What Is Matched in Direct Matching? Intention Attribution Modulates Motor Priming

Roman Liepelt and D. Yves Von Cramon Max Planck Institute for Human Cognitive and Brain Sciences Marcel Brass

Max Planck Institute for Human Cognitive and Brain Sciences
and Ghent University

Converging evidence has shown that action observation and execution are tightly linked. The observation of an action directly activates an equivalent internal motor representation in the observer (direct matching). However, whether direct matching is primarily driven by basic perceptual features of the observed movement or is influenced by more abstract interpretative processes is an open question. A series of behavioral experiments tested whether direct matching, as measured by motor priming, can be modulated by inferred action goals and attributed intentions. Experiment 1 tested whether observing an unsuccessful attempt to execute an action is sufficient to produce a motor-priming effect. Experiment 2 tested alternative perceptual explanations for the observed findings. Experiment 3 investigated whether the attribution of intention modulates motor priming by comparing motor-priming effects during observation of intended and unintended movements. Experiment 4 tested whether participants' interpretation of the movement as triggered by an external source or the actor's intention modulates the motor-priming effect by a pure instructional manipulation. Our findings support a model in which direct matching can be top-down modulated by the observer's interpretation of the observed movement as intended or not.

Keywords: motor priming, direct matching, mirror neurons, action goal, intention attribution

In social interactions, we often end up in a pose, a gesture, or a facial expression similar to that of our interaction partner. Imitative behavior seems to take place automatically and without the person's intention (Lakin & Chartrand, 2003). Such automatic imitative behavior was already described on a phenomenological level by Charles Darwin (1872/1965), referring to imitative tendencies of spectators when observing athletes. On a theoretical level, the assumption of a strong link between perception and execution of action goes back to the 19th century (James, 1890; Lotze, 1852) but was widely neglected until the second half of the 20th century. William James considered the ideomotor principle of voluntary action as a fundamental mechanism of motor control primarily meant to account for internally induced, voluntary actions. He claimed that the movements of the body follow the notion of the movement's consequences in the mind immediately (James, 1890). According to the ideomotor principle, every representation of a

Roman Liepelt and D. Yves Von Cramon, Max Planck Institute for Human Cognitive and Brain Sciences, Department of Cognitive Neurology, Leipzig, Germany; Marcel Brass, Max Planck Institute for Human Cognitive and Brain Sciences, Department of Cognitive Neurology, Leipzig, Germany, and Ghent University, Department of Experimental Psychology, Ghent, Belgium.

This research was supported by a European-funded project aimed at understanding the evolutionary, developmental, and intentional control of imitation (EDICI-12929). We express our appreciation to Helge Gillmeister and Caroline Catmur for proofreading.

Correspondence concerning this article should be addressed to Roman Liepelt, Max Planck Institute for Human Cognitive and Brain Sciences, Department of Cognitive Neurology, Stephanstrasse 1A, 04103, Leipzig, Germany. E-mail: liepelt@cbs.mpg.de

movement awakens to some degree a movement that is its object (James, 1890, Vol. II, p. 526). This principle can likewise be applied to externally induced actions when the term representation refers not only to anticipatory representations of one's own planned action but also to perceptual representations of ongoing actions of other's. Observing certain actions in somebody else tends to stimulate a tendency in the perceiver to perform a movement himself that accords with the movement being observed. In the 1950s, Alvin Liberman postulated the motor theory of speech perception, in which he claimed that, in all kinds of communication, sender and receiver must be bound by a common understanding about what counts (Liberman, 1957; Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967; for a more recent version, see Liberman & Mattingly, 1985). He proposed that speech perception is facilitated by an automatic activation of a corresponding motor representation in the receiver. In this sense, the motor theory of speech perception extended the ideomotor principle to externally induced actions. In the 1970s, Greenwald postulated a sensory feedback mechanism in performance control referring to the ideomotor principle. In his ideomotor theory, Greenwald assumed that all actions are represented in the form of images of the sensory feedback they produce and that such representations are used to initiate and control body movements (Greenwald, 1970). Based on a further extension of ideomotor theory by Wolfgang Prinz (Prinz, 1997), a group of cognitive psychologists developed the theory of event coding (TEC), proposing that perceptual contents and action goals are cognitively represented by composite codes of their distal features. Perception and intended or to-be-generated events (actions) are coded within a common representational medium (Hommel, Müsseler, Ascherschleben, &

Prinz, 2001; Prinz, 1990, 1997). All these theories assume a tight relationship between perception and execution of action.

Triggered by the finding of mirror neurons located in premotor and parietal cortices of the macaque monkey (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), the idea of shared representations of perception and action attracted attention in the neuroscientific community. These neurons are active during action execution and action planning, as well as during observation of actions performed by others. Functional Magnetic Resonance Imaging (fMRI) has revealed a similar mirror system in humans (Buccino et al., 2001; Iacoboni et al, 1999). It is now widely accepted that observing somebody else executing an action leads to an activation of an internal motor representation in the observer because of the similarity of the perceived action and the motor representation used to control action execution (Brass, Bekkering, Wohlschläger, & Prinz, 2000; Brass, Zysset, & von Cramon, 2001; Press, Bird, Flach, & Heyes, 2005; Press, Gillmeister, & Heyes, 2006; Stürmer, Aschersleben, & Prinz, 2000; Vogt, Taylor, & Hopkins, 2003; for an overview, see Blakemore & Frith, 2005; Brass & Heyes, 2005). Iacoboni referred to this idea as the direct matching hypothesis (Iacoboni et al., 1999). Direct matching indicates that action observation and action execution share some cognitive as well as neuronal representations (Aziz-Zadeh, Maeda, Zaidel, Mazziotta, & Iacoboni, 2002; Decety & Grezes, 1999; di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Iacoboni et al., 2001; Iacoboni et al., 1999; Jarvelainen, Schurmann, Avikainen, & Hari, 2001; Rizzolatti et al., 1996).

Although direct matching is assumed to be a simple automatic mechanism, it was thought to play a crucial role in social cognition (Decety & Jackson, 2004), imitation learning (Rizzolatti & Craighero, 2004) and action understanding (Iacoboni et al, 2005). Furthermore, it was proposed to provide the basis for empathy (Gallese, 2006) and a bridge from action to language (Rizzolatti & Arbib, 1998, 1999). This would imply that a number of complex sociocognitive skills are resolved on a rather low functional level involving basic mechanisms such as mirroring and simulation.

Even though there is strong empirical evidence for the direct matching hypothesis, little is known about the representational level on which actions are automatically mapped onto the observer's motor representation. The question arises, "which aspects or features of the action being observed are actually taken up and how are they mapped onto aspects or features of the action being performed?"

Direct Matching and Movement Kinematics

A view that has recently gained evidence is that movement kinematics are directly mapped onto the internal motor representation of the observer during observation of an action (Castiello, Lusher, Mari, Edwards, & Humphreys, 2002; De Maeght & Prinz, 2004; Dijkerman & Smit, 2007; Edwards, Humphreys, & Castiello, 2003; Kilner, Paulignan, & Blakemore, 2003). For example, it was shown that viewing incongruent movements interferes with the execution of nonobject-directed arm movements (Kilner et al., 2003) and with object-directed prehension movements (Dijkerman & Smit, 2007). Although the observation of an incongruent biological motion automatically influences kinematic characteristics in the observer, no interference effect was observed

when subjects saw robotic arm movements (Kilner et al., 2003). Recently De Maeght & Prinz (2004) tested whether ideomotor movements are induced through watching the outcome of one's own as well as somebody else's action. The authors used a computer-animated bowling task in which participants saw a ball travelling toward a target. The ball always missed the target if participants did not intervene. Corrective interventions, which could only be made in the initial period of the ball's travel, were horizontal shifts to the left or right either applied to the travelling ball or to the stationary target, depending on the condition (ball vs. target). Their findings indicated that watching the ball's travel induced participants to move in accordance with the direction of that travel. When people watch other people's actions, they cannot help but move in accordance with those actions.

Direct matching effects induced by movement kinematics were mainly tested with motor-priming paradigms measuring an interference effect produced by an automatic matching of an observed task-irrelevant movement to the observer.

Perception Action Coupling and Action Goals

However, evidence from imitation research in children provides strong support for the idea that the influence of action observation on action execution might also be affected by higher order processes such, as goal inference and intention attribution (Bekkering, Wohlschläger, & Gattis, 2000; Meltzoff, 1995). Work by Bekkering and colleagues, for example, showed that preschool children imitated the most salient action goal and not the action kinematics when imitating hand gestures (Bekkering et al., 2000; see also Bekkering & Prinz, 2002; Gattis, Bekkering, & Wohlschläger, 2002; Gergely, Bekkering, & Király, 2002).

Even more interestingly, Meltzoff (1995) demonstrated that 18-month-old infants already imitate the goal of an action that had to be inferred on the basis of an observed unsuccessful action attempt (hands slipping several times off an object) rather than the observed action kinematics. It seems as if humans implicitly infer goals and intentions associated with movements by predicting how a movement will continue (Wolpert, Doya, & Kawato, 2003). This raises the fundamental question whether such higher order influences of intention attribution and goal inference can be observed on the direct-matching level where the intention of the observer is not to imitate the observed movement.

The aim of the present study was to test if participants' interpretation of an observed movement in terms of inferred goals and intentions modulates automatic motor-priming effects. Following the imitation study of Meltzoff (1995), we used simple, tiny, finger-lifting movements as stimuli differing with respect to the goal to assess effects of participants' interpretation on direct matching effects. We used two different approaches to achieve this aim: (a) We presented an intention without a movement and (b) a movement without an intention.

Using the Motor-Priming Effect to Measure Direct Matching

A paradigm that has been used effectively to determine the amount of automatic motor priming is the imitation-inhibition paradigm (Brass et al., 2000). Participants have to respond to a symbolic stimulus, "1" or "2," with their finger while observing a

task-irrelevant interfering finger-lifting movement. The size of the motor-priming effect can be determined by a comparison of responses that are either congruent or incongruent to the observed movement, which is task irrelevant. The term *motor priming* refers to the activation of a corresponding motor response by movement observation. This can either lead to a facilitation effect, an interference effect, or both. Even small effects produced by finegrained context manipulations on the task-irrelevant dimension can be detected by measuring the changes they produce on the task-relevant choice-reaction task.

In the first experiment, we tested whether direct matching as indexed by motor priming is influenced by the goal that is attributed to the observed action. In the present study, goal refers to the inferred end position of a movement.

Experiment 1

The aim of Experiment 1 was to test whether the observation of an unsuccessful attempt to move the index or middle finger produces a motor-priming effect. Participants observed a hand the index and middle fingers of which were restrained by two metal clamps. A brief picture sequence was presented showing the model's attempt to lift the index or middle finger against the metal clamp (attempted movement condition, AMC). Even though only a tiny movement was visible, the observed movement gives the impression that the model tries to lift the index or middle finger. In order to ensure that a potential effect was not caused by the movement itself but rather by the interpretation of the movement, we introduced a control condition in which the same movement was demonstrated without the clamp. Unlike the restrained movement, the movement in the micromovement condition (MMC) does not give the impression that the model tries to completely lift the index or middle finger. We compared these two conditions with a condition where the model lifted the index and middle fingers completely (standard movement condition, SMC). If inferred action goals modulate direct matching effects, one should expect (a) a motor-priming effect in the AMC and (b) this effect to be larger in the AMC compared to the MMC.

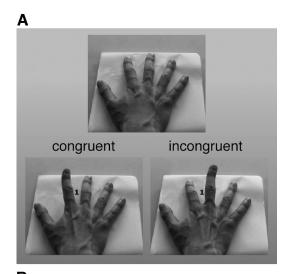
Method

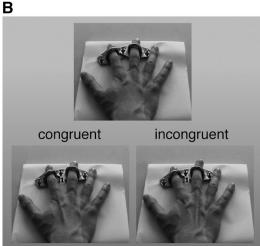
Participants

A group of 18 undergraduate students (9 men; mean age, 24.1 years) participated in this experiment. All were right handed, had normal or corrected-to-normal vision, and were naive with regard to the hypotheses of the experiment. Participants were paid $\[mathbb{e}\]$ 7 for their participation.

Apparatus and Stimuli

Stimuli were presented on a 17-in. color monitor that was connected to a Pentium I PMC. Experiments were carried out using ERTS software (Experimental Runtime System; Beringer, 2000). The sequence of hand movements consisted of two pictures of a right hand positioned in the same perspective as the hand of the participant that executed the action (see Figure 1 and Figure 2). The presented sequence produced realistic finger movements. As stimuli, photos of a hand were presented. At a viewing distance of 80 cm, the hand subtended a visual angle of $9.57^{\circ} \times 10.27^{\circ}$.





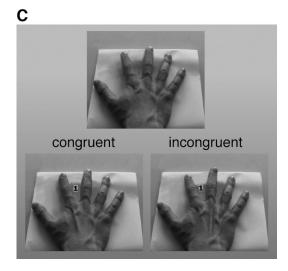


Figure 1. (A) Standard, (B) Attempted and (C) micromovements in congruent and incongruent conditions of Experiment 1.

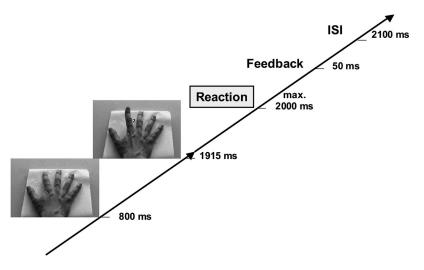


Figure 2. The stimulus sequence for each trial, depicting a finger movement as used in all experiments. Each trial started with a picture (displayed for 800 ms) showing a static hand. In the second frame (displayed for 1,915 ms) the symbolic imperative stimulus '1' or '2' appeared between the index and middle finger, one of which was lifted. The symbolic stimulus and the moving finger appeared together. Participants had to respond within 2,000 ms. The reaction was followed by a tonal feedback for 50 ms and a constant interstimulus interval.

Simultaneously with the presentation of the imperative number stimulus, a second photo of a finger-lifting movement was presented. The number subtended a visual angle of $0.72^{\circ} \times 0.36^{\circ}$.

The observed hand on the display was given in three different conditions: The SMC, the AMC, and the MMC. In the SMC, the second photo consisted of a complete lifted finger (see Figure 1A). In the AMC, the observed fingers were physically restrained by a metal clamp mounted over index and middle fingers (see Figure 1B) so that only small finger-lifting movements were observed. The goal of the action (lifting the finger) could easily be inferred based on this action context. In the MMC, the identical finger-lifting movement was presented as in the AMC. The conditions only differed with respect to action context. In the MMC, the clamp was removed from the photo by using a graphic program (see Figure 1C).

Procedure and Design

An adopted version of the paradigm developed by Brass et al. (2000) was used in Experiment 1. Participants had to lift either the index or the middle finger of their right hand in response to a number (1, index; 2, middle). The number was displayed together with a photo of a right hand on a computer screen. The observed hand was oriented in exactly the same way as the participant's response hand. The number always appeared at the same position, located between the index finger and the middle finger of the observed hand. As the number appeared, either the index or the middle finger of the observed hand was lifted either congruently or incongruently to the required response indicated by the number (see Figure 1). In congruent trials, the observed and the required response finger were identical. In incongruent trials, the observed and the required response finger differed. Participants were instructed to respond to the numbers irrespective of the observed finger-lifting movements.

Each movement condition was given in separate blocks for 120 trials. Within each block, a short break was given after the first half of the trials. Block order was counterbalanced across participants. Participants performed 360 trials in total.

Each trial began with a frame lasting for 800 ms showing a resting hand. The second frame showed the same hand with one of the fingers having moved in a transverse position for 1,915 ms. At the same time as the movement was presented, a digit appeared between the index and the middle finger of the observed hand. A tonal feedback that informed participants about the correct use of the response board was given for 50 ms followed by a blank screen of 2,100 ms. Thus, each trial lasted 4,865 ms (see Figure 2).

Results

Data Analysis

In all experiments prior to statistical analyses, all trials in which responses were incorrect or slower than 2,000 ms were excluded from statistical Reaction Time (RT) analyses. This resulted in the elimination of 1.2% of trials from the data set. A Greenhouse-Geisser correction was used to assess the significance of each effect in all experiments as well as a cutoff criterion. Participants whose mean RT fell outside of a range of more than 2.5 standard deviations from the group mean were excluded from data analysis. This resulted in the exclusion of no participants in the present experiment. RTs and percentage error for all conditions of Experiment 1 are presented in Figure 3.

RT Analysis

A 3×2 factorial design was used to analyze the present data, including the three-level factor *Observed Movement* (SMC, AMC, and MMC) and the two-level factor *Congruency* (congruent, incongruent) as within-subject variables. An equivalent analysis was

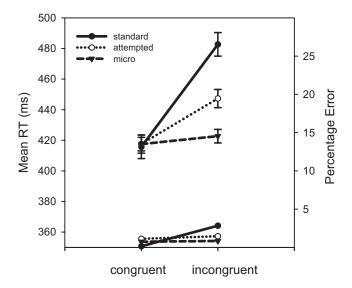


Figure 3. Mean reaction times (RTs) in ms and percentage error in Experiment 1 as a function of observed movement type (standard, attempted, and micromovements) and congruency (congruent and incongruent). Error bars represent standard errors of the mean differences.

conducted for accuracy data. The RT analysis showed that RTs for different types of observed movements differed, indicated by a significant effect of observed movement, F(2, 34) = 7.74, MSE = 1171.33, p < .01, partial $\eta^2 = .31$. RTs for congruent and incongruent trials differed as indicated by an effect of congruency, F(1, 17) = 66.55, MSE = 468.35, p < .001, partial $\eta^2 = .80$, with faster RTs in congruent trials. The congruency effect differed for different types of observed movements as indicated by a significant interaction of Movement Type \times Congruency, F(2, 34) =31.15, MSE = 346.38, p < .001, partial $\eta^2 = .65$. Planned t tests indicated a congruency effect in the SMC amounting to 67 ms, t(17) = -8.71, p < .001. In the AMC, we also observed a significant congruency effect, 30 ms, t(17) = -4.99, p < .001. However, no significant congruency effect was observed in the MMC, t(17) = -1.18, p = .253. The difference between different kinds of observed movements is due to a difference in incongruent trials between conditions, F(2, 34) = 23.52, MSE = 695.65, p <.001, partial $\eta^2 = .58$. In congruent trials we found no differences between conditions, F < 1 (for an overview of RTs in congruent and incongruent conditions of Experiment 1 see Table 1).

Most important, for the present research question was the comparison of motor-priming effects between the AMC and the MMC. This comparison indicated an increased motor-priming effect in the AMC compared to the MMC, amounting to 25 ms, t(17) = -4.09, p < .001.

Error Analysis

Error analysis showed that errors for different types of observed movements did not differ. No significant effect of observed movement was observed, F(2, 34) = 2.13, MSE = 2.22, p > .1, partial $\eta^2 = .11$. Participants made more errors in incongruent compared with congruent trials, indicated by an effect of congruency, F(1, 17) = 15.92, MSE = 1.85, p < .001, partial $\eta^2 = .48$. The congruency

effect differed for different types of observed movements, indicated by a significant interaction of Movement Type \times Congruency, F(2, 34) = 8.16, MSE = 2.25, p < .001, partial $\eta^2 = .32$.

For errors, we observed a congruency effect in the SMC. Participants made 2.7% more errors in incongruent trials compared to congruent trials, t(17) = -4.34, p < .001. We observed no congruency effect in the AMC, t(17) = -0.37, p = .72, and in the MMC, t(17) = -0.69, p = .50. In line with the RT analysis, the motor-priming effect for errors was increased in the SMC compared to the AMC by 2.3%, t(17) = 2.79, p < .05.

Most importantly, motor-priming effects in the AMC and the MMC did not differ for errors, t(17) = -0.46, p = .66. The error pattern confirms that the RT results cannot be attributed to a speed-accuracy trade-off (SAT).

Discussion

The aim of Experiment 1 was to test whether the observation of an attempted movement that allows an inference about the goal of the action produces a significant motor-priming effect. The experiment revealed a significant motor-priming effect for the AMC condition, indicating that indeed the observation of a movement attempt is sufficient to trigger motor priming. However, the size of the effect was smaller than in the SMC condition, where the whole movement path was presented. Crucially, no motor-priming effect was observed in the MMC condition, suggesting that it was not the movement kinematics themselves that triggered motor priming in the AMC condition but rather the contextual manipulation. Although we interpret this finding as evidence for the assumption that motor priming can be induced by the inferred action goal rather than the kinematics alone, there are two alternative explanations for the present results.

First, one might argue that the metal clamp attentionally cued the relevant fingers in the AMC condition and therefore the movement was easier to detect in the AMC than in the MMC. Another potential confounding variable might be that the tiny movement is easier to detect in the AMC condition because the metal clamp provides a reference for the motion. If that holds true, relative motion perception might be improved in the AMC compared to the MMC condition. In order to rule out these two alternative explanations for the motor-priming effect in the AMC, we performed a second experiment in which we tried to control for these perceptual confounds.

Experiment 2

In Experiment 2, we compared the AMC of Experiment 1 with another condition where we presented the same stimuli but with the clamp open. This resulted in two versions of the same condi-

Table 1
RTs (and SDs in Parentheses) in ms for Standard-, Micro- and
Attempted-Movement Conditions of Experiment 1

| | Congruent | Incongruent |
|-----------|-----------|-------------|
| Standard | 415 (53) | 483 (63) |
| Micro | 417 (43) | 423 (42) |
| Attempted | 418 (32) | 447 (42) |

tion: AMC (clamp closed) and AMC-clamp open (AMC-CO; Figure 4). In both conditions the clamp worked as an attentional cue directing participant's attention to the finger movements as well as a perceptual reference system improving movement perception.

In line with the findings of Experiment 1, we predicted a larger motor-priming effect in the AMC condition than in the AMC–CO condition.

Method

Participants

A new group of 17 undergraduate students (8 men; mean age, 24.1 years) participated in this experiment. All were right handed, had normal or corrected-to-normal vision, and were naive with regard to the hypotheses of the experiment. Participants were paid €7 for participation.

Apparatus and Stimuli

Apparatus and stimuli were identical to those used in Experiment 1, except that we opened the clamp in the AMC-CO condition.

Procedure and Design

The procedure and design were identical to Experiment 1. Each movement type was presented in separate blocks, with 120 trials in each. Participants performed 240 trials in total. Trial timing was identical to Experiment 1.

Results

RT Analysis

The same outlier procedure as in Experiment 1 was applied to the data of Experiment 2. This resulted in the exclusion of 2.7% of

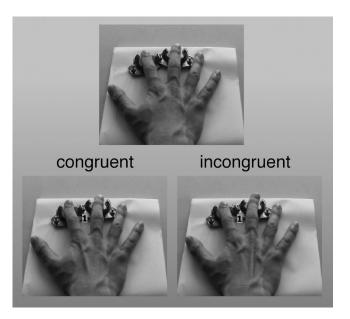


Figure 4. The attempted-movement clamp open condition in congruent and incongruent conditions of Experiment 2.

trials from the RT data analysis. No participant was excluded from data analysis due to the cutoff criterion. RTs and percentage error in the AMC and AMC–CO conditions are presented in Figure 5.

To test effects of observed movement, we used a 2×2 factorial design with a two-level factor, Observed Movement (AMC, AMC–CO), as well as Congruency (congruent, incongruent) as within-subject variables. The same analyses were performed for the error data.

We observed no strong main effect of observed movement, F(1, 16) = 4.42, MSE = 1,084.30, p = .052, partial $\eta^2 = .22$, but a significant effect of congruency, F(1, 16) = 20.0, MSE = 1,407.93, p < .001, partial $\eta^2 = .56$, due to faster RTs in congruent compared to incongruent trials. The most important finding was a significant interaction of Observed Movement × Congruency, F(1, 16) = 4.80, MSE = 279.21, p < .05, partial $\eta^2 = .23$, indicating different motor-priming effects for conditions.

Planned t tests indicated a congruency effect in the AMC amounting to 50 ms, t(16) = -4.21, p < .001. We also observed a significant congruency effect in the AMC–CO amounting to 32 ms, t(16) = -4.12, p < .001. The motor-priming effect in the AMC condition was 18 ms larger then in the AMC–CO condition, t(16) = 2.19, p < .05.

Error Analysis

Error analyses indicated no main effect of observed movement (F < 1), no main effect of congruency, F(1, 16) = 1.10, MSE = 4.51, p = .31, partial $\eta^2 = .06$, as well as no significant interaction of Observed Movement \times Congruency, (F < 1), indicating no difference in motor priming for errors between conditions ruling out an SAT.

Discussion

With Experiment 2, we aimed to test if motor priming can be modulated by inferred action goals when perceptual artifacts of Experiment 1 are controlled. These were attentional cuing effects and an improved movement perception through a visual reference system. As predicted, we found a smaller motor-priming effect in the AMC–CO conditions than in the AMC condition, indicating that the larger compatibility effect in the AMC condition is not due to perceptual or attentional confounding variables. However, we also found a motor-priming effect in the AMC–CO condition, which was of comparable size to the AMC condition of Experiment 1. This indicates that movement perception per se, improved through visual reference, is another important variable modulating motor-priming effects, as previously shown by Kilner et al., (2003).

Experiment 3

The results of Experiments 1 and 2 suggested that direct matching can be modulated by inferred action goals. In Experiment 3, we aimed to extend these findings with a reversed logic. If perceived intention modulates motor priming, removing the perceived intentionality should decrease the size of the motor-priming effect. In Experiment 3, we compared motor-priming effects during observation of a movement where the finger was passively lifted by a mechanical device, the passive movement condition (PMC), with

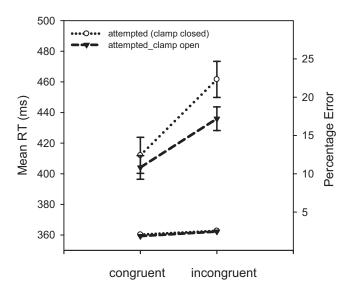


Figure 5. Mean reaction times (RTs) in ms and percentage error in Experiment 2 as a function of observed movement type (attempted movement clamp closed and attempted movement clamp open and congruency (congruent and incongruent). Error bars represent standard errors of the mean differences.

that of the SMC condition. The former reflects a nonintended, the latter an intended, movement.

We used explicit task instructions to ensure that participants would interpret the presented movements as intended or not. During the preexperimental experience, participants had to produce both kinds of movements (SMC and PMC). For the SMC, participants were instructed to lift their own fingers two times. For the PMC, participants' fingers were passively moved by the tension of the wires using the same device presented as stimuli during the experimental session. Each finger was raised twice.

Participants

A new group of 21 undergraduate students (10 men; mean age, 23.1 years) participated in this experiment. All were right handed, had normal or corrected-to-normal vision, and were naive with regard to the hypotheses of the experiment. Participants were paid €7 for participation.

Apparatus and Stimuli

Apparatus and stimuli were identical to those of the previous experiments. Additionally, we added the PMC, in which the fingers of the observed hand were passively lifted by small pulleys (see Figure 6).

Procedure and Design

The procedure and design were identical to previous experiments. However, in Experiment 3, the SMC and the PMC were randomly presented within each block (mixed design). Each type of movement was presented for 40 trials within one block so that one block consisted of 80 trials. In total, two blocks were given, intermitted by a short break, so that each participant performed 160

trials during the entire experiment. The trial timing was identical to previous experiments.

Results

RT Analysis

The same outlier procedure as in the previous experiments was applied to the data of Experiment 3. This resulted in the exclusion of 1.9% of trials from the RT data analysis. One participant was excluded from the data analysis due to the cutoff criterion. RTs and percentage error for SMC and PMC of Experiment 3 are presented in Figure 7.

We used a 2×2 factorial design including the two-level factor observed movement (SMC, PMC) as well as the two-level factor congruency (congruent, incongruent) as within-subject variables. The same analysis was conducted for accuracy data.

In the present experiment, we observed a main effect of observed movement, F(1, 19) = 6.16, MSE = 92.17, p < .05, partial $\eta^2 = .25$, with a larger effect in the SMC, as well as a main effect of congruency, F(1, 19) = 134.71, MSE = 901.46, p < .001, partial $\eta^2 = .88$, due to increased RTs in incongruent compared to congruent conditions. Most importantly, a significant interaction of Observed Movement \times Congruency was observed, F(1, 19) = 4.63, MSE = 344.42, p < .05, partial $\eta^2 = .20$, indicating a difference in motor priming between the SMC and the PMC.

Planned t tests indicated a congruency effect in the SMC amounting to 87 ms, t(19) = -9.40, p < .001. In the PMC we also observed a significant congruency effect of 69 ms, t(19) = -11.01, p < .001. The motor-priming effect in the PMC condition was 18 ms smaller compared to the SMC, t(19) = -2.15, p < .05.

Error Analysis

For errors, we observed no main effect of observed movement, (F < 1), but a main effect of congruency, F(1, 19) = 30.01,

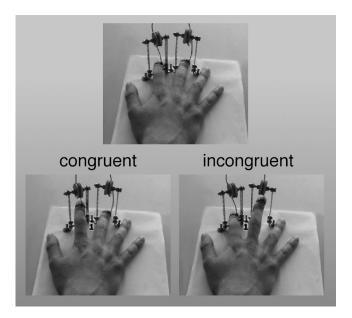


Figure 6. The figure displays the passive movement condition where the fingers were seen raised by small pulleys in congruent and incongruent conditions of Experiments 3 and 4.

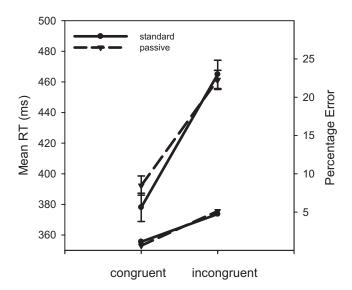


Figure 7. Mean reaction times (RTs) in ms and percentage error in Experiment 3 as a function of observed movement type (standard and passive movements) and congruency (congruent and incongruent) after directing participants' attention to the different kinds of observed movements. Error bars represent standard errors of the mean differences.

MSE = 10.10, p < .001, partial $\eta^2 = .61$, due to an increased error rate in incongruent compared to congruent conditions. Most importantly, no significant interaction of Observed Movement \times Congruency was observed (F < 1), indicating no differences in motor priming between conditions for errors.

In the SMC, the congruency effect amounted to 3.6%, t(19) = -3.56, p < .05. In the PMC, we observed a congruency effect of 4.5%, t(19) = -5.75, p < .001. In both conditions, people made more errors in incongruent trials compared to congruent trials.

Importantly, for errors, the motor-priming effects in the PMC and the SMC did not differ, t(19) = .84, p = .41. The error analyses showed no evidence for an SAT as an explanation for the observed RT effects.

Discussion

Experiment 3 revealed different motor-priming effects for observing intended (SMC) and nonintended (PMC) movements. This suggests that motor-priming effects were modulated by the perceived intention. This extends our previous findings concerning inferred action goals on motor-priming effects with respect to the modulation effect of the participants' interpretation about other's intentions on automatic motor-priming processes.

However, the perception of the movement in the PMC could have been attenuated by the distraction of the wires and the pulleys in the stimulus pictures. Perceptual attenuation might alternatively explain the smaller motor-priming effect in the PMC compared to the SMC. In order to definitively rule out this possibility, we performed a last experiment.

Experiment 4

To test whether it is actually participants' interpretation of the finger movements that modulate motor-priming effects rather than any perceptual or attentional differences between conditions, we employed a pure instructional manipulation in Experiment 4. We used exactly the same stimuli in all conditions, but varied participants' interpretation of the movement as unintentional (passive) or intentional (active). We presented the stimuli of the PMC used in Experiment 3, but gave two different groups of participants' different preexperimental experience with two variants of the apparatus. During the preexperimental experience for one group, the fingers were moved passively by the tension of the wires attached to the fingers, whereas, for the other group, participants were asked to move the fingers actively against a constant tension on the wires. Any differences between groups are unambiguously attributable to the difference in participants' interpretation of the source of the movement (passive vs. intentional). By controlling effects of perceptual attenuation, we can directly extract effects of top-down modulation on motor priming. Preexperimental experience given as a task instruction can also be viewed as a kind of action context. If direct matching is modulated by intention attribution, we expect a smaller motor-priming effect for the passive group compared to the intentional group. If, in contrast, the smaller motor-priming effect in the PMC condition of Experiment 3 was due to perceptual attenuation (distraction of the wires and the pulleys in the stimulus pictures), we would expect equal motorpriming effects for both groups.

Method

Participants

A new group of 26 undergraduate students (13 men; mean age, 23.4 years) participated in this experiment. Thirteen were given preexperimental experience in which their fingers were moved up passively by tension of the wires attached to the fingers (external source group) and thirteen were asked to move the fingers actively against constant tension on the wires (internal intention group). Participants were randomly assigned to the groups. All were right handed, had normal or corrected-to-normal vision, and were naive with regard to the hypotheses of the experiment. Participants were paid €7 for participation.

Apparatus and Stimuli

Apparatus and stimuli were identical to those used in Experiment 3, but in this experiment we only presented passive movements

Procedure and Design

Procedure and design were identical to that used in the previous experiments. However, in Experiment 4, the PMC condition was presented to two groups with different preexperimental experience (between-group design). In each group, the movement was presented for two blocks each consisting of 60 trials. In total, two blocks were given, intermitted by a short break, so that each participant performed 120 trials during the entire experiment. The trial timing was identical to previous experiments.

Results

RT Analysis

The same outlier procedure as in both previous experiments was applied to the data set of Experiment 4. This analysis resulted in

the exclusion of 1.3% of trials from the RT data analysis. No participants were excluded from data analysis due to the cutoff criterion. RTs and percentage error for the conditions of Experiment 4 are presented in Figure 8.

We used a 2×2 factorial design including the two-level between-subject factor Group (external source, internal intention), as well as the two-level factor congruency (congruent, incongruent) as a within-subject variable. The same analysis was conducted for accuracy data.

In the present experiment, we observed no main effect of group (F < 1) but a main effect of congruency, F(1, 24) = 253.54, MSE = 212.45, p < .001, partial $\eta^2 = .91$, due to increased RTs in incongruent compared to congruent conditions. Most importantly, a significant Group × Congruency interaction was observed, F(1, 24) = 7.49, MSE = 212.45, p < .05, partial $\eta^2 = .24$, indicating a difference in motor priming between the external-source group and the internal- intention group.

In the external-source group attributing the movement as passively lifted, the congruency effect amounted to 53 ms, t(12) = -7.98, p < .001. In the internal-intention group attributing the movement as actively lifted, we observed a significant congruency effect of 75 ms, t(12) = -16.57, p < .001. The motor-priming effect in the external-source group was 22 ms smaller compared to the internal-intention group, t(24) = -2.74, p < .05.

Additional evidence for effects of participants' interpretation on motor priming can be taken from a correlation analysis, in which we correlated the size of the motor-priming effect and perceived self-determination of participants as prompted by a questionnaire. The correlation was computed for overall participants (n=26) independent of group. We found a significant correlation between motor priming and perceived self-determination (r=.43, p=.03).

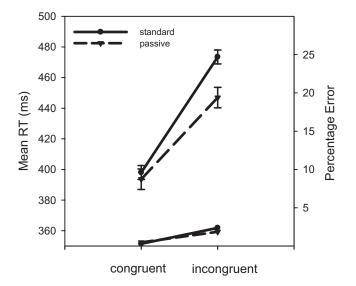


Figure 8. Mean reaction times (RTs) in ms and percentage error in Experiment 4 as a function of observed movement type (external source and internal intention) and congruency (congruent and incongruent) after excluding a perceptual attenuation effect. Error bars represent standard errors of the mean differences.

Error Analysis

For errors, we observed no main effect of group, (F < 1), but a main effect of congruency, F(1, 24) = 42.94, MSE = 0.91, p < .001, partial $\eta^2 = .64$, due to an increased error rate in incongruent compared to congruent conditions. Most importantly, no significant interactions between Group \times Congruency were observed, F(1, 24) = 1.78, MSE = 0.91, p = .19, partial $\eta^2 = .07$, indicating no differences in motor priming between the external-source group and the internal-intention group for errors.

The congruency effect in the external-source group amounted to 1.4%, t(12) = -5.30, p < .001. In the internal-intention group, we observed a congruency effect of 2.1%, t(12) = -4.53, p < .001. In both groups, participants made more errors in incongruent trials compared to congruent trials.

Importantly, for errors, the motor-priming effects between both groups did not differ statistically, t(24) = -0.13, p = .19, and had a tendency in the same direction as RT effects. Error analyses showed no evidence for an SAT as an explanation for the observed RT effects.

Discussion

The aim of Experiment 4 was to test top-down modulation effects on motor priming excluding perceptual or attentional alternative explanations for previous results. We varied only participants' interpretation of the movement as passive or intentional, while the stimuli remained equal between groups.

As in Experiment 3, the motor-priming effect was smaller in a group in which participants' fingers were moved passively compared to a group that was asked to move their fingers actively during preexperimental experience. By controlling effects of perceptual attenuation, this difference is attributable to the difference in participants' interpretation of the source of the movement (passive or intentional).

Taken together, the present findings suggest that direct matching can be top-down modulated by intention attribution (participants' interpretation of the observed movement) and suggest that the findings of Experiment 3 cannot be attributed to perceptual attenuation.

General Discussion

Previous research suggested that a tendency to imitate occurs instantly and automatically in humans when observing an action (Brass et al., 2000; 2001; Chartrand & Bargh, 1999; Lakin & Chartrand, 2003; Stürmer et al., 2000). Evidence from cognitive and neuroscience has accumulated indicating that the underlying mechanism producing this imitative response tendency is direct matching of the observed action to the motor representation of the observer. Direct matching is assumed to be an automatic process, which takes place even when people have no intention to imitate. Although there is plenty of evidence for the existence of direct matching, the basic factors that drive this mechanism are still poorly understood. In particular, effects of higher order inferential processes, such as goal inference and intention attribution, have not to our knowledge been systematically investigated in the context of direct matching. Most studies investigating the impact of higher order inferential processes have been carried out in the

context of imitation paradigms, in which participants were explicitly instructed to imitate observed actions (Bekkering et al., 2000; Meltzoff, 1995). We used a modified version of the so-called imitation-inhibition paradigm (Brass et al. 2000) to test effects of inferred goals and intentions on direct matching. Using this paradigm, direct matching is indexed by measuring the motor-priming effect produced by a task-irrelevant observed movement on the actually executed movement. There are at least two possible factors that might trigger direct matching effects: observed movement kinematics and inferred action goals. Whereas effects of observed movement kinematics on direct matching were recently demonstrated (Kilner et al., 2003), the present study focused on higher order processes of participants' interpretation of an observed movement. In Experiment 1, we tested if attempted but unsuccessful actions that allow the inference of an action goal can modulate motor-priming effects. In Experiment 2, we tried to rule out alternative perceptual explanations for these effects. In the following two experiments, we tested top-down modulation effects of attributed intentions on motor priming (Experiment 3) also controlling for perceptual artifacts (Experiment 4).

Our findings indicate that inferred action goals can trigger direct matching effects. Furthermore, we found that intention attribution modulates direct matching effects in a top-down way after giving participants different preexperimental experience influencing their interpretation about the observed movement as externally or internally triggered.

Motor Priming Induced by Inferred Action Goals

In Experiment 1, we observed a motor-priming effect induced by a task-irrelevant finger-lifting movement, which produced a response tendency congruent to the response finger replicating previous findings of Brass et al. (2000) with the present stimuli and design. We also found motor-priming effects for observed, tiny, finger-lifting movements, where the fingers were attached to a table with clamps so that the full movement was prevented. However, the motor-priming effect was smaller compared to a condition where a full movement was presented. To test whether motor priming in the attempted condition was produced by the inferred action goal we compared motor-priming effects in this condition with those in which kinematically identical micromovements were presented. The movement types differed only with respect to the presence or the absence of a clamp over the fingers. When the clamp was present, participants could easily infer the action goal (lifting the finger), because the clamp provided an interpretative context for the small movement. In the micromovement condition, the action was ambiguous, increasing the difficulty of inferring the action goal. We only observed significant motor-priming effects when the clamp was present and the action goal could be inferred, not when the clamp was absent. These data provide evidence for the assumption that motor priming cannot only be induced by movement kinematics (Kilner et al., 2003) but seems also be guided by the observer's interpretation of the motor pattern in terms of the perceived action goal (Bekkering et al., 2000).

Because we used tiny movements as stimuli, we tried to control for perceptual artifacts, such as attentional cuing effects and effects of improved perceptual movement detection due to a perceptual reference of the clamp. Under perceptually controlled task conditions, we could replicate our finding of a larger motor-priming effect when the action goal could be inferred compared to a condition where the goal was more ambiguous. However, we also observed a motor-priming effect in the latter condition, indicating that movement kinematics seem to be another important variable, as has recently been shown by Kilner et al. (2003). This also explains why we found smaller motor-priming effects guided by perceived action goals in the tiny finger-lifting movement condition where the fingers were attached to a table compared to the condition where the full movement was presented.

Our findings suggest that not only is the movement kinematic important for motor priming but so is how this kinematic is perceived by the observer. In the present study, we found larger motor-priming effects when tiny movements were cued and movement perception was improved by perceptual reference points. The most parsimonious interpretation for our findings is that both action kinematics and inferred action goals contribute to motorpriming effects. Depending on the stimulus features and its context, one or the other route can trigger motor-priming effects, a phenomenon named attentional weighting, which has previously been proposed for spatial-compatibility effects (Hommel et al., 2001). The magnitude of the compatibility effect seems to be affected by the manner in which responses are described to participants. The size of the compatibility effect was shown to be larger when participants were instructed to code responses spatially than when they were instructed to code responses in terms of color (Wenke & Frensch, 2005). Our findings are in line with the idea of attentional weighting and suggest that similar weighting effects also modulate direct matching effects in automatic imitation tasks.

Motor Priming Modulated by Attributed Intentions

In Experiment 3, we presented full finger-lifting movements as priming stimuli and tested if motor-priming effects differ for observed intended and unintended movements. In this experiment the motor-priming effect was significant smaller for movements that were passively pulled up compared with the model's intentional movements. Nevertheless, one can argue that this modulation of motor priming was due to perceptual differences in the stimulus display. Therefore, we tested top-down modulation of intention attribution more directly by presenting identical stimulus pictures excluding all possible perceptual confounding variables. In Experiment 4, only participants' interpretations of the movement as driven by an external source or by internal intention were varied. The end position of the movement as well as its kinematic was identical between conditions. Experiment 4 indicated smaller motor-priming effects when participants interpreted the observed movement as externally driven then when they attributed the movements as internally generated by the actors' own intention. This pattern of results suggests that motor-priming effects can be top-down modulated by perceived and inferred intentions, participants' interpretation of the observed movement. In the present study, the interpretation of the movement was varied by task instruction.

This modulation of motor priming by changing the interpretation of an action by mere instruction is consistent with recent findings of a study performed by Longo, Kosobud, & Bertenthal (in press). They showed that the same motor-priming effects are observed for biologically possible and impossible movements (see also Bertenthal, Longo, & Kosobud, 2006). When attention was drawn to differences between possible and impossible movements, however, only possible movements elicited automatic imitation effects. In line with our findings of Experiments 1 and 2, this suggests that actions are coded at the goal level, which is in line with common coding theories (e.g., Hommel et al., 2001; Prinz, 1990). Automatic imitation was eliminated for impossible but not for possible actions after instructing participants that they would see both natural and impossible movements. In contrast we still observed automatic imitation effects for passive movements after instructing participants that these movements were nonintended, although the effects were smaller for passive movements than for active movements. However, a direct comparison of the absolute motor-priming effect between studies cannot be made because the mere compatibility effect was subtracted from the automatic imitation effect in the Longo study, which was not the case in the present study. It seems as if attentional shifting from goals to movements is easier then an attentional shift from intentional to nonintentional movements. However, this is a topic which needs further evidence to be validated. Due to the fact that the majority of actions we perceive in daily life are intended, a default intentional mode seems to be rather plausible.

Importantly, our findings indicate that attention cannot only be shifted from actions to goals, as has been previously been proposed (Arbib, 1985; Jeannerod, 1997), but also to intentions, reflecting a more abstract level in the hierarchy.

This is in line with recent neuroimaging data showing effects of action context on the human mirror system (Iacoboni et al., 2005). However, our findings go far beyond these results by demonstrating an influence of attributed intentions on motor-priming effects even when no visual contextual information triggers this process, when it is induced by mere instruction. These findings suggest that attentional weighting can modulate motor priming on several hierarchical nested levels (Hommel, 2006). It can be induced by the perception of stimulus features (Experiments 1 and 2), visual context information (Experiments 1 and 3), and top-down influences (Experiment 4). Important for attentional weighting is how a stimulus is perceived and interpreted by the observer. As shown in the present study changes in perceived intentionality can be induced in various ways.

Taken together, the present findings suggest that, even at a very early level of processing, attributing goals and intentions do modulate direct matching effects. This indicates that automatic imitation is not purely automatic as can be suggested from the basic idea of automaticity (Schneider & Shiffrin, 1977). One main criteria of automatic processing is that such processes are purely stimulus driven. In contrast to this, our findings show a clear influence of top-down modulation on direct matching, which is assumed to be an automatic process. Our findings suggest that even very low-level processes, such as direct matching, are not purely automatic in a strict sense. Moreover, attentional modulation affects direct matching.

Facilitation Versus Interference

The pattern of results in Experiments 1, 2, and 4 seems to suggest that our experimental manipulations were primarily effective in incongruent trials. Even though this interpretation has to be handled with care without an appropriate neutral baseline, the

consistency of this finding across experiments seems to support this claim. One possible interpretation of this finding might be that the transformation of the symbolic stimulus in a motor representation becomes so automatic that in congruent trials an activation of the corresponding motor representation has no additional facilitatory effects on the initiation of the movement. This is consistent with previous findings suggesting that the motor-priming effect develops relatively slowly (Brass et al., 2001). However, if an incongruent motor representation is externally triggered, a time-consuming reevaluation process is required in order to determine which response is intended and which is externally triggered (Brass, Derrfuss, & von Cramon, 2005).

The Goal Concept in Automatic and Intentional Imitation

A goal-related approach of direct matching suggests that the specific movement path is interpreted as a means to achieve a goal whereas the action goal is represented independently as the potential end state of the action. The action is conceived in relation to the end state destined to achieve it even if this end state is not attained in every particular instance of an action (Csibra & Gergely, 2007). The interpretation of an action in terms of its goals provides us with an explanation for the action. Furthermore, attributing a goal to an observed action allows us to predict its further course, to evaluate the action's causal efficacy in terms of its outcomes, and justifies the action (Csibra & Gergely, 2007; Keil, 2006; for underlying social functions of goal attribution, see Tomasello, Carpenter, Call, Behne, & Moll, 2005).

Our findings are also in line with evidence reviewed in the introductory section coming from imitation studies (Meltzoff, 1995), showing that infants imitate the most rational action that the demonstrator should use to achieve the goal (see also Gergely et al., 2002; Meltzoff, 1988; 1995). The present study extends these findings by showing that higher order inferential processes, such as context-related goal inference, seem to take place by default and already modulate behavior at a very early processing level, such as direct matching. Humans automatically interpret elemental movements in terms of the actor's goals, which are central to action planning. The processes underlying imitation take into account what others intend. Our findings seem to suggest that action goals and attributed intentions also play an important role in understanding the functional architecture underlying imitation.

Our interpretation of automatic goal inference in action observation is in line with recent evidence coming from single-cell studies in monkeys (Umiltà et al., 2001) and neuroimaging studies in humans (Hamilton & Grafton, 2006). These studies show that movement observation leads to the generation of a motor representation in the observer even when a visual description of the final part of the observed movement is lacking.

Intention Attribution in Nonintended Actions

Whether goals and intentions are automatically attributed to all kinds of observed movements is by no means a trivial question and was not frequently investigated. Michotte (1946, 1963) was one of the first to study automatic attribution of intentions to moving shapes. He separated intentional causality from the principle of perceptual causality, in which an event is seen as causing another event. The best known example is the so called launch event, in

which a shape, A, moves toward a shape, B, that is stationary. After contact, A is stationary and B moves away. This appears as A launching or pushing B. Michotte argued that perceptual causality is an innate foundation for the idea of cause independent of learning. It maps on physical mechanical causation, in which an action is seen as caused by material processes. However, if A is a person that hits B and B moves away, one interpretation could be that B moved to avoid further blows. The motion would then be seen as goal directed, to be explained in terms of the agents' perceptions and intentions; this is also referred to as psychological, social, or intentional causality. According to Michotte, it seems as if the mode of causality is determined by the nature of the agent, as if an animate agent implies an intentional action. The theory emphasized its automaticity, its strict dependence on subtle display details, and its relative immunity from higher level intentions and beliefs (Michotte, 1946; 1963). Contrary to that, our findings indicate that an instruction changing the observer's belief about the observed action leads to differences in motor priming in kinematically identical human finger-lifting movements. It seems as if this effect is produced by an interaction of the belief the observer possesses about the observed action (intended or not) and the perceptual context.

Previous research showed increased motor-priming effects for human movements compared to robotic movements (Press et al., 2005, 2006). These studies suggest that certain stimulus properties indicating the concept of animacy lead to automatic motor priming in a bottom-up way (Press et al., 2006). Our findings suggest that another factor, which might be crucial to test, besides the kinematics of a robotic movement, is whether such a movement is intentionally triggered or not.

Theoretical Framing: Intention Attribution Modulates Motor Priming

The present results are in line with theories that can explain automatic imitation effects triggered by inferred action goals (Hommel et al., 2001) and complement previous findings of action goals on intentional imitation (Bekkering et al., 2000; Meltzoff, 1995; Wohlschläger, Gattis, & Bekkering, 2003).

However, our findings go even beyond this assumption, by showing that not only the attributed action goal but also the attribution of intentionality modulates direct matching. We do not want to claim that intention attribution is the only factor that affects direct matching. Another important factor triggering direct matching is the kinematic of an action (Kilner et al., 2003; see also Rumiati & Bekkering, 2003; Tessari, Rumiati, & Haggard, 2002), a factor which is needed to fully explain motor-priming effects. These two mechanisms do not compete but may complement each other. Whereas other studies focused on the impact of action kinematics on direct matching effects (Kilner et al., 2003), the present study provides evidence (a) for an effect of inferred action goals and (b) for an effect of top-down modulation of the observer's interpretation about the actor's intention on direct matching effects (see also Grezes, Costes, & Decety, 1998; Zentgraf et al. 2005). A framework that offers an opportunity to incorporate both routes is ideomotor theory (Hommel et al., 2001; James, 1890; Lotze, 1852; Prinz, 1990, 1997). This theory describes the importance of action effects for action planning and control. Prior to performing a goal-directed action, the agent holds a representation of the environmental changes that he/she wants to produce by the movement. Actions are represented in terms of their perceptual effects. These action effects can be very proximal and strongly related to the action itself or more distal and abstract. Within this framework, action perception can modulate action execution on a proximal level, such as action kinematics, as well as on a more abstract and distal level, such as inferred goals and attributed intentions.

According to a more recent version of ideomotor theory, the theory of event coding of Hommel et al. (2001), perceptual and motor events are coded in terms of a shared set of features varying in salience. Feature weighting can be induced by both intentional and attentional modulation, resulting from highlighting of features of the response or the stimulus, respectively. The theory of event coding can explain a modulation of motor-priming effects by perceived goals and inferred intentions through intentional highlighting of certain stimulus features.

References

- Arbib, M. A. (1985). Schemas for the temporal organization of behaviour. Human Neurobiology, 4, 63–72.
- Aziz-Zadeh, L., Maeda, F., Zaidel, E., Mazziotta, J., & Iacoboni M. (2002). Lateralization in motor facilitation during action observation: A TMS study. Experimental Brain Research, 144, 127–131.
- Bekkering, H., & Prinz, W. (2002). Goal representations in imitative actions. In K. Dautenhahn, & E. Nehaniv (Eds.), *Imitation in animals* and artifacts (pp. 555–573). Cambridge, MA: MIT Press.
- Bekkering, H., Wohlschläger, A., & Gattis, M. (2000). Imitation of gestures in children is goal-directed. *Quarterly Journal of Experimental Psychology A*, 53(1), 153–164.
- Beringer, J. (2000). Experimental Runtime System (Version 3.32). [Computer software]. Frankfurt am Main, Germany: BeriSoft Corporation.
- Bertenthal, B. I., Longo, M. R., & Kosobud, A. (2006). Imitative response tendencies following observation of intransitive actions. *Journal of Experimental Psychology: Human Perception and Performance*, 32(2), 210–225.
- Blakemore, S. J., & Frith, C. (2005). The role of motor contagion in the prediction of action. *Neuropsychologia*, 43, 260–267.
- Brass, M., Bekkering, H., Wohlschläger, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: Comparing symbolic, spatial, and imitative cues. *Brain Cognition*, 44(2), 124–143.
- Brass, M., Derrfuss, J., & von Cramon, D. Y. (2005). The inhibition of imitative and overlearned responses: A functional double dissociation. *Neuropsychologia*, 43, 89–98.
- Brass, M., & Heyes, C. M. (2005). Imitation: Is cognitive neuroscience solving the correspondence problem? *Trends in Cognitive Science*, 9, 489–495.
- Brass, M., Zysset, S., & von Cramon, D. Y. (2001). The inhibition of imitative response tendencies. *Neuroimage*, *14*(6), 1416–1423.
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. European Journal of Neuroscience, 13, 400–404.
- Castiello, U., Lusher, D., Mari, M., Edwards, M. G., & Humphreys, G. W. (2002). Observing a human or a robotic hand grasping an object: Differential motor priming effects. In W. Prinz & B. Hommel (Eds.) Attention and performance, Vol. 19 (pp. 315–333). Cambridge, MA: MIT Press.
- Chartrand, T. L., & Bargh, J. A. (1999). The chameleon effect: The perception-behavior link and social interaction. *Journal of Personality* and Social Psychology, 76, 893–910.
- Csibra, G., & Gergely, G. (2007). 'Obsessed with goals': Functions and

- mechanisms of teleological interpretation of actions in humans. *Acta Psychologica*, 124 (1), 60–78.
- Darwin, C. (1965). The expression of the emotions in man and animals. Chicago: University of Chicago Press. (Original work published 1872).
- Decety, J., & Grezes, J. (1999). Neural mechanisms subserving the perception of human actions. *Trends Cognitive Science*, 3(5), 172–178.
- Decety, J., & Jackson, P. L. (2004). The functional architecture of human empathy. Behavioral and Cognitive Neuroscience Reviews, 3(2), 71– 100.
- De Maeght, S., & Prinz, W. (2004). Action induction through action observation. Psychological Research, 68, 97–114.
- Dijkerman, H. C., & Smit, M. C. (2007). Interference of grasping observation during prehension, a behavioural study. *Experimental Brain Research*, 176, 387–396.
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, 91(1), 176–180.
- Edwards, M. G., Humphreys, G. W., & Castiello U. (2003). Motor facilitation following action observation: A behavioural study in prehensile action. *Brain Cognition*, 53, 495–502.
- Gallese, V. (2006). Intentional attunement: A neurophysiological perspective on social cognition and its disruption in autism. *Brain Research*, 1079(1), 15–24.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. Brain, 119 (Pt 2), 593–609.
- Gattis, M., Bekkering, H., & Wohlschläger, A. (2002). Goal-directed imitation. In A. Meltzoff, & W. Prinz (Eds.), *The imitative mind: Development, evolution, and brain bases* (pp. 183–205). Cambridge, England: Cambridge University Press.
- Gergely, G., Bekkering, H., & Király, J. (2002). Developmental psychology: Rational imitation in preverbal infants. *Nature*, 415(6873), 755.
- Greenwald, A. G. (1970). Sensory feedback mechanisms in performance control: With special reference to the ideo-motor mechanism. *Psychological Review*, 77, 73–99.
- Grezes, J., Costes, N., & Decety, J. (1998). Top-down effect of strategy on the perception of human biological motion: A PET investigation. Cognitive Neuropsychology, 15, 553–582.
- Hamilton, A. F., & Grafton, S. T. (2006). Goal representation in human anterior intraparietal sulcus. *Journal of Neuroscience*, 26, 1133–1137.
- Hommel, B. (2006). Bridging social and cognitive psychology? In P. A. M. Van Lange (Ed.), *Bridging social psychology: The benefits of transdisciplinary approaches* (pp. 167–172). Hillsdale, NJ: Erlbaum.
- Hommel, B., Müsseler, J., Ascherschleben, G., & Prinz, W. (2001). The Theory of Event Coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences*, 24, 849–937.
- Iacoboni, M., Koski, L. M., Brass, M., Bekkering, H., Woods, R. P., Dubeau, M. C., et al. (2001). Reafferent copies of imitated actions in the right superior temporal cortex. *Proceedings of the National Academy of Sciences*, USA, 98(24), 13995–13999.
- Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biology*, 3(3), e79.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, 286(5449), 2526–2528.
- James, W. (1890). The principles of psychology (Vols. 1–2). New York: Holt.
- Jarvelainen, J., Schurmann, M., Avikainen, S., & Hari, R. (2001). Stronger reactivity of the human primary motor cortex during observation of live rather than video motor acts. *Neuroreport*, 12, 3493–3495.
- Jeannerod, M. (1997). The cognitive neuroscience of action. Cambridge, MA: Blackwell.
- Keil, F. C. (2006). Explanation and understanding. Annual Review of Psychology, 57, 227–254.

- Kilner, J., Paulignan, Y., & Blakemore, S. (2003). An interference effect of observed biological movement on action. *Current Biology*, 13 (6), 522– 525.
- Lakin, J. L., & Chartrand, T. L. (2003). Using nonconscious behavioral mimicry to create affiliation and rapport. *Psychological Science*, 14(4), 334–339.
- Liberman, A. M. (1957). Some results of research on speech perception. Journal of the Acoustical Society of America, 29, 117–123.
- Liberman, A. M., Cooper, F. S., Shankweiler, D. P., & Studdert-Kennedy, M. (1967). Perception of the speech code. *Psychological. Review*, 74, 431–461.
- Liberman, A. M., & Mattingly, I. G. (1985). The motor theory of speech perception revised. *Cognition*, 21(1), 1–36.
- Longo, M. R., Kosobud, A., and Bertenthal, B., I. (in press). Automatic imitation of biomechanically impossible movements: Effects of priming movements vs. goals. *Journal of Experimental Psychology: Human Perception and Performance*.
- Lotze, R. H. (1852). Medicinische psychologie oder physiologie der seele [Medical psychology or mental physiology]. Leipzig, Germany: Weidmann.
- Meltzoff, A. N. (1988). Infant imitation after a 1-week delay: Long-term memory for novel acts and multiple stimuli. *Developmental Psychology*, 24, 470–476.
- Meltzoff, A. N. (1995). Understanding the intentions of others: Reenactment of intended acts by 18-month-old children. *Developmental Psychology*, 31, 838–850.
- Michotte, A. (1946). La Perception de la Causalité. Louvain, France: Institut Superieur de Philosophie.
- Michotte, A. (1963). *The perception of causality*. (T. R. Miles & E. Miles, Trans.). London: Methuen. (Original work published 1954)
- Press, C., Bird, G., Flach, R., & Heyes, C. (2005). Robotic movement elicits automatic imitation. *Cognitive Brain Research*, 25(3), 632–640.
- Press, C., Gillmeister, H., & Heyes, C. (2006). Bottom-up, not top-down, modulation of imitation by human and robotic models. *European Jour*nal of Neuroscience 24(8), 2415–2419.
- Prinz, W. (1990). A common coding approach to perception and action. In O. Neumann & W. Prinz (Eds.), *Relationships between perception and action: Current approaches* (pp. 167–201). Berlin: Springer.
- Prinz, W. (1997). Perception and action planning. European Journal of Cognitive Psychology, 9(2), 129–154.
- Rizzolatti, G., & Arbib, M. A. (1998). Language within our grasp. Trends in Neurosciences, 21(5), 188–194.
- Rizzolatti, G., & Arbib, M. A. (1999). From grasping to speech: Imitation might provide a missing link: Reply. *Trends in Neurosciences*, 22(4), 152.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. Annual Review of Neuroscience, 27, 169–192.
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, 3, 131–141.
- Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu, E., Perani, D., et al. (1996). Localization of grasp representations in humans by PET: 1. Observation versus execution. *Experimental Brain Research*, 111(2), 246–252.
- Rumiati, R. I., & Bekkering, H. (2003). To imitate or not to imitate? How the brain can do it, that is the question! *Brain and Cognition*, 53(3), 479–482.
- Schneider, W., & Shiffrin, R. M. (1977). Controlled and automatic human information processing: 1. Detection, search, and attention. *Psychological Review*, 84, 1–66.
- Stürmer, B., Ascherschleben, G., & Prinz, W. (2000). Correspondence effects with manual gestures and postures: A study of imitation. *Journal of Experimental Psychology*, 26, 1746–1759.

- Tessari, A., Rumiati, R. I., & Haggard, P. (2002). Imitation without awareness. *Neuroreport*, *13*(18), 2531–2535.
- Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. Behavioral and Brain Sciences 28, 675–735.
- Umiltà, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., et al. (2001). I know what you are doing: A neurophysiological study. *Neuron*, *31*(1), 155–165.
- Vogt, S., Taylor, P., & Hopkins, B. (2003). Visuomotor priming by pictures of hand postures: Perspective matters. *Neuropsychologia*, 41, 941–951.
- Wenke, D., & Frensch, P. A. (2005). The influence of task instruction on action coding: Constraint setting or direct coding? *Journal of Experimental Psychology: Human Perception and Performance*, 31, 803–819.Wohlschläger, A., Gattis, M., & Bekkering, H. (2003). Action generation

- and action perception in imitation: An instance of the ideomotor principle. *Philosophical Transitions of the Royal Society of London: B Biological Science*, 358, 501–515.
- Wolpert, D. M., Doya, K., & Kawato, M. (2003). A unifying computational framework for motor control and social interaction. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, 358(1431), 593–602.
- Zentgraf, K., Stark, R., Reiser, M., Kunzell, S., Schienle, A., Kirsch, P., et al. (2005). Differential activation of pre-SMA and SMA proper during action observation: Effects of instructions. *Neuroimage*, 26(3), 662–672.

Received November 16, 2006
Revision received September 24, 2007
Accepted October 1, 2007

Low Publication Prices for APA Members and Affiliates

Keeping you up-to-date. All APA Fellows, Members, Associates, and Student Affiliates receive—as part of their annual dues—subscriptions to the *American Psychologist* and *APA Monitor*. High School Teacher and International Affiliates receive subscriptions to the *APA Monitor*, and they may subscribe to the *American Psychologist* at a significantly reduced rate. In addition, all Members and Student Affiliates are eligible for savings of up to 60% (plus a journal credit) on all other APA journals, as well as significant discounts on subscriptions from cooperating societies and publishers (e.g., the American Association for Counseling and Development, Academic Press, and Human Sciences Press).

Essential resources. APA members and affiliates receive special rates for purchases of APA books, including the *Publication Manual of the American Psychological Association*, and on dozens of new topical books each year.

Other benefits of membership. Membership in APA also provides eligibility for competitive insurance plans, continuing education programs, reduced APA convention fees, and specialty divisions.

More information. Write to American Psychological Association, Membership Services, 750 First Street, NE, Washington, DC 20002-4242.