Action intentions modulate visual processing during action perception

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ABSTRACT

The current debate on mechanisms of action understanding and recognition has re-opened the question of how perceptual and motor systems are linked. It has been proposed that the human motor system has a role in action perception; however, there is still no direct evidence that actions can modulate early neural processes associated with perception of meaningful actions. Here we show that plans for action modulate the perceptual processing of observed actions within 200 ms of stimulus onset. We examined event-related potentials to images of hand gestures presented while participants planned either a matching (congruent) or non-matching (incongruent) gesture. The N170/VPP, representing visual processing of hand gestures, was reliably altered when participants concurrently planned congruent versus incongruent actions. In a second experiment, we showed that this congruency effect was specific to action planning and not to more general semantic aspects of action representation. Our findings demonstrate that actions encoded via the motor system have a direct effect on visual processing, and thus imply a bi-directional link between action and perception in the human brain. We suggest that through forward modelling, intended actions can facilitate the encoding of sensory inputs that would be expected as a consequence of the action.

1. Introduction

Motor theories of perception state that the motor system is intrinsically involved in action recognition. According to these theories, we recognize actions performed by others by matching the perceived action into our own motor system and simulating the motor plan needed to produce the same action (Rizzolatti, Fogassi, & Gallese, 2001; Rizzolatti & Sinigaglia, 2010). Empirical evidence for this concept comes from the observation of increased activity within the motor system during perceptual tasks in which hand actions are presented, as shown both in macaques (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) and in humans (Decety & Grezes, 1999; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Grezes & Decety, 2001). A critical prediction of motor theories of perception is that motor plans have the potential to modulate the perceptual processing of observed actions. If the motor system has a functional role in action recognition, changes in the motor system should modulate the process of action perception.

Such effects of the motor system on perception have been well studied in behavioural tasks examining perceptual judgments (see Schutz-Bosbach & Prinz, 2007 for an overview). Typically in such tasks, actions planned or executed by participants facilitate the perceptual judgments of visual stimuli that are compati-

ble or congruent with the goals of the action (Blaesi & Wilson, 2010; Lindemann & Bekkering, 2009). According to feed-forward or common-coding models of action–perception, it is suggested that a representation of the outcome of the action formed during action planning can influence the perceptual processes associated with sensory feedback of the action (Hommel, Musseler, Aschersleben, & Prinz, 2001).

However, such behavioural measures alone cannot reveal how these action–perception linkages are mediated in the brain. Therefore an open question is what stages of visual or perceptual processing are modulated by activity in the motor system, leading to changes in conscious perceptual judgements. For example, a common representation of action goals or intentions, from observed actions and planned or executed actions (Rizzolatti & Sinigaglia, 2010), may lead to changes in perceptual judgments arising from late-stage higher-order processes associated with extracting meaning and intention from the visual stimulus. Alternately, it is possible that motor representations of planned actions may be transformed to sensory representations or predictions of the outcomes of the action, and may therefore exert top-down control to directly influence the earliest stages of visual processing (Stanley & Miall, 2007).

Event-related potentials (ERPs) can provide a direct measure of neural activity associated with different stages of visual perceptual processing. Two recent ERPs studies have shown that early stages of visual processing are modulated by the congruency of concurrently performed actions during the observation of meaningless actions

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(Press, Gherri, Heyes, & Eimer, 2010) and objects (van Elk, van Schie, Neggers, & Bekkering, 2010). Meaningful and meaningless actions, however, are thought to involve different processing routes to motoric representations, with meaningless actions involving a direct route via visuo-motor transformation, and meaningful actions via both the direct route and an indirect, semantic route (Press & Heyes, 2008; Rumiati & Tessari, 2002). Viewing meaningful hand gestures results in the activation of brain areas associated with semantic processing (Ozyürek, Willems, Kita, & Hagoort, 2007; Willems, Ozyürek, & Hagoort, 2007), while Lingnau, Gesierich, and Caramazza (2009) even argue that activation of the motor system when observing actions follows only as a consequence of action understanding via semantic representation. Therefore, it is not clear whether the effect of action execution on the visual processing of meaningful actions could be mediated by the semantic representation of the action or by its motoric representation associated with action planning.

Here, we specifically use ERPs to test whether motor plans can influence the early stages of perceptual processing of observed meaningful hand gestures, within the first 200 ms following stimulus presentation. Moreover, we extend on previous studies by using a novel paradigm in which we separated motor planning and execution stages of action, so that we could measure visual evoked potentials to observed actions purely during motor planning and without any overlapping of motor components relating to the initiation and execution of actions. Using this paradigm, we specifically examined the direct effect of motor representations for intended actions on early stages of visual processing of observed actions.

In this study, we measured the early components of visual ERPs, namely P1, N170 and Vertex Positive Potential (VPP), while participants viewed static images of hand gestures that matched (congruent condition) or did not match (incongruent condition) planned gestures. Participants prepared familiar hand gestures indicated by an initial word cue in a Go/NoGo paradigm (Fig. 1A). During the motor planning interval we presented a visual image of a hand gesture that was either congruent or incongruent with the concurrently planned action. This hand gesture image was irrelevant to the participant's task, but was the crucial stimulus to which we measured event-related potentials (ERPs). We therefore examined neural activity associated with the visual processing of actions that were either congruent or incongruent with concurrently planned actions. If the motor system and plans for action play a role in the perception of observed actions, then the congruency of the planned actions should modulate the perceptual processing of visually presented actions.

2. Experiment 1

2.1. Materials and methods

2.1.1. Participants

Twenty healthy, young volunteers participated in Experiment 1 (age range 18–30 years, 11 females). All participants were right-handed and had normal or corrected-to-normal visual acuity. Volunteers gave informed consent prior to entering the study, and the study was approved by the Medical Research Ethics Committee of The University of Queensland. One participant was excluded from analyses due to excessive EEG artefacts requiring rejection of more than 30% of trials.

2.1.2. Procedure

Participants were comfortably seated in a dimly lit, sound-attenuated room, and faced a 22-inch LCD screen placed 70 cm in front of them. All participants first completed a brief training session to allow them to learn and practice the hand gestures

required in the experimental task. In the training session, one of four target words representing the four required gestures ('OK', 'Peace', 'Thumbs-up', and 'Point') was displayed, followed by the corresponding hand gesture image. Participants silently read the word and, upon receiving the "go" signal, imitated the hand gesture exactly as depicted in the images. Each stimulus was repeated six times.

For the experimental task, during EEG measurement, participants performed a delayed Go/NoGo task, referred to as the Gesture task (Fig. 1A). For each trial, one of the four word cues was initially presented (500 ms duration), indicating which of the four hand gestures the participant should perform. Following a delay period (1500 ms duration), a Go or NoGo cue was presented, consisting of a solid green or red circle, respectively. Participants were required to release a resting-position button and perform the indicated gesture as quickly as possible in response to the Go cue (75% of trials), and to withhold any response to the NoGo cue (25% of trials). During the action preparation interval, 500 ms prior to the Go/NoGo cue, a static visual image of one of the four hand gestures was presented. This gesture image was either congruent (50% of trials) or incongruent (50% of trials) with the hand gesture participants were preparing to perform. These gesture images were irrelevant to the participant's task but were the crucial stimulus to which event-related potentials (ERPs) were examined. In addition, catch trials were included (25% of all trials) in which the Go cue was presented in place of the hand gesture image to ensure that participants maintained attention to the stimuli at the time of presentation of the gesture image. Gestures were performed with the left and the right hand in separate blocks and consistently with the observed actions, i.e., when gestures were performed with the left hand, gesture images depicted a left hand and when gestures were performed with the right hand, gesture images depicted a right hand. Thirteen blocks of 24 trials were performed alternately for each hand, with order counterbalanced between participants. The first block with each hand was excluded as practice, leaving a total of 288 trials for each hand: 108 congruent trials, 108 incongruent trials, and 72 catch trials in which no gesture image was presented.

2.1.3. Recording and analyses

Electroencephalographic (EEG) activity was recorded continuously from 64 electrodes in a standard, extended 10-20 cap using a BioSemi Active Two EEG system. Eye movements were detected by recording horizontal and vertical electro-oculogram. The EEG signal was digitised at a sampling rate of 512 Hz, re-referenced offline to an average reference, band-pass filtered at 0.1–50 Hz, and blink-artefact corrected (Berg & Scherg, 1994; Ille, Berg, & Scherg, 2002). Epochs were obtained from 100 ms before gesture image presentation to 500 ms after stimulus onset, with the first 100 ms used as baseline. Epochs were rejected from further analyses if the EEG signal exceeded ±100 μV or if they contained eye-movement or other kinds of artefacts, as identified by visual inspection. Average event-related potentials (ERPs) were calculated separately for congruent and incongruent trials, and for the left and right hands.

Peak amplitudes of three ERP components were measured within specific time windows: P1 was measured between 90 and 150 ms over PO3, PO4, PO7, PO8, O1, O2; N170 was measured between 140 and 200 ms over P7, P8, P9, P10, PO7, PO8; VPP was measured in the same time window as N170, over frontocentral electrodes, FCz, F1, Fz, F2, FC1, FCz, FC2, Cz. These electrode selections were based on previous studies investigating visual processing of hands and faces (Kovacs et al., 2006; Letourneau & Mitchell, 2008; Rossion & Jacques, 2008).

2.1.4. Statistical analyses

Amplitudes of both the P1 and N170 components were analysed by 4-way repeated-measures ANOVA, with factors of Hand
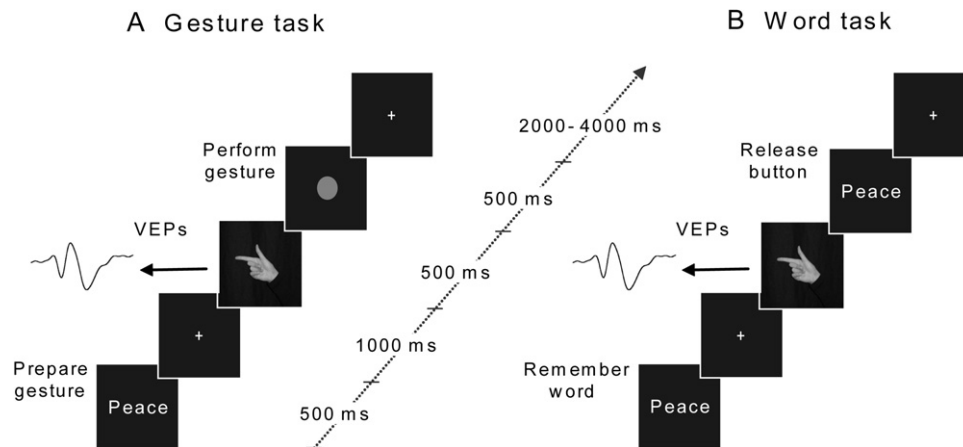
A Gesture task

B Word task

Fig. 1. Time course of a typical trial of the Gesture task (A) and the Word task (B). Experiment 1 involved only the Gesture task, performed with the right or left hand in separate blocks. Experiment 2 involved both the Gesture task and the Word task, performed with the right hand only. For all trials, an initial word cue indicated one of four possible hand gestures ('OK', 'Peace', 'Thumbs-Up', 'Point'). In the Gesture task, participants prepared and performed the cued gesture as quickly as possible in response to a Go cue (green circle; 75% of trials) and withheld responses to NoGo cues (red circle; 25% of trials). In the Word task, participants remembered the cued action and released a resting-position button in response to a matching action word (Go cue; 75% of trials) and withheld responses to non-matching words (NoGo cues; 25% of trials). During the delay interval, 500 ms prior to the Go cue, a visual image of a hand gesture that was either congruent or incongruent with the cued action was presented. Visual evoked potentials in response to these congruent and incongruent hand gesture images were measured and compared.

(left hand, right hand), Congruency of gesture images (congruent, incongruent), Hemisphere of electrodes (ipsilateral, contralateral to performing hand), and Electrode site (electrodes PO3/4, PO7/8, O1/2 for the P1; electrodes P7/8, P9/10, PO7/8 for the N170). Since the VPP was recorded centrally over midline electrodes, and not separately over left and right lateral sites, the amplitudes for this component were analysed using a 3-way repeated-measures ANOVA, with factors of Hand (left hand, right hand), Congruency of gesture images (congruent, incongruent), and Electrode site (FCz, F1, Fz, F2, FC1, FCz, FC2, Cz). Greenhouse–Geisser correction was applied when appropriate, and significant main effects and interactions involving congruency were followed up with planned t-tests to compare ERPs to congruent and incongruent hand-gesture images. Partial eta squared (η^2) was calculated as index of effect size.

We considered the possibility that viewing action images during motor preparation could influence neural activity associated with motor preparation, i.e., a visual-to-motor effect. We therefore tested whether any congruency effects on fronto-central electrodes, which might reflect activity associated with motor preparation, were specific to the time interval of the N170/VPP, or whether they extended over the entire preparatory interval leading up to movement execution. We ran an additional analysis in which the signal across eight fronto-central electrodes (FCz, F1, Fz, F2, FC1, FCz, FC2, Cz) was averaged in eight, 50 ms time windows over the period from 100 post-stimulus (the time of the early P1 component) to 500 ms post-stimulus (the time of the Go cue to initiate movement). The average signal in each time window was analysed using 3-way repeated-measures ANOVA, with factors of Hand (left hand, right hand), Congruency of gesture image (congruent, incongruent), and Time window (from 100 ms to 500 ms after stimulus presentation). Post hoc comparisons (Newman–Keuls correction) were conducted to further examine differences in ERPs to congruent and incongruent images within each time interval.

2.2. Results and discussion

Event-related potentials to the images of hand gestures showed the typical sequence of P1 and N170/VPP components (Kovacs et al., 2006; Mouchetant-Rostaing, Giard, Bentin, Aguera, & Pernier, 2000) (Fig. 2A). Analysis of the amplitudes of these ERP peaks showed no significant effects of action congruency on the early P1 component,

approximately 100 ms after stimulus presentation ($p > .05$), but significant effects of action congruency in both the N170 and Vertex Positive Potential (VPP) components, approximately 170 ms after stimulus presentation.

The N170 measured over left and right lateral parieto-occipital regions was influenced by both the congruency and the laterality of the planned action [Congruency × Hemisphere interaction, $F(1, 18) = 5.40$, $p < .05$, partial $\eta^2 = .23$]. As can be seen in Fig. 2B, N170 amplitude was significantly larger over the hemisphere contralateral to movement, for both left and right hand actions, and was significantly larger for incongruent hand actions (i.e., where intended and observed actions did not match) than for congruent actions (in which intended and observed actions matched) over the contralateral hemisphere ($p < .05$). The N170 is suggested to reflect high-level visual processing of faces, hands and body parts, corresponding to the structural encoding of the stimulus (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000; Kovacs et al., 2006). Our results suggest that this high-level visual processing of hand actions integrates information concerning intended actions from the motor system. In other words, motor representations of action in the contralateral hemisphere influence neural responses of occipito-temporal areas (Peelen & Downing, 2007) associated with perception of hands and body parts. This sensory-motor integration, which was strongly lateralised to the contralateral hemisphere, is unlikely to be due to the hand (left versus right) depicted in the gesture-image, as previous studies have shown left hemisphere predominance for the visual processing of hand actions regardless of the hand presented (McCarthy, Puce, Belger, & Allison, 1999; Wheaton, Pipingas, Silberstein, & Puce, 2001). Instead, the difference in the N170 over the contralateral hemisphere suggests an enhanced responsiveness of posterior associative areas in the hemisphere involved in preparing the action.

The VPP measured over the fronto-central midline region also showed a significant congruency effect [$F(1, 18) = 8.49$, $p < .01$, partial $\eta^2 = .32$]. VPP amplitude was significantly larger in response to gesture-images that were incongruent with the planned action than for those triggered by congruent images (Fig. 2C). The origin of the VPP is still unknown, and it is a matter of debate whether the VPP represents activity of the same neural source as the N170 or a parallel but independent neural process (Bentin et al., 1996; Joyce & Rossion, 2005; Tang, Liu, Li, Qiu, & Zhu, 2008). The topography of the congruency effect evident in the VPP (Fig. 2D) suggests that
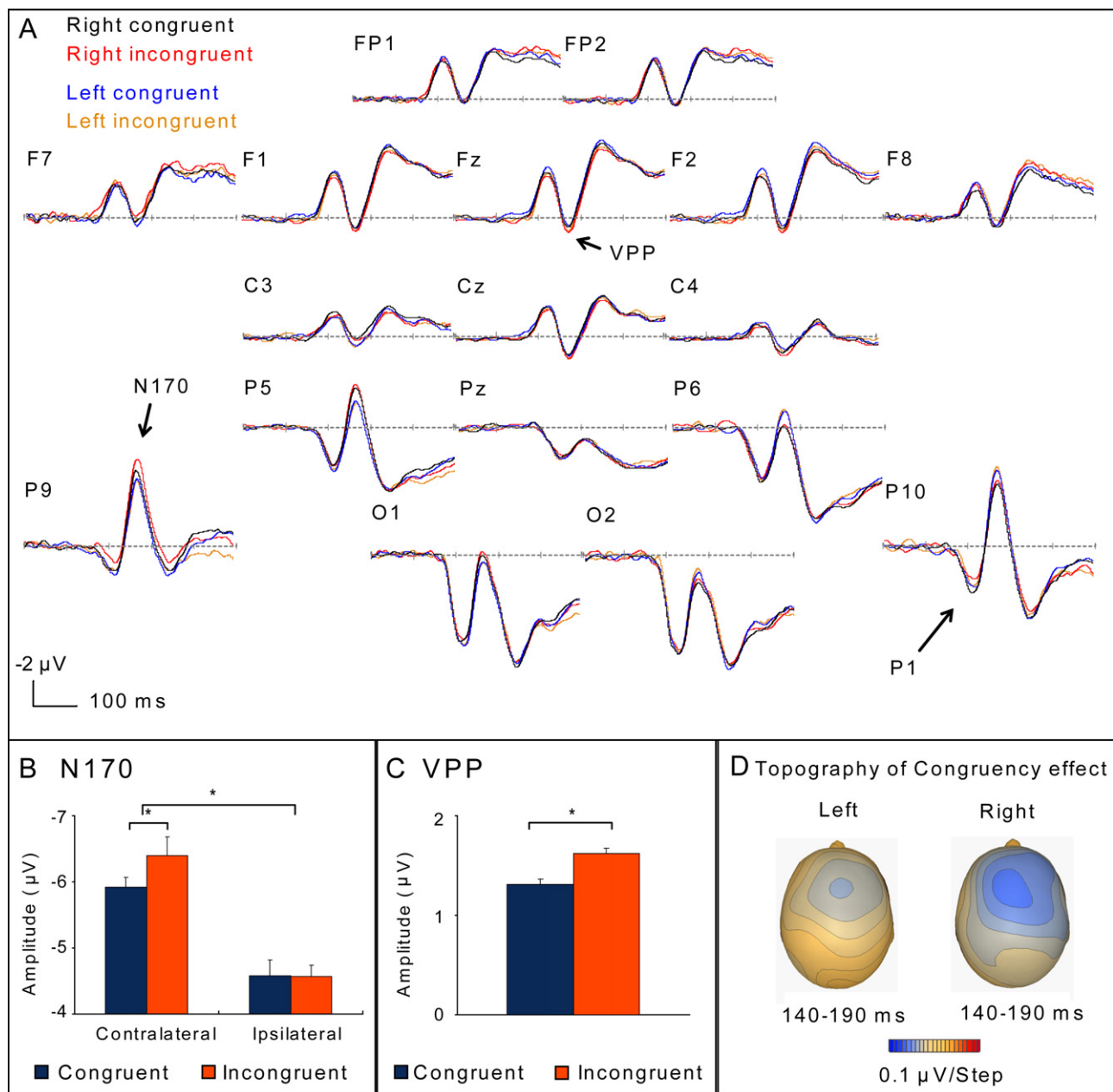
Fig. 2. Visual evoked potentials for the Gesture task in Experiment 1. (A) Grand-average visual evoked potentials over 17 scalp electrode sites, shown for both congruent and incongruent gesture images with actions performed with the left or right hand. (B) Mean and standard error of N170 amplitudes elicited by gesture images that were congruent or incongruent with planned actions, measured over lateral parieto-occipital areas ipsilateral and contralateral to movement. (C) Mean and standard error of VPP amplitudes for congruent and incongruent hand gesture images, measured over the fronto-central region. (D) Topography of the difference between incongruent and congruent gesture images at the time of the N170/VPP complex, from 140 ms to 190 ms following presentation of the hand gesture image.

it might represent changes in activity in premotor areas. Indeed, premotor cortex has been suggested to contribute to perception of action over this same time interval, from 150 ms following stimulus presentation (Cattaneo et al., 2010; Urgesi, Candidi, Ionta, & Aglioti, 2007).

The additional analyses conducted over the entire preparatory interval leading up to movement execution (from 100 to 500 ms post-stimulus), showed that the congruency effect recorded on the fronto-central electrodes was restricted to the VPP time interval. Significant differences in ERP amplitudes to incongruent compared with congruent stimuli were found only in early time intervals, from 100 to 150 ms ($p < .05$) and from 150 to 250 ms ($p < .01$) [Congruency × Time interaction, $F(7, 126) = 5.18$, $\varepsilon = .58$, $p < .05$, partial $\eta^2 = .22$], implying that the congruency effect was driven by early

visual responses to the images of hand gestures. This result rules out the possibility that the fronto-central congruency effect was related to a modulation of activity related to action preparation (i.e., a visual-to-motor effect), as in that case the congruency effect would have lasted throughout the preparation period up to the execution of the movement.

3. Experiment 2

Taken together, the results of our first experiment suggest that motor representations that arise from action planning can influence the visual processing of observed meaningful actions within 200 ms after stimulus onset. A potential alternative interpretation, however, is that the effect of congruency on visual processing of gesture

images might arise from a more abstract or semantic-level representation of the gestures evoked by the action-word, rather than from motoric representations associated specifically with action plans. In other words, the meaning of the word indicating the gesture could activate a visual representation of that gesture, therefore modulating the visual processing of the subsequently presented congruent/incongruent gesture image. In this case, the effect of congruency observed on the N170/VPP would not necessarily rely on the activation of the motor system. We therefore conducted a second experiment in which we repeated the Gesture Task for the right hand, exactly as in Experiment 1, but included an additional Word Task as a semantic control condition (Fig. 1B). The Word Task involved identical cue- and gesture-image stimuli, but required participants to remember and maintain the cued gesture in working memory rather than to prepare the gesture for execution. Moreover, in this experiment we controlled for possible effects driven by a disparity in the frequency of presentation between congruent and incongruent gestures. Indeed, because for each action word there were one congruent and three possible incongruent images, congruent gestures may have been more predictable than incongruent gestures. In Experiment 2, we paired each action with one of the other actions (with different pairings for each participant) and within blocks showed only congruent images with their paired incongruent image. All possible different pairings of action images were used and counterbalanced between participants.

3.1. Materials and methods

3.1.1. Participants

Experiment 2 involved 24 healthy young participants (age range 18–27 years, 14 females), two of whom had previously participated in Experiment 1. All participants were right-handed and had normal or corrected-to-normal visual acuity. Volunteers gave informed consent prior to entering the study, and the study was approved by the Medical Research Ethics Committee of The University of Queensland. One participant was excluded from analyses due to excessive EEG artefacts requiring rejection of more than 30% of trials.

3.1.2. Procedure

Participants were seated comfortably in front of a 20-inch CRT monitor, at a distance of 80 cm, in a dimly lit room for EEG measurement. After a brief training session, as in Experiment 1, participants performed both the Gesture Task of Experiment 1 and the additional Word Task control condition (Fig. 1B). These tasks were completed in two separate runs of 13 blocks each, with the order counterbalanced between participants. The Gesture Task was repeated exactly as in Experiment 1, but with the right hand only. In the Word Task, the Go and NoGo cues were replaced with matching and non-matching word cues respectively. All other stimuli were identical to those used in the Gesture Task, as was the timing of successive displays within each trial. Matching word cues (Go trials) were the same gesture names as presented in the initial word cue, whereas non-matching word cues (NoGo trials) were the names of one of the other gestures. Participants were required to release the resting-position button as quickly as possible for matching words (75% of trials) and to withhold responses for non-matching words (25% of trials). In this way, the Word Task involved encoding the cued action-word in memory rather than preparing the action for execution. As in Experiment 1, each task included a total of 288 trials: 108 congruent trials, 108 incongruent trials, and 72 catch trials in which no gesture image was presented.

3.1.3. ERPs and statistical analyses

EEG recording and preprocessing of event-related potentials (ERPs) were performed as in Experiment 1. Statistical analyses on

the N170 and VPP were also conducted as in Experiment 1, except that experimental Task was included as a factor in place of the Hand. The order in which the two tasks were performed was also included in the ANOVA as a between-subjects factor. The N170 was therefore analysed using a 5-way, mixed design ANOVA that included within-subject factors of Task (Gesture Task, Word Task), Congruency of gesture images (Congruent, Incongruent), Hemisphere of electrodes (Ipsilateral, Contralateral to performing hand), and Electrode site (electrodes P7/8, P9/10, PO7/8 for the N170), and a between-subjects factor of Order (Gesture task first, Word task first). VPP was analysed using a 4-way, mixed design ANOVA, with all of the same factors except for Hemisphere. Greenhouse–Geisser correction was applied where appropriate, and significant main effects and interactions involving Congruency were followed up with planned t-tests to compare ERPs to congruent and incongruent hand-gesture images. Partial eta squared (η^2) was calculated as index of effect size. Reaction times to the go stimulus were recorded and analysed in a 3-way mixed design ANOVA that included within-subject factors of Task (Gesture Task, Word Task), Congruency of gesture images (Congruent, Incongruent), and a between-subjects factor of Order (Gesture task first, Word task first).

3.2. Results

As in Experiment 1, both the N170 and VPP elicited by the gesture images were influenced by the congruency of concurrently planned actions. Crucially, however, there was no congruency effect for ERPs in the Word Task control condition (Fig. 3). For the N170, the congruency effect also interacted with task order [three-way interaction Task × Congruency × Order, $F(1, 21) = 7.66$, $p < .05$, partial $\eta^2 = .27$], such that only the participants who completed the Gesture Task first showed a significant difference between congruent and incongruent stimuli [planned comparisons: $p < .05$]; for the Word Task, there was no significant effect of congruency, regardless of the order of conditions. Also, as in Experiment 1, N170 amplitudes were larger over the hemisphere contralateral to the planned hand movement, and this lateralization was more pronounced for the Gesture Task than for the Word Task [Task × Hemisphere × Order interaction, $F(1, 21) = 8.07$, $p < .05$, partial $\eta^2 = .28$]. For the VPP, again those participants who completed the Gesture Task first showed larger amplitudes for incongruent compared with congruent stimuli [Task × Congruency, $F(1, 11) = 5.31$, $p < .05$, partial $\eta^2 = .33$; planned comparison: $p = .053$]. In the Word Task, there were no significant effects of stimulus congruency on VPP amplitudes, independent of the task order.

At behavioural level, the congruency between the perceived action and the planned action facilitated the initiation of the response and this effect was evident both in the Gesture task and in the Word task. Indeed, reaction times in response to the go stimulus were faster when the action image matched the planned action than when it was incongruent [Congruency effect, $F(1, 21) = 20.93$, $p < .001$]. Therefore, consistent with previous studies, motor representations of actions (Craighero, Bello, Fadiga, & Rizzolatti, 2002; Miall et al., 2006) and semantic representations of actions (McPherson & Holcomb, 1999) both induce priming effects to facilitate the initiate of the subsequent action. Crucially only motor representations of the action affected visual cortical activity during the processing of observed actions. The lack of any congruency effect for the Word task on the P1 and N170/VPP components is not inconsistent with previous findings of semantic priming effects. Indeed, electrophysiological studies have shown that neural correlates of semantic priming are only seen more than 200 ms following stimulus presentation and therefore may have occurred at later stages of processing that we have not investigated (Chauncey & Holcomb, 2009).
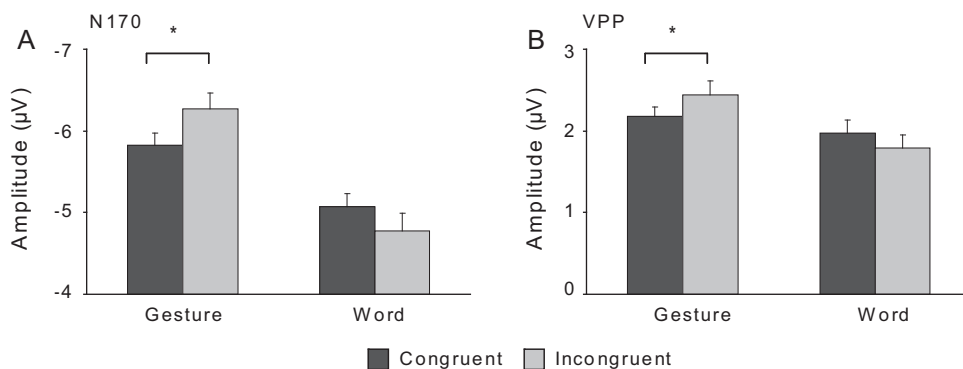
Fig. 3. Visual evoked potential results for Gesture and Word tasks in Experiment 2, shown only for those participants who completed the Gesture task first. (A) Mean and standard error of N170 amplitudes elicited by gesture images that were congruent or incongruent with the cued action for both the Gesture and Word tasks. (B) Mean and standard error of VPP amplitudes for congruent and incongruent hand gesture images for both Gesture and Word tasks.

To summarise, we replicated the congruency effect of Experiment 1 in those participants who completed the Gesture Task first. Crucially, there was no effect of stimulus congruency on ERPs in the Word Task, regardless of task order. This result suggests that the effect of congruency on observed actions can be attributed to action planning processes rather than to an abstract or semantic-level representation of the actions.

The absence of any congruency effect on the ERPs for the Gesture Task when preceded by the Word Task was unexpected, but not inconsistent with our conclusion. One possible explanation is that when the Word Task was completed first the strategy adopted by participants for remembering the gesture names carried over into the subsequent Gesture Task. When the Gesture Task was completed first, however (as it was for all participants in Experiment 1), the congruency effects of Experiment 1 were replicated.

4. General discussion

Overall, our results show that the early stages of visual processing of observed meaningful actions, within 200 ms of stimulus onset, are influenced by the motor representations of intended actions, during concurrent action planning. Crucially, this effect appears to be specifically related to activity within the motor system itself, rather than to a more abstract or semantic-level representation of action. Thus, our study provides evidence that action preparation via the motor system has a direct effect on visual processing of meaningful actions. Taken together with previous studies, our data suggest that action and perception are linked bi-directionally, so that, as others have shown, visual perception can directly influence the execution of actions (Brass, Bekkering, Wohlschlager, & Prinz, 2000; Kilner, Paulignan, & Blakemore, 2003), but also crucially that motor plans can influence the visual processing of observed actions (Press et al., 2010).

This motor-to-visual modulation suggests that the motor system has a functional role in perception of meaningful actions, even when the perceived actions are irrelevant to the task. Indeed, evidence for the influence of motor representations on visual perception emerged during the first 200 ms of visual encoding, at a stage during which the visual system differentiates between different types of action (Wheaton et al., 2001). Specifically, we found that visual ERPs were enhanced for images of actions that did not match the concurrent motor plan, and that visual ERPs generated in associative areas were enhanced in the hemisphere contralateral to the intended movement.

It is interesting to note that visual ERPs were increased for incongruent actions compared with congruent actions. This effect, although surprising, is in line with the results reported by Press

et al. (2010) for intransitive actions. The direction of this effect is not consistent with the involvement of attentional effects on visual processing. It is well known that attention modulates neural activity associated with visual processing and, consequently, affects the amplitude of visual event-related potentials (Clark & Hillyard, 1996; Mangun & Hillyard, 1991). Previous studies have shown that both manual and saccadic response preparation are associated with shifts in attention toward response-relevant locations (Gherri, Driver, & Eimer, 2008; Gherri & Eimer, 2008). Moreover, preparing a specific action may implicitly trigger non-spatial attention for stimulus features, such as orientation, shape or color. Several studies have shown that both spatial attention (Eimer & van Velzen, 2006; Eimer, Van Velzen, Gherri, & Press, 2006) and non-spatial attention (Karayanidis & Michie, 1997; Proverbio, Esposito, & Zani, 2002) result in enhanced N1 amplitudes. Accordingly, one would expect that preparing a specific hand gesture automatically facilitates the processing of action-congruent visual features. However this explanation does not match with our results, in which an increased amplitude of N170 and VPP was found for incongruent stimuli compared with congruent stimuli.

Another possible explanation is that the increased neural activity for incongruent gestures may represent the detection of a mismatch between the anticipated outcome of the planned action and sensory input from the observed action. The anticipation of upcoming sensory outcomes of action has been suggested by forward models (Hommel et al., 2001), according to which motor representations of intended actions are fed forward to influence sensory processing associated with action outcomes. This representation may be considered a form of sensory anticipation of the action, that is created during action preparation. Accordingly, in our experiment the effect of the motor system on visual processing of actions was not limited only to the execution of movements as in the study by Press et al. (2010), but was caused by motor representations of intended actions during motor preparation. In this way, the motor system may shape the perceptual processing of observed actions through a process of matching with the predicted sensory consequences of the action. This mechanism could explain how perception of an action that is congruent with the motor plan is facilitated, as shown in previous studies (Craighero et al., 2002; Miall et al., 2006) and in our reaction times results. The detection of a visuo-motor mismatch during movement planning and control may be important in allocating cognitive resources to the action in order to adjust the motor output according to the changing visual information.

There are several neural mechanisms that may mediate this influence of the motor system on visual processing of observed actions. Mirror neurons, which fire during both the execution and observation of actions (Gallese et al., 1996), could mediate this

sensory-motor integration when actions are observed. Through mirror neuron activation, when a motor act is observed, the action may be automatically processed and represented in the motor system. Therefore, mirror neurons may allow not only a direct matching of observed actions to the motor system, as suggested by Rizzolatti et al. (2001), but also a reverse link from intended actions encoded in the motor system to sensory representations of the action. Behavioural studies have shown that planned or executed actions can also facilitate perception of graspable objects (Craighero, Fadiga, Rizzolatti, & Umilta, 1999) or abstract shapes (Wohlschlager, 2000). Canonical neurons that fire both during the grasping of objects and the observation of graspable objects (Rizzolatti, Fogassi, & Gallese, 2000) may therefore mediate similar sensory-motor integration when objects are observed. Importantly, the interactions between planned actions and abstract shapes are not always facilitatory. Musseler and Hommel (1997) suggested that the generation of predicted sensory feedback during action planning may interfere with the perception of congruent stimuli (Musseler & Hommel, 1997). Whatever the mechanism, here we have shown that motor representations during action planning have a direct influence on the visual processing of observed actions.

Acknowledgments

References

Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, *6*(8), 551–565.

Berg, P., & Scherg, M. (1994). A multiple source approach to the correction of eye artifacts. *Electroencephalography and Clinical Neurophysiology*, *90*(3), 229–241.

Blaesi, S., & Wilson, M. (2010). The mirror reflects both ways: action influences perception of others. *Brain and Cognition*, *72*(2), 306–309.

Brass, M., Bekkering, H., Wohlschlager, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: Comparing symbolic, spatial, and imitative cues. *Brain and Cognition*, *44*(2), 124–143.

Cattaneo, L., Barchiesi, G., Tabarelli, D., Arfeller, C., Sato, M., & Glenberg, A. M. (2010). One's motor performance predictably modulates the understanding of others' actions through adaptation of premotor visuo-motor neurons. *Social Cognitive Affective Neuroscience*, doi:10.1093/scan/nsq099

Chauncey, K., & Holcomb, P. (2009). Primed picture naming within and across languages: An ERP investigation. *Cognitive Affective and Behavioral Neuroscience*, *9*(3), 286–303.

Clark, V. P., & Hillyard, S. A. (1996). Spatial selective attention early extrastriate but not striate components of the visual evoked-potential. *Journal of Cognitive Neuroscience*, *5*(8), 387–402.

Craighero, L., Bello, A., Fadiga, L., & Rizzolatti, G. (2002). Hand action preparation influences the responses to hand pictures. *Neuropsychologia*, *40*(5), 492–502.

Craighero, L., Fadiga, L., Rizzolatti, G., & Umilta, C. (1999). Action for perception: A motor-visual attentional effect. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(6), 1673–1692.

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

Eimer, M. (2000). Effects of face inversion on the structural encoding and recognition of faces. Evidence from event-related brain potentials. *Brain Research. Cognitive Brain Research*, *10*(1–2), 145–158.

Eimer, M., & van Velzen, J. (2006). Covert manual response preparation triggers attentional modulations of visual but not auditory processing. *Clinical Neurophysiology*, *117*(5), 1063–1074.

Eimer, M., Van Velzen, J., Gherri, E., & Press, C. (2006). Manual response preparation and saccade programming are linked to attention shifts: ERP evidence for covert attentional orienting and spatially specific modulations of visual processing. *Brain Research*, *1105*(1), 7–19.

Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, *73*(6), 2608–2611.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*(Pt 2), 593–609.

Gherri, E., Driver, J., & Eimer, M. (2008). Eye movement preparation causes spatially-specific modulation of auditory processing: New evidence from event-related brain potentials. *Brain Research*, *1224*, 88–101.

Gherri, E., & Eimer, M. (2008). Links between eye movement preparation and the attentional processing of tactile events: An event-related brain potential study. *Clinical Neurophysiology*, *119*(11), 2587–2597.

Grezes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Human Brain Mapping*, *12*(1), 1–19.

Hommel, B., Musseler, J., Aschersleben, G., & Prinz, W. (2001). The Theory of Event Coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences*, *24*(5), 849–937.

Ille, N., Berg, P., & Scherg, M. (2002). Artifact correction of the ongoing EEG using spatial filters based on artifact and brain signal topographies. *Journal of Clinical Neurophysiology*, *19*(2), 113–124.

Joyce, C., & Rossion, B. (2005). The face-sensitive N170 and VPP components manifest the same brain processes: The effect of reference electrode site. *Clinical Neurophysiology*, *116*(11), 2613–2631.

Karayanidis, F., & Michie, P. T. (1997). Evidence of visual processing negativity with attention to orientation and color in central space. *Electroencephalography and Clinical Neurophysiology*, *103*(2), 282–297.

Kilner, J. M., Paulignan, Y., & Blakemore, S. J. (2003). An interference effect of observed biological movement on action. *Current Biology*, *13*(6), 522–525.

Kovacs, G., Zimmer, M., Banko, E., Harza, I., Antal, A., & Vidnyanszky, Z. (2006). Electrophysiological correlates of visual adaptation to faces and body parts in humans. *Cerebral Cortex*, *16*(5), 742–753.

Letourneau, S. M., & Mitchell, T. V. (2008). Behavioral and ERP measures of holistic face processing in a composite task. *Brain and Cognition*, *67*(2), 234–245.

Lindemann, O., & Bekkering, H. (2009). Object manipulation and motion perception: Evidence of an influence of action planning on visual processing. *Journal of Experimental Psychology: Human Perception and Performance*, *35*(4), 1062–1071.

Lingnau, A., Gesierich, B., & Caramazza, A. (2009). Asymmetric fMRI adaptation reveals no evidence for mirror neurons in humans. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(24), 9925–9930.

Mangun, G. R., & Hillyard, S. A. (1991). Modulations of sensory-evoked brain potentials indicate changes in perceptual processing during visual–spatial priming. *Journal of Experimental Psychology: Human Perception and Performance*, *17*(4), 1057–1074.

McCarthy, G., Puce, A., Belger, A., & Allison, T. (1999). Electrophysiological studies of human face perception. II: Response properties of face-specific potentials generated in occipitotemporal cortex. *Cerebral Cortex*, *9*(5), 431–444.

McPherson, W., & Holcomb, P. (1999). An electrophysiological investigation of semantic priming with pictures of real objects. *Psychophysiology*, *36*, 53–65.

Miall, R. C., Stanley, J., Todhunter, S., Levick, C., Lindo, S., & Miall, J. D. (2006). Performing hand actions assists the visual discrimination of similar hand postures. *Neuropsychologia*, *44*(6), 966–976.

Mouchetant-Rostaing, Y., Giard, M. H., Bentin, S., Aguera, P. E., & Pernier, J. (2000). Neurophysiological correlates of face gender processing in humans. *European Journal of Neuroscience*, *12*(1), 303–310.

Musseler, J., & Hommel, B. (1997). Blindness to response-compatible stimuli. *Journal of Experimental Psychology*, *3*(23), 861–872.

Ozyürek, A., Willems, R. M., Kita, S., & Hagoort, P. (2007). On-line integration of semantic information from speech and gesture: Insights from event-related brain potentials. *Journal of Cognitive Neuroscience*, *19*, 605–616.

Peelen, M. V., & Downing, P. E. (2007). The neural basis of visual body perception. *Nature Reviews Neuroscience*, *8*(8), 636–648.

Press, C., Gherri, E., Heyes, C., & Eimer, M. (2010). Action preparation helps and hinders perception of action. *Journal of Cognitive Neuroscience*, *22*(10), 2198–2211.

Press, C., & Heyes, C. (2008). Stimulus-driven selection of routes to imitation. *Experimental Brain Research*, *188*, 147–152.

Proverbio, A. M., Esposito, P., & Zani, A. (2002). Early involvement of the temporal area in attentional selection of grating orientation: An ERP study. *Brain Research. Cognitive Brain Research*, *13*, 139–151.

Rizzolatti, G., Fogassi, L., & Gallese, V. (2000). Cortical mechanisms subserving object grasping and action recognition: A new view on cortical motor functions. In M. S. Gazzaniga (Ed.), *The new cognitive neurosciences* (2nd ed., pp. 539–552). Cambridge, MA: MIT Press.

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, *2*(9), 661–670.

Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nature Reviews Neuroscience*, *11*(4), 264–274.

Rossion, B., & Jacques, C. (2008). Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. *Neuroimage*, *39*(4), 1959–1979.

Rumiati, R. I., & Tessari, A. (2002). Imitation of novel and well-known actions: The role of short-term memory. *Experimental Brain Research*, *142*, 425–433.

Schutz-Bosbach, S., & Prinz, W. (2007). Perceptual resonance: Action-induced modulation of perception. *Trends in Cognitive Neuroscience*, *11*(8), 349–355.

Stanley, J., & Miall, R. C. (2007). Functional activation in parieto-premotor and visual areas dependent on congruency between hand movement and visual stimuli during motor-visual priming. *Neuroimage*, *34*(1), 290–299.

Tang, Y., Liu, D., Li, Y., Qiu, Y., & Zhu, Y. (2008). The time-frequency representation of the ERPs of face processing. *Conference Proceeding of the IEEE Engineering Medical Biological Society*, *2008*, 4114–4117.

Urgesi, C., Candidi, M., Ionta, S., & Aglioti, S. M. (2007). Representation of body identity and body actions in extrastriate body area and ventral premotor cortex. *Nature Neuroscience*, *10*(1), 30–31.

van Elk, M., van Schie, H. T., Neggers, S. F. W., & Bekkering, H. (2010). Neural and temporal dynamics underlying visual selection for action. *Journal of Neurophysiology*, *104*(2), 972–983.

Wheaton, K. J., Pipingas, A., Silberstein, R. B., & Puce, A. (2001). Human neural responses elicited to observing the actions of others. *Visual Neuroscience*, *18*(3), 401–406.

Willems, R. M., Ozyürek, A., & Hagoort, P. (2007). When language meets action: The neural integration of gesture and speech. *Cerebral Cortex*, *17*, 2322–2333.

Wohlschlager, A. (2000). Visual motion priming by invisible actions. *Vision Research*, *40*, 925–930.