the position of the object that is available, rather than attend to the grip adopted by the partner. In order to investigate the possible contribution of color cueing to the observed differences between the two tasks, in Experiment 2, actions were cued using a color cue appearing on the manipulandum, instead of the hand. By cueing the manipulandum, the spatial emphasis on the virtual actor's grasp that may have confounded Experiment 1 was removed from the design.

Experiment 2

Method

The experimental method was identical to Experiment 1 except for the fact that color trials were no longer indicated by coloring the hand, but rather by coloring (aluminum wires wrapped around) the object. A different group of 16 subjects (3 male, 13 female) from the same population as in Experiment 1, volunteered to participate in the experiment. Subject age varied between 18 and 35 ($M = 23$, $SD = 4.2$).

Results

As was the case for Experiment 1, subjects made a small number of grip selection errors: only 31 trials out of 6400 included an incorrect grasp of the manipulandum. In 66 trials (1%) RT or MT was found to exceed the 2.5 SD from the subject mean and excluded from statistical analysis.

Similar to Experiment 1, RTs in normal trials were found to be significantly faster in the imitation (516 ms) than in the complementary action task (553 ms), $F(1, 15)=4.65$, $p < .05$, $\eta_p^2=.23$, although the difference (37 ms) between the two task conditions was less pronounced as compared to the difference in Experiment 1 (63 ms). An additional repeated measures ANOVA to investigate this difference between experiments, however, was not found significant, $F(1, 30)=1.29$, $p = .266$, $\eta_p^2=.041$. For color trials the RT effect of Action Context was even more reduced (25ms), and no longer significant, $F(1, 15)=2.03$, $p = .17$, $\eta_p^2=.12$. No effect of Congruency was found, $F(1, 15)=1.40$, $p = .26$, $\eta_p^2=.09$. Importantly, as in Experiment 1, a highly significant interaction effect of Action Context * Congruency was observed, $F(1, 15)=40.06$, $p < .001$, $\eta_p^2=.73$, reflecting the reversal of congruency effects in the two action contexts. As in Experiment 1, no significant main effects or interactions were found in subjects' movement times.

Discussion

The results of Experiment 2 replicated the main findings of Experiment 1 revealing a reversal of congruency effects between

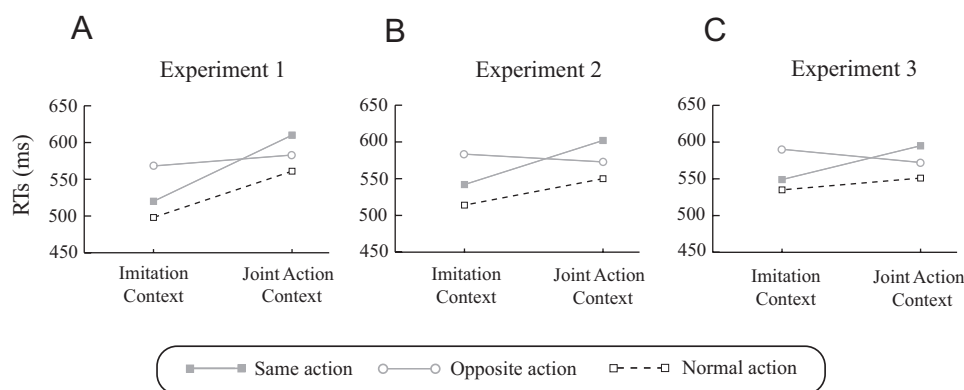


Figure 2. Response latencies in Experiments 1, 2, and 3 for normal trials (dotted lines) and color trials (solid lines). In normal trials, subjects generated imitation or complementary actions depending on the action context. In color trials, subjects performed a preinstructed action (either a precision grip or a full grip) independently from the action of the virtual actor. In color trials, subjects' actions could either be the same as the virtual actor (filled squares) or the opposite action (unfilled circles).

the two tasks. Again, in context of the imitation task subjects were faster to respond if movements overlapped with actions of the coactor, but slowed down for nonoverlapping or opposite movements. In the complementary action blocks the reversed pattern was found where subjects were faster to respond to the observation of dissimilar actions than to similar actions.

Color cueing of the manipulandum did not reverse or eliminate the RT advantage in the imitation block. This suggests that the difference between the two action conditions that was observed in Experiment 1 can not be explained by the hypothesis that emphasizing the hand of the coactor was the main cause of facilitated responses in the imitation blocks. Interestingly, the RT advantage for imitation over complementary action blocks was smaller than in the previous experiment, although the difference between experiments was not significant. For color trials, however, the main effect of Action context was even more reduced and the difference no longer significant. This suggests that emphasizing the hand may have partly contributed to the RT difference between the two task contexts in Experiment 1. However, considering that differences between normal imitation and complementary action were still highly significant, we consider it likely that some other factor was involved.

Previous research has shown that one of the most important factors to influence the speed of response in a choice reaction time task is the stimulus–response compatibility (Hommel & Prinz, 1997; Kornblum, Hasbroucq, & Osman, 1990). Perhaps the most known form of stimulus–response compatibility (SRC) is the Simon effect, referring to the RT advantage that results when there is a spatial correspondence between stimulus and a response (Simon & Rudell, 1967), even if the position of the stimulus is irrelevant for the task. Within the present experiment, spatial congruency between the subject's and coactor's movements (e.g. both moving in upward direction in case of a precision grip) may have facilitated responses in the imitation task, as compared to the complementary action task in which movements of subject and coactor are incongruent by definition. Consistent with this suggestion, Brass, Bekkering, and Prinz (2001) identified two components that may contribute to facilitation of imitative actions: a spatial compatibility component (related to movement direction), and an ideomotor component (related to movement type).

Previous work by Nicoletti and Umiltà (1994) has shown that Simon effects may be obviated when the movement of visual attention is controlled, e.g. by presenting an additional stimulus below fixation that captures attention, or allocating attention to a position different from fixation. We decided to adopt a similar strategy in a subsequent experiment to try and limit the contribution of Simon effects to our effects of interest. Rather than presenting color cues at the coactor's hand or at the manipulandum we decided to cue the table on which the manipulandum was presented. Both the size of the table and its peripheral distribution are likely to provide a strong attentional capture that may override automatic allocation of attention in the direction of the coactors' hand. By overriding spatial attention to be drawn in the direction of the hand, any spatial cueing advantage that may have existed for the imitation condition was hypothesized to be circumvented.

Experiment 3

Method

The experimental method was identical to Experiment 1 and 2 except for the fact that color trials were indicated by coloring the table. A different group of 16 subjects (6 male, 10 female), drawn from the same population as in Experiment 1 and 2, volunteered to participate in the experiment. Subject age varied between 18 and 30 ($M = 23$, $SD = 3.4$).

Results

Subjects made 46 errors (<1%) in grip selection. An additional 62 trials (1%) were excluded from analysis because either RT or MT exceeded the 2.5 SD criterion.

Different from Experiment 1 and 2 in which a RT advantage was found for the responses in the imitation block as compared to the complementary action block, neither RTs in normal trials, nor the RTs in colored trials showed an effect of Action Context, $F(1, 15) = 0.499$, $p = .50$, $\eta_p^2 = .03$ and $F(1, 15) = 0.25$, $p = .62$, $\eta_p^2 = .02$, respectively. As in Experiment 1, analysis of color trials showed a small but significant main effect of Congruence, $F(1, 15) = 5.82$, $p < .05$, $\eta_p^2 = .28$, indicating slightly faster RTs for same (572ms) than for opposite actions (581ms) on average. As in the previous two experiments a significant interaction effect of Action Context * Congruence, $F(1, 15) = 29.76$, $p < .001$, $\eta_p^2 = .34$, was found reflecting the reversal of the congruency effect between the two action conditions. As was the case in the previous experiments, no significant main effects or interactions were found in subjects' movement times.

Discussion

Consistent with the hypothesis that a Simon effect may have contributed to the difference between the imitation task and the complementary action task in the previous two experiments, changing the assignment of the color cue to the table successfully eliminated the main difference between the two tasks. This suggests that when Simon effects are controlled for, complementary actions may be performed as quickly as imitative actions.

Elimination of the Simon effect did not affect the nature of the reversed congruency effect, suggesting the operation of two independent factors, consistent with Brass, Bekkering, and Prinz (2001), who suggested two independent components (one spatial, one related to movement type) to contribute to imitation. However, in contrast with the conclusions drawn by Brass et al., in the current study, observation of specific movement types did not automatically facilitate movements of a comparable type, but could also facilitate movements of the opposite type depending on the context in which the observed actions were embedded.

General Discussion

The aim of the present study was to investigate automatic effects of action observation in imitative and complementary contexts. Contrary to previous studies that emphasized automatic tendencies for imitation following action observation (review in Hurley & Chater, 2005a, 2005b) the results of the present study suggest that a) complementary actions may be performed as readily as imitative

actions when Simon effects are controlled, and b) that motor activation resulting from action observation does not necessarily introduce an imitative bias, but can as well prime activation of complementary actions depending on social and contextual factors. These findings suggest that the mapping between action perception and action execution is more flexible than typically assumed by most action observation models.

A long literature has shown the ability of people to flexibly learn arbitrary stimulus–response relations (Fitts & Deininger, 1954), where learned relations may bias or trigger the selection of future responses (Hommel, 1996). On the contrary, research on imitation has found evidence for an inflexible coupling between perception and action, where the observation of a human movement automatically causes a motor response in the observer that matches the observed behavior (Fadiga, Craighero, & Olivier, 2005). Brass, Zysset, & von Cramon (2001) reported that for generating a response that is different from the one observed, the automatic tendency for imitation first needs to be inhibited. Furthermore, whereas research on stimulus–response compatibility typically focused on relatively simple (nonbiological) stimulus features (e.g. the correspondence between spatial properties of stimulus and response; Hommel, 1993), studies on imitation and action observation typically assumed existence of a special mechanism for the processing of biological stimuli that is different from mechanisms subserving nonbiological stimuli (e.g. Puce & Perrett, 2003). In the present study we found no support for the existence of a specialized mechanism for automatic imitation of biological stimuli. Rather, the observation of the virtual actor was found to bias responses of subjects in accordance with the stimulus–response relations that were set between the two actors. These findings are in contradiction with current theoretical views on imitation and action observation.

In agreement with the idea that perception and execution of actions are intimately linked, models dealing with action observation have typically been phrased in accordance with congruency (matching) effects between observation and execution of actions. According to the *associative sequence learning* (ASL) theory (Heyes, 2001) the cortical connections mediating motor activation through action observation arise primarily through correlated experience of observing and executing the same actions. Consistent with the importance of experience, Heyes et al. (2005) recently showed that automatic imitation may be abolished after incompatible training when subjects were trained to respond to opening and closing hands with a movement in the opposite direction. Training however only stopped the congruency effects from occurring (no reversal of effects was found) which was argued to support the idea that it may be difficult to counteract a lifetime of correlated experience between executed actions and perceptual consequences with only limited incongruent training. Similar findings using nonbiological stimuli were reported by Tagliabue, Zorzi, Umiltà and Bassignani (2000) who were able to eliminate the Simon effect (the tendency to respond faster if there is spatial congruency between stimulus and response) after limited incongruent training in 72 trials during which subjects practiced responding with their (left/right) hand opposite to the position of the stimulus that was presented left or right from fixation. Proctor and Lu (1999) furthermore showed that with prolonged incongruent training (900 trials) a robust reversal of the Simon effect can be obtained (e.g. subjects responding faster with a left hand to a stimulus appearing

on the right). The present study further extends these findings by showing that flexible stimulus–response adjustments may just as well work for biological stimuli, e.g. in conditions where people need to cooperate with and respond to others in an opposite manner.

Interestingly, the current study managed to reverse congruency effects without the requirement of prolonged training or practice. The reason for the successful reversal of congruency effects in the present case appears to be the dual task paradigm that was used. The primary task rule to imitate or complement the actions of the coactor in 60% of the trials probably persisted during the color trials (40%) where subjects only needed to respond to color but in fact were still influenced by the stimulus–response association set by the primary task. Furthermore, the ability of subjects to successfully switch between imitation and complementary action blocks without much effort, suggests that people are rather flexible in selecting and adopting different sets of stimulus–response associations to accommodate different tasks. Although we do not deny that learning is important to establish associations between stimuli and responses (ASL), our findings suggest that there is much more flexibility in the system to modify and select stimulus–response associations in accordance with task constraints, than is assumed by ASL.

Ideomotor theories of action control (e.g. Greenwald, 1970; Prinz, 1987) suggest that actions are closely associated with the sensory consequences they produce, such that observation of other peoples' actions and their effects may automatically trigger similar responses in the observer. Although the ideomotor approach is rather liberal with respect to the sorts of stimuli that may induce action in an observer (both biological and nonbiological stimuli can be effective), it may be difficult for this theory to explain why identical stimulus–response combinations produced facilitation of responses in one condition, and inhibition of actions in the other. Interestingly, recent studies have distinguished between two principles for ideomotor action: perceptual induction and intentional induction (De Maeght & Prinz, 2004; Knuf, Aschersleben, & Prinz, 2001). Perceptual induction refers to the classical ideomotor concept that people tend to perform movements that are congruent with the effects they perceive (e.g. moving to the left if a tennis ball is played to the left part of the court). Intentional induction, however, refers to the fact that people sometimes perform movements that are congruent with the effects they would like to see (e.g. move to the right if the tennis ball is played just left to the sideline). Possibly, intentional induction and the complementary action effects found in the present study rely on similar mechanisms, since both appear to reflect the active involvement (or task) of the subject.

Furthermore, the present results could be explained by more general principles of stimulus–response coding, e.g. as reflected by the *theory of event coding* (Hommel, Musseler, Aschersleben, & Prinz, 2001) instead of having to resort to specialized models for the processing of biological stimuli. Reversed congruency effects in the present study could be explained by task specific stimulus–response relations between the observed virtual behavior and the response selected by the subject. Previous research on task-switching has shown that practiced stimulus–response relations can persist to influence behavior on a subsequent task when subjects are required to respond to a different feature within the same stimulus (Allport, Styles, & Hsieh, 1994; Waszak, Hommel,

& Allport, 2003). In the current experiment, task specific stimulus–response associations likely persisted during color trials to influence execution of subjects' grasping movements.

Lastly, the present results are in apparent contradiction with the operation of a *mirror neuron system* (MNS) in man that directly matches motor representations to the observation of goal-directed actions (Rizzolatti et al., 2001). More specifically, our data argue against the idea that observed actions automatically and obligatorily lead to the activation of an imitative or matching action (Brass, Zysset, & von Cramon, 2001; Gallese, 2005). Rather, the present findings suggest that, depending on the task, complementary responses, as well as imitative responses may become activated during action observation. Remarkably, the properties of mirror neurons, although usually regarded from a direct matching or imitation (mirror) perspective, may also, in principle, underlie the performance of complementary actions. One group of mirror neurons (about one third) shows a strict congruence between action observation and action execution, to the level of the means of the action (e.g. grasping with a precision grip), whereas for other mirror neurons (the remaining two thirds) the congruence between observation and execution is much broader and often linked to the goal of the action (Rizzolatti & Craighero, 2004). Mirror neurons with a broad congruency usually have selective motor characteristics (e.g. grasping with finger opposition), but are more broadly tuned in action observation. E.g. a mirror neuron that is activated for finger opposition in execution may become activated in response to seeing a whole hand grasping action or manipulation of an object with a different effector (Gallese et al., 1996). In line with these observations, Fogassi and Gallese (2002) suggest that broadly congruent mirror neurons could be important “to appropriately react within a social environment” since “these neurons ‘recognize’ one or more observed actions and produce a response that can be ethologically related to them” (p. 19). These findings suggest that, in addition to imitation, mirror neurons may play a role in translating between different types of actions that are complementary or logically related in the sense that they lead to the same action goal (e.g. observing an experimenter placing a piece of food on a tray may be considered by the monkey as a precursor for subsequent eating). In accordance with these suggestions, a recent fMRI study using the design of Experiment 1 (Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007) found greater activation in MNS areas (inferior parietal and inferior frontal cortices) during the preparation of complementary as compared to imitative actions, supporting the involvement of the MNS in complementary behavior in addition to imitation. Further analyses directed at the neural basis of response facilitation however suggest that the MNS is not the only structure that is responsible for the reversal of congruency effects reported here, as other areas (outside of the classical MNS) supporting goal-directed action were also found to be activated. Further research is needed to determine the relative contribution of these different networks to the flexible coupling between stimuli and responses in accordance with task constraints.

Finally, one alternative explanation that needs to be considered is that the reversal of congruency effects as reported here might have occurred because the manipulandum offered a natural scenario or condition for complementary action benefits to occur. This is an interesting point considering that most imitation studies typically require subjects to perform unusual actions that are not associated with any meaningful behavior in real life (e.g. people do not typically lift their middle finger in response to seeing another

person lifting an index finger). Instead, the setup of the present study may have helped subjects to relate their actions more easily to ordinary situations where people hand over objects (e.g. handing over a bottle) or grasp objects simultaneously (e.g. grasping a bottle for toasting). On the basis of their recent PET findings Rumiati et al. (2005) proposed that imitation of meaningful and meaningless behavior are probably effectuated through different pathways: a direct (dorsal) pathway for transforming visual input to motor output and a semantic (ventral) pathway for reactivating stored action knowledge. However, contrary to the suggestion that subjects may have used a semantic strategy while performing the two tasks, fMRI data accompanying experiment 1 (Newman-Norlund et al., 2007) yielded no support for the use of areas supporting activation of “action semantics” as compared with activations reported by Rumiati et al. (2005). Rather, and in line with traditional views in experimental psychology (cf. Fitts & Deininger, 1954), behavioral and neuroimaging results suggests that subjects successfully adopted arbitrary stimulus–response associations between observed actions and their own behavior to maximize their task performance.

In sum, the present results make a case against the common scientific belief that action observation automatically yields imitation in the observer. Instead, our findings argue for flexible models of action observation that are responsive to the relations that exist between individuals, either within the circumscribed domain of a common task, or with respect to the social conditions that guide the interaction between persons beyond imitation.

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