Effector-specific Motor Interference in Action Simulation

Peggy Tausche, Anne Springer and Wolfgang Prinz
(Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany)

Abstract

Neuroscientific findings suggest that observing temporally occluded actions evokes a mental simulation of the occluded action part. This action simulation may involve corresponding motor programs in the observer and is suggested to run in real time. The present study aimed to investigate whether real-time action simulation relies on effector-specific motor representations. Our participants watched transiently occluded actions performed either with the arms or the legs and had to predict the action course after occlusion. Participants also responded to the task with a movement involving either their arms or legs. Simulation performance broke down when the observed effector and the moved effector corresponded. In contrast, simulation was intact when the effectors did not correspond. The results are in line with previous research and extend it by showing that interference effects can occur within the real-time course of action simulation. Furthermore, shared representations between action simulation and action execution are effector specific.

Introduction

In everyday life, humans experience hundreds of situations in which other people's actions are temporally or partially occluded. Nevertheless, observers perceive the actions in a fluent manner. It is suggested that humans fill the perceptual gap with a mental simulation of the unseen action parts. This action simulation implies the establishment of a mental representation of the unseen part that is equivalent to the visual representation during visual perception.

In the Common Coding framework, it has been argued that action execution and action perception share a common coding system (Prinz, 1990, 1997). This might enable observers to understand, anticipate and predict others' ongoing behavior (Blakemore & Frith, 2005; Prinz, 2006; Wilson & Knoblich, 2005; Wolpert & Flanagan, 2001). Behavioral studies supported this assumption by showing that concurrent action execution and action observation can interact with each other (Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschlager, & Prinz, 2000; Kilner, Paulignan, & Blakemore, 2003; Stürmer, Aschersleben, & Prinz, 2000). An influence of action observation on action execution was shown by Brass et al. (2000). They showed that the observation of a lifting movement of the index finger led to faster execution of a lifting movement with the index finger

relative to the middle finger, even when the observed movement was irrelevant to the task. Other studies have investigated the influence of action execution on action perception (Daprati, Wriessnegger, & Lacquaniti, 2007a, 2007b; Jacobs & Shiffrar, 2005). Jacobs and Shiffrar (2005) showed that the ability to discriminate between two observed walking speeds is selectively impaired in walking observers as compared to cycling and standing observers. Taken together these findings propose a bi-directional link between action perception and action production.

While several studies support a bi-directional link between action perception and action production on the level of movements (Brass, et al., 2001; Brass, et al., 2000; Kilner, et al., 2003; Stürmer, et al., 2000), others were able to provide evidence for a link on the level of goals (Bekkering, Wohlschlager, & Gattis, 2000; Hamilton & Grafton, 2006; Woodward, 1998). This suggests that a common representational system of action execution and action observation might be hierarchically organized (1990).

Neurophysiologic findings support this idea by showing a different nature of the so called mirror neurons. These neurons are located in area F5 in the macaque monkey brain (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) and fire both when the monkey observes an action and when it performs this action on its own. Studies using functional magnet resonance imaging (fMRI) and transcranial magnetic stimulation (TMS) have provided significant evidence that such a mirror neuron system also exists in the human brain (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Grezes, Armony, Rowe, & Passingham, 2003; Rizzolatti & Craighero, 2004). Moreover, there is evidence that there are "strictly congruent" mirror neurons which fire only when the observed and the executed action correspond in means and goals. In contrast, "broadly congruent" neurons generalize across different means and goals (Gallese, et al., 1996).

Other studies have addressed the question of the underlying processes of action simulation itself (Graf, et al., 2007; Prinz & Rapinett, 2008). For instance, Graf and colleagues (2007) recently proposed that the internal simulation of observed actions runs in real-time. The authors used a paradigm in which the participants perceived temporally occluded sequences of point-light actions. In their studies they presented the beginning of an action sequence which was interrupted by an occluder. The occluder was followed by a static test posture. Two independent variables

were manipulated: occluder time (100, 400 or 700 ms) and test posture time (the time which would pass behind the occluder) (100, 400 or 700 ms). The participants' task was to decide whether the test posture was a continuation of the previous seen action in the same visual angle, or whether it was rotated in depth. In accordance with the real-time simulation hypothesis, the participants showed best performance when occluder and test posture time corresponded. Furthermore, performance decreased as the time distance between occluder and test posture time increased. The authors argued that the internal representation of the action is updated in real time and that this leads to high task performance when the upcoming test posture corresponds to a real-time outcome. Furthermore, task performance decreases with increasing dissimilarity in the internal representation and the test posture.

Our study connects to this work by investigating the role of motor representations in this action simulation process. In extension to previous research on motor interference in action observation and action discrimination (Daprati, et al., 2007a, 2007b; Jacobs & Shiffrar, 2005), we focussed on motor interference effects *within the real-time course* of action simulation (as proposed by Graf et al., 2007). Moreover, we wondered whether motor representations, which might be used in action simulation, are organized on an effector-specific level.

It has been suggested that humans have a long-term body representation which contains the basic spatial arrangement of different body parts (Reed & Farah, 1995). A structural overlap between one's own and another person's body enables humans to represent visual, motor and proprioceptive inputs from both bodies within a common code in a shared representational system which in turn would lead to more interactions between both processes. When a common code is used for one process (e.g., action execution), it is not or less available for the other process (e.g., action perception), which should lead to interference. Accordingly, we hypothesized that a structural overlap on the effector-specific level (i.e., the same effector is involved in action simulation and action execution) would lead to increased interference effects as compared to no structural overlap (i.e., different effectors are involved in action simulation and action execution).

In order to investigate this, we adopted the action prediction task used by Graf et al. (2007) and combined it with a secondary motor task. This motor task was performed simultaneously to the action prediction task and involved either the same effector as the relevant effector in the point-light action or a different effector.

Methods

Participants: Thirty right-handed participants (mean 25 years; range 20 – 35 years; 14 female) were tested. One participant's data had to be excluded from the analysis, because of a faulty response device which caused the loss of a part of the data set. Thus, data analysis was based on a total number of 29 participants. All participants reported normal or corrected-to-normal vision and were naive with respect to the purpose of the study. They were paid for their participation. Informed written consent was obtained from each participant prior to the experiment.

Material: We used six film sequences showing a point-light character (Johansson, 1973, 1975) performing familiar actions. These were three arm-related actions (tennis, throwing something with one hand, throwing something with both hands) and three leg-related actions (knee-bends, standing up from a chair, standing up from the floor). We chose actions which were rated on a visual analogue scale as being highly arm- or leg-related by an independent sample (N = 15). All actions of the present study were familiar everyday actions and all participants could easily recognize and name them. This is unique and contrasts with other studies using very simplistic and artificial movements (Brass, et al., 2000; Kilner, et al., 2003; Reed & Farah, 1995; Reed & McGoldrick, 2007), thus allowing us to investigate the involvement of effector-specific motor representations in action simulation of complex and familiar actions.

We used point-light stimuli (instead of real films), because these stimuli are known to emphasize motion information instead of alternative sources of information like social information. The videos were taken from a stimulus set provided by Graf et al. (2007) and showed a male right-handed agent recorded using a motion capture system (Vicon Motion Systems Ltd., Oxford, UK). Each point-light display consisted of 13 black dots that were located at the major joints and were 2 mm in diameter. The point-light character was about 7 cm in height and actions were performed within an area of 340 pixels width and 312 pixels height at the center of the screen. An occluder of the same size was presented as a square.

Design and Data Analysis: As in the original paradigm of Graf et al. (2007), we manipulated the factors occluder time (100, 400 and 700 ms) and test posture time (TPT; 100, 400 and 700 ms). A combination of each level of both factors resulted in a condition in which occluder time and TPT correspond (i.e., time distance of 0 ms) and conditions in which occluder time and TPT did not correspond (i.e., time distance of 300 ms and 600 ms, respectively). Participants had to decide whether the test posture was a continuation in the same visual angle, or whether it was rotated in depth. In accordance with Graf et al. (2007), we used

this task, because no explicit judgments about the timing of the actions were requested. Therefore subjects were explicitly instructed to decide whether the test posture was a correct or rotated continuation at any point in time which avoids that task instruction generates potential real-time effects. In order to investigate effector-specific interference effects in action simulation, we introduced a secondary motor task, which was either performed with the arms or with the legs. Participants were instructed to hold their hands/feet on two home buttons during the action sequence of the action prediction task and to perform a discrete bimanual/bipedal movement in order to provide a response to the action prediction task. The movement was a reaching movement towards two diagonally opposite buttons of an arrangement of four different target buttons (e.g., pressing the right upper key with the right hand and pressing the left lower key with the left hand simultaneously in order to give a "correct continuation" response) (Figure 1). The location of the target keys were randomized across participants. Participants were asked to respond immediately when the static test posture appeared and a time out for their response was set at 4000 ms (time out trials were excluded from data analysis).
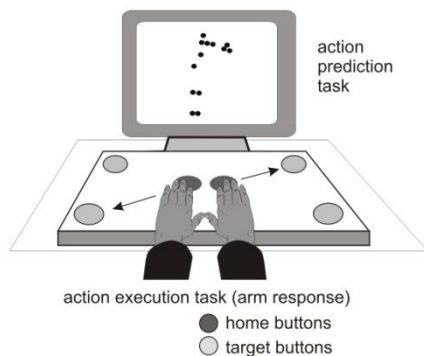
Figure 1: Schema of the experimental setting (exemplary for arm responses). The actions for the action prediction task were presented on the screen. The hands or feet rested on the home buttons (dark gray). The motor task involved a discrete bimanual/bipedal movement towards two diagonally opposite target keys in order to give a response to the action prediction task.

The experiment consisted of 648 trials (3 occluder times x 3 test posture times x 2 response devices [same, rotated] x 2 video effector [arm versus leg] x 2 response effector [arm versus leg] x 9 repetitions) divided into two experimental sessions with a break of one to two hours in between. Each session consisted of 324 trials divided into 12 blocks. The factor response effector (arm versus leg) was constant within one session. The order of the sessions was randomized across participants. The factor occluder time was blocked and the order of blocks was balanced across participants, with the restriction that two identical

occluder times did not follow each other. The factors video effector (arm versus leg) and test posture time were completely randomized. Prior to the first session, participants received an initial familiarization phase where all actions were presented twice. This was followed by a practice phase containing different actions as in the experiment (knee-bends, leapfrog, basketball). The practice phase consisted of 30 trials and was performed with the same effector that was required in the first experimental session. Prior to the second session, a practice phase of 15 trials was performed again using the other effector, which was required in the second session. The experimental sessions lasted about 1.5 and 1 hour, respectively. Feedback was given to the participants during the practice and the experimental phases.

Data analysis focused on error rates and reaction times (RTs). RTs were defined as the time between TPT onset and leaving the home buttons. RTs were only analyzed for correct responses. Due to the fact that spatial and temporal aspects were mixed in the rotated trials, the analysis included only unrotated trials.
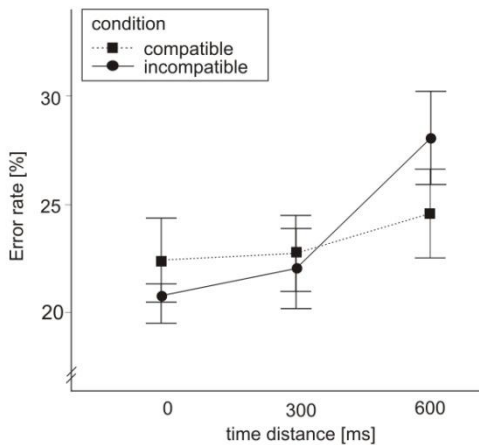
Our analyses were based on compatibility between the relevant effector in the action prediction task and the effector in the action execution task. Compatible trials were those trials in which the video effector and the response effector corresponded (arm/arm and leg/leg); incompatible trials were the trials in which the video effector and the response effector did not correspond (arm/leg and leg/arm). Compatibility was considered to be an adequate factor for the analysis because participants were required to predict exactly the same actions and to answer with their arms and legs in both compatible and incompatible trials. This allowed us to control for stimulus-dependent effects (due to variability within the point-light actions) and to control for response-dependent effects (due to variability between arm and leg responses), which are not in the center of interest in this study.

Results and Discussion

Error rates: We performed an analysis-of-variance (ANOVA) with the factors occluder time, test posture time (TPT) and compatibility. Error rates showed a significant main effect of TPT ($F(2, 56) = 38.395$; $p < .001$; $Eta^2 = .578$) with significantly higher error rates in the long TPT as compared to short and medium TPTs (ps $< .001$; Bonferroni corrected). No main effect of occluder time and no main effect of compatibility were found (Fs $< .1$). A significant two-way interaction between the factors occluder time and test posture time was found ($F(2, 112) = 2.835$; $p < .05$; $Eta^2 = .092$). In line with Graf et al. (2007), lowest error rates were found when occluder time and test posture time corresponded. No other two-way interaction reached significance (Fs < 1). Most importantly, the three-way interaction between the factors occluder time, TPT and

compatibility was significant ($F_{(4, 112)}$ = 2.664; p < .05; Eta^2 = .087). There was no significant occluder time x TPT interaction in the compatible condition (F < 1.8), while this interaction was reliable in the incompatible condition ($F_{(4, 112)}$ = 3.660; p < .01; Eta^2 = .116). This indicates that incompatible trials, in contrast to compatible trials, involved real-time action simulation processes.

A way of confirming this effect and to increase power is the analysis of the time distance effect. In a further step, we collapsed the different occluder times and TPTs across time distances (time distance of 0 ms, 300 ms and 600 ms, respectively) and performed an ANOVA with the factors time distance (0, 300 and 600 ms) and compatibility. Data showed a significant main effect of time distance ($F_{(2, 56)}$ = 11.235; p < .001; Eta^2 = .286). As put forward in the real-time hypothesis, error rates were significantly higher in the greatest time distance as compared to the short and medium time distance (ps < .001; Bonferroni corrected). Again, there was no main effect of compatibility (F < .1). Most interestingly, data showed a significant interaction between the factors time distance and compatibility $F_{(2, 56)}$ = 5,050; p < .05; Eta^2 = .153), with a significant main effect of time distance in the incompatible trials ($F_{(2, 56)}$ = 13.461; p < .001; Eta^2 = .325), while there was no reliable effect of time distance present in the compatible trials (F < 1.9) (Figure 2). Again, this indicates that incompatible trials, in contrast to compatible trials, involved real-time action simulation processes.
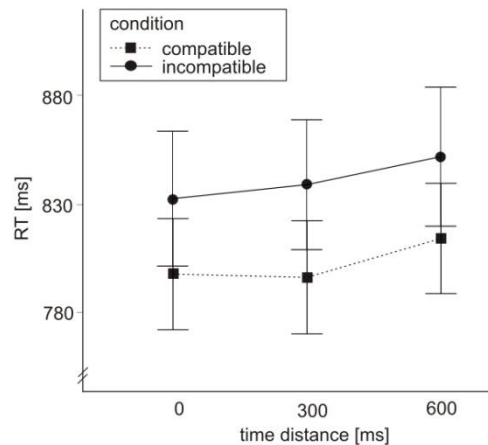
main effect of occluder time ($F_{(2, 56)}$ = 4.745; p < .05; Eta^2 = .145), with significantly shorter RTs in the medium as compared to the short occluder time (p < .05; Bonferroni corrected). A significant main effect of TPT ($F_{(2, 56)}$ = 23.389; p < .001; Eta^2 = .455) was found with increasing RTs with increasing TPT (ps < .01; Bonferroni corrected). Furthermore, a significant main effect of compatibility was found ($F_{(1, 56)}$ = 6.362; p < .05; Eta^2 = .185), with shorter RTs in compatible as compared to incompatible trials. A significant two-way interaction between the factors occluder time and test posture time was found ($F_{(2, 112)}$ = 6.568; p < .001; Eta^2 = .19), with longest RTs when occluder time and test posture time did not correspond. Neither other two-way interactions nor the three-way interaction reached significance (Fs) < 1.

Again, we collapsed the different occluder times and TPTs across time distances (time distance of 0 ms, 300 ms and 600 ms, respectively) and performed an ANOVA with the factors time distance (0 ms, 300 ms and 600 ms) and compatibility. Data showed a significant main effect of time distance ($F_{(2, 56)}$ = 5.337; p < .01; Eta^2 = .160). RTs were significantly higher in the long time distance as compared to the short and medium time distance (p < .05; Bonferroni corrected). There was a main effect of compatibility ($F_{(1, 56)}$ = 6.123; p < .05; Eta^2 = .179), with significantly faster RTs in compatible as compared to incompatible trials. No significant time distance x compatibility interaction was found (F < .4) (Figure 3).

Figure 2: Error rates plotted as a function of time distance dependant on the compatibility between video effector and response effector. Error rates showed a significant time distance effect in incompatible trials, while no reliable time distance effect was present in compatible trials.

Figure 3: Reaction times plotted as a function of time distance dependant on the compatibility between video effector and response effector.

General Discussion
The present study aimed to investigate the role of motor representations in action simulation by focussing on motor interference within the real-time course of action simulation. Furthermore, it was investigated whether motor representations, which might be used in

Reaction times: We performed an ANOVA with the factors occluder time, test posture time (TPT) and compatibility. Reaction times showed a significant

real-time action simulation, are organized on an effector-specific level.

Overall, the results showed two major findings: First, our data showed that action simulation and action execution share a common representational system. Action simulation is considered to run in real time (Graf, et al., 2007), but we could show interference in the time course of action simulation in an online action prediction task. To our knowledge, our results are the first to demonstrate that a secondary motor task leads to an interference effect within the real-time course of action simulation. We assume that the preparation of the to-be-executed action takes resources of the same representational system as action simulation, which in turn leads to a lack of resources which might be necessary for an action simulation to run in real time.

Second, we were successfully able to show that this motor interference effect was effector-specific. That is, real-time action simulation broke down when the action prediction task and the action execution task involve the same type of effector as compared to a different type of effector, although the predicted and the executed actions differed in terms of the kind of action, the exact trajectory and action goals. This allows us to specify that shared representations are coded on an effector-specific level and that they can generalize across different kinds of actions, trajectories and goals. This finding is in line with other studies (Reed & Farah, 1995; Reed & McGoldrick, 2007). For example, Reed and McGoldrick (2007) showed that the task performance in a body posture memory task is selectively impaired when a concurrent movement task is applied that involves the same type effector as the body posture memory task as compared to a different type of effector. In this study the only structural overlap regards the effector while the kind of the action, the trajectory and the goals differs between both tasks. The idea that shared representations might be organized hierarchically is also supported by imaging studies showing that parts of the mirror neuron system are organized in a somatotopic pattern which resembles the classical motor homunculus (Buccino, et al., 2001; Buccino, et al., 2004). In line with the common coding framework (cf. Introduction), these results suggests the existence of a hierarchically organized matching system of action observation and action execution.

As mentioned above, real-time simulation was no longer applied in trials, in which the relevant effector in the action prediction task and in the action execution task corresponded. Nevertheless, it is reasonable to assume that real-time action simulation was replaced by another process because task accuracy was comparable between compatible and incompatible trials. Possible candidates of processes are either the memorizing of the arrangement of certain points of the point-light display and matching them onto the test posture which was presented after the occluder or memorizing the test postures and the according feedback and applying a memory process without any simulation process. Although we cannot make any assumptions about the type of process which was applied in compatible trials, we can completely rule out a real-time simulation process. One could speculate that real-time simulation is the default process and that a blocking of a common coding system by a secondary motor task leads to a breakdown of such a process and requires the application of an alternative process.

However, the motor interference effect in real-time action simulation was statistically reliable only in error rates. There are several reasons which might account for that fact. First, we used quite a demanding task. Participants' error rates were relatively high (about 23 percent). This is in contrast to other studies that involve very simplistic and easy tasks showing a compatibility effect in the RTs, which could show floor effects in error rates (Brass, et al., 2001; Brass, et al., 2000). Second, we used a decision task. It is likely that this requires higher cognitive processes in order to reach the decision rather than a reaction towards a certain stimulus. An indication of this is the fact that RTs were much longer (average of 820 ms) than RTs for simple reactions towards a certain stimulus (about 300 ms) (Brass, et al., 2001; Brass, et al., 2000). Third, although we instructed our participants to respond as fast and as accurately as they could, it is possible that they focused more on task accuracy. They had a quite long time in which to give a response (time out of 4000 ms) and participants received feedback on the basis of accuracy while no explicit feedback was given regarding speed. It is likely that this caused participants to focus on task accuracy rather than task speed, which in turn lead to a visible effect of compatibility on action simulation in error rates.

In conclusion, this study demonstrates for the first time motor interference *within the real-time course* of action simulation. This indicates that real-time action simulation of temporally occluded actions and action execution share a common representational system. Preparation for action execution leads to the activation of these shared representations, which in turn leads to a lack of representations for action simulation. This, in turn, causes interference in the real-time cause of action simulation. Finally, we were successful in showing that this representational system is specific on the level of effectors, even when the actions differ in terms of the kind of the movement, trajectories and goals.

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