

Functional activation in parieto-premotor and visual areas dependent on congruency between hand movement and visual stimuli during motor-visual priming

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Electrophysiological studies in monkeys and neuroimaging studies of humans have shown that action execution and action observation share neural processing sites traditionally thought to be responsible for motor execution alone. This experiment investigates a behavioral phenomenon in which a visual discrimination task is influenced by concurrent motor performance. Functional magnetic resonance imaging (fMRI) was used to determine whether this discrimination task uses components of the motor system. Participants viewed and responded to an animated hand while performing either congruent or incongruent right hand actions; the visual presentation was either a sequence showing a hand opening and closing, or randomly ordered frames from this series. The participant responded to onscreen target hand postures on a left footpedal. Previous behavioral results have shown a reaction time advantage on this discrimination task when performing congruent compared to incongruent hand actions, but only for sequential visual presentation. Left superior parietal lobule (SPL) and dorsal premotor cortex were more strongly activated when visual series and hand action did not match, as were dorsal premotor cortex and primary visual cortex. These results suggest that mismatches between performed action and visual feedback produce an inaccurate neural representation of limb state, which we suggest causes the contralateral SPL activation. This representation could not be used in the visual discrimination task, requiring increased reliance on direct visual inputs in order to perform the discrimination task accurately.

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It has been suggested that action execution automatically engages a forward modeling process in the brain. This process combines efference copy of the executed movement with information about the motor system's current state and dynamics, and then produces a prediction of the action outcome (Miall and Wolpert, 1996). The current experiment is based on research that suggests that the predictive output resulting from this forward model can be made available to other brain areas for use in a visual

discrimination task (Miall et al., 2006), and aims to identify the neural systems involved in this task.

There is a large body of evidence showing that motor task performance can be influenced by perceiving another person executing an action. The most intuitive example of this is that observation of another person's action allows one to learn new motor programs (e.g., Mattar and Gribble, 2005; Buccino et al., 2004). A more complicated situation arises when performed and simultaneously observed actions differ. Kilner et al. (2003) showed that if a participant moves his or her arm in a horizontal plane, then observing another person moving their arm in the perpendicular vertical plane introduces additional vertical variability into the participant's fingertip position.

Similarly, movement initiation speed can be influenced by presenting a prime stimulus that is either matched or mismatched with a preordained movement. Congruent prime/movement combinations facilitate movement onset, while incongruent pairings delay movement onset, both when the prime represents the target object (e.g., a bar rotated to a particular angle; Craighero et al., 1999, 2002), as well as when the prime stimulus represents a congruent/incongruent hand position or movement (Brass et al., 2000; Vogt et al., 2003).

There are two competing explanations for these behavioral effects. Craighero et al. (1999) proposed that preparing a motor response will increase the speed of processing for congruent visual stimuli, allowing faster movement initiation—a process referred to as motor-visual priming. Alternatively, viewing a hand position or target object may automatically prime the production of that hand action, or the hand action required to interface with the target—referred to as visuo-motor priming (Craighero et al., 2002).

In our own experiments, we have investigated motor priming of visual processing during a combined hand movement/visual discrimination task (Miall et al., 2006). Participants viewed an ongoing presentation of an animated hand opening and closing, and were asked to detect an oddball hand position inserted in this series. They were faster at this task when performing a congruent hand action, compared to when performing an incongruent hand action.

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This paradigm provides evidence for a motor-visual priming effect, an effect also reported for detecting apparent motion by Wohlschläger (2000). Unlike the earlier priming studies (Craigheo et al., 1999, 2002; Vogt et al., 2003), in our task the required response was distinct from the ongoing motor/visual task, both in effector (participants gave a vocal response on detection of the oddball) and in the relationship between prime and response (i.e., participants did not have to produce a response that was related to either the visual stimulus or the performed action). A visuo-motor interpretation of this phenomenon is not convincing: the observed visual stimuli would prime the performance of similar hand movements, rather than priming the vocal responses to the oddball target (Miall et al., 2006).

This evidence pointing towards motor-visual priming led us to hypothesize that performing a congruent hand action produces a forward model representation of the upcoming hand position in the visual sequence; this congruent representation then allows more rapid discrimination of the oddball stimulus. Performing an incongruent hand action would lead to forward modeling of the next incongruent hand position, and this modeling could only provide conflicting information to the discrimination task.

The aim of the present study was then to investigate how the brain processes underlying action performance and action observation interact to produce this behavioral phenomenon, which has been replicated across four separate experiments (Miall et al., 2006).

Recent research in motor control has found that motor execution circuits in the brain are also active during action observation (for an in-depth review, see Rizzolatti and Craighero, 2004). Mirror neurons were first reported for the ventral premotor cortex in the macaque monkey (Rizzolatti et al., 1996), and a similar area has been identified in the human brain as being active during imitation tasks (Iacoboni et al., 1999). In a meta-analysis of functional brain imaging studies on motor performance, observation, or imagery, Grezes and Decety (2001) identified reasonably consistent brain activation during these tasks in the superior parietal lobule (BA 7), supramarginal gyrus (BA 40, but only for fine finger movements), supplementary motor area (SMA), and dorsal premotor areas (although this activation was less consistent for action observation, across studies).

This suggests a common neural framework for action performance and observation. Iacoboni (2005; see also Miall, 2003) provides a framework for how these areas might interact during imitation, starting with a visual representation of the to-be-imitated action in the superior temporal sulcus (STS), an area that is responsive to biological motion, and is active during action observation but not execution (Iacoboni et al., 1999, 2001). Visual information from the observed action passes from the STS to the posterior parietal cortex (specifically the inferior parietal lobule, or IPL), which codes for the predicted somatosensory outcome of the intended action; this passes to the ventral premotor cortex, where the action's goal is translated into a motor program; an efferent copy of this planned action then returns to the STS where it is compared to the original visual representation of the observed movement to determine whether these match.

We have previously proposed that our simultaneous hand movement and visual stimulus discrimination task (Miall et al., 2006) makes use of a similar forward model network, the output of which can be used to aid the visual discrimination process. When hand movement and visual series are congruent, the output of the forward model will be a more accurate predictor of the next part of

the visual sequence, and it is hypothesized that these areas of the mirror neuron network will be differentially activated when participants are performing movements congruent with the onscreen visual series, compared to performing incongruent movements.

In the current study, participants performed our hand-movement/visual-discrimination task while correlates of brain activity were recorded with functional magnetic resonance imaging (fMRI). We hypothesize that the subjects will show differential activity in one or more of the forward model/mirror neuron areas (ventral premotor cortex, STS, IPL), for the contrast between congruent and incongruent movements. We have no a priori position on whether this difference will be manifest as some of these areas being active under congruent movement conditions but not under incongruent conditions, or as a difference in the level of activation in these areas across conditions.

Materials and methods

Participants

A total of 16 participants completed the experiment (8 male, 8 female), ranging in age from 18 to 48 years (median = 26.5 years). Four of the participants had previously participated in unrelated fMRI experiments. All had either normal visual acuity or wore corrective lenses during the testing session.

Stimuli

The visual series (see Fig. 1A) consisted of 15 frames (frame duration = 1 s) of an animated right hand (Poser software package, Curious Labs), arranged in the Sequential visual condition to form a series simulating a hand opening and closing at .133 Hz (i.e., the hand completed two movements in 15 s). In the Random visual condition, the same pictures were presented in a random order, at the same display rate, forming an unpredictable pattern.

The visual display was projected onto a screen located 3 m from the end of the head coil, and was viewed through prism glasses. The left side of the display area included a fixation crosshair/pointer, with the hand visual series displayed on the right of the screen.

Visual stimulus presentation was controlled by Presentation (Neurobehavioral Systems) and was synchronized to the EPI volumes. Oddball target stimuli consisted of the hand shown with the index and middle fingers extended (see Fig. 1); reaction time (response with left foot on a pedal) was recorded by Presentation. The timing of these target stimuli within a block was pseudorandomized, so that target times were balanced across each experimental condition and across all trials in the two functional scanning runs.

Experimental task

The experimental task required participants to perform one of two hand movements while viewing a series of pictures of hand positions presented on the projection screen. This picture series was presented either sequentially, reproducing a right hand opening and closing, or as a random ordering of the same frames. Performed hand actions are displayed in Fig. 1B. The first hand movement was congruent with the picture series (i.e., opening and closing the hand), while the second hand movement was

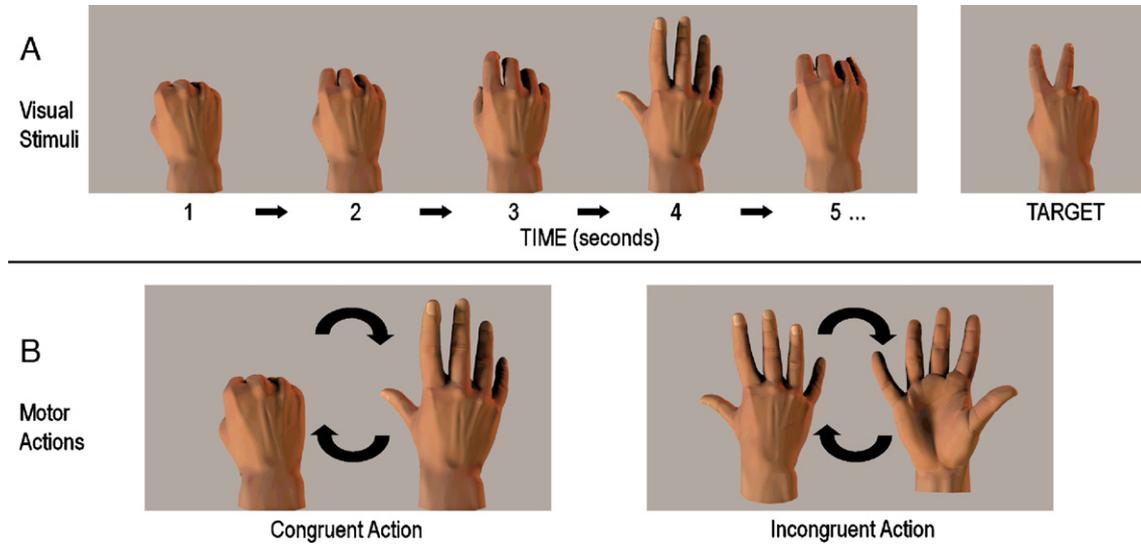


Fig. 1. (A) The hand images as displayed in the sequential visual series, with target hand position. Participants moved in time with a metronome displayed on the left of the projector screen, while hand pictures appeared on the right of the screen. Images were displayed at 1 Hz. (B) Congruent and incongruent motor actions.

incongruent with the picture series (rotating the wrist with the palm open, from pronation to supination). The participant performed these hand actions with his or her right hand held above the right thigh; thus processing of both motor task and visual stimuli should be lateralized to the left hemisphere.

Fig. 2 shows the timecourse of each trial. A trial began with an instruction screen (5 s) indicating the hand movement to be performed for that block. This was replaced by the initial hand position picture and crosshair display (static presentation for 3 s), after which presentation of the picture series began at 1 frame per second. During the hand movement period, the fixation pointer on the left hand side of the screen slowly rotated through a 180° angle at the same frequency as the visual series, and the participant was asked to time their movements on the basis of this pointer (thus synchronizing the phase of hand movements to that of the visual series presentation in the sequential condition, and providing matched pacing in the random visual condition). The hand movement/visual series presentation lasted for 31 s (active period), and was followed by further presentation of the static hand and crosshair for 18 s (passive period), during which period the participant kept his or her hand still.

On each trial, two target pictures were presented at pseudorandom times within the 31 s active period, and one target was presented within the passive period. Participants were instructed to respond as quickly as possible to these target stimuli by pressing on a foot-pedal with their left foot. A pillow was placed under the left leg to minimize body movement from this response.

Procedure

Each participant completed a safety screening form and was provided with the task instructions. He or she then completed one practice trial for each of the four conditions before entering the scanner, and two practice trials in the scanner prior to the start of recording. During the earlier practice sessions, the experimenter monitored the participant's eye movements to ensure that they followed the instructions to fixate the metronome during the task. No recordings of eye movements were made during the scanning sessions. The experiment was split into two 14-min recording sessions, consisting of 15 trials each (three trials each of the four factorial conditions described, plus three trials of a no-movement

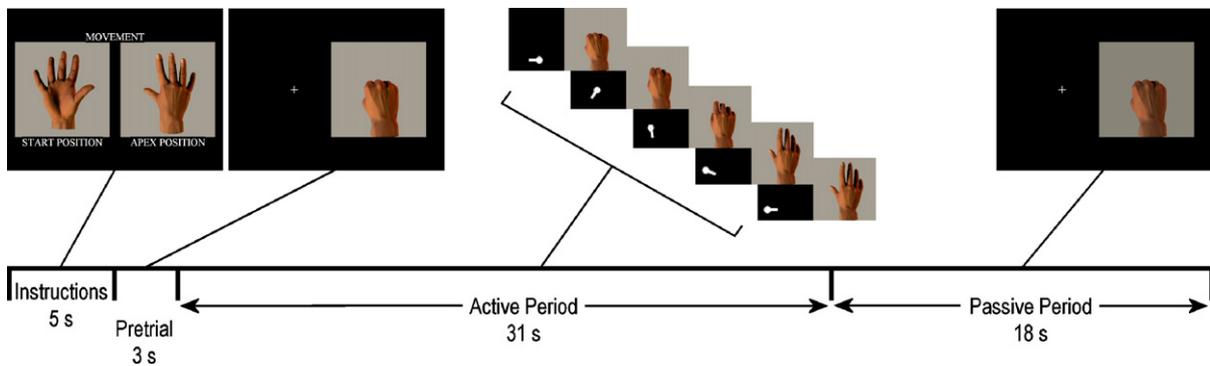


Fig. 2. Task structure for a single trial—the instruction screen indicates the hand movement to be performed on the trial. Following a pre-trial display, the Active period lasts for 31 s, with visual images as in Fig. 1 (note that the pointer size and position have been changed for clarity in this figure). The Passive period lasts for 18 s, during which period target pictures are still presented, but the hand image is otherwise static.

condition with the sequential visual series, which is not reported in this paper).

Image acquisition parameters

Functional and anatomical images were acquired on a 3 T Varian/Siemens magnet system at FMRIB, Oxford. The functional imaging sequence collected T2* weighted EPI images (30 ms echo time, 87° flip angle). Twenty-five 5.5 mm axial slices provided whole-brain coverage for each volume, with 3×3 mm in-plane resolution. For each of two runs, 4 dummy volumes were followed by 283 functional volumes, with a 3 s TR. Structural images were acquired following completion of both functional imaging runs (1 run=15 trials, as described above), using a T1-weighted sequence with 1×1×1 mm voxel size.

fMRI processing and analysis

All fMRI signal processing and analysis was performed using the FMRIB software library (FSL; FMRIB, Oxford). The initial four dummy volumes of each functional data collection run were discarded prior to analysis to ensure T1 saturation had been achieved. Prior to processing, slice timing was corrected and the volumes in each run were motion-corrected and realigned to the middle volume of the run using MCFLIRT. The BOLD signals were then high-pass filtered with a 60 s Gaussian-weighted filter, and spatially filtered with a 5 mm FWHM kernel. Epochs associated with the instruction screens preceding each trial, and with the target presentation period (including the participant's response to this), were entered into the GLM as two separate covariates of no interest. The target presentation period was defined as starting at target onset, and terminating at the time of the foot pedal response (or the onset of the following picture, if participants failed to respond to the target on that trial).

Four explanatory variables associated with each of the active conditions¹ were convolved with a gamma-derived hemodynamic response function (standard deviation of 3 s, mean lag of 6 s). The motion correction parameters calculated by MCFLIRT were also entered into the model at this stage as covariates of no interest (3 rotation parameters, and 3 translation parameters), without convolution by the HRF, and orthogonalized with respect to one another.

The first level of analysis was performed separately for each 14-min run. Within each run, contrasts testing the factorial combination of the two main factors and their interaction were calculated (Congruent vs. Incongruent, and Sequential vs. Random).

At the second level of the analysis, contrasts were combined for each participant from the first-level analysis of the two functional imaging runs with a mixed effects treatment of the variance (FMRIB's Local Analysis of Mixed Effects, FLAME, stage 1 processing). The third level of the analysis combined the second level output across all participants, again with mixed effects treatment of the variance (full FLAME processing). Voxels were initially thresholded at a Z-score value of 2.6 (equivalent to a p of .005, single sided), and then subjected to a cluster threshold with a significance level of $p < 0.05$.

¹ Epochs associated with the no-movement condition, sequential visual series, as described in the Procedure, were also entered into the analysis as covariates of no interest.

A traditional factorial analysis of these data overlooks some aspects of the experimental design, and risks overlooking areas where main effects are additive across factors. The final stage of the analysis therefore tested the conjunction of the main effects for hand movement and visual series. The conjunction was calculated by taking the contrast results for the factorial analysis main effects (Incongruent minus Congruent hand movement, and Random minus Sequential visual series), and multiplying the binary images of these two sets of results to identify voxels that were responsive to both factors of the design.

The brain areas revealed by this conjunction approach can be missed when emphasis is placed on interaction terms as the critical test of experimental tasks, but these areas remain of interest as representing parts of the brain that are additively responsive to more than one main effect of an experimental design, where one factor does not mediate/modulate the activity due to the other factor; this point is continued in the Discussion.

Results

Behavioral responses

Mean reaction times for identifying the target stimulus in the active hand movement conditions are presented in Table 1. Missed targets occurred on 2.6% of all trials, and late responses (i.e., longer than 1 s) made up 2.99% of all trials.

A 2×2 ANOVA (Visual Series×Performed Movement) unexpectedly indicated faster RTs to the target for the Incongruent condition ($M=618.3$ ms, $SE=24.8$) than for the Congruent condition ($M=635.7$ ms, $SE=25.1$), $F(1,15)=7.17$, $p=0.017$. The main effect for Visual Series and the interaction between this factor and Performed Movement were not significant, $F_s(1,15) < 1.96$, $ps > 0.18$.

Factorial analysis of functional imaging data

Local maxima for the six contrasts of the factorial design are listed in Table 2. We first compared the Congruent and Incongruent hand movement conditions (across both Sequential and Random visual conditions) and revealed differential activation of sensorimotor cortex over the left hemisphere (Fig. 3; congruent hand movement activation is represented in the red to yellow spectrum, Incongruent hand movement activation in the blue to green spectrum). For the Incongruent–Congruent contrast (Table 2B), this sensorimotor activation extended into the posterior parietal cortex; a second cluster of activity was found in the primary visual cortex (mainly located in the left hemisphere). The Congruent–Incongruent (Table 2A) contrast also showed activation in the left hemisphere anterior superior cerebellum. Note that the congruent

Table 1
Reaction time means and standard errors (ms) for responses to target stimuli, organized by visual series (Seq/Rand) and performed hand movement (Con/Incon)

	Seq Con	Seq Incon	Rand Con	Rand Incon
Mean	627.49	614.93	643.98	621.67
Standard error	25.02	26.97	25.83	23.81

Note. Seq=Sequential visual series; Rand=Random visual series. Con=Congruent movement; Incon=Incongruent movement.

Table 2
Significant functional brain activations from factorial analysis

Cluster	Cluster volume (cm ³)	Cluster <i>p</i> value	Area for local maxima	Brodmann's area	Max <i>Z</i> score	MNI coordinate (mm) of max voxel (x, y, z)
<i>A. Congruent–Incongruent</i>						
1. Left hemisphere cerebellum	3.25	<0.019	LH cerebellum 6th lobule		5.13	–24, –54, –28
			LH cerebellum 1st Crus		4.26	–46, –62, –34
2. LH sensorimotor areas	6.88	<0.001	LH primary motor cortex	4	8.5	–42, –14, 62
			LH central sulcus	4/3	6.88	–40, –20, 52
			LH postcentral gyrus	3	6.59	–42, –20, 58
<i>B. Incongruent–Congruent</i>						
1. Visual cortex	17.77	<0.001	Bilateral primary visual cortex	17	5.21	–2, –86, 2
				17	5.04	10, –80, 4
2. Left hemisphere sensorimotor	37.20	<0.001	LH postcentral gyrus	3	8.84	–36, –36, 60
			LH primary motor cortex	4	5.98	–22, –16, 62
			LH superior parietal gyrus	7	5.62	–36, –44, 60
			LH supplementary motor area	6	5.47	–4, –20, 54
			LH precuneus/sup. parietal gyrus	5	4.7	–12, –60, 58
<i>C. Sequential–Random</i>						
No activation sites.						
<i>D. Random–Sequential</i>						
1. Right MT/V5	3.14	<0.023	RH area MT [V5]	Border 37/19	3.99	52, –68, –2
2. Right ventral premotor areas	3.41	<0.015	RH inferior frontal gyrus (pars operculum)	44	3.64	48, 6, 32
			RH precentral gyrus	6	3.55	56, 8, 30
3. Left superior parietal cortex	5.10	<0.002	LH superior parietal gyrus	7	4.16	–28, –54, 58
4. Right dorsal premotor areas	5.28	<0.002	RH dorsal premotor	6	5.63	28, –4, 48
			RH dorsal premotor	6	3.37	52, –8, 52
5. Left dorsal premotor areas	6.07	<0.001	LH dorsal premotor	6	4.92	–42, –6, 50
			LH dorsal premotor	6	4.23	–30, –4, 48
6. Bilateral anterior cingulate	7.02	<0.001	LH anterior cingulate cortex	32	5.04	–2, 2, 54
			RH anterior cingulate cortex	32	3.97	8, 2, 48
7. Right superior parietal cortex	8.05	<0.001	RH superior parietal cortex	7	5.12	28, –62, 60
			RH inferior parietal cortex	40	3.62	34, –46, 38
			RH precuneus	5	3.24	14, –70, 62
8. Left lateral visual areas and cerebellum	12.13	<0.001	LH area MT [V5]	19	4.58	–46, –72, 2
			LH cerebellum		4.41	–10, –76, –28
			LH visual cortex	18	4.12	–28, –72, –16
<i>E. Positive interaction [Seq Con–Seq Incon]–[Rand Con–Rand Incon]</i>						
No activation sites.						
<i>F. Negative interaction [Seq Incon–Seq Con]–[Rand Incon–Rand Con]</i>						
1. Bilateral primary visual cortex	8.98	<0.001	RH primary visual cortex	17	4.54	4, –84, 0
			LH primary visual cortex	17	3.49	–6, –82, 0

and incongruent conditions required different actions by the participant, and hence different activation of sensorimotor areas was expected.

The second pair of contrasts compared the Sequential and Random visual series conditions (on average over both hand movements). No areas were identified with stronger activation for the Sequential than the Random visual series (Table 2C).

For the contrast showing areas with greater activation for the Random compared to the Sequential visual series (across both movement conditions, Table 2D), there were multiple clusters of activity, including bilateral dorsal premotor areas, right hemisphere ventral premotor cortex, bilateral superior parietal cortex, and bilateral anterior cingulate cortex. Increased activity in visual areas

was seen in the right hemisphere V5/MT area (on the border of Brodmann's areas 19 and 37), as well as in the corresponding areas in the left hemisphere (extending caudally towards V1).

The final two contrasts were the positive and negative interaction terms (Tables 2E and F, respectively). For the positive interaction [Sequential Congruent–Sequential Incongruent]–[Random Congruent–Random Incongruent], there were no significantly activated areas. Bilateral primary visual cortex was identified as significantly activated for the negative interaction, [Sequential Incongruent–Sequential Congruent]–[Random Incongruent–Random Congruent]. The extent of this activation is displayed in Fig. 4; percentage signal change from baseline for the individual conditions is displayed on the right hand side of Fig. 4.

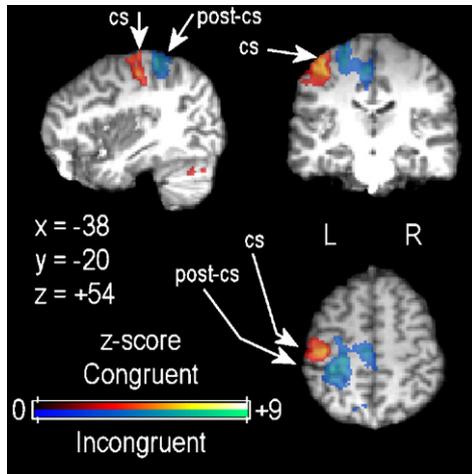


Fig. 3. Differential sensorimotor cortex activation for congruent (red to yellow shading) and incongruent (blue to green shading) hand movements, thresholded at $Z > 2.6$, with a cluster threshold set at $p < 0.05$. Group functional data are projected onto a single participant's structural scan, registered to standard MNI-space coordinates. Sulci are marked as follows: cs=central sulcus; post-cs=postcentral sulcus.

Conjunction analysis of functional imaging data

Figs. 5 and 6 show the two areas identified by the conjunction of the main effects, with greater magnitude BOLD signal changes for both incongruent hand movements (compared to congruent hand movements) and random visual series presentation (compared to sequential visual presentation).

Fig. 5 shows the first of these areas (volume: 2.5 cm^3) in the posterior parietal cortex, located behind the posterior bank of the postcentral sulcus, and towards the midline from the intraparietal sulcus. This included activation in the superior parietal lobule (BA 7; $-26, -46, 58$), the precuneus (BA 5; $-16, -60, 58$), and the inferior parietal cortex (BA 40; $-34, -44, 52$). The bar graph attached to Fig. 5 shows percentage signal change in this area for the four conditions for this conjunction. It can be seen that the conjunction in this superior parietal site is based on additive main effects (Incongruent > Congruent, Random > Sequential).

The second area highlighted by the conjunction analysis (Fig. 6) was located in dorsal premotor cortex (PMd, Brodmann's area 6), posterior to the precentral sulcus (cluster volume: $.8 \text{ cm}^3$). The bar graph attached to Fig. 6 shows percentage signal change in PMd for the individual conditions of the conjunction.

Discussion

We aimed to investigate the neural processes underlying the performance advantage for judging visual images of hands while simultaneously performing the same hand movement, compared to performing a distinct hand movement (Miall et al., 2006). The key results indicated that when the visual series and the performed hand movement were in disagreement, there was greater activation in the superior parietal lobule and primary visual cortex, compared to the Sequential Congruent condition.

Addressing the factorial analysis of the results first, activation differences between the congruent (open and close hand) and incongruent (rotate wrist) movements clearly revealed two separate areas of activation for these movements (see Fig. 3). These

corresponded to known localizations within primary motor cortex for hand vs. wrist movements, with the congruent (hand) activation located anterior and lateral on the central sulcus relative to the incongruent (wrist) activation.

Increased activity for the random compared to the sequential visual presentation (averaged across the two hand movement conditions) was observed for several areas, including bilateral dorsal premotor cortex, bilateral posterior parietal cortex, anterior cingulate cortex, and bilateral motion processing regions of visual cortex (Table 2D). It is likely that performance demands in this random condition were more complex than in the sequential condition (as indicated by the anterior cingulate activation); studies show that increasing the complexity of unimanual motor tasks will lead to increased recruitment of ipsilateral motor cortex (Seidler et al., 2004), including dorsal premotor cortex (Winstein et al., 1997).

The negative interaction term showed lower BOLD signal magnitude in primary visual cortex for the Sequential Congruent condition relative to all other conditions, suggesting that there is differential activation of early visual areas when there is a change in the relationship between performed action and observed images. This may be the neural basis of the performance differences in the discrimination of the target images.

While this appears to be a negative signal change relative to baseline, it is worth remembering that the baseline condition is a visual discrimination task (without any hand movement) rather than a truly passive condition. Thus it is not clear whether the BOLD differences in V1 (relative to baseline) indicate a negative BOLD signal in the active conditions, or instead indicate a stronger, positive BOLD signal in the baseline condition. Given that the passive baseline task allows the participant to fully concentrate on the visual discrimination task, we suggest the latter hypothesis is more likely. This would mean that the difference between the active conditions represents an increase in BOLD for all of the Sequential Incongruent/Random Congruent/Random Incongruent conditions relative to Sequential Congruent.

However, several studies on cross-modal attention have shown that activity in primary sensory cortex (visual or auditory) is inhibited when the participant attends to another sensory modality (Johnson and Zatorre, 2005; Shulman et al., 1997). In the present experiment, the Sequential Congruent condition may allow the participant to focus on non-visual (proprioceptive or motor efference) information to perform the task while discounting visual inputs, thus leading to reduced V1 activation.

Conjunction of main effects

The factorial analysis obscures the fact that in only one of the four experimental conditions is the action a true match with the visual series (Sequential Congruent). In all of the three other conditions, there is either a categorical or temporal mismatch between the visual series and the performed hand movement. The conjunction analysis of the main effects allowed us to test for those areas where activity increased during a mismatch between the performed hand movement and the observed visual stimuli. This approach identified activation differences in two areas: left hemisphere superior parietal lobule (SPL) and left dorsal premotor cortex (PMd), and indicated that both the SPL and PMd are sensitive to both factors of the experimental design. It should be noted that an overemphasis on interaction effects as being the critical points for interpreting fMRI data means that such areas are

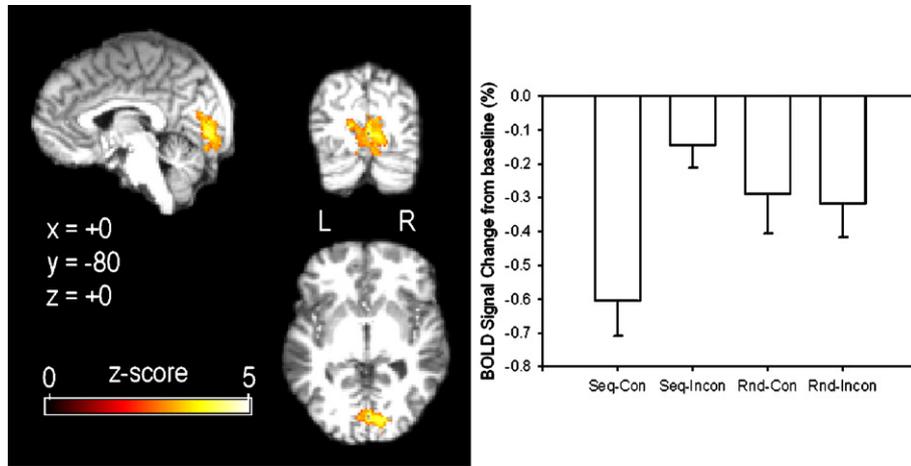


Fig. 4. Visual cortex activation for the negative interaction term of the factors Visual Series and Hand Movement. Brain activations were thresholded at $Z > 2.6$, with clusters thresholded at $p < 0.05$. The bar graph shows mean BOLD signal changes for this region (% change relative to baseline) for all four conditions. Group data are projected onto a single participant's structural scan, registered to standard MNI-space coordinates.

frequently ignored or summarily treated in descriptions of the non-critical main effects.

As visual stimuli were presented in the right hemifield, and hand movements were performed with the right hand, the lateralization of this activity to the left hemisphere is consistent with contralateral coding of this information; if the task was performed with the left hand and visual stimuli presented to the left hemifield, we would predict increased right hemisphere SPL activity for this conjunction (see discussion of Fink et al., 1999, below), although PMd is often bilaterally activated (Hoshi and Tanji, 2006).

It is unlikely that the superior parietal lobule activation is related solely to differences in motor or sensory processes related to the performed movement. Firstly, the site of activation is located posterior to the postcentral sulcus, and therefore lies behind primary motor and somatosensory cortices, so sensory reafference from the hand action is unlikely to contribute (compare Figs. 3 and

5). Secondly, taking the conjunction of the main effects balances the visual and proprioceptive aspects of the task, and highlights areas that are responsive to both of these factors. Therefore, it appears that these areas are responding to the discrepancy between the visual representation and the performed hand movement, and are not driven simply by task-dependent motor or visual signals alone. We propose that the SPL is actively combining motor efference copy with feedback from visual inputs – and possibly somatosensory and proprioceptive feedback – in order to produce an accurate predictive model of hand state/position (Wolpert et al., 1998).

The role of the SPL in combining motor and visual signals has been shown in several studies. MacDonald and Paus (2003) asked participants to judge whether virtual-reality visual feedback of their right-hand finger movement was delayed with respect to the movement itself. Following disruption of processing in SPL, using repetitive transcranial magnetic stimulation (rTMS), participants

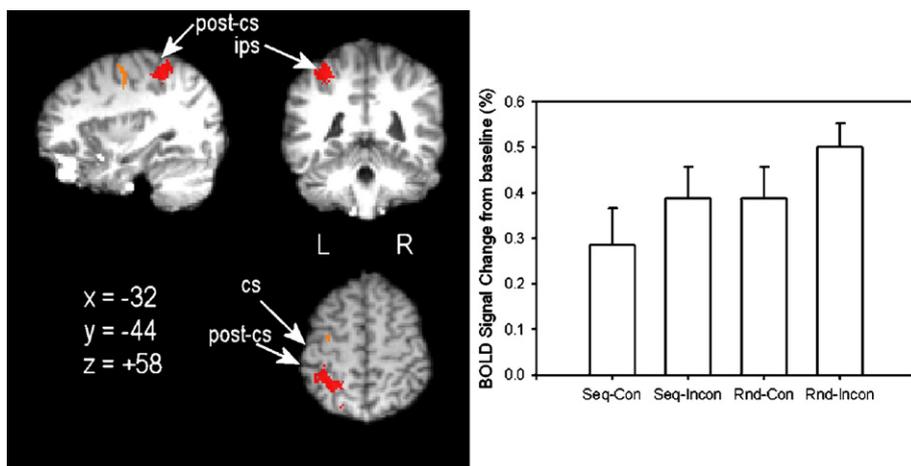


Fig. 5. Left hemisphere superior parietal lobule activation (red areas) for conjunction of the main effects of Visual Series and Hand Movement. Orange areas represent dorsal premotor cortex (see Fig. 6). Thresholds for activation in the main effect contrasts were as described in the main text (at $Z > 2.6$, with clusters thresholded at $p < 0.05$). The bar graph shows mean BOLD signal changes for this region (% change relative to baseline) for all four individual conditions. Group data are projected onto a single participant's structural scan, registered to standard MNI-space coordinates. Sulci are marked as follows: cs=central sulcus; post-cs=postcentral sulcus; ips=intraparietal sulcus.

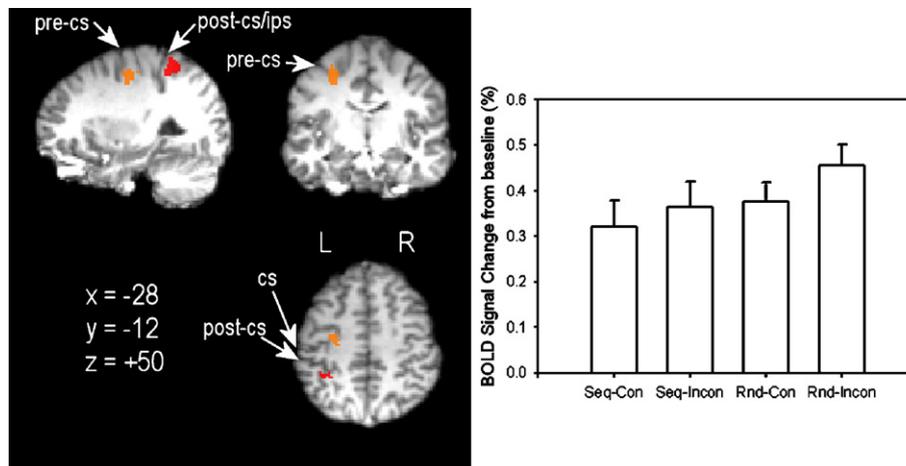


Fig. 6. Left hemisphere dorsal premotor activation (orange areas) for conjunction of the main effects of Visual Series and Hand Movement. Red areas represent superior parietal lobule (see Fig. 5). Thresholds for activation in the main effect contrasts were as described in the main text (at $Z > 2.6$, with clusters thresholded at $p < 0.05$). The bar graph shows mean BOLD signal changes for this region (% change relative to baseline) for all four individual conditions. Group data are projected onto a single participant's structural scan, registered to standard MNI-space coordinates. Sulci are marked as follows: pre-cs=precentral sulcus; cs=central sulcus; post-cs=postcentral sulcus; ips=intraparietal sulcus.

reported fewer delayed trials than in the pre-rTMS baseline condition—but only for the active finger movement condition, and not for a passive finger movement condition. Thus the comparison must take place between visual feedback and motor efference copy, and not from somatosensory or proprioceptive information (MacDonald and Paus, 2003).

Fink et al. (1999) asked participants to perform a modified version of Luria's bimanual coordination task: opening and closing both hands either in-phase or out-of-phase with each other, while looking at their left hand. On half of all trials, the view of the left hand was occluded with a mirror so that the participant viewed a reflection of their right hand. SPL activity (contralateral to the observed hand) increased when viewing the right hand's mirror image compared to viewing the left hand, and also when moving out-of-phase compared to moving in-phase. The SPL was not implicated in the interaction of these two factors (Fink et al., 1999). This means that the effects of mirror and phase relationship on SPL activity were additive (an interpretation not emphasized by the authors), and suggest that SPL activation may be parametrically related to the level of unreliability of the visual feedback. Other work with congruent/incongruent bimanual movement tasks has shown both SPL and PMd activation when movement angles are incompatible, suggesting activity due to premotor inhibition of default interlimb coordination patterns (Wenderoth et al., 2004).

Wolpert et al. (1998) proposed that the SPL is involved in maintaining limb position estimates. They reported the case of a patient who perceived her arm position as gradually drifting following cessation of movement, in the absence of vision; hence the idea that the SPL is maintaining or storing limb position estimates in the absence of new inputs. Data from clinical populations of participants with widespread lesions to parietal cortex suggest that this area may also be critical for distinguishing one's own movements from the movements of others when visual feedback is ambiguous (Sirigu et al., 1999), with some patients with damage to the angular gyrus of parietal cortex also showing poor ability to report when they formed the intention to perform a motor action (Sirigu et al., 2004). These data are also consistent with parietal cortex playing an important role in forward modeling

and the combination of visual information with motor efference copy.

All of these results suggest that motor efference and visual information are combined in the SPL to form a model or representation of the current position/state of the contralateral limb. We propose that our finding of an increase in SPL activation across the mismatch conditions represents changes in processing to ensure that the mismatched visual sequences are not incorporated in the forward model process for coding current hand state. This provides an explanation for the increased visual cortex activation in the mismatch conditions, as revealed by the significant interaction in the factorial analysis: when the visual series and performed hand action are congruent, the information from the forward model of hand state can be used to predict the next image in the visual sequence, leading to an RT advantage (Miall et al., 2006; the incompatible RT data in the present experiment are dealt with in the following section). When hand-action and visual series disagree, the model of hand state is of no use for the discrimination task, prompting an increased reliance on the visual inputs in order to perform the target detection task and increasing the length of time required to respond to these targets.

In the monkey, the superior parts of posterior parietal cortex are well connected to the dorsal premotor cortex (Wise et al., 1997; Marconi et al., 2001), and so it is unsurprising that our conjunction analysis identified PMd in addition to SPL. However, PMd is more typically activated in functional imaging studies by complex visuo-motor associative tasks (Ramnani and Miall, 2003) or by sequence learning paradigms (Grafton et al., 1995). In monkeys, PMd is active in similar tasks, as well as showing eye–hand interactions (Caminiti et al., 1991). PMd is also associated with response selection in both monkeys (Kurata and Hoffman, 1994) and humans (Chouinard et al., 2005). Neuronal activity in monkeys shows that two conflicting responses are encoded here prior to response selection (Cisek and Kalaska, 2005). We cannot be certain which aspects of our task would lead to the PMd activation. It may be that this activation represents additional processing to allow performance of the instructed action, by inhibiting imitation of the unwanted observed action.

It should be noted that eye movement information was not recorded during this task; however, during the practice trials, all participants maintained fixation on the crosshair/metronome position (as assessed by experimenter observation). The activations in visual and parietal cortex could possibly be explained by greater frequency or magnitude of saccadic eye movements during the mismatched trials, but such parietal activation during saccadic eye movements tends to be bilateral (Law et al., 1997; Matsuda et al., 2004).

Reaction time data

The reaction time data measured in the present study are only partly consistent with our previously reported findings from four separate experiments (Miall et al., 2006). In comparing the present results with those of our previous report (left panel of Fig. 4, in Miall et al., 2006), we find in both cases that RTs are longer in the random conditions than in the sequential conditions. However, in our present study, the Sequential Congruent mean RT is longer than expected.

Our earlier behavioral results suggest that the congruency advantage is a real phenomenon, and has been demonstrated in repeated experiments with three independent participant groups (Miall et al., 2006). Differences in the experimental task were necessary in the shift from the laboratory to the scanner environment—participants responded on a footpedal (lab: vocal response), and hand movements were performed with the right hand (lab: left hand). The earlier laboratory tests also included a larger number of trials, which allowed the full factorial combination of the two hand movements (as in the present study) and the two corresponding visual series (one showing the hand opening and closing; the other showing rotation of the wrist). In adapting the paradigm for use in the fMRI scanner, only one visual series was used (of the hand opening and closing). This meant that hand movement and visual series were not completely counterbalanced, as they were in the behavioral studies.

Closer inspection of the earlier experiments behavioral data, however, shows an RT difference between the two hand movements used, irrespective of their congruency with the visual series. Participants responded faster to the target when performing the “rotate wrist” movement than when performing the “open and close hand” movement, on average over congruent and incongruent trials—that is to say, the congruency effect was intact for both of these hand movements, but was also accompanied by generally faster responses during the “rotate wrist” action trials than during the “open and close hand” action trials. It is unclear why this should be the case.

Because the present experiment only utilized the one visual series (“open and close hand” animation), the RT data appear to have been confounded by this difference in responding due to the nature of the hand movement, operating independently of the congruency effect. The abbreviated design meant that the hand movement for Sequential Congruent trials was always “open and close hand”, and for Sequential Incongruent trials it was always the “rotate wrist” movement. Thus the Sequential Congruent trials had (1) an RT advantage from the congruency between movement and visual stimuli, and (2) an RT disadvantage from the actual movement performed (open and close hand). The Sequential Incongruent trials had (1) an RT disadvantage from the incongruency between movement and visual stimuli, and (2) an RT advantage from the exact movement performed (rotate wrist).

This interpretation is supported by the 22 ms difference in RT between Random Congruent and Random Incongruent trials (where no difference was apparent in the earlier behavioral data; Miall et al., 2006); we suggest that this 22 ms difference represents an RT cost for responding while performing the “open and close hand” movement compared to the “rotate wrist” movement.² As outlined above, the abbreviated design for the fMRI version of our task appears to have obscured the expected RT effects.

Conclusions

The experiment showed increased activity in SPL, PMd, and primary visual cortex when there is a mismatch between a performed movement and a simultaneously viewed visual stimulus compared to the matched condition. This is consistent with the hypothesis that the SPL is involved in combining motor efference copy and visual feedback to produce a forward model estimate of hand state, which can be compared with a target hand state (in this case the visual stimulus). In the presence of incongruent visual feedback, processing in the SPL has to ensure that the forward model represents the actual hand state, rather than incorporating invalid information from the visual stimuli. At the same time, when the hand movement is not related to the target detection task, the forward model cannot be used to prime the visual system for target detection and hence there is an increased reliance on direct visual cortical processing under these conditions. We speculate that activation in dorsal premotor cortex may represent inhibition of the incompatible movement observed on mismatch trials.

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² If the RT difference between the Sequential Congruent and Sequential Incongruent conditions is corrected using this 22 ms RT difference (representing the RT cost for the “hand open and close” movement compared to the “rotate wrist movement”), the data show a 9.75 ms advantage for Sequential Congruent trials over Sequential Incongruent.

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