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Authorship effects in the prediction of handwriting strokes: Evidence for action simulation during action perception

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Does the action system contribute to action perception? Recent evidence suggests that actions are simulated while being observed. Given that the planning and simulating system are the same only when one observes one's own actions, it might be easier to predict the future outcomes of actions when one has carried them out oneself earlier on. In order to test this hypothesis, three experiments were conducted in which participants observed parts of earlier self- and other-produced trajectories and judged whether another stroke would follow or not. When the trajectories were produced without constraints, participants accomplished this task only for self-produced trajectories. When the trajectories were produced under narrow constraints, the predictions were equally accurate for self- and for other-generated trajectories. These results support the action simulation assumption. The more the actions that one observes resemble the way one would carry them out oneself, the more accurate the simulation.

Some of the events that we observe are caused by our own actions, and some are caused by the actions of others. It is important for us to know which events are caused by whom. Otherwise, it would be impossible for us to effectively plan, monitor, and evaluate our actions and we would certainly lack a sense of self. Essentially, there are two different situations in which the cognitive system is confronted with self-produced or self-authored events. Most of the time, such events are the result of an action that one has carried out immediately before the event occurs. For instance, when one touches one's arm with one's finger, one sees and feels one's finger touching one's arm, very shortly after having intended to touch one's arm with one's finger. In this type of situation the problem is one of attributing the perceived results of one's own actions to oneself, online (Frith, 1992; Jeannerod, 1999).

The second condition, the offline processing of self-generated actions, is probably most familiar to celebrities. In this situation one perceives events that one has produced oneself

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earlier on. Examples are listening to a recording of oneself playing the piano, or watching a video that shows oneself playing tennis. Although the average person encounters such situations quite rarely, they are very interesting from a theoretical point of view. They provide an opportunity to investigate what happens when the cognitive system is confronted with events that are the results of its own workings, without having intended to produce these events shortly before (Blakemore & Decety, 2001; Knoblich & Flach, 2001; Knoblich & Prinz, 2001). Should one expect that they can be recognized as self-produced? Are they more informative for the cognitive system than other-produced events? Before we address these questions, we briefly review earlier work on online and offline processing of self- and other-generated events.

On-line attribution of events to oneself

One fundamental problem in event perception is to determine which of the events that are currently observed in the environment result from self-produced actions, and which do not. But is there really a problem at all? Following Gibson's (1979) ecological approach to perception, there is none. According to this approach, no internal processing is needed to couple perceived events to one's own actions. Because perception arises from the interaction of an active observer with the environment, the action of the observer and the perception of the environment are inextricably linked. Hence, no attribution problem arises. Therefore, people should not have problems attributing events to their own actions. This is clearly not the case, however (see later).

More promising approaches to explain self-attribution of events go back to von Holst's (1954) efferent copy theory. It was originally developed to explain why we perceive a stable world, although the retinal image of the world changes with each eye movement. The theory claims that an efferent copy is derived from each eye movement to be executed. This signal allows the perceptual system to compensate for the movement of the eyes and therefore to stabilize the image of the world.

Frith (1992) proposed that a similar process, namely the automatic prediction of the future sensory consequences of actions, might be implemented in a central self-monitoring system. According to Frith, this system serves two important functions. The first is to monitor the relationship between actions and external events, and the second is to monitor intentions, in order to distinguish between willed and stimulus-driven actions. According to Frith, both functions are necessary to correctly attribute events in the environment to oneself or to other sources. Failure of either of the two can produce symptoms of schizophrenia, because it leads to errors in the self-or-other-attribution of external events (Daprati et al., 1996; Frith & Done, 1989).

A study of Fourneret and Jeannerod (1998) demonstrates that normal participants also have problems in attributing events to themselves under certain conditions. Their participants were not able to consciously monitor their motor performance when a trajectory they were currently producing was spatially perturbed (bent to the left or right). Rather, they automatically compensated for the perturbation without noticing. Hence, there also seem to be limits to the functioning of the self-monitoring system in normal individuals.

The idea that we use the prediction of the sensory consequences of our actions to determine which events are caused by ourselves has been further developed and implemented in terms of a forward model during the last years (Frith, Blakemore, & Wolpert, 2000; Wolpert, Ghahramani, & Jordan, 1995). The forward model takes an efferent copy produced in parallel with each motor command as its input and simulates the sensory consequences that should follow the execution of the command. Hence, whereas self-produced events are predicted by the model, other-generated events are not (Blakemore & Decety, 2001). This additional signal allows one to attribute events to oneself.

It has also been proposed that sensations induced by self-generated movements are cancelled by the prediction of the forward model and therefore experienced as less intense. A recent study by Blakemore, Wolpert, and Frith (1998) provides striking evidence for this claim. They investigated the phenomenon that external tactile stimulation is experienced as more intense than self-produced stimulation. In accordance with their cancellation hypothesis, an fMRI (functional magnetic resonance imaging) experiment showed less activity for self-produced tactile stimuli in the somatosensory cortex (related to experience of intensity of a tactile stimulus) and more activity in the cerebellum (related to the prediction of the future consequences of an action). Their results support the claim that the cerebellum is involved in predicting the sensory consequences of a movement and provides a signal that is used to cancel sensory responses to self-generated stimulation.

Recently, Blakemore and Decety (2001) speculated that forward models might also play an important role in the off-line processing of events. This idea implies that the action system contributes to the perception of actions even in situations where humans are just observing the actions of others. In the next section, we review some evidence supporting this claim and spell out some predictions regarding off-line effects of authorship.

Off-line processing of self-produced events

When we observe the actions of another person, we do not necessarily have a related intention to produce the observed actions ourselves. This is also true when the person observing is the same as the person observed—that is, when one watches oneself from a third-person perspective. However, a growing number of theories suggest that the action system might actually contribute to the perception and understanding of actions. One assumption that has been made is that actions are coded in terms of the perceivable effects they should generate (Hommel, Müsseler, Aschersleben, & Prinz, in press; Prinz, 1997). Moreover, these representations of actions effects do not only govern action production but are also involved in action perception (common coding assumption). In action production, the actual movement is determined by representations coding action effects. These event representations automatically activate the motor codes that generate the respective event in the environment. In action perception, the same representations are activated and allow one, for instance, to detect the intended action goals. As a consequence, the motor codes that generate the observed effect also become activated in action perception.

Earlier versions of this assumption can be traced back to James' ideomotor principle (James, 1890; Knuf, Aschersleben, & Prinz, 2001) and Liberman's motor theory of speech perception (Liberman & Mattingly, 1985; Liberman & Whalen, 2000). Empirical evidence from the area of stimulus–response compatibility (Hommel, 1995; Müsseler & Hommel, 1997), temporal synchronization (Aschersleben & Prinz, 1995), bimanual coordination (Mechsner, Kerzel, Knoblich, & Prinz, 2001), imitation (Bekkering, Wohlschläger, & Gattis, 2000; Kerzel & Bekkering, 2000), and serial learning (Koch & Hoffmann, 2000) is consistent with this approach. The assumption that a level of common event representations mediates the interplay between perception and action is also supported by neuro-physiological evidence (Decety & Grezes, 1999; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Jeannerod, 1997).

The common coding assumption also suggests that perceiving one's own actions from a third-person perspective is different from perceiving somebody else's actions from this perspective, at least under certain conditions. Whenever people's way of performing an action varies, the similarity between external events and the common event representations is maximized when one observes events that are the result of one's own earlier generated actions. The reason is that idiosyncratic aspects of the common representations are also reflected in the perceivable outcomes of the actions they code (Knoblich & Prinz, 2001). Hence, when one observes events that result from one's own actions there should be a superior match between these representations and the perceptual input during action perception. The accuracy of the match should allow one to recognize whether the perceived events are self-produced or other-produced.

One way to test this prediction is to investigate whether people can recognize their own actions based on their kinematics. This procedure largely reduces the likelihood that static features (such as one's own face or other anatomical features) guide recognition. Beardsworth and Buckner (1981) investigated whether one can distinguish kinematic displays of oneself from another person walking, using Johannson's (1973) point light technique. They found that participants could identify themselves better than their acquaintances, despite the fact that one sees one's acquaintances much more often than oneself from a third-person perspective (Wolff, 1931, obtained similar results).

More recently, we have demonstrated that one can distinguish between self- and other-produced drawings based on the kinematics of a single moving dot (Knoblich & Prinz, 2001). In this study, participants drew familiar and unfamiliar symbols without receiving visual feedback. Later, the same participants watched kinematic displays of their own movements, or those produced by others. The results showed that the participants could recognize their own trajectories reliably better than chance. The main cues to determine authorship were characteristic changes in velocity (but not familiarity of a symbol, overall duration of the trajectory, or form information). These results support the claim that the accuracy of match between the perceptual input and common event representations allows one to determine authorship of earlier produced actions.

Authorship effects in action simulation?

The results described earlier raise the question of whether authorship effects are restricted to judging whether an action that one currently perceives is self- or other-generated. Alternatively, similar effects might be present when the future consequences of an observed action are simulated, based on previously or currently perceived events. Before we address the question of authorship, we briefly review some evidence that gives us reason to believe that action perception is often accompanied by action simulation (Barresi & Moore, 1996; Blakemore & Decety, 2001; Gallese & Goldman, 1998).

The functional value of such simulations is obvious. They could generate predictions that are useful for shifting one's attention or for directing one's actions to critical locations, for anticipating the occurrence of critical events, or for coordinating one's own actions with somebody else's (Knoblich & Jordan, 2002). Neuro-physiological evidence supports the action simulation assumption. First, there are mirror neurons in the monkey premotor cortex that discharge when the monkey carries out certain hand actions but also when the monkey observes the experimenter perform the same action (Gallese et al., 1996; Gallese & Goldman, 1998). The discharge in the observation condition already starts in early phases of the movement (Umiltà et al., 2001). Moreover, several regions in the human brain are activated during action generation, action simulation, and action observation. These areas include the premotor cortex, the posterior parietal cortex, and the cerebellum (Decety et al., 1997; Ruby & Decety, 2001).

Further evidence comes from a study by Orliaguet, Kandel, and Boé (1997). These authors demonstrated that when one observes the kinematics of certain handwriting trajectories one can generate accurate anticipations about the identity of forthcoming letters. In a recent study, Kandel, Orliaguet, and Viviani (2000) extended these results by demonstrating that correct predictions were possible only for trajectories that complied to the two-thirds power law (Lacquaniti, Terzuolo, & Viviani, 1983). In other words, accurate predictions were possible only if the movement was biologically plausible. Both studies support the claim that people can use action-related representations to simulate the future outcomes of an action.

If one combines these results with our earlier assumptions regarding the recognition of self-generated actions, one can derive the prediction that authorship effects should also be present in action simulation. The rationale behind this prediction is that the superior match between self-produced actions and common event representations should also affect the accuracy of action simulation. Based on the common coding assumption, action perception and simulation could be linked in the following manner: First, common event representations become activated by the perceptual input. Second, there is an automatic activation of the motor codes attached to these event representations. Third, the activation of the motor codes results in a prediction of the action results in terms of future events. If this is the case, the superior match for self-produced actions should also result in a more accurate simulation of future events.

To sum up, the present study aims at providing evidence for action simulation during action perception. One way to support this claim is to demonstrate that when observing the outcomes of actions from third-person perspective, one can more accurately predict the future outcomes of self-produced actions.

EXPERIMENT 1

The aim of Experiment 1 was to provide a first test of the assumption that there are authorship effects for action simulation. Our experimental task was based on the one reported by Orliaguet et al. (1997). However, we used a stroke instead of a letter anticipation task because the results of our earlier experiments suggest that authorship effects arise at a stroke rather than at a letter level (Knoblich & Prinz, 2001). In our stroke anticipation task, individuals observed a single stroke and predicted whether this stroke had been produced in isolation or followed by another stroke, in order to produce a certain symbol. If there are differences in the kinematics of single strokes produced in isolation or as a part of a symbol, one should be able to predict whether another stroke will follow or not.

The kinematics of different strokes of one type (isolated or part) might contain regularities that hold across different individuals, and regularities that hold only across different productions of one individual. Both types of regularity might be used to accurately predict whether another stroke follows or not. If only general regularities enter into the predictions their accuracy should be above chance for self- and other-generated strokes, but there should be no authorship effects. If general and individual regularities enter into the predictions they should be above chance for self- and other-generated strokes and significantly greater for self- than for other-generated strokes. If individual regularities enter into the predictions, exclusively, they should be more accurate for self- than for other-generated trajectories and not different from chance for the latter.

When assessing self–other differences it is important to make sure that these differences are not related to differences in the stimulus material. We did so by creating sets of trajectories for pairs of participants. In each set, one half of the trajectories was produced by Participant A, and the other half of the trajectories was produced by Participant B. Hence, two participants in a pair judged exactly the same set of trajectories. Therefore, any authorship effects that we report cannot be explained by differences in the stimulus material.

Method

Participants

A total of 18 participants, all students of the University of Munich, took part in the experiment, 4 of them male. They ranged in age from 19 to 36 years. All participants were right-handed and had normal or corrected-to-normal vision. They received payment for their participation.

Materials and procedure

Recording session. In the first session, writing samples were collected. Participants were seated in front of a computer monitor at a distance of about 70 cm. The graphics tablet was located between the participant and the monitor. After the participants had made themselves familiar with writing on a graphics tablet, the actual data recording started. The participants were asked to reproduce four different models as material for the stroke anticipation task (see Figure 1). A total of 20 reproductions of each symbol (e.g., the number 2) were collected. The order of blocks was counterbalanced across participants.

At the beginning of each block, the symbol to be produced was displayed. Five seconds later, a button appeared on the screen. As soon as the button was touched by the pen cursor, the stimulus vanished from the screen, and the first trial started. At the beginning of each trial, two auxiliary lines were displayed on the screen. Given a viewing distance of 70 cm, they subtained 8 visual degrees to the left and the right

Figure 1. Stimuli in the recording session of Experiment 1.

of the screen centre, horizontally. The upper line was 4 degrees above and the lower 4 degrees below screen centre. Additionally, a start button appeared at the left end of the auxiliary lines. Its vertical position varied depending on the shape of the symbol to be copied. As soon as participants moved the pen cursor to that position and increased pen pressure, the button vanished, and data sampling was initiated. Participants had 3 s to produce the given symbol in their own handwriting. At the end of this interval, a 100-ms beep indicated that the trial was over.

While writing, participants observed the emerging trajectory on the monitor. The trace given on the monitor was a 1:1 copy of the trace recorded by the graphics tablet with a 10-ms delay. The experimenter also watched the emerging of each trajectory on a control monitor. There were three conditions under which a trial was repeated: (1) The symbol was not written correctly (different symbol, features neglected, etc.); (2) a written trace largely exceeded or fell short of the auxiliary lines (by 10% of the distance between the two lines on either of the two sides); or (3) the writing was not fluent.

The stimuli and traces were presented on an Apple Vision 17" monitor with a horizontal resolution of 800 and a vertical resolution of 600 pixels. The vertical sync frequency was 100 Hz. Movements were recorded using a WACOM A3 graphics tablet with a sampling rate of 100 Hz (equal to vertical sync frequency). The resolution of the tablet was 15,000 dots horizontally and 11,250 dots vertically. These devices as well as a second Apple Vision 17" monitor (which displayed the emerging trajectories to the experimenter) were connected to an Apple Power PC. The sampling rate of the graphics tablet was synchronized with the screen refresh rate, so that the samples could be copied to the screen in real time by scaling tablet resolution to screen resolution, in the later recognition session.

Stimulus preparation. The raw kinematic data were prepared for the recognition session in several steps. In a first step, pen velocity at each point in time was determined. To decrease noise, data were smoothed before estimating velocity. We used the 7RY routine proposed by Mottet, Bardy, and Athènes (1994) for data smoothing. This routine consists of two steps. First, a moving median is computed over seven points, until the recursive routine converges. Second, a weighted moving average is computed over seven points to eliminate high-frequency components let through by the moving median. The advantage of this routine is that it deals better with aberrant points in the kinematic data, than do linear routines.

In the second step, the starting point of each trajectory was determined as the first sample for which velocity and pen pressure were greater than zero. To determine the endpoint of a trajectory, different criteria were used for the production of different symbols. The endpoint for trajectories reproducing single strokes was determined as the first sample in which either velocity or pen pressure was zero. In trajectories reproducing the symbol *2*, the first stroke was segregated from the second stroke by determining the first velocity minimum in the lower half of the trajectory. The trajectory was segregated at the sample at which the velocity minimum occurred. The use of a minimum-velocity criterion for stroke segmentation is standard practice in handwriting research (Maarse, Van Galen, & Thomassen, 1989; Van Galen, 1991).

The resulting trajectories were inspected, and 10 out of 20 were chosen for each of the four conditions. The criteria for including a trajectory in the stimulus set were that it had a regular form and a regular speed curve without major discontinuities, and that it had been correctly segregated. The number of faulty segregations was very low (< 1%). Hence, more elaborate criteria, as used for the segmentation of continuous handwriting trajectories (Van Galen, 1991), were not needed.

Recognition session. One week after the recording session participants returned for the recognition session. They were not informed whether or not the trajectories were self-produced. Participants were seated in front of a computer monitor at a distance of 70 cm. They went through two blocks of trials. In one block, they observed the first stroke of the upright symbol *2* and judged whether this stroke had been written in isolation or as part of the production of the symbol *2*. In a further block they observed the first stroke of the rotated symbol *2* and judged whether this stroke had been written in isolation or as part of the production of the symbol *2*. The order of blocks was counterbalanced across participants.

The participants were organized into pairs. Both participants of a pair observed their own trajectories half of the time and the trajectories of the other participant half of the time. Therefore, two participants judged exactly the same stimulus material. Each block consisted of 80 trials presented in random order. A trial was initiated by a 100-ms beep, followed by the key assignment displayed for 1 s in the centre of the screen. Next, a dot appeared on the screen and remained still for 500 ms. Afterwards, it reproduced the kinematics of a trajectory. The dot left no trace on the screen. Hence, the participants observed a single point moving across the screen. Afterwards, they pressed one of two keys on the button box to indicate their judgement. The next trial started after an intertrial interval of 2000 ms.

Results

The raw judgements were converted into *d′* sensitivity measures (including the correction required for 2AFC designs, Macmillan & Creelman, 1991). This measure stands for the ability to correctly predict forthcoming strokes. It is free from general response biases that could, for instance, stem from a general preference to judge strokes as being produced in isolation. Hence, it provides us with a bias-free estimate of the accuracy of action simulation for self- and other-generated trajectories. The *d′* measure was computed separately for each condition. The left-hand panel in Figure 2 displays the results. The predictions were more accurate when a horizontal stroke was observed (0.39) than when a vertical stroke was observed (0.13). The accuracy of predictions for other-generated strokes was almost at chance level (0.04). In contrast, it was clearly above chance level for self-generated strokes (0.47). The difference between predictions for self- and other-generated strokes was greater for horizontal (0.70) than for vertical strokes (0.15).

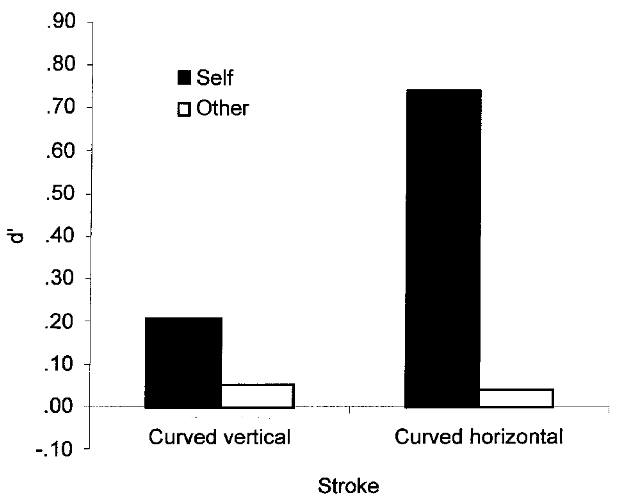

Figure 2. Accuracy of stroke prediction in Experiment 1 for self- and other-generated trajectories.

The d' measures were entered into a 2×2 within-subjects analysis of variance (ANOVA) with the factors orientation (vertical vs. horizontal) and authorship (self- vs. other-generated). There was a significant main effect for orientation, $F(1, 17) = 5.11$, $p < .05$, the accuracy of prediction being significantly greater for horizontal strokes. There was also a significant main effect for authorship, $F(1, 17) = 15.8$, $p < .001$, the accuracy of prediction being significantly greater for self-generated strokes. There was also a significant interaction between the two factors, $F(1, 17) = 10.3$, $p < .01$, the difference in accuracy between self- and other-generated trajectories being significantly greater for horizontal strokes. Post hoc tests confirmed that the difference between self- and other-generated trajectories was present for horizontal strokes ($p < .001$) and vertical strokes ($p < .05$).

Discussion

The results of Experiment 1 show that participants were able to predict strokes when observing self-generated trajectories. They could only guess for other-generated trajectories. This suggests that the kinematics of different types of stroke do not contain regularities that hold across persons. However, they do contain intra-individual regularities that enable one to generate accurate predictions when observing the results of one's own actions. A further result is that, although the accuracy of predictions was significantly above chance level for the vertically and horizontally oriented symbol *2*, it was clearly greater for the latter. One possible reason for the asymmetry is that the use of horizontal auxiliary lines may have constrained the production of the vertical version more strongly than the production of the horizontal version. Another possibility is that the production of the vertical version of the symbol *2* is better trained. Because training increases the adaptation to task constraints (Ericsson & Lehmann, 1996), individual regularities may become weaker with more training. Experiment 2 was conducted to address these two alternative explanations and to provide further evidence for authorship effects in stroke prediction.

EXPERIMENT 2

The first aim of Experiment 2 was to replicate the authorship effect for action simulation obtained in Experiment 1, under conditions in which trajectory production was even less constrained. Therefore, no auxiliary lines were displayed during the recording session. The same authorship effect as observed in Experiment 1 should also be obtained under these circumstances. Moreover, completely unconstrained drawing should remove the asymmetry between the vertical and horizontal version, if the auxiliary lines caused the asymmetry in Experiment 1, and should have no effect, if better training for the vertical version removed individual regularities.

A second aim was to exclude an alternative explanation related to the visual feedback that participants received in the recording session of Experiment 1. Obviously, they received visual feedback only for self-generated trajectories but not for other-generated trajectories. Therefore, they might have formed episodic representations of the trajectories they produced and used these representations to generate their predictions. Although this explanation seems somewhat unlikely, given the fact that the recognition session took place one week after the recording session, it is a viable explanation for the authorship effect obtained in Experiment 1.

We attempted to rule out this alternative explanation by providing no visual feedback during the recording session of Experiment 2.

Using trajectories produced without visual feedback also greatly decreases the possibility that form information is used to generate predictions. Form information becomes quite distorted in trajectories produced without visual feedback (Smyth, 1989; Smyth & Silvers, 1987). Hence, if authorship effects are detected in trajectories that were produced without visual feedback, it is quite likely that temporal parameters provide the distinctive features as suggested by the study of Orliaguet et al. (1997) and our earlier studies (Knoblich & Prinz, 2001). Finally, we added four further symbols to the symbol set to generalize the results of Experiment 1 to predictions derived from the observation of a straight vertical or straight horizontal stroke (Figure 3 shows the additional stimuli).

Method

Participants

A total of 18 participants, all students at the University of Munich, took part in the experiment, 6 of them male. They ranged in age from 21 to 38 years. All participants were right-handed and had normal or corrected-to-normal vision. They received payment for their participation.

Materials and procedure

Recording session. The recording session was the same as that in Experiment 1, except for a few modifications due to changes in the material. The participants now reproduced eight symbols as material for the stroke anticipation task. The first four symbols were the same as those in Experiment 1. Figure 3 displays the additional symbols. A further modification, compared to Experiment 1, was the use of a cover that kept participants from seeing their hand on the writing pad. Moreover, participants could not watch the emerging trajectory on the computer screen (there was no visual feedback). The experimenter watched the emerging trajectory on a control monitor. A trial was repeated when the symbol was not written correctly or the writing was not fluent.

Stimulus preparation. The stimulus preparation was the same as that in Experiment 1. The endpoints for trajectories that reproduced the newly introduced symbols were determined in the same manner as that for the other symbols (see Method section of Experiment 1). Again, the number of faulty segregations of stroke compounds was very low (< 1%).

Recognition session. The recognition session was the same as that in Experiment 1 except for changes necessary due to the modified material. The participants went through four blocks of trials. In the first block, they observed vertical, curved strokes. In a second block, they observed horizontal, curved strokes. In a third block, they observed vertical, straight strokes. Finally in a fourth block, they observed horizontal, straight strokes. In each block they judged whether the respective stroke had been written in isolation or as part of the production of a symbol. Again, the order of blocks was counterbalanced.

Figure 3. Additional stimuli in Experiments 2 and 3.

Results

In addition to the accuracy of predictions, we also analysed the trajectories with respect to inter-individual and intra-individual regularities that they might contain. We included spatial (*x* to *y* ratio of the trajectory) and temporal parameters (duration, peak velocity, end velocity) in the analysis. We report only the results for the analysis of peak velocity, because this parameter contained the most reliable regularities.

Accuracy of predictions. Figure 4 displays the results of Experiment 2. The predictions were more accurate for self-generated (0.34) than for other-generated strokes (0.02). Again, for other-generated trajectories, the accuracy of prediction did not deviate substantially from chance level. The difference between predictions for self- and other generated-strokes was somewhat greater for straight horizontal (0.49) than for straight vertical (0.33), curved vertical (0.16), and curved horizontal strokes (0.29).

The d' measures were entered into a 2 × 2 × 2 within-subjects ANOVA with the factors type of stroke (curved vs. straight), orientation (vertical vs. horizontal), and authorship (self- vs. other-generated). There was no significant main effect for type of stroke, $F(1, 17) = 0.73$, $p = .41$, and orientation, $F(1, 17) = 1.05$, $p = .32$. There was however, a significant main effect for authorship, $F(1, 17) = 21.0$, $p = .001$; the accuracy of prediction was significantly greater for self-generated strokes. None of the interactions was significant (all $p > .10$). Post hoc tests confirmed that the difference between self- and other-generated trajectories was statistically significant for curved horizontal ($p < .05$), straight vertical ($p < .01$), and straight horizontal strokes ($p < .001$). The difference was not significant for curved vertical strokes ($p = .14$).

Peak velocity. To determine whether the trajectories contained general differences in peak velocity that may have informed the predictions, we analysed whether there were

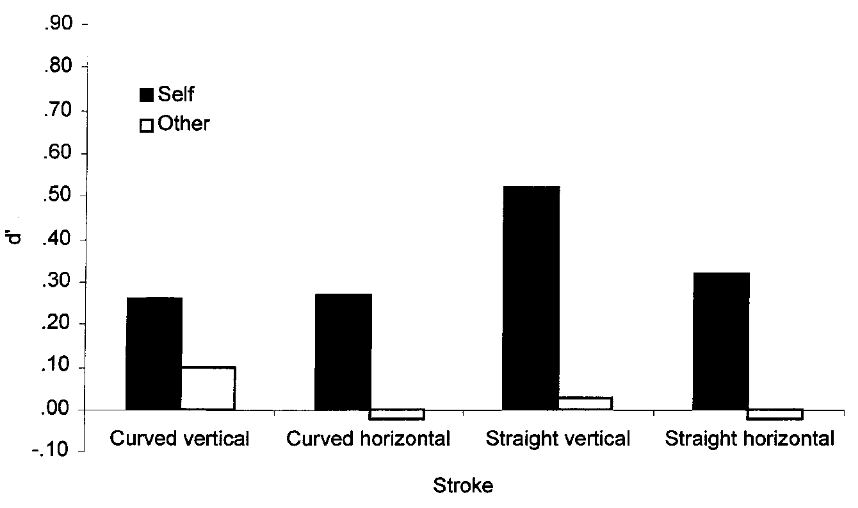

Figure 4. Accuracy of stroke prediction in Experiment 2 for self- and other-generated trajectories.

detectable differences in peak velocity between isolated strokes and strokes produced as part of a symbol. Figure 5 shows the results. Peak velocity was highest in trajectories of curved vertical strokes. The remaining strokes had comparable peak velocities. There were almost no differences in peak velocity between strokes produced in isolation and strokes produced as part of a symbol.

To assess statistical significance, the peak velocities were entered into a 2 × 2 × 2 within-subjects ANOVA with the factors type of stroke (curved vs. straight), orientation (vertical vs. horizontal), and context (isolated vs. part of symbol). There were significant main effects for type of stroke, $F(1, 17) = 14.0$, $p < .01$, and orientation, $F(1, 17) = 22.2$, $p < .001$, and a significant interaction between these two factors, $F(1, 17) = 5.4, p < .05$. However, there was no significant main effect for context, $F(1, 17) = 1.5, p = .23$. Thus, there were no significant overall differences between strokes produced as part of a symbol and strokes produced in isolation that could have guided the predictions. None of the further interactions was significant (all $p > .10$).

In a further step, we analysed whether there were intra-individual differences between the peak velocities for strokes produced in isolation and strokes produced as part of a symbol in self-generated directories. To do so, we determined a detectability index for each person. The rationale for this index is as follows. Given a set of trajectories produced by a person, greater differences in peak velocity between strokes produced in isolation and those produced as a part of a symbol should increase the accuracy of prediction. The difference is easier to detect when overall velocity and the variability in the production of different exemplars of the same stroke are low. This leads to the following formula:

$$D = \frac{Abs(x_{pi} - x_{ps})}{[x_{pi} + x_{ps} / 2] * [s_{pi} + s_{ps} / 2]}$$

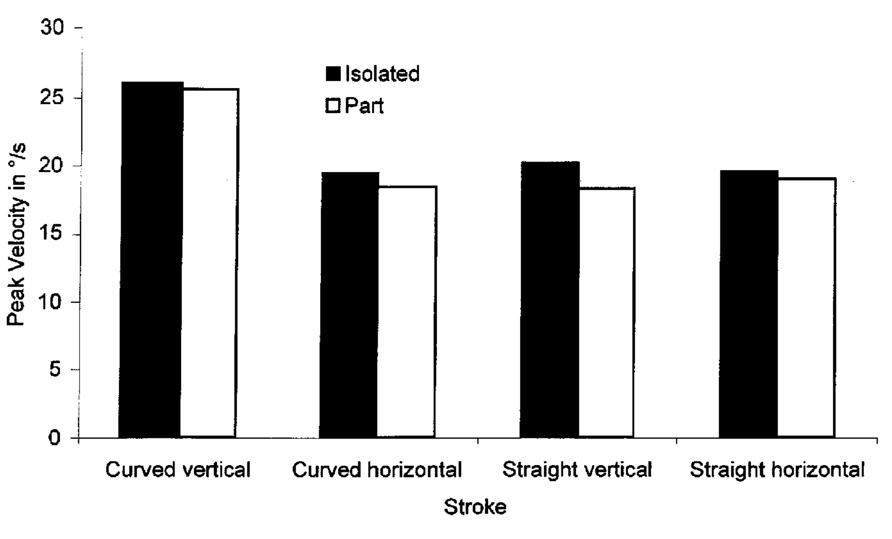

Figure 5. Peak velocity for isolated and part-strokes in Experiment 2.

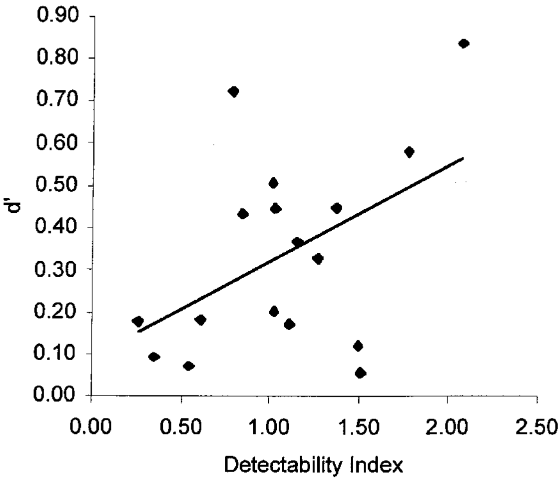

Figure 6. Accuracy of prediction for self-generated trajectories as a function of the detectability index (each data point stands for one person) in Experiment 2.

where x_{pi} and x_{ps} stand for the mean of the peak velocity for different strokes produced as part of a symbol and in isolation, respectively, and s_{pi} and s_{ps} stand for the standard deviations. Because there were only few exemplars of each type of stroke, we collapsed the detectability indices across different types of stroke. Figure 6 plots d' as a function of the detectability index, for each individual. There was a significant correlation between these two variables, $r = .47$, $z = 2.41$, $p < .05$. Prediction accuracy was greater when the detectability index was greater.

Discussion

The results replicate and extend the results of Experiment 1. Participants were able to predict forthcoming strokes only when they observed self-generated trajectories. This pattern is also seen for trajectories that reproduce straight strokes. The authorship effect was again smaller or almost not present for curved vertical strokes—that is, the first part of the number *2*. This supports the interpretation that individual regularities may become weaker with more training.

The results of Experiment 2 demonstrate that authorship effects can also be obtained when participants receive no visual feedback while producing a trajectory. Therefore, it is unlikely that episodic or form information plays a crucial role in predicting forthcoming action effects. Rather, peak velocity seems to be the crucial parameter. Across participants, there were no systematic differences in peak velocity between strokes produced as a part of a symbol and those produced in isolation. Hence, the prediction accuracy was zero for other-generated trajectories. However, there was a systematic relationship between the detectability index and the prediction accuracy for self-generated trajectories. The accuracy of prediction was greater when participants' strokes (isolated and part) differed in peak velocity, the variability in the production of different exemplars of the same stroke was low, and the overall velocity was low.

EXPERIMENT 3

In the previous experiments, the constraints to produce a stroke in a certain way were never really narrow. Although there were auxiliary lines in Experiment 1, the remaining unconstrained dimension gave participants a lot of freedom to produce strokes in different ways. In Experiment 2 the production was completely unconstrained. To create a situation in which stroke production is more constrained we added horizontal and vertical auxiliary lines in the production session and asked participants to fit the respective strokes or stroke combinations within these lines. Under these conditions, the pattern of results should change. Because of the narrow constraints, the variability between participants should decrease. This implies that the detectability of cues that hold across individuals should increase. Therefore, participants should be better able to accurately predict whether a stroke was produced as part of a symbol when observing other-generated trajectories. At the same time, the difference in prediction accuracy between self- and other-generated trajectories should decrease, because the trajectories contain fewer cues that hold only intra-individually.

Method

Participants

A total of 18 participants, all students at the University of Munich, took part in the experiment, 9 of them male. They ranged in age from 20 to 48 years. All participants were right-handed and had normal or corrected-to-normal vision. They received payment for their participation.

Material and procedure

The material for the recording session was the same as that in Experiment 2. The set-up and the procedure were the same as those in Experiment 1 (the graphics tablet was not covered, and participants received feedback about the emerging trace that they produced). The only difference was that the auxiliary lines constrained symbol production not only vertically, but also horizontally. Depending on the symbol, the additional auxiliary lines were located between 2° and 5° of visual angle to the left and right of the screen centre, given a viewing distance of 70 cm. During the recording session, the experimenter watched the emerging trajectory on a control monitor. The participant was asked to repeat a trial under the following conditions: (1) The symbol was not written correctly; (2) the written trace largely exceeded or fell short of the horizontal or vertical auxiliary lines (by 10% of the distance between the two lines on either of the two lines, respectively); or (3) the writing was not fluent. The stimulus preparation and the recognition session were the same as those in Experiment 2.

Results

Accuracy of predictions. Figure 7 displays the results of Experiment 3. Overall, the accuracy was greater than that in the preceding experiments. However, there was no clear advantage for self-generated strokes (0.56) compared to other-generated strokes (0.50). The predictions were more accurate for straight (0.70) than for curved strokes (0.35). For curved strokes, the accuracy of prediction was greater when they were vertical (difference: 0.22), for straight strokes the accuracy of prediction was greater when they were horizontal (difference: 0.19).

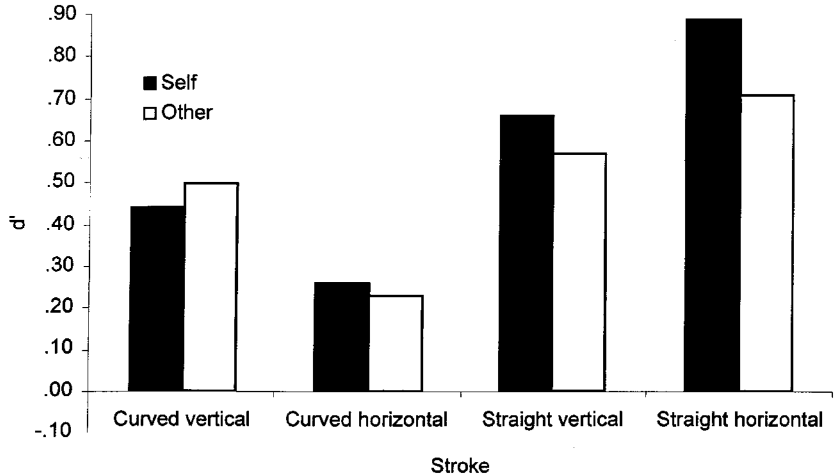

Figure 7. Accuracy of stroke prediction in Experiment 3, for self- and other-generated trajectories.

The d' measures were entered into a 2 × 2 × 2 within-subjects ANOVA with the factors type of stroke (curved vs. straight), orientation (vertical vs. horizontal), and authorship (self- vs. other-generated). There was a significant main effect for type of stroke, $F(1, 17) = 27.5$, $MSE = 0.16$, $p < .001$; the predictions were significantly more accurate for straight strokes. There were no significant main effects for orientation, $F(1, 17) = 0.06$, $MSE = 0.25$, $p = .81$, and authorship, $F(1, 17) = 21.0$, $MSE = 0.28$, $p = .61$. There was, however, a significant interaction between type of stroke and orientation, $F(1, 17) = 7.6$, $MSE = 0.20$, $p < .05$. All further interactions were not significant (all $p > .10$).

Peak velocity. Again, we analysed whether there were detectable differences in peak velocity between isolated strokes and strokes produced as part of a symbol. Figure 8 shows the results. Peak velocity was greater in trajectories of curved strokes. The differences in peak velocity between strokes produced as part and those produced in isolation were greater for straight than for curved strokes.

To assess statistical significance, the peak velocities were entered into a 2 × 2 × 2 within-subjects ANOVA with the factors type of stroke (curved vs. straight), orientation (vertical vs. horizontal), and context (isolated vs. part of symbol). There were significant main effects for type of stroke, $F(1, 17) = 105.8$, $p < .001$, and context, $F(1, 17) = 30.7$, $p < .001$; peak velocity was significantly greater for curved strokes and for strokes that were produced as part of a symbol. There was also a significant interaction between these two factors, $F(1, 17) = 18.3$, $p < .001$; the difference between isolated and part strokes was greater when they were straight. There was no significant main effect for orientation, $F(1, 17) = 1.5$, $p = .23$, but there was a significant interaction between type of stroke and orientation, $F(1, 17) = 53.6$, $p < .001$. Peak velocity in straight vertical strokes was greater than that in straight horizontal strokes. In curved strokes, peak velocity was greater when they were horizontal. All other interactions were not significant (both $p > .10$).

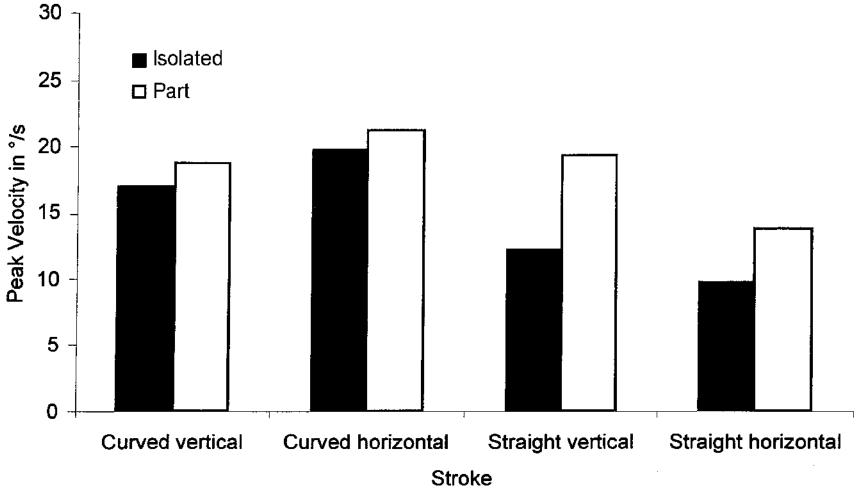

Figure 8. Peak velocity for isolated and part-strokes in Experiment 3.

Discussion

The pattern of results in Experiment 3 is quite different from the patterns obtained in the first two experiments. When stroke production was narrowly constrained, the prediction of forthcoming strokes became more accurate. Moreover, the predictions were equally accurate for self- and for other-generated trajectories. This result indicates that the trajectories contained kinematic cues that were the same across individuals, and that there were no cues specific to certain individuals. The analysis of peak velocity indicates that this parameter was an important cue. Peak velocity was systematically lower for strokes produced in isolation. Moreover, peak velocity served as an especially good cue in trajectories of straight strokes, and the predictions for straight strokes were more accurate, accordingly.

GENERAL DISCUSSION

The main question addressed by the present research was whether there is action simulation during action perception. If so, the prediction of future events should be more accurate when this prediction is based on actions that one produced earlier oneself, at least if these actions share regularities when repeatedly carried out by a certain individual, and should differ for different individuals. The three experiments reported here provide a clear answer to this question. In a stroke prediction task, prediction accuracy varied depending on production constraints and authorship. When the participants were allowed to copy strokes or symbols without narrow production constraints there were only intra-individual regularities in the production of different types of stroke. These regularities could later be used to generate accurate predictions for self-generated trajectories (see Experiments 1 and 2). If stroke production was narrowly constrained, thus prompting each individual to write in the same manner, the predictions were accurate for self- and for other-generated trajectories (see Experiment 3). The fact that accuracy increased for other-generated trajectories without decreasing for self-generated trajectories underlines the fact that the prediction is informed by one's own action system. If everybody complies with the same norms somebody else's actions are as good as one's own.

In the present study, stroke production was spatially constrained by auxiliary lines. It is quite likely that other constraints—for example, asking participants to draw as fast as they can, or frequent repetitions of the same movement (e.g., Viviani & Mounoud, 1990)—might also reduce intra-individual regularities and therefore allow one to make accurate predictions for one's own as well as for others' actions. The earlier results by Orliaguet et al. (1997) suggest that social norms and rules can also impose constraints on action production. As stimuli for their letter prediction task, they used trajectories of a high-school teacher whose writing best reflected the norms of writing of a whole sample of high-school teachers. This is exactly the type of stimulus that one would expect to be informative for everybody else's action system.

In our view, the authorship effects observed in the present experiments are best explained by the assumption that action perception is accompanied by concurrent action simulation (Blakemore & Decety, 2001; Gallese & Goldman, 1998; Knoblich & Flach, 2001; Liberman & Whalen, 2000). In order for action simulation to be useful (e.g., in order to make accurate predictions of future events, shift attention, or coordinate one's own actions with somebody else's), the output of the simulation has to be commensurate with the perceptual input. Representations of distal events as postulated by the common coding assumption (cf., Prinz, 1997), could provide a level on which the perceptual input and the simulation results could be integrated (Knoblich & Flach, 2001; Knoblich & Jordan, 2002). However, the common coding assumption alone is not sufficient to explain the present results. It does predict that the perception of an event leads to the activation of motor codes that could produce the same event. However, in order to fully explain the results it is necessary to also postulate that the activation of motor codes results in turn in a prediction of future events. This additional assumption is completely in line with the assumption that forward models derive the sensory consequences of motor commands (cf., Blakemore & Decety, 2001; Frith, 1992; Frith et al., 2000; Wolpert et al., 1995). From the point of view of common coding there is no reason to believe that such predictions are restricted to situations in which a person is currently acting. They could also accompany the activation of event representations during action perception.

This interpretation also sheds new light on our earlier studies that provided evidence for the claim that people can recognize their own drawing trajectories (Knoblich & Prinz, 2001). It is quite possible that self-recognition is based on a comparison between observed and simulated events. The participants might have judged those trajectories in which there was a discrepancy between simulated and observed events as other-generated and those in which there was no discrepancy as self-generated.

One obvious question is whether authorship effects can also be observed in domains other than handwriting. In a recent series of experiments we found that participants predicted the landing position of a dart more accurately after watching self-generated throwing actions recorded on video (Knoblich & Flach, 2001). However, the differences between the handwriting and the throwing domain are also reflected in somewhat different results. When a participant observed a stroke trajectory in the present experiment, the perspective was the same as that experienced while actually producing the stroke. In the dart experiments, the participants observed a video displaying themselves or others from a side perspective—that is, a perspective that one could never take while throwing a dart at the target board. The results showed that initially the participants predicted the landing position equally well for self- and other-generated trajectories. In later trials, the predictions became more accurate for self-generated but not better for other-generated throws, leading to a reliable authorship effect in later trials, although no feedback was given. These results can be explained by the assumption that people initially use overt cues like head position for their predictions. Later on, they integrate the perceived events with a simulation of future action outcomes (Barresi & Moore, 1996; Knoblich & Flach, 2001). An analysis of training effects for the present experiments showed that the authorship effect was present right from the start and did not vary across consecutive blocks. Hence, it seems that such integration is not necessary to predict future strokes.

The ability to predict letters and strokes from earlier parts of a trajectory is quite similar to phenomena in the domain of speech perception where the same phoneme is perceived differently depending on the context created by the preceding phoneme (Liberman & Whalen, 2000). This implies that the same acoustical input can be perceived as different phonemes depending on the earlier context (Kerzel & Bekkering, 2000). The motor theory of speech perception (Liberman & Mattingly, 1985; Liberman & Whalen, 2000) claims that ambiguities in the acoustical input are resolved by co-articulation processes. Adapted to our terminology, the idea is that while one perceives a phoneme sequence one concurrently runs a simulation of producing the same sequence. Hence, there might also be authorship effects in phoneme anticipation. From our explanation of the present results there follows a clear prediction for this situation. Authorship effects should also occur in speech perception if there are intra-individual regularities for the production of different types of phoneme that are not shared by different speakers. Because phonemes are important for communicating with others it is unlikely that prediction accuracy would completely break down for other-generated actions, but there could still be an advantage for self-generated speech. To the best of our knowledge, there are no studies that have addressed the question of whether the prediction of the next phoneme in a co-articulated syllable is more accurate if one hears a tape of oneself speaking. The only study that addressed authorship effects in the acoustical domain was conducted by Repp (1987). He provided some evidence for the claim that people can recognize their own clapping. Hence, it might be worthwhile to address authorship effects in the acoustical domain. Our first attempt at doing so provided encouraging results. In a pilot study that basically replicated Repp's study, we observed substantial authorship effects in the clapping domain.

To conclude, we think that authorship effects not only are interesting in themselves but also provide a way to address the issue of whether the action system contributes to action perception. The present study suggests that these contributions might take the form of action simulations that provide the perceptual system with predictions of future events. It has been speculated that action simulation is also important for understanding the meaning of actions (Rizzolatti & Arbib, 1998) and empathy (Barresi & Moore, 1996; Preston & Waal, in press). The fact that action simulation is more accurate for one's own actions might therefore also be relevant in explaining why it is sometimes so hard to understand what other people are doing.

REFERENCES

Aschersleben, G., & Prinz, W. (1995). Synchronizing actions with events: The role of sensory information. *Perception & Psychophysics*, *57*(3), 305–317.

Barresi, J., & Moore, C. (1996). Intentional relations and social understanding. *Behavioral and Brain Sciences*, *19*, 107–154.

Beardsworth, T., & Buckner, T. (1981). The ability to recognize oneself from a video recording of one's movements without seeing one's body. *Bulletin of the Psychonomic Society*, *18*(1), 19–22.

Bekkering, H., Wohlschläger, A., & Gattis, M. (2000). Imitation of gestures in children is goal-directed. *Quarterly Journal of Experimental Psychology*, *53A*(1), 153–164.

Blakemore, S.-J., & Decety, J. (2001). From the perception of action to the understanding of intention. *Nature Reviews*, *2*, 561–567.

Blakemore, S.J., Wolpert, D.M., & Frith, C.D. (1998). Central cancellation of self-produced tickle sensation. *Nature Neuroscience*, *1*(7), 635–640.

Daprati, E., Franck, N., Georgieff, N., Proust, J., Pacherie, E., Dalery, J., & Jeannerod, M. (1997). Looking for the agent: An investigation into consciousness of action and self-consciousness in schizophrenic patients. *Cognition*, *65*(1), 71–86.

Decety, J., Grèzes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., Grassi, F., & Fazzio, F. (1997). Brain activity during action observation. Influence of action content and subject's strategy. *Brain*, *120*, 1763–1777.

Decety, J., & Grèzes, J. (1999). Neural mechanisms subserving the perception of human actions. *Trends in Cognitive Sciences*, *3*(5), 172–178.

Ericsson, K.A., & Lehmann, A.C. (1996). Expert and exceptional performance: Evidence of maximal adaption to task constraints. *Annual Review of Psychology*, *47*, 273–305.

Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, *73*, 2608–2611.

Fourneret, P., & Jeannerod, M. (1998). Limited conscious monitoring of motor performance in normal subjects. *Neuropsychologia*, *36*(11), 1133–1140.

Frith, C.D. (1992). *The cognitive neuropsychology of schizophrenia*. Hove, UK: Lawrence Erlbaum Associates Ltd.

Frith, C.D., Blakemore, S.-J., & Wolpert, D.M. (2000). Abnormalities in the awareness and control of action. *Philosophical Transactions of the Royal Society*, *London*, *B355*, 1771–1788.

Frith, C.D., & Done, D.J. (1989). Experiences of alien control in schizophrenia reflect a disorder in the central monitoring of action. *Psychological Medicine*, *19*, 359–363.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609.

Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind reading. *Trends in Cognitive Science*, *2*, 493–501.

Gibson, J.J. (1979). *The ecological approach to visual perception*. Boston, MA: Houghton Mifflin.

Hommel, B. (1995). Stimulus response compatibility and the Simon effect: Towards an empirical clarification. *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 764–775.

Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (in press). The theory of event coding: A framework for perception and action. *Behavioral and Brain Sciences*.

James, W. (1890). *The principles of psychology*. New York: Holt.

Jeannerod, M. (1997). *The cognitive neuroscience of action*. Oxford, UK: Blackwell Publishers.

Jeannerod, M. (1999). The 25th Bartlett Lecture: To act or not to act: Perspectives on the representation of actions. *Quarterly Journal of Experimental Psychology*, *52A*(1), 1–29.

Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception & Psychophysics*, *14*(2), 201–211.

Kandel, S., Orliaguet, J.-P., & Viviani, P. (2000). Perceptual anticipation in handwriting: The role of implicit motor competence. *Perception & Psychophysics*, *62*(4), 706–716.

Kerzel, D., & Bekkering, H. (2000). Motor activation from visible speech: Evidence from stimulus response compatibility. *Journal of Experimental Psychology: Human Perception and Performance*, *26*(2), 634–647.

Knoblich, G., & Flach, R. (2001). Predicting action effects: Interactions between perception and action. *Psychological Science*, *12*, 467–472.

Knoblich, G., & Jordan, J.S. (2002). *Individual and joint conflict resolution*. Manuscript submitted for publication.

Knoblich, G., & Prinz, W. (2001). Recognition of self-generated actions from kinematic displays of drawing. *Journal of Experimental Psychology: Human Perception and Performance*, *27*, 456–465.

Knuf, L., Aschersleben, G., & Prinz, W. (2001). An analysis of ideomotor action. *Journal of Experimental Psychology: General*, *130*, 779–798.

Koch, I., & Hoffmann, J. (2000). The role of stimulus-based and response-based spatial information in sequence learning. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *26*(4), 863–882.

Lacquaniti, F., Terzuolo, C., & Viviani, P. (1983). The law relating the kinematic and figural aspects of drawing movements. *Acta Psychologica*, *54*(1–3), 115–130.

Liberman, A.M., & Mattingly, I.G. (1985). The motor theory of speech perception revised. *Cognition*, *21*(1), 1–36.

Liberman, A.M., & Whalen, D.H. (2000). On the relation of speech to language. *Trends in Cognitive Sciences*, *4*, 187–196.

Maarse, F.J., Van Galen, G.P., & Thomassen, A.J. (1989). Models for the generation of writing units in handwriting under variation of size, slant, and orientation. *Human Movement Science*, *8*, 271–288.

Macmillan, N.A., & Creelman, C.D. (1991). *Detection theory: A user's guide*. Cambridge, UK: Cambridge University Press.

Mechsner, F., Kerzel, D., Knoblich, G., & Prinz, W. (2001). What is coordinated in bimanual coordination. *Nature*, *414*(6859), 69–73.

Mottet, D., Bardy, G.B., & Athènes, S. (1994). A note on data smoothing for movement analysis: The relevance of a nonlinear method. *Journal of Motor Behavior*, *26*(1), 51–55.

Müsseler, J., & Hommel, B. (1997). Blindness to response-compatible stimuli. *Journal of Experimental Psychology: Human Perception and Performance*, *23*(3), 861–872.

Orliaguet, J.-P., Kandel, S., & Boé, L.-J. (1997). Visual perception of motor anticipation in cursive handwriting: Influence of spatial and movement information on the prediction of forthcoming letters. *Perception*, *26*(7), 913–928.

Preston, S.D., & Waal, F.B.M. (in press). Empathy: Its ultimate and proximate bases. *Behavioral and Brain Sciences*.

Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology*, *9*(2), 129–154.

Repp, B.H. (1987). The sound of two hands clapping: An exploratory study. *Journal of the Acoustical Society of America*, *81*, 1100–1109.

Rizzolatti, G., & Arbib, M.A. (1998). Language within our grasp. *Trends in Neurosciences*, *21*(5), 188–194.

Ruby, P., & Decety, J. (2001). Effect of the subjective perspective taking during simulation of action: A PET investigation of agency. *Nature Neuroscience*, *4*, 546–550.

Smyth, M.M. (1989). Visual control of movement patterns and the grammar of action. *Acta Psychologica*, *70*(3), 253–265.

Smyth, M.M., & Silvers, G. (1987). Functions of vision in the control of handwriting. *Acta Psychologica*, *65*(1), 47–64.

Umiltà, M.A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., & Rizzolatti, G. (2001). I know what you are doing: A neurophysiological study. *Neuron*, *31*, 155–165.

Van Galen, G.P. (1991). Handwriting: Issues for a psychomotor theory. *Human Movement Science*, *10*, 165–191.

Viviani, P., & Mounoud, P. (1990). Perceptuomotor compatibility in pursuit tracking of two-dimensional movements. *Journal of Motor Behaviour*, *22*(3), 407–443.

von Holst, E. (1954). Relations between the central nervous system and the peripheral organs. *British Journal of Animal Behaviour*, *2*, 89–94.

Wolff, W. (1931). Zuordnung individueller Gangmerkmale zur Individual-Charakteristik [Assignment of individual attributes of gait to the individual characteristic]. *Beihefte zur Zeitschrift für angewandte Psychologie*, *58*, 108–122.

Wolpert, D.M., Ghahramani, Z., & Jordan, M.I. (1995). An internal model for sensorimotor integration. *Science*, *269*, 1880–1882.

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