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Visuomotor priming by pictures of hand postures: perspective matters

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Abstract

Observing hand postures interacts with the preparation of similar actions. This may be due to motor encoding of the observed displays and/or to enhanced visual processing induced by motor planning. We studied the effects of the observer's perspective on motor representation, using a visuomotor priming task with simple responses. Participants were asked to grasp a bar in horizontal or vertical orientation. In Experiment 1, the prime stimuli were pictures of a hand in either 'Own' or 'Other perspective', and their orientation could be congruent or incongruent with the pre-specified grasping action. An overall effect of congruency was found, providing strong evidence for the automatic encoding of the primes. The effects of prime perspective were moderated by the availability of preview of the hand stimuli: with preview, congruency effects only occurred for 'Own perspective' stimuli. Conversely, without preview, congruency effects were restricted to 'Other perspective' primes. In Experiment 2, we replicated the 'Own perspective advantage' with hand preview. In addition, we manipulated the stimulus onset asynchrony between prime stimulus and go-signal and found congruency effects to be restricted to the shorter asynchronies. We interpret the 'Own perspective advantage' as the result of an enhancement of action relevance of the prime stimuli during the preview interval, driven by motor planning. In contrast, we explain the 'Other perspective advantage' as a stimulus-driven visuo-motor effect, based on more frequent experience with suddenly appearing hands of conspecifics than with suddenly appearing own body parts.

Keywords: Motor preparation; Perception and action; Mirror system; Prehensile actions; Action observation; Human

1. Introduction

Observing the actions of conspecifics involves predictive motor representations on the side of the observer, even in the absence of the observer's intention to respond with an imitative or complementary behaviour. Also during observation of graspable objects and tools, motor cortical areas have been shown to code the object in terms of one or more potential actions with these objects [21,29]. In both instances of motor involvement during observation of actions and objects, actions are internally simulated by the observer [19].

The experimental methods employed over the last decade to study these visuomotor couplings include a number of neurophysiological methods (single cell recordings, [14,27,33]; brain imaging methods, see reviews [11,19,26,28]; transcranial magnetic stimulation, [13,31]) as well as behavioural methods (transfer paradigms, [17,34–36]; stimulus-response compatibility paradigms, [3,4,7,32]). As a result, the basic phenomenon of motor involvement during action observation is now well documented, led by the research on 'mirror neurons' [14,27,33]. This work has further contributed to raising interest in action imitation and observational learning, both of which are likely to build on a mirror system architecture [1,20,28,37,38].

In this general context, we pursued two aims with the present, behavioural study. Firstly, we were seeking to clarify the impact of the observer's perspective on motor representation, by employing a visuomotor priming task. Secondly, we wanted to gather further evidence for the automaticity of these priming effects.

With respect to our first aim, we used, as prime stimuli, pictures of a hand that matched the end posture of the observer's own hand when performing the displayed action ('Own perspective'). We contrasted these with pictures of hand end postures in the perspective of another person, facing the participant with a mirror-symmetric hand posture ('Other perspective'). The observer's perspective has not been systematically manipulated in previous research on visuomotor priming. Its study is of practical relevance for the design of displays in observational learning procedures. In addition, we were hoping to gain further insight into the neuro-cognitive mechanisms that underlie the documented priming effects. In the following, we outline the two main

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explanations offered for these effects, and ask what these might predict for the two perspectives.

Based on the work by Craighero et al. [9] on object priming, we distinguish 'visuo-motor' and 'motor-visual' priming, and use 'visuomotor' as a neutral umbrella term for both. Motor-visual priming was the preferred interpretation in Craighero et al.'s [7] recent study with hand posture primes. They demonstrated that the initiation of a pre-specified reach-to-grasp action can be modulated by pictures of a hand that matched or did not match the planned effector end orientation. According to them, motor preparation biases visual processing. As an underlying neurophysiological mechanism, they suggested that motor preparation not only involves premotor cortical areas, but "should evoke also a representation of the prepared action in visual terms" (p. 498), located in posterior parietal and superior temporal areas. Responses to hand pictures that match this anticipatory visual representation should be facilitated, due to the priming effects of the internal representation on the visual processing of the picture stimuli. Although these priming effects arise, in a strict sense, from competing visual representations, the label 'motor-visual' adequately refers to their motor origin, in that the internal expected sensory consequences derive from motor preparation.

Given that, in motor-visual priming, motor and visual representations refer to the actor's own hand, one would expect 'Own perspective' displays to produce stronger effects than 'Other perspective' displays for this type of priming. It is thus surprising that Craighero et al. [7] only used hand postures in 'Other perspective', which do not resemble the expected sensory consequences as directly as 'Own perspective' stimuli. Clearly, a comparison of both perspectives, as undertaken in the present study, is called for.

Craighero et al.'s [7] results are also open to a visuo-motor interpretation. In this account, which has been prevalent in the interpretation of mirror neurons and related behavioural findings, visual hand postures automatically activate a corresponding motor representation, regardless of whether the observer has already prepared a response or not. A visuo-motor account thus includes situations where the observer has little advance knowledge about the visual event (e.g. an unexpected social signal), whereas a motor-visual account presupposes the observer's own motor preparation.

What can be predicted from a visuo-motor account regarding the impact of perspective? Rizzolatti and Luppino [29] recently suggested that the congruency between premotor neurons and visual descriptions of seen actions in temporal and parietal cortex might take its origin from action execution: "in the case of mirror neurons, the matching should occur between the hand action commanded by a certain motor prototype and the vision, by the agent of the action, of his/her own hand. Once this initial visuomotor link is established, it is progressively generalized to the hands of other individuals" (ibid, p. 897). Thus, associating the actions of others with the observer's motor repertoire is seen to develop on the basis of links between motor commands and visual input from one's own hand. Accordingly, also from a visuo-motor interpretation, one might expect a primacy of 'Own perspective' displays. However, a lifetime's experience with body parts in both 'Own' and 'Other perspective' is likely to result into strong visuo-motor associations for both perspectives. Thus, effects of visuomotor priming should not necessarily differ for the two perspectives. Given the massive exposure to the actions of others, and the need for their rapid interpretation, it is even possible that 'Other perspective' displays produce stronger visuomotor priming effects than 'Own perspective' displays.

Also in other work with hand displays [3,4,32], perspective has not been systematically manipulated. Again, the basic finding in these studies was that responses congruent with a (task-irrelevant) hand posture were initiated faster than responses in the presence of incongruent displays. Stürmer et al. [32] interpreted their results with reference to Greenwald's [16] ideomotor principle and Prinz' [23] common coding approach, in the sense that actions become automatically activated by visual events that correspond to their effects, i.e. as a visuo-motor effect. Unlike in motor-visual priming, interference here arises between competing motor representations that are concurrently activated by different features of the display.

Whereas Stürmer et al. [32] used, as prime stimuli, pictures of hand gestures that resembled the participants' view of their own hand, 'Other perspective' stimuli have been used in subsequent work by Brass et al. [3,4], namely pictures of others' hands with a lifting index or middle finger. Again, a symbolic instruction was facilitated by finger movement displays that were congruent with the required response [4]. Also these authors entertain a visuo-motor account and explicitly state "that a motor-visual priming mechanism . . . is unlikely to be able to explain fully the RT patterns of the present experiments" (ibid, p. 139).

In summary, we can expect 'Own perspective' primes to exert stronger effects than 'Other perspective' primes for motor-visual priming, and presumably equal effects for visuomotor priming. In the available studies, both perspectives proved effective, but a direct comparison between 'Own' and 'Other perspective' has not yet been undertaken. The results of the present study indicate that priming mechanisms can differ substantially for 'Own' and 'Other perspective' stimuli.

Turning to the second aim of the present study, we employed a simple response task in order to obtain more clearcut evidence for the automaticity of the priming effects than previously available. Amongst the existing behavioural studies, only Brass et al. [3] used a simple response task, whereas choice response tasks were adopted by Brass et al. [4] and Stürmer et al. [32], and a go/no-go choice task by Craighero et al. [7]. In agreement with Brass et al. [3], we find choice response tasks not as convincing as simple response tasks in providing evidence for automatic response activation by visual stimuli, simply because participants in choice tasks are actively seeking information about the required response from the visual array. The demonstration that this search can be ‘misled’ by stimulus attributes that are task-irrelevant but that specify aspects of the required response, is, in our view, a less convincing indicator of automatic response activation than the impact of the same gesture on a response that does not require further specification. Also the go/no-go task employed by Craighero et al. [7] compromises an interpretation in terms of automatic processing. This is because their task required the visual analysis of precisely that stimulus attribute (hand orientation) which was expected, and shown, to impact on response latencies.

2. Experiment 1

We adopted a simple response procedure in order to further substantiate the automaticity of priming by observed hand postures. The task was closely modelled after Craighero et al.’s [8,10] earlier studies on object priming. In addition to perspective of the primes, and congruency between instructed hand orientation and prime, we also manipulated the location where the prime stimuli were shown (on a monitor above the hand’s target location, or, via a mirror, precisely at the target location), and the type of fixation precue. Our initial prediction regarding the prime location was that ‘Own perspective’ displays would be affected more strongly by location than ‘Other perspective’ displays. We used two fixation precues, a fixation point, as did Craighero et al. [7], and a pictorial hand precue which matched the hand’s neutral start position. With the latter, we wanted to reduce global effects of the sudden onset of the hand prime stimulus, which might mask the more specific effects of hand orientation that we were interested in. Driver et al. [12] had found earlier and more robust effects of a face’s gaze on visual orienting when a neutral face precue, rather than a fixation asterisk was used. Also in our experiment, the type of fixation precue turned out to be a potent variable. In summary, we pursued four main research questions in Experiment 1:

(1) Can priming effects by pictures of hand postures be demonstrated in a simple response task, as previously shown for object priming?
(2) Do prime stimuli in ‘Own perspective’ produce equal or stronger effects than stimuli in ‘Other perspective’?
(3) Are the effects of ‘Own perspective’ primes particularly sensitive to presentation location?
(4) Can more robust priming effects be obtained by using a neutral hand picture as fixation precue, instead of a fixation point?

2.1. Method

2.1.1. Participants

Twenty-four students (14 female, 10 male) from Lancaster University volunteered for this study, for which they received £5 payment. Ages ranged between 19 and 37 years (mean age = 22.7), and all were right-handed and had normal or corrected-to-normal vision.

2.1.2. Design

A four-factorial within-subjects design was used, with the factors congruency between instructed hand orientation and prime (congruent versus incongruent), perspective of prime stimuli (own versus other hand), location of prime stimuli (at the hand’s target location, versus on a monitor above that), and fixation precue (fixation point versus neutral hand). We manipulated the factors perspective and location across four main blocks of trials. The fixation precue was manipulated in two sub-blocks within each main block.

2.1.3. Stimuli and apparatus

Participants sat at a table (80 cm × 80 cm) in a dimly lit room in front of a computer monitor, with a viewing distance of 50 cm (Fig. 1). E-Prime software (Psychology Software Tools Inc.) was used for stimulus presentation and measurement of reaction times (RTs). Stimuli consisted of colour pictures of hands captured using a digital camera and edited on a standard green background. The four pictures that were used as primes (Fig. 2, lower right frame) represented hands that matched the end positions required to grasp the response bar as seen from the participants’ point of view. Two of the four pictures showed an end position that matched the required grasps as participants would see their own hand (cf. Fig. 4). The other two pictures showed the same hand postures as though it was the hand of another person grasping the bar from across the table (or as their own hand seen in a mirror, cf. Fig. 2). The three fixation pictures used the same standard background, on which either a white fixation point was placed, or pictures of a hand that matched the hand’s start position in either ‘Own’ or ‘Other perspective’, with the same fixation point superimposed. All pictures (28 cm × 21 cm) were presented on a 15 in. monitor (Sony Multiscan 15sf, 800 × 600 pixel, 16 bit colour) to appear life-size.

The monitor was mounted onto a box so that the centre of the screen sat 43 cm above the plane of the table (Fig. 1). On the front of the box a bar was mounted (18 cm × 6 cm) that could be turned by the experimenter to a horizontal or vertical orientation. The starting point for the reaching movement was a button fixed on the table and aligned to the centre of the bar, with a reaching distance of 20 cm. Participants were seated so that the start position and bar were in line with their right shoulder. An occluding surface (40 cm × 26 cm) was positioned horizontally over the start position at a height of 27 cm to block vision of the hand throughout the movement. For presenting stimuli at the hand’s target location, the images were displayed upside-down on the monitor, and a mirror (20 cm × 25 cm) was placed on the occluding surface. The mirror was aligned so that the stimuli appeared at the location of the target object, that is, as though the displayed hand was grasping the (invisible) response bar. A shield was placed in front of the monitor to prevent participants from

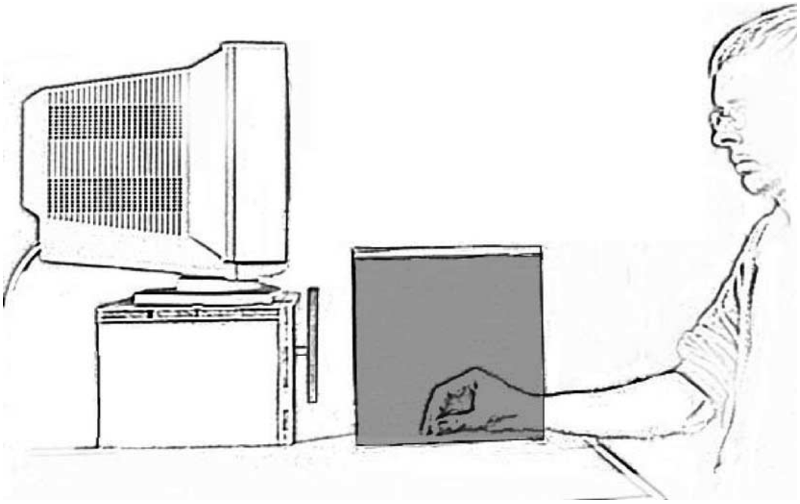

Fig. 1. Experimental setup. The response bar is shown in vertical orientation and is hidden from the participant's view by an occluder. A mirror could be placed on the occluding surface for presentation of the hand stimuli at the target location.

looking directly at it. In all conditions, RTs were collected from prime onset until release of the start button.

2.1.4. *Task and procedure*

At the beginning of each trial, participants placed their right index finger on the start button with their thumb placed alongside and touching their index finger so that the button remained depressed. This position ensured that the orientation of the opposition space between thumb and index was approximately 45° relative to the table surface and therefore allowed for a similar amount of wrist rotation for either movement. The response bar, which was always invisible to the subject, was positioned by the experimenter to be either vertical or horizontal. The bar orientation always corresponded to the instruction word for this trial ("clockwise" or "anticlockwise"), which was shown on the monitor for 2500 ms (Fig. 2). During this interval participants had been instructed to imagine themselves performing the grasp in

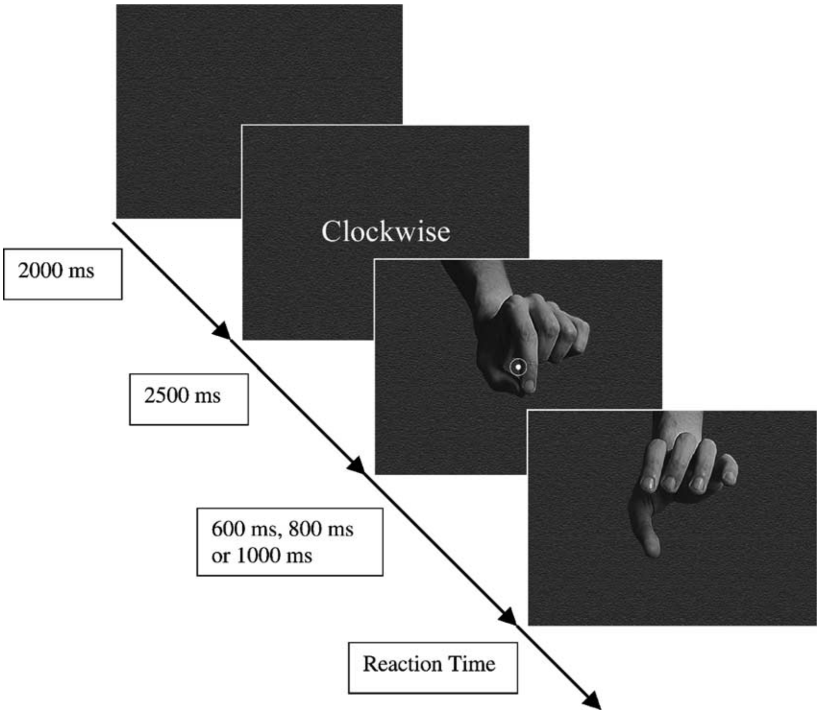

Fig. 2. Sequence of stimuli in Experiment 1, shown for 'Other perspective' and hand fixation trials. On appearance of the prime (lower right picture), participants were to reach for the response bar in the pre-instructed orientation.

the required orientation. This procedure ensured that the response was fully prepared before the remaining events commenced (simple responses on a trialwise basis).

The instruction word was replaced by a fixation stimulus to alert the participant that the go-signal was about to appear and to focus their attention to the centre of the screen. The duration of the fixation period was randomised (600, 800 or 1000 ms) to prevent participants from anticipating the onset of the go-signal. The fixation stimulus was then replaced by the relevant prime stimulus for that trial, which acted as go-signal and was either congruent or incongruent to the prepared movement. Participants had been instructed to respond as quickly as possible to the go-signal by grasping the bar in the pre-specified orientation and to ignore the orientation of the prime stimulus. When the bar was in horizontal orientation, participants grasped with their thumb on the bottom edge of the bar and all four fingers on the top edge. With a vertical bar orientation, the required grasp was with the thumb on the left edge and fingers placed on the right edge. Finally, the prime stimulus was replaced by a blank screen 500 ms after movement onset (or 2000 ms after prime onset in case of no response), and participants returned their hand to the start position, ready for the next trial.

Prior to running the four main experimental blocks, participants completed 40 practice trials in which they were trained to grasp the bar in the two different orientations without vision of their hand. In the first half of these practice trials, stimuli were presented using the mirror, and participants were asked to reach for the bar using the same hand orientation as that presented via the mirror. In the second half, stimuli were presented on the screen, bar orientations were pre-instructed as in the main experiment, and a large circle was used as go-signal.

Each of the four main blocks, across which location and perspective of the hand stimuli were manipulated, consisted of 44 trials. Each block was divided into two halves to allow the type of fixation to be varied. In the hand fixation trials, the perspective of the fixation picture was always matched to that of the perspective of the prime stimulus that followed it. The order of the blocks was counterbalanced between participants using a Latin square design. Also the order of fixation conditions was counterbalanced between participants. The first two trials of a half block were practice trials to allow participants to adapt to changes of the display, and were discarded from the analysis. The remaining 20 trials consisted of 10 clockwise grasps and 10 anticlockwise grasps in random order, which were made in the presence of either congruently or incongruently oriented prime stimuli. The same number of congruent and incongruent trials was used so that the primes were not informative about the true bar orientation. Responses with RTs shorter than 120 ms were classified as anticipation errors and responses with RTs longer than 1000 ms as omission errors. Trials containing such errors or errors in hand orientation were discarded from the RT analysis.

2.2. Results

2.2.1. Error analysis

Anticipation, omission and movement error rates were acceptably small: 3.3, 0.01, and 1.0%, respectively. No main effect or interaction in the corresponding four-factorial ANOVA reached significance. There was a trend for more frequent errors when stimuli were presented on the screen rather than at the target location, $F(1, 23) = 2.75$, $P > 0.10$. All other effects were non-significant ($P > 0.10$), indicating the absence of a speed-accuracy tradeoff.

2.2.2. RT analysis

The mean RTs were calculated for all conditions and each participant. A five-factorial repeated measures ANOVA was performed on the data. The additional, fifth factor resulted from a median split of the RT data (Vincentization procedure [9,25]). For each participant and factor, separate bins for short and long RTs were formed, and means were calculated for each bin. With an odd number of cases, the median value was placed in both bins and given a half weight relative to that of the other values.

A significant main effect of congruency was found $F(1, 23) = 12.81$, $P = 0.002$, with shorter latencies for congruent primes than for incongruent primes (300 ms versus 307 ms). The only other significant main effect resulted from the binning procedure, $F(1, 23) = 221.71$, $P < 0.001$. Trivially, latencies in the 'early bin' were shorter than in the 'late bin' (264 ms versus 344 ms). The main effect of location failed to reach significance, $F(1, 23) = 2.27$, $P > 0.10$, though there was a trend for shorter latencies with stimuli presented via the mirror (301 ms versus 307 ms).

The interaction between congruency and 'bin' was significant, $F(1, 23) = 10.85$, $P = 0.003$. Contrast analyses indicated that congruency effects were pronounced in the 'late bin', $F(1, 23) = 14.80$, $P < 0.001$, and absent in the 'early bin', $F(1, 23) < 1.00$. None of the other two-way interactions was significant, including that between congruency and location.

A marginally significant three-way interaction between congruency, fixation and perspective was found, $F(1, 23) = 4.74$, $P = 0.040$, as shown in Fig. 3. Contrast analyses revealed that, for hand fixation trials, only prime stimuli in 'Own perspective' produced a significant congruency effect, $F(1, 23) = 6.24$, $P = 0.020$, while stimuli in 'Other perspective' did not, $F(1, 23) < 1.00$. The opposite pattern was observed for dot fixation trials: stimuli in 'Own perspective' produced no effect, $F(1, 23) < 1.00$, but a significant congruency effect was found for stimuli in 'Other perspective', $F(1, 23) = 9.48$, $P = 0.005$. All remaining three-way interactions, including that between congruency, location and perspective, failed to reach significance. More specifically, 'Own perspective' stimuli were not affected by presentation location, $F(1, 23) < 1.00$, thus providing a clearcut, negative answer to our third question. None of the higher-order interactions reached significance.

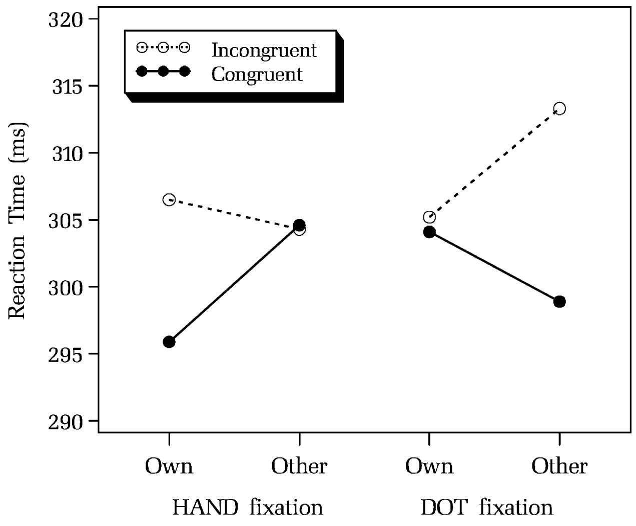

Fig. 3. Results of Experiment 1 for the factors congruency, perspective, and fixation.

2.3. Discussion

Our first research question can be answered positively in that we found a reliable main effect of congruency: pre-planned responses made to pictures matching the orientation of the required grasp were made faster than to pictures showing an incongruent orientation. Thus, our study provides further evidence for the automatic involvement of motor encoding of visual gestures by using a simple response task. More specifically, we demonstrate priming effects for hand orientation in the absence of a choice task. Only one previous study showed such effects, but for finger selection [3].

The median split indicated that congruency effects were more pronounced for long compared to short latencies. A likely explanation for this finding is that, for short latencies, the time for processing the orientation of the hand stimuli exceeded the time required to respond to the go-signal, and thus could not affect responses. In contrast, in the slower responses, the orientation of the hand primes was sufficiently processed for congruency effects to arise. Larger congruency effects for slower responses were also reported by Brass et al. [3]. Nevertheless, even our 'slow' responses (mean = 344 ms) were 100–150 ms faster than those observed in choice [32] or go/no-go tasks [7] with hand gesture stimuli.

Regarding our second research question, both perspectives produced, overall, similarly strong congruency effects. However, the type of fixation precue moderated the impact of perspective on congruency effects. When participants watched a hand precue, we found effects for 'Own perspective', but not for 'Other perspective' primes. Conversely, with dot precues, there were congruency effects for only 'Other perspective' primes (see Fig. 3). The latter effect replicates Craighero et al.'s [7] basic finding, who used a cross as fixation precue. But why does this effect disappear when primes are shown in 'Own perspective'? Given that we only used pictures of another individual's hand and not those of the participant's hand, one might argue that our participants were more familiar with our stimuli when they appeared in 'Other perspective' than in 'Own perspective'.

However, a problem with the latter interpretation is that it would predict the same pattern of results for the dot and hand fixation conditions, which is contradicted by our results. A more tenable, and more specific explanation for the perspective differences in our dot fixation conditions builds on the very short inspection time for the prime stimuli: the stronger congruency effects for 'Other perspective' primes may result from different amounts of experience with suddenly appearing stimuli, rather than from 'hand ownership' per se. That is, it is behaviourally relevant to rapidly encode unexpectedly appearing body parts of conspecifics, which do typically appear in 'Other perspective'. In contrast, body parts in 'Own perspective' rarely appear unexpectedly, and individuals are thus hardly ever confronted with the requirement to encode such stimuli de novo.

So far, our discussion has focused on the results from the dot fixation conditions (right side in Fig. 3), which are well in line with previous studies [3,7]. The finding that this 'Other-perspective advantage' turns into an 'Own-perspective advantage' when the body part is shown in advance (left side of Fig. 3) may appear puzzling at first sight. Since we did not predict this pattern of results, and since the relevant three-way interaction was only marginally significant, we sought to replicate the 'Own perspective advantage' in Experiment 2.

Our third question concerned the potential differential effects of presentation location for the two perspectives. However, the data provide no support for the idea that 'Own perspective' stimuli should exert stronger congruency effects when shown at the effector end location.

Our fourth question addressed the effect of the fixation precue on visuomotor priming. Unexpectedly, congruency effects were equally pronounced in both fixation conditions. Nevertheless, the type of precue significantly moderated perspective effects, as indicated earlier. Before discussing this finding further, we now present the results of the second experiment.

3. Experiment 2

The main objective of Experiment 2 was to replicate the 'Own-perspective advantage' for hand fixation precues. In addition, we wanted to identify the time window over which congruency effects could be observed. Experiment 1 revealed such effects despite the rapid responses typical of simple response tasks. For the automatic modulation of hand orientation, latencies of approximately 300 ms are likely to represent the lower boundary at which congruency effects can be observed (see median split analysis). In Experiment 2, we sought to determine the upper boundary for these effects. Accordingly, we probed congruency effects at different stimulus onset asynchronies (SOAs) between presentation of the prime and the go-signal.

3.1. Method

3.1.1. Participants

Twenty-four students (11 female, 13 male) from Lancaster University volunteered for this study and received £5 payment. Ages ranged between 19 and 48 years (mean age = 25.8 years) and all were right-handed with normal or corrected-to-normal vision. One participant was later excluded from analysis due to a data collection problem, leaving 23 participants (10 female, 13 male; mean age = 25.3 years).

3.1.2. Design

A three-factorial within-subjects design was used, with the factors congruency, perspective of prime stimuli, and SOA between onset of prime and go-signal (0, 200, 400, and 600 ms). Perspective was manipulated across blocks of trials, and congruency and SOA within blocks.

3.1.3. Stimuli and apparatus

The same stimuli as in Experiment 1 were used, with the exception that only the neutral hand pictures were used as fixation stimuli and that no fixation point was superimposed on the hand fixation stimuli. In addition, greyscale versions of the prime stimuli now served as go-signals. The same apparatus was used as in Experiment 1 with the exception that stimuli were always viewed directly on the monitor. Also, participants were now instructed about the required grasp orientation via a pre-recorded voice ("clockwise" or "anticlockwise") from two speakers connected to the PC.

3.1.4. Procedure

Once the participant had placed the index finger on the start button, a blank screen appeared in the beginning of each trial, and after 500 ms the verbal instruction was presented through the speakers (Fig. 4). The screen remained blank for a further 2000 ms to allow the experimenter to position the bar to the corresponding orientation. The blank screen was then replaced with the neutral hand fixation stimulus in either 'Own' or 'Other perspective'. As before, the duration of the fixation interval was randomised (600, 800 or 1000 ms), and was followed by the prime stimulus ('Own' or 'Other perspective' hand in horizontal or vertical orientation). Participants then had to respond to the appearance of a greyscale hand image as go-signal. In the 0 ms SOA condition, the prime stimulus appeared in greyscale immediately, whereas in the remaining SOA conditions, it appeared in colour for 200, 400 or 600 ms and then turned to greyscale. Participants were instructed to respond as quickly as possible to the appearance of the greyscale image and to ignore any

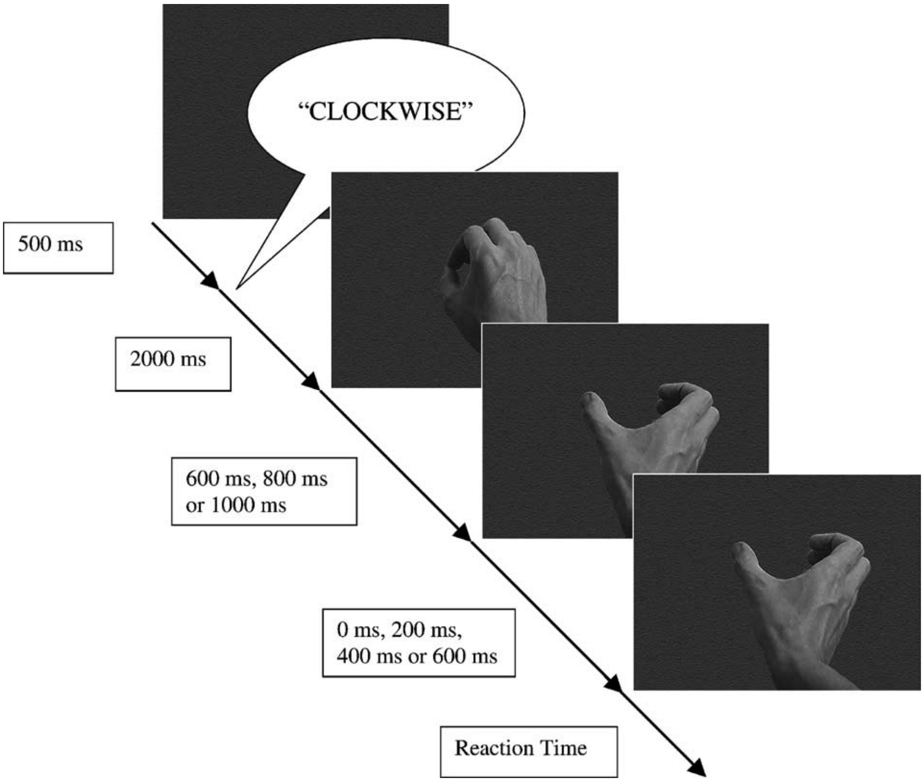

Fig. 4. Sequence of stimuli in Experiment 2, shown for 'Own perspective' trials. The prime stimulus (third frame from top; hand presented in colour) is followed with an SOA of 0, 200, 400 or 600 ms by the go-signal (lower right frame; hand in greyscale).

change in the hand's orientation. Finally, the greyscale hand picture was replaced by a blank screen 500 ms after movement onset, or 2000 ms after appearance of the go-signal if a participant had not responded. RT collection and error monitoring procedures were the same as for Experiment 1.

Prior to the main experimental conditions, practice trials were once again completed. Half of these were made using 'Other perspective' stimuli and the remaining using 'Own perspective' stimuli, so that the practice session ended with the perspective that the particular participant would start the main experiment with. This consisted of two blocks of 80 trials, one for each perspective. These blocks were divided into 10 sub-blocks of eight trials in which each of the four SOAs appeared twice. The order of SOAs was randomised within a sub-block, and the order of perspective was counterbalanced across participants. Prior to starting the second main block, participants were given a further eight practice trials that matched the perspective they were about to encounter.

3.2. Results

3.2.1. Error analysis

Anticipation, omission and movement error rates were 1.3, 0.25, and 2.3%, respectively. Again, no main effect or interaction in the corresponding four-factorial ANOVA reached significance (all $F < 1.2$, $P > 0.32$).

3.2.2. RT analysis

The RT data were subjected to a $2 \times 4 \times 2$ repeated measures ANOVA with the factors congruency, SOA and perspective. Where appropriate (d.f. > 1), probabilities were adjusted as suggested by Greenhouse and Geisser [15]. Since we expected congruency effects only for 'Own perspective' stimuli and only for the shorter SOAs [32], planned comparisons between congruent and incongruent trials were run separately for each perspective and SOA.

A highly significant main effect of congruency was found, $F(1, 22) = 28.13$, $P < 0.001$. Participants responded faster in congruent (416 ms) than in incongruent trials (434 ms). Also SOA had a highly significant effect on response times, $F(3, 66) = 163.28$, $P < 0.001$. Responses were faster as SOA increased (see Fig. 5), which reflects the standard temporal warning effect seen after any cue event at longer intervals [24]. The main effect of perspective did not reach significance, $F(1, 22) = 3.85$, $P = 0.063$, but a trend for faster responses with 'Own perspective' (419 ms) than with 'Other perspective' stimuli (432 ms) was apparent.

Importantly, there was a significant interaction between congruency and perspective, $F(1, 22) = 7.20$, $P = 0.014$. The interaction between congruency and SOA did not approach significance, $F(3, 66) = 2.27$, $P = 0.105$, but a trend for congruency effects to reduce at larger SOAs was present. The three-way interaction was not significant, nor was the interaction between perspective and SOA. The planned comparisons indicated that the interaction between congruency and perspective was largely restricted to SOAs of 0 and 200 ms (see also Fig. 5). For 'Own perspective', the contrasts for SOAs of 0, 200 and 600 ms were significant, $F(1, 22) = 9.98$, $P = 0.005$; $F(1, 22) = 15.92$, $P = 0.001$; $F(1, 22) = 5.36$, $P = 0.03$, respectively. None of the four contrasts for 'Other perspective' was significant. Thus, the congruency effects obtained were relatively short-lived.

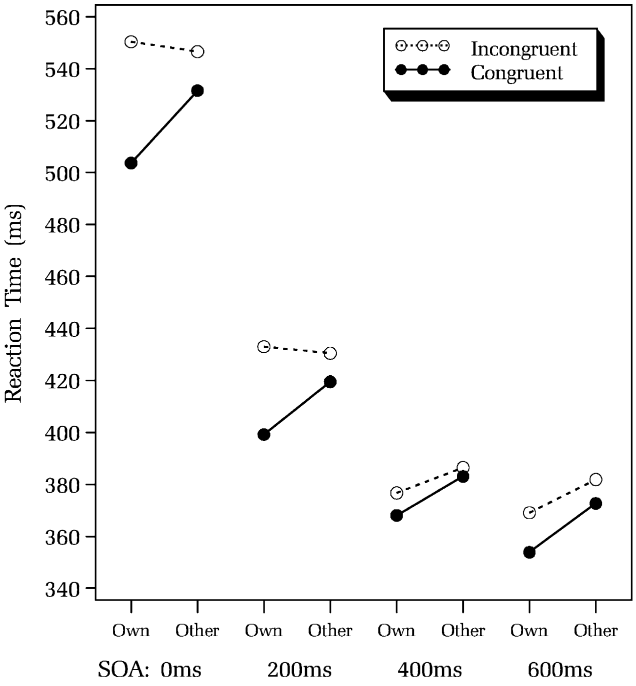

Fig. 5. Results of Experiment 2 for the factors congruency, perspective, and stimulus onset asynchrony (SOA).

We also explored if congruency effects were equally pronounced for horizontal and vertical grasp orientations. This was indeed the case, as indicated by a separate two-way ANOVA with the factors congruency and orientation. Neither the main effect of orientation, $F(1, 22) = 3.14$, $P = 0.09$, nor, more importantly, the interaction, $F(1, 22) = 1.19$, $P = 0.29$, were significant.

3.3. Discussion

RTs were generally longer in the present experiment than in the first, which is, at least partially, due to the task of selectively responding to the colour change as go-signal [22]. When the change in hand orientation occurred simultaneously with the go-signal (0 ms SOA), responses were particularly long. This might indicate that participants tended to generally suppress responses to the more salient, but task-irrelevant orientation change and to react only to the more subtle colour change.

More importantly, congruency effects were only found for 'Own perspective' stimuli. This result nicely replicates the 'Own perspective advantage' found in Experiment 1 when hand fixation stimuli were used (compare Fig. 3, left side, and Fig. 5, SOAs of 0 and 200 ms). In addition, the congruency effects in 'Own perspective' were more robust and numerically larger than in Experiment 1, which is likely due to the longer RTs in Experiment 2, for which larger congruency effects can be expected [3].

Experiment 2 also confirms that the effect of the prime stimuli is short-lived, in that it was most pronounced for SOAs of 0 and 200 ms and disappeared between 616 and 772 ms after prime onset (200 ms SOA plus mean RT of 416, and 400 ms SOA plus mean RT of 372 ms, respectively). Given that the effect begins to manifest approximately 300 ms after prime onset (see median split analysis in Experiment 1), we infer that it spans a time window from roughly 300 to 700 ms after prime onset, with a peak just above 500 ms (47 ms effect size between congruent and incongruent trials for 0 ms SOA). In this respect, our findings for 'Own perspective' are in good agreement with the data by Stürmer et al. [32], Experiment 1, who used open versus closed hand postures in 'Own perspective' as primes and provided preview of a neutral hand posture before prime onset, as we did.

4. General discussion

Three main findings were obtained in the present study: firstly, in both experiments priming effects by hand postures were demonstrated in a simple response task. We interpret this as strong evidence for the automatic encoding of the orientation of observed hand postures, as Brass et al. [3] did for finger selection. In other related studies [4,7,32], choice or go/no-go tasks were used that compromise an interpretation in the sense of automatic encoding.

Secondly, we have tentatively identified the time window of this priming effect to extend from approximately 300 to 700 ms after prime onset, being most pronounced for latencies of approximately 500 ms between go-signal and response (SOA of 0 ms in Experiment 1). One possible reason why our effects were relatively short-lived is that, with increasing likelihood of the go-signal to appear, motor preparation might proceed from an initial focus on the hand's target orientation towards representing the concurrent state of the hand (in its initial, neutral hand orientation [2]). Consequently, the congruency effect would reduce with increasing temporal proximity to movement onset, which is in line with our results (for complementary explanations see [32]).

The third main finding was that the effects of prime perspective were moderated by the type of fixation precue. When preview of a neutral hand stimulus was given, congruency effects only occurred with 'Own perspective' stimuli (Experiments 1 and 2). Conversely, when the prime stimuli appeared without preview (dot fixation conditions in Experiment 1), congruency effects were restricted to 'Other perspective' primes. We have interpreted the latter effect as a specific case of experience-dependent priming, namely in terms of the more frequent exposure to unexpected stimuli in 'Other' than in 'Own perspective'. Although more direct evidence would be desirable, we provisionally classify this effect as a stimulus-driven *visuo-motor* priming effect. In contrast to motor-visual priming, motor planning is not causal for visuo-motor priming.

Our explanation of the 'Own perspective advantage' in the hand preview condition builds on the fact that body parts which appear in 'Own perspective' can typically be predicted from the observer's own motor planning. Based on this anticipatory internal representation, we propose that during motor preparation, actors selectively enhance the visual processing of those (body) parts in the visual array that are plausibly associated with the prepared action. Their relevance for subsequent visuomotor control is high [6]. In contrast, when a body part cannot be associated with a planned action, visuomotor processing of this body part is not enhanced and possibly even suppressed.

In our hand preview conditions, the perspective in which the precue was shown was likely used as a criterion for action relevance: 'Own perspective' stimuli have typically higher action relevance than 'Other perspective' stimuli. Note that this does not generally exclude the usage of body parts in different perspectives, e.g. when seen in a mirror, from visuomotor processing. Rather, when the two perspectives are directly contrasted, as in our experiments, 'Own perspective' wins. Why was this only the case when preview of the hand was available? As described earlier, we assume that the 'Other perspective advantage' found reflects a dominance of experience-dependent visuo-motor priming in the no-preview conditions. This 'default' mechanism is overridden when visual contact with an action-relevant body part is made during the preview interval. In addition, our no-preview conditions might simply not have provided sufficient time for this upwards modulation to take place.

It should be clear from the above that we classify the 'Own-perspective advantage' as a genuine *motor-visual* effect. Without motor planning, a modulation of visual processing according to action-relevance makes little sense. However, we have no certain evidence that the previewed hand needs to validly precue the perspective of the prime. It is thus unknown whether hand preview per se, regardless of perspective, would substantially reduce the 'Own perspective advantage', as we currently assume.

To conclude, contrasting the two perspectives of prime stimuli has led us to propose two distinct mechanisms: (1) a stimulus-driven visuo-motor priming effect that does not depend on motor planning and rapidly encodes body parts that appear unexpectedly; and (2) a planning-driven motor-visual priming effect that selectively enhances the visual processing of body parts in 'Own perspective', and presumably overrides the first, 'default' mechanism. Our interpretation of the 'Other perspective advantage' (1) is thus at variance with Craighero et al.'s [7] preferred interpretation of the same effect in terms of motor-visual priming. Also our interpretation of the ‘Own perspective advantage’ in terms of enhanced visual processing deserves further study. Differentiating self-produced actions from the actions of others has been shown to be one of the functions of neurons in the superior temporal sulcus [5]. Furthermore, cortical activations in inferior parietal, precuneus and somatosensory cortex differ when humans imagine actions in first- or third-person perspective [30]. Our specific proposal is that the action relevance of seen body parts is already processed before motor execution, and that visual processing is modulated accordingly. This agency judgement [18], or, more precisely, ‘ownership judgement’ presumably serves the pragmatic visuomotor processing during action execution.

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