Contextual movement constraints of others modulate motor preparation in the observer

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ABSTRACT

Previous research demonstrated that observing an action seems to automatically activate a corresponding motor representation in the observer. It has been argued that this direct matching of observed on executed actions is modulated by contextual factors. An open question is whether observing another person being physically restrained has an influence on action execution in the observer. Using performance measures we found a slowing of response times when perceiving others' hands being physically restrained (Experiment 1). We did not find a slowing effect when participants responded with their feet ruling out a general perceptual interpretation of the present findings (Experiment 2). To further test our hypothesis, we measured event-related brain potentials (ERPs). The ERP results demonstrate that the observed slowing effect is reflected in a decrease of motor-related ERP components (Experiment 3). Perceiving others' hands physically restrained impairs motor preparation in the observer. Our findings suggest that observed environmental constraints are automatically mapped onto the observer's motor system. Such a mapping of motor restraints might facilitate action understanding.

1. Introduction

Recently, evidence from different fields of cognitive neuroscience has revealed that perception and execution of action have a common representational basis. Moreover, the finding of mirror neurons has stimulated extensive research on the relationship between perception and action (Rizzolatti & Craighero, 2004). In macaque monkeys it was shown that neurons in the ventral premotor and inferior parietal cortex are active both when the monkey executes a goal-directed action, as well as when he observes the same action performed by others. Neuroimaging evidence suggests that the observation of another person's action also evokes activity in motor execution related brain areas in humans (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti et al., 1996). This finding indicates that observed actions are directly mapped onto an internal motor representation of the observer (Iacoboni et al., 1999). According to ideomotor theory (IM; James, 1890; Prinz, 1997), direct matching of observed actions results from a general overlap of sensory and motor representations because actions are controlled

via 'images' of the sensory feedback they produce (Greenwald, 1970). Behavioural evidence for common coding is provided by a range of studies showing that, during observation of an action, a corresponding representation in the observer's action production system is activated (Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschläger, & Prinz, 2000; Press, Bird, Flach, & Heyes, 2005; Stürmer, Aschersleben, & Prinz, 2000). However, observing the actual action does not seem to be necessary for motor simulation. Instead, assuming that someone else is intending to move seems to be sufficient (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004; Liepelt, von Cramon, & Brass, 2008). This suggests that participants generate an action representation of anticipated actions (Sebanz, Bekkering, & Knoblich, 2006). Theories of embodied social cognition assume that motor simulation is necessary (Wilson, 2002) and sometimes even sufficient for understanding higher-level cognition (Barsalou, Niedenthal, Barbey, & Ruppert, 2003). Motor simulation may help to retrieve situated conceptualizations that are useful for processing the current situation (Dijksterhuis & Bargh, 2001). Accordingly one predominant functional interpretation of the 'mirror system', for example, suggests that motor simulation is involved in action understanding (Gallese & Goldman, 1998; Rizzolatti, Fogassi, & Gallese, 2001). In accordance with this view, it has recently been shown that contextual

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information seems to be represented in the mirror system as well, and can be used to disambiguate the meaning of an observed action (Iacoboni et al., 2005). However, if contextual information is also automatically mirrored in the observer's motor system, observing somebody else being restrained should restrain the observer.

In the present study we wanted to directly test the influence of observed motor restraints on the observer's behaviour. We predicted that when fingers are shown that are tied to a table by a clamp, the observation of these motor restraints (1) should lead to a slowing of reaction time (RT) in the observer. (2) Furthermore, we predicted that observing such restraints should lead to a decrease in the event-related brain potential (ERP) amplitude of the motor response. We tested the first prediction in two behavioural experiments modifying a motor priming paradigm based on Brass et al. (2000). In Experiment 3 we carried out an EEG study to test whether the observed behavioural differences are really related to changes in motor processing by investigating motor-related ERP components.

2. Experiment 1

2.1. Materials and methods

2.1.1. Participants

A group of 26 undergraduate students (mean age 24 years; 13 female) 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 their participation.

2.1.2. Apparatus and stimuli

Stimuli were presented on a 17-in. color monitor that was connected to a Pentium I PC. Experiments were carried out using ERTS software (*Experimental Runtime System*; Beringer, 2000). The stimuli consisted of a picture of a right hand positioned in the same perspective as the hand of the participant (egocentric perspective) with which the action was executed (see Fig. 1). At a viewing distance of 80 cm, the hand subtended a visual angle of $9.57° \times 10.27°$. An imperative number stimulus appeared between index and middle finger. The number subtended a visual angle of $0.72° \times 0.36°$. The observed hand on the display was given in three different conditions: The "no restraint", "corresponding restraint" and "non-corresponding restraint" condition.

In the no-restraint condition a simple hand picture was displayed statically positioned on a table (left panel of Fig. 1). In the corresponding restraint conditions the picture on the computer screen showed a hand where the index and middle finger were tied to the table with metal clamps (middle panel of Fig. 1). The restrained fingers corresponded to participant's response fingers. In the non-corresponding restraint condition the thumb and the ring finger were restrained to the table with metal clamps (right panel of Fig. 1). These fingers did not cor-

respond to participants' response fingers. None of these conditions contained any movement.

2.1.3. Procedure

An adopted version of the paradigm developed by Brass et al. (2000) was used in Experiment 1. Participants had to lift their index or middle finger in response to a number presented between the index and the middle finger of a photographed static hand (see Fig. 1). If a '1' appeared, participants had to lift the index finger, and if a '2' appeared, they had to lift the middle finger. Crucially, participants were required to react to the number and could ignore the hand on which the number was projected.

Each trial started with a picture (displayed for 800 ms) showing either the hand with no restraints (NR), a restrained index and middle finger (corresponding restraint, CR) or a restrained thumb and ring finger (non-corresponding restraint, NCR). In the second frame (displayed for 1900 ms) the imperative stimulus '1' or '2' appeared between the index and middle finger of the hand picture. Stimuli were presented in two separate experimental blocks which were counterbalanced across subjects. In one block 60 NR and 60 CR trials were randomly intermixed. In the other block 60 NCR trials were mixed with 60 NR trials. The lower panel of Fig. 1 shows the mean reaction time for each condition (for sake of simplicity the NR condition was averaged across blocks).

2.1.4. Data analysis

In all experiments prior to statistical analyses, all trials in which responses were incorrect or slower than 2000 ms were excluded from statistical reaction time analyses. This resulted in the elimination of 2.4% of trials from the data set. A Greenhouse–Geisser correction was used to assess the significance of each effect in all experiments. RTs for all conditions of Experiment 1 are presented in Fig. 1. A 2-factorial design was used to analyse the present data, including the 2-level factor *Restraint* (Restraint, Unrestrained) and the 2-level factor *Clamp Correspondence* (CR, NCR), both as within-subject variables. Further, we performed planned *t*-tests.

2.2. Results

We found a main effect of Restraint, $F_{1,25} = 29.09$, MSe = 78.42, $p < 0.001$, as well as a significant interaction of *Restraint × Clamp Correspondence*, $F_{1,25} = 7.13$, $p < 0.05$. Compared to the unrestrained condition (lower panel of Fig. 1) participants were significantly slower, $t_{25} = 5.49$, $p < 0.001$, when the fingers corresponding to the response fingers of the subject were restrained to the table. This indicates that observing someone else being restrained leads to a slowing of RTs in the observer. Furthermore, the slowing effect was absent, $t_{25} = 0.93$, $p = 0.36$, when the non-corresponding fingers (the thumb and ring finger) were restrained to the table leading to a significantly larger slowing effect in the corresponding restraint condition compared to the non-corresponding restraint condition ($t_{25} = 2.67$, $p < 0.05$).
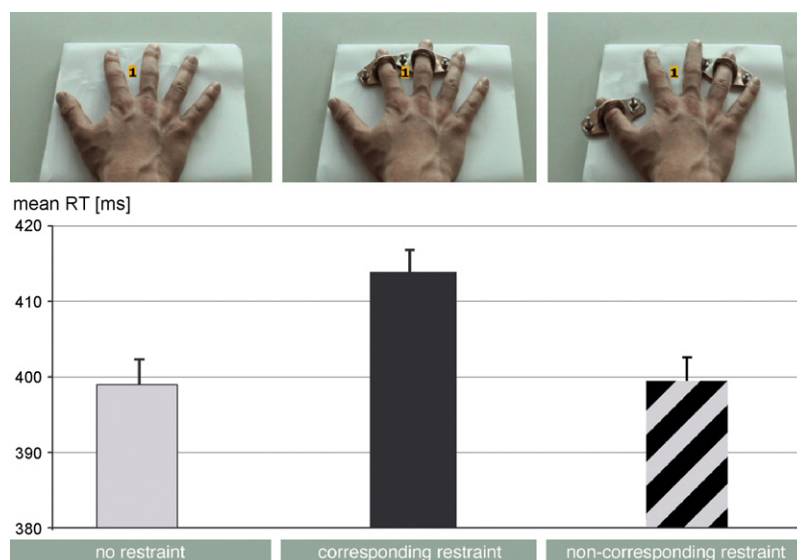

Fig. 1. Experimental design and results for finger responses of Experiment 1.

For errors, we found no significant effect of Restraint, $F_{1,25} = 3.04$, MSe = 3.52, $p > 0.09$. Numerically the error effect goes in the same direction as for RTs. Further, we found no significant interaction of *Restraint × Clamp Correspondence*, $F < 1$. Error rates did not differ across conditions confirming that the RT results cannot be attributed to a speed-accuracy trade-off (SAT).

2.3. Discussion

The aim of Experiment 1 was to test the influence of observed motor restraints on the observer's behaviour with a motor priming paradigm (Brass et al., 2000). In line with our prediction we found a slowing of reaction time in the observer when the shown fingers that correspond to the observer's response fingers are tied to a table by a clamp. We did not find such a slowing effect when the fingers of the observed hand that did not correspond to participants' response fingers were restrained. These findings suggest that the restraint-related slowing is not a general semantic effect but only affects the fingers which correspond to the restrained fingers. However, one might argue that the position of the restraint might have caused the slowing effect due to a higher perceptual difficulty to perceive the number in the corresponding restraint condition.

3. Experiment 2

In order to rule out a perceptual alternative interpretation for the slowing effect in Experiment 1, we carried out a control experiment. Participants saw exactly the same stimuli as presented in the no-restraint condition (left panel of Fig. 2) and the corresponding-restraint condition (right panel of Fig. 2) of Experiment 1. In contrast to Experiment 1, participants had to respond with their left and right foot rather than their index or middle finger to the identity of the number. If the restraint-related slowing effect was due to a higher difficulty to perceive the number in the display, it should occur regardless of whether participants react with their hand or feet. Conversely, if the effect was due to the automatic mapping of the restraint onto the observer's motor representa-

tion, the feet responses should be unaffected by the restraint of the fingers.

3.1. Materials and methods

3.1.1. Participants
A new group of 19 undergraduate students (mean age 24.1 years; 9 female) 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.

3.1.2. Apparatus and stimuli
The visual displays were identical to the no-restraint condition and the corresponding restraint condition of Experiment 1 (see Fig. 2).

3.1.3. Procedure
The procedure, design and trial timing were identical to Experiment 1. Participants reacted with their left and right foot to the restraint condition (60 trials) and the no-restraint condition (60 trials). The non-corresponding restraint condition of Experiment 1, however, was not given in Experiment 2.

3.1.4. Data analysis
Data analysis was identical to Experiment 1. Responses which were incorrect or slower than 2000 ms were excluded from statistical RT analyses. This resulted in the elimination of 4.9% of trials from the data set. We used a 1-factorial design to analyse the present data, including the 2-level factor *Restraint* (Restraint, Unrestrained) as a within-subject variable. Further, we performed planned *t*-tests.

3.2. Results

In Experiment 2, we found no main effect of Restraint ($F < 1$). As can be seen in Fig. 2 (lower panel), the RTs for the no-restraint condition and the restraint condition were nearly identical (496 ms versus 497 ms) and did not even show a tendency for a statistical difference, $t_{18} = -0.16$, $p = 0.87$. The same was observed for errors ($p > 0.05$), indicating no evidence for a SAT of observed RT effects.

3.3. Discussion

The aim of Experiment 2 was to test if effects of observed motor restraints on the observer's behaviour as found in Experiment 1 are due to perceptual slowing, a higher perceptual difficulty to perceive the number in the corresponding restraint condition. When participants responded with their left and right feet, we did not find a slowing effect for the corresponding restraint condition as compared to the no-restraint condition. These findings suggest that the restraint-related slowing effect as found in Experiment 1 was not due to a general perceptual slowing and an increased difficulty of perceiving the number in the corresponding restraint condition.

However, in the present experiment one could argue that response times as a measure might not be sensitive enough to precisely test effects of other's movement restraints on the observer's motor system. Furthermore, the overall reaction time was substantially higher in the second experiment. In order to directly test the hypothesis that the movement restraint effect is located at the motor processing stage, we investigated effects of other's movement constraints on the observer's motor system by measuring motor-related ERP components.

4. Experiment 3

To test effects of environmental constraints with EEG, we had to adapt our experimental design. We recorded EEGs of 25 right-handed subjects who prepared a left- or right-hand response to a static display of another person's left- or right-hand. As in the previous experiments, the hand on the display was presented from an egocentric perspective (see Fig. 3). In the present study, we used the lateralized readiness potential (LRP, Coles, 1989; Gratton, Coles,
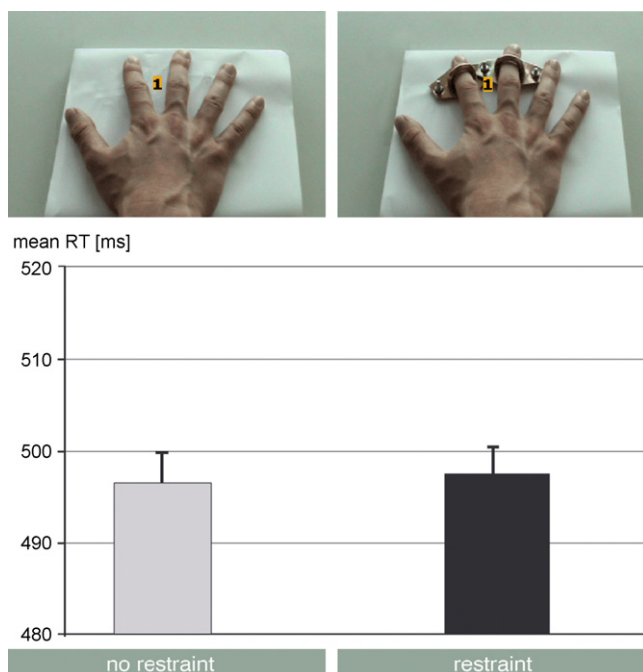

Fig. 2. Experimental design and results for foot responses of Experiment 2.
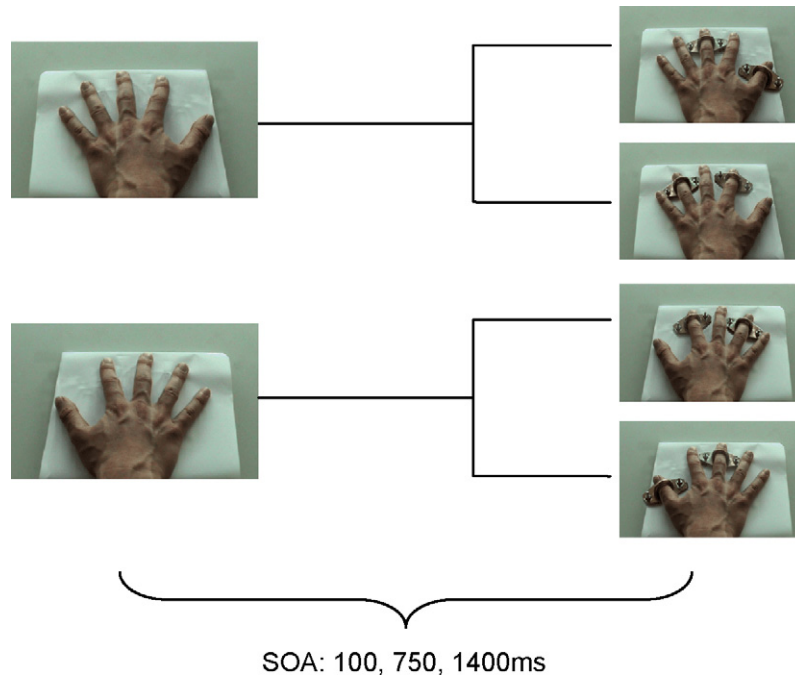
SOA: 100, 750, 1400ms

Fig. 3. Experimental design of Experiment 3. A left-hand indicates preparation of left-hand responses, a right-hand preparation of right-hand responses. The appearance of the clamps reflects the go stimulus. Onset time of the go stimulus varied between 100, 750 and 1400 ms. Depending on block type (index finger responses or middle finger responses), the go stimulus could reflect either corresponding restraint (Restraint) or non-corresponding restraint (Unrestrained) conditions.

Sirevaag, Eriksen, & Donchin, 1988), a temporal electrophysiological marker of motor preparation to test effects of environmental constraint on a finer-grained level. We extracted the LRP during motor preparation from the EEG signal by dividing responses over both hands. Participants were instructed to prepare their responses to the identity of a static hand presented on the display. They had to withhold their response until a metal clamp (motor restraint) appeared over some of the observed fingers of the static hand. Responses were to be given independently of the finger on which the restraint appeared. Depending on the response finger (index or middle finger), the clamp correspondingly restrained the response finger or not. We predicted a smaller motor-related ERP amplitude for the corresponding restraint condition as compared to the unrestrained condition.

4.1. Materials and methods

4.1.1. Participants

A new group of 25 undergraduate students (mean age 24 years; 11 female) 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.

4.1.2. Apparatus and stimuli

The stimuli were adapted to the present design. They consisted of a picture of a left- or right-hand positioned in an egocentric perspective (preparation stimulus). The clamp (imperative response stimulus) appeared either over index and ring or thumb and middle finger of the static hand (see Fig. 3).

4.1.3. Procedure

The preparation stimulus was presented with a variable length of 100, 750 or 1400 ms. The clamp, acting as the imperative response stimulus appeared for 800 ms (see Fig. 4). This created a variable stimulus onset asynchrony (SOA) of 100, 750 or 1400 ms between the preparation stimulus and the imperative response stimulus (the clamp). This clamp restrained the other person's possible finger movements, respectively (either thumb and middle finger or index and ring finger). Trial length varied between 3 s (SOA 100 ms) and 4.3 s (SOA 1400 ms). The subject's task was to prepare (but not to execute) a finger lifting movement with their left-hand when observing a left-hand and with their right-hand when observing a right-hand. Subjects had to withhold their response until the imperative response stimulus (the metal clamp) appeared. When the imperative stimulus appeared they had to respond with the prepared finger lifting movement. The task was given in two kinds of blocks differing with respect the response finger. In one block type participants were instructed to respond with left or right index fingers (index finger blocks), in the other block type with their middle fingers (middle finger blocks). Depending on the fingers that were restrained on the observed hand, responses were either *Restraint* or *Unrestrained*. Eight blocks were given in total. Each block contained 120 trials leading to 960 trials and an experimental duration of 1 h in total. Using a 3 (SOAs) × 2 (Observed hand) × 2 (Restraint) design, each condition was presented for 10 times per block and for 80 times in total. Due to lateralization of responses, there were 40 trials per condition and response hand throughout the entire experiment.

4.1.4. Data recording

The EEG was recorded in an acoustically and electrically shielded, dim-lit room. Stimuli were presented with a Pentium 4 3 GHz computer on a 17 in. monitor with a picture repetition rate of 75.3 Hz. Subjects were seated approximately 110 cm before
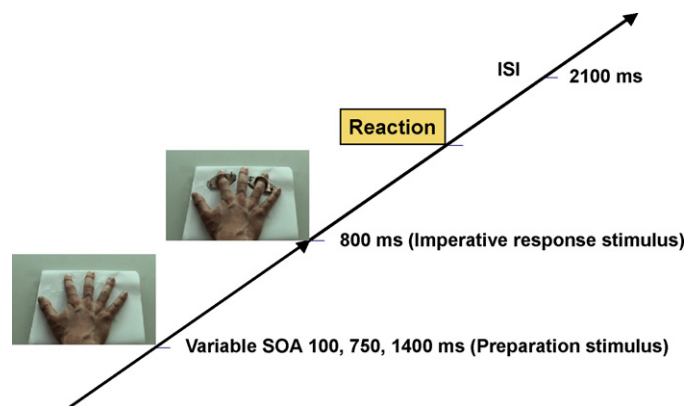

Fig. 4. Shown is the stimulus sequence for each trial as used in Experiment 3. Each trial started with a picture (displayed for a variable amount of time: 100, 750, 1400 ms) showing a static left or right-hand acting as a preparation stimulus. In the second frame (displayed for 800 ms), the imperative response stimulus (a clamp) appeared either over thumb and middle finger or index and ring finger. This created a variable SOA between the preparation stimulus and the imperative response stimulus. Participants had to respond to the appearance of the clamp independently of the finger on which the restraint appeared. The reaction was followed by a constant inter-stimulus interval (ISI).
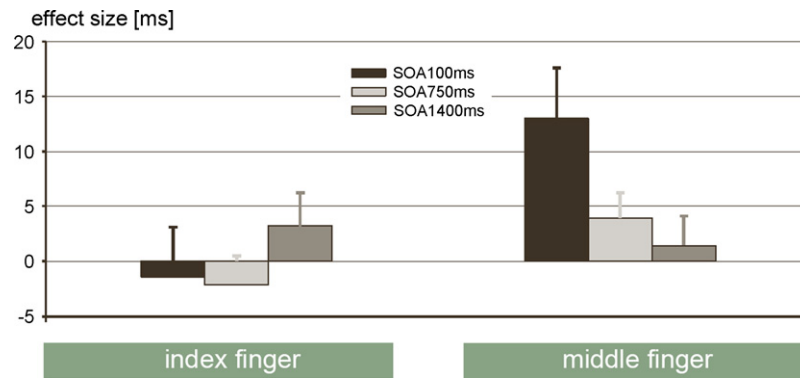
Fig. 5. Behavioural results of Experiment 3. Effect sizes estimated by *Reaction Times (ms) Restraint* minus *Reaction Times (ms) Unrestrained* for index finger responses (left graph) and for middle finger responses (right graph) for three SOAs (1400 ms in dark grey, 750 ms in light grey and 100 ms in black).

the monitor. The stimulus (a picture of a left- or right-hand) subtended a visual angle of 6.98° × 7.50°. For stimulus presentation and response recording we used ERTS (version 3.33). EEG data were recorded with a pass band of DC to 70 Hz at 16 bit resolution and a sampling rate of 500 Hz from 64 Ag/AgCl scalp electrodes spread out across the scalp arranged according to an extension of the 10–20-principle (Jasper, 1958) and four ocular electrodes at the outer canthi and above and below the left eye. EEG data were recorded with BrainAmp MR+ (BrainProducts, Herrsching, Germany) using an elastic cap (Easy Cap Herrsching, Germany) and analyzed with the software EEP (ERP Evaluation Package). All EEG channels were referenced to the left mastoid and were re-referenced offline to the average of the left and right mastoids. In a first analysis step, the EEG epochs were scanned for muscular and large EOG artifacts. Whenever the standard deviation in a 200-ms interval exceeded 50 μV, the epoch was rejected. In a second step, small horizontal and vertical EOG artifacts, which were still present in the EEG signal, were corrected by an eye movement correction procedure (Pfeifer, 1993) based on a linear regression method described by Gratton, Coles, and Donchin (1983). A 200 ms pre-stimulus interval relative to S1 served as baseline.

4.1.5. Data analysis

RTs and errors were measured with an optical response device. Responses which were incorrect or slower than 2000 ms were excluded from statistical RT analyses. This resulted in the elimination of 2.9% of trials from the data set. As there is known to be a lateralized potential prior to a predictable response, the lateralized readiness potential, we used the averaging method of Rugg and Coles (1995) to test effects of observed restraint on movement preparation of the specific response finger over C3 and C4: LRP = {mean (C4′ − C3′)$_{\text{left-hand movement}}$ + mean (C3′ − C4′)$_{\text{right-hand movement}}$}/2 (Rugg & Coles, 1995). Average EEG amplitudes in all trials were analysed in the time window −200 ms to +200 ms around the response separately for the different restraint and finger conditions. In addition to effects of specific motor preparation we recorded the readiness potential (RP) representing effects of general motor preparation.

Statistical analyses were performed by entering average RTs and LRP amplitudes into repeated measures ANOVA. We used a 3-factorial design to analyse the present data. We included the 3-level factor *SOA* (SOA 100, 750, 1400 ms), the 2-level factor *Response Finger* (index finger, middle finger) and the 2-level factor *Restraint* (Restraint, Unrestrained) in a repeated-measures ANOVA as within-subject variables. Further, we performed planned *t*-tests to test for possible differences between both response hands.

4.2. Results

4.2.1. Behavioural results

The mean RT decreased with increasing SOA (SOA 100, 443 ms; SOA 750, 297 ms; SOA 1400, 276 ms; $F_{2,48} = 282.7$; $p < 0.01$). Mean RT under conditions of Restraint (339 ms) overall SOAs were slower as compared to Unrestrained conditions (336 ms) ($F_{1,24} = 4.8$; $p < 0.05$). Most importantly we observed a three way interaction (SOA × Restraint × Response Finger) in the omnibus ANOVA, $F_{2,48} = 3.6$; $p < 0.05$, indicating stronger effects of the observed Restraint on Response finger in short SOAs.

Planned *t*-tests indicated that the three-way interaction resulted from restraint effects in SOA 100 ms (for effect sizes see Fig. 5), and middle finger responses. Middle finger response RT in the Restraint condition (453 ms) were increased compared to the Unrestrained

condition (440 ms), $t_{24} = 2.8$; $p < 0.05$. No such effect was observed when taking into account only index finger responses, $p = 0.75$. Additional analyses showed stronger effects of observed restraint for left-hand compared to right-hand responses, $t_{24} = 2.4$; $p < 0.05$.

Overall errors were made in only 2.9% of the trials. The error analysis also indicated a significant three-way interaction (SOA × Restraint × Response Finger), $F_{2,48} = 5.0$; $p < 0.05$. This analyses indicates similar differential effects of observed Restraint on Response finger for different SOAs as we observed for RTs. Errors decreased with increasing SOA ($F_{2,48} = 21.3$; $p < 0.01$).

4.2.2. EEG results

As expected, lateralization for SOA 1400 ms started at the earliest point in time relative to the response and latest at the shortest SOA of 100 ms (see Fig. 6). Results revealed a significant interaction of Restraint × Response finger $F_{1,24} = 4.6$; $p < 0.05$, due to effects of SOA 100 ms and middle finger responses, $t_{24} = 2.9$, $p < 0.01$ (see Fig. 7).

In SOA 100 ms the amplitude of the LRP for middle finger responses without restraint was 0.6 μV higher compared to the restraint condition ($t_{24} = 2.9$; $p < 0.05$). The restraint condition reached a maximum amplitude of −2.5 μV in comparison to −3.1 μV for the unrestrained condition (both: SOA 100 ms and a middle finger response) which is in line with response time data.
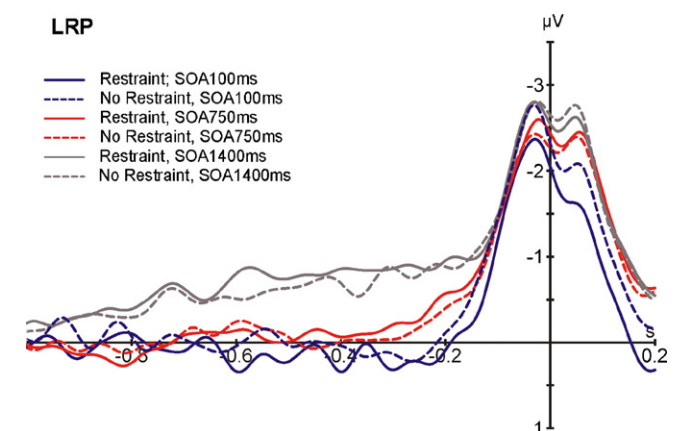

Fig. 6. Lateralized readiness potentials for three SOA conditions (100, 750 and 1400 ms) in Restraint and Unrestrained conditions of Experiment 3. The late component of the lateralized readiness potential reflects the time at which the exact movement is specified. Shown are response-locked LRPs averaged over electrodes of interest (C3 and C4) and subjects. The different lines represent the Restraint (straight lines) and the Unrestrained (dashed lines) condition for three SOAs (1400 ms in grey, 750 ms in red and 100 ms in blue aligned to the response).
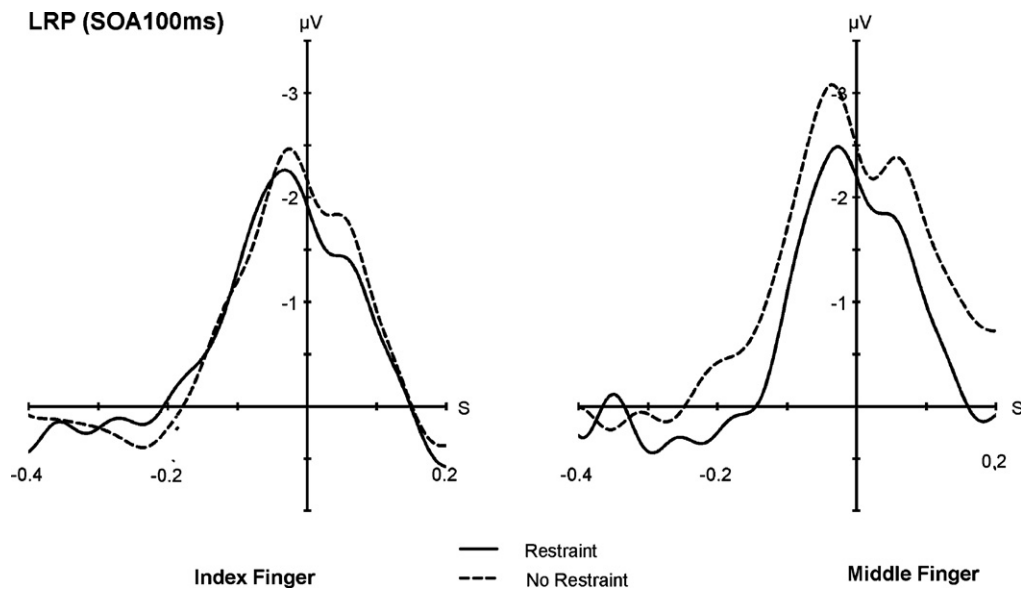
Fig. 7. Lateralized readiness potentials for index finger (left) and middle finger (right) responses in the Unrestrained (dashed lines) and the Restraint (straight lines) condition for SOA 100 ms of Experiment 3.

Effects of observed restraint were increased for left-hand compared to right-hand responses in the readiness potential (measured over the contralateral (pre)motor cortex at electrodes C4 and C3, respectively) in SOA 100 ms (t_{24} = 3.3; $p < 0.05$). We found stronger effects of observed restraint for less prepared responses as shown by effects of SOA, response hand and response finger.

5. Discussion

Previous research on shared representations showed that observation of an ongoing movement leads to activity in areas that are also active during action execution (Gallese et al., 1996; Iacoboni et al., 1999; Rizzolatti et al., 1996). Such motor activity has also been shown to occur when anticipating someone acting (Kilner et al., 2004). Moreover, recent evidence suggests that this 'mirror activity' is modulated by contextual information, indicating that the context in which an action is embedded is also represented in the observer's motor system (Iacoboni et al., 2005). However, it is an open question whether observed context that constrains a potential action space is also mapped onto the observer's motor representation. The aim of the present study was to investigate this question by using performance measures and EEG. We devised a series of three experiments in which participants saw somebody else's fingers restrained to the table while the subject had to respond to a number presented between the index and the middle finger of the model (Experiments 1 and 2). In Experiment 3, we measured EEG while participants carried out a slightly modified version of the paradigm allowing to compute LRPs.

Using a motor priming paradigm (Brass et al., 2000), we show that observing another person's restraint leads to a finger-specific slowing of reaction time in the observer, even when this restraint was response irrelevant. Importantly the slowing effect was absent when the fingers that did not correspond to the participants response fingers were restrained. This pattern of results suggests that the restraint-related slowing is not a general semantic effect but only affects response fingers which correspond to the restrained fingers.

However, the findings of Experiment 1 could alternatively be explained by an increased perceptual difficulty to perceive the number in the corresponding restraint condition as compared to

the non-corresponding restraint condition. These two conditions differ perceptually. To rule out this perceptual alternative interpretation, we carried out a control experiment in which participants saw exactly the same stimuli as presented in the no-restraint condition of Experiment 1. However, in this experiment participants had to respond with their left and right foot rather than their index or middle finger to the identity of the number. In Experiment 2 we found no difference in reaction times for the no-restraint condition and the restraint condition, ruling out a perceptual alternative explanation for the observed effect in Experiment 1.

In order to directly test the hypothesis that the movement restraint effect is located at the motor stage rather than the perceptual stage, we measured the lateralized readiness potential while participants prepared their responses to the identity of a static hand. The LRP results revealed a modulation of motor-related LRP components when the clamp appeared on the fingers that corresponded to participant's response finger. Furthermore, our data suggest that the size of the effect was modulated by the dominance of the responding effector. First, we found stronger effects when participants responded with their non-dominant left-hand. Moreover, the effect was stronger for the middle finger rather than the extremely practiced index finger. In addition the effect of motor restraint on the LRP was modulated by the amount of motor preparation. The less the subject was prepared the stronger the restraint effect.

One potential critique of Experiment 3 might be that the motor restraint effects both behaviourally and in LRP were restricted to specific fingers and SOA. However, in order to adapt the design to the ERP logic, we had to modify the stimuli in Experiment 3 as compared to the previous experiments. We think that the procedure we adapted in Experiment 3 was less optimal to reveal behavioural effects. In Experiments 1 and 2, the imperative stimulus was a number appearing over the restrained or unrestrained finger, respectively. The restraint was present from the beginning of the stimulus presentation. Opposed to that in Experiment 3 an unrestrained left- or right-hand was presented that indicated the response participants had to prepare. The clamp appeared later acting as the imperative stimulus after the motor response had been selected. In the first two experiments, however, the clamp was present at an earlier stage of response selection. This could explain

the stronger and more reliable behavioural effects of the observed restraint in Experiments 1 and 2 as compared to Experiment 3. These findings suggest that the effect of observed restraint becomes stronger the less parameters of the observer's motor response are prepared.

However, in general we could replicate the behavioural findings of Experiments 1 and 2. In addition the LRP findings strongly suggest that the influence of motor restraint on response times is primarily located on the motor level and not on the perceptual level.

Overall, this study provides converging behavioural and ERP evidence for the assumption that environmental constraints of others are automatically mapped onto the observer's motor representation. This finding is consistent with recent imaging results indicating that the mirror system is not only sensitive to the action itself but also to action context (Iacoboni et al., 2005).

5.1. Functional mechanisms underlying automatic mapping of action restraints

Our findings provide evidence that not only other's actions are mirrored in the observer's motor system but also contextual information relevant for potentially upcoming actions. But how can we explain direct matching of contextual information in the context of theories of motor control and mirror system research? One potential explanation for this finding is based on IM (James, 1890; Prinz, 1997). IM proposes that actions are planned and controlled by anticipation of the sensory consequences of the action. When planning a finger lifting movement, for example, one anticipates how it looks or feels to lift the finger. At an early stage of motor preparation one thus represents the finger in the starting position (e.g. resting on the table). At that point, observing a hand in the same position might lead to a confusion of the observed hand with the response hand. When the observed hand includes a context that restraints a potentially upcoming action, as in the present study, the observed restraint is automatically mapped onto one's own motor representation. Confusion effects between perceptual and motor representations should be stronger the less parameters of the response (such as the end state of the movement) are specified and the higher the overlap between perceptual and motor representations.

Comparable "representational confusion effects" are well known from a phenomenon called the "rubber hand illusion" (Tsakiris, Prabhu, & Haggard, 2006). Here, a participant sees a rubber hand plausibly positioned to extend from her real arm which is hidden. If the rubber hand and the real hand are stroked simultaneously, the participant sometimes feels the stroking in the location of the faked hand, not the real hand (Botvinick & Cohen, 1998). Such effects are stronger the higher the overlap between the external perceptual and the internal motor representation (Costantini & Haggard, 2007; Tsakiris et al., 2006). Self/other confusion can occur even though the subject is completely aware of the identity of his/her own hand.

5.2. The affordance of action restraints

Importantly, the present findings also extend the affordance concept (Gibson, 1977). Recent findings show that action-related object affordances can activate specific motor schemas related to an action (Di Pellegrino, Rafal, & Tipper, 2005). We show that observing objects indicating possible movement restraints lead to an impairment of the respective motor plan in the observer. Object affordances do not only activate motor schemas related to possible actions with the object, but also restrict the degrees of freedom of how to act upon it. Our findings suggest that mental representations of restraining context automatically involve encodings of the

motor programs not to act in the intended way and may be used as a signal to start alternative motor programs.

Theories of embodied social cognition (Wilson, 2002) assume that mimicry may not be an end in itself (Barsalou et al., 2003), at least in complex social situations. It may help to retrieve situated conceptualizations that are useful for processing the current situation effectively. Just like action mimicry induces social contagion (Dijksterhuis & Bargh, 2001) matching of action restraints may induce physical contagion. When people share a physical state they are likely to activate the same conceptualization, thereby achieving synchrony, coordination and common physical understanding important in social interactions (Sebanz et al., 2006). To our knowledge our results show for the first time that action context indicating possible movement restraints affect the observer's motor response even in the absence of any observed movement.

One could speculate that direct mapping of action-related environmental context onto the observer's motor representation plays a crucial role in action understanding, prediction of future actions (Blakemore & Frith, 2005; Wilson & Knoblich, 2005) and setting up anticipatory re-actions before the other's action have occurred.

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