Action outcomes are represented in human inferior fronto-parietal cortex

Antonia F. de C. Hamilton & Scott T. Grafton
Dartmouth College, Hanover, NH, 03755, USA.

The simple action of pressing a switch has many possible interpretations – the actor could be turning on a light, deleting critical files from a computer or even turning off a life-support system. In each of these cases, the motor parameters of the action are the same but the physical outcome differs. We report evidence of suppressed responses in right inferior parietal and right inferior frontal cortex when participants saw repeated movies showing the same action outcome, but these regions did not distinguish the kinematic parameters by which the action was accomplished. Thus these brain areas encode the physical outcomes of human actions in the world. These results are compatible with a hierarchical model of human action understanding in which a cascade of specialised processes from occipital to parietal and frontal regions allow humans to understand the physical consequences of actions in the world and the intentions underlying those actions.

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Corresponding Author:
Dr Antonia Hamilton antonia.hamilton@nottingham.ac.uk
School of Psychology, University of Nottingham, University Park, Nottingham, NG7 2RD, UK

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Introduction

Hierarchical theories of human motor control have an august history (Bernstein, 1996; Hebb, 1949; Sherrington, 1906). Such models distinguish between different levels of motor representation, for example, a muscle level, a kinematic level (reach and grasp), an object-goal level (grasp a hammer) and an outcome level (hammer a nut). The distinction between these four levels is not only descriptive, but is likely to reflect the fundamental organisation of action in the central nervous system.

Much is know about the organisation of the lowest levels of the motor hierarchy, including the representation of muscle force (Evarts, 1968; Porter and Lemon, 1993) and reach and grasp actions (Jeannerod et al., 1995) in the primary and premotor cortex. In contrast, few studies have attempted to examine the higher levels of the motor hierarchy, in particular the levels of goals and outcomes. Increasing evidence suggests that this more abstract level of representation is important for both motor and social cognition. Several psychophysical studies have shown that human actions are encoded in terms of their outcomes (Hommel et al., 2001; Mechsner et al., 2001), and observed outcomes provide an important cue to an actor's mental state (Frith and Frith, 2006). The aim of the current paper was to examine the neural representation of action outcomes in the human brain based on action observation. By doing so, we can advance our knowledge of both hierarchical motor control and social action understanding.

The parallel study of social and motor cognition is made possible by discovery of mirror neurons in the macaque brain, which encode actions of the self and others (di Pellegrino et al., 1992; Gallese et al., 1996). Several theorists have suggested that mirror neurons may be important for representing action goals, intentions and outcomes for the self and for others (Gallese and Goldman, 1998; Rizzolatti and Fadiga, 1998). However, empirical demonstrations of neurons encoding a goal or outcome other than object grasping in the macaque brain are rare. Mirror neurons in the macaque inferior frontal gyrus respond when an action is inferred even it is not seen (Umilta et al., 2001), while neurons in macaque inferior parietal lobule encode specific action sequences for the self and others (Fogassi et al., 2005). These results suggest that inferior frontal or inferior parietal cortex might contain goal or outcome representations. Unfortunately, the macaque experiments did not record from both regions under the same conditions, and did not systematically separate goals from the underlying kinematics which achieve the goal, so the relative contribution of these different cortical regions to understanding goals and intentions remains undefined.

In the human brain, a mirror neuron system has been localised to the inferior frontal gyrus (IFG) and inferior parietal lobule (IPL) (Rizzolatti and Craighero, 2004). Many studies have shown that IFG and IPL respond when hand actions are performed (Grafton et al., 1992), imagined (Grafton et al., 1996), observed (Buccino et al., 2001), planned (Johnson et al., 2002) and imitated (Aziz-Zadeh et al., 2006; Buccino et al., 2004; Iacoboni et al., 1999). However, these studies are limited in two critical ways. The majority of studies activated all four putative mirror neuron regions (left and right IPL and IFG), and do not help us understand the differential processing of information within and between these regions. Similarly, none of these studies were able to distinguish between different levels of the action hierarchy, in particular between the kinematic level and the goal or outcome level. This is because all actions are made up of a wide variety of features including low level kinematic parameters such as hand speed and finger configuration, as well as more abstract goals, intentions and outcomes. It is almost impossible to constrain natural and rich stimuli in order to separate different types of action representation with simple subtraction designs, because an ‘action without a goal’ or an ‘outcome without an action’ is seldom plausible.

Recognising this confusion between kinematic, goal and outcome representations, Jacob and Jeannerod (Jacob and Jeannerod, 2005) recently argued that the mirror neuron system provides only kinematic representations (motor intentions), which are insufficient to determine a ‘prior’ intention. For example, pressing a switch might in one situation turn on a light, but in another might turn off a life-support machine, and presumably the intention of the actor is very different in each case. Under Jacob’s theory, when you see a person press a switch, the mirror neuron regions should encode the kinematic parameters of the pressing action such as the shape of the hand as it grasps, but not the outcome of that action – turning on the light – nor the prior intention to turn on the light which guided the outcome. If this interpretation is correct, bold theories which attempt to link the mirror neuron system to intentionality and theory of mind (Gallese, 2003; Gallese and Goldman, 1998) would have to be re-assessed.

A new way to discriminate between kinematic, goal and outcome levels of representation is to measure repetition suppression (RS) of the BOLD signal in response to observed videos showing novel or repeated kinematics, goals and outcomes. In two previous studies using an RS method, we showed that left anterior intraparietal sulcus (aIPS) represents object-goals. Object goal was defined by the identity of the object grasped by a person, for example, a ‘take-cookie’ goal compared to a ‘take-diskette’ goal (Hamilton and Grafton, 2006; Hamilton and Grafton, in press). The present study generalizes and extends this result by examining the neural representation of outcomes in relation to kinematic parameters. We define an outcome as the (desired) physical consequence of an action in the world, for example: pushing a light switch results in the outcome of a lit lamp in one case, or the outcome of a dim lamp in another. In the current study we did not attempt to isolate a representation at the object-goal level (grasping the light switch), which precedes the action outcome. Instead we examined the representation linked to the outcome of lighting the lamp, which completes the action. Thus, outcomes involve more complex actions with differing effects in the world, and may be represented at a higher level of the action hierarchy than object-goals.

The current paper distinguishes the representation of outcomes from those related to the kinematic components of actions used to generate those outcomes (e.g., pushing versus pulling, etc.). In order to localise brain activity at these two levels, we carried out an fMRI study measuring RS to sets of action movies with novel and repeated outcomes and novel and repeated kinematic parameters. This achieves two objectives. First, we could address Jacob’s challenge and determine if the putative human mirror neuron system represents intentions and outcomes rather than just kinematics. Second, we would be able to extend our knowledge of the motor hierarchy for action observation, building on our previous work examining goal representations (Hamilton and Grafton, 2006; Hamilton and Grafton, in press). We tested if the representation of observed outcomes was found in a different part of the putative mirror neuron system from the representation of observed kinematic features within each movement. Given the variability of recruitment of local cortical areas within the MNS in prior studies of action observation, we compared the relative involvement of inferior frontal and parietal cortex and also tested for differences in hemispheric involvement.

Methods

We used repetition suppression in an event-related fMRI experiment to localise the neural representation of action outcomes. First, twelve distinct sets of action movies were generated (See Supplementary Figure 1). Within every set, there were two possible outcomes and two possible kinematic means of achieving that outcome. For example, a box with a sliding lid can be opened or closed by either pushing the lid with a finger or pulling with both finger and thumb (Figure 1). The sets differed in low level stimulus characteristics such as lighting and the precise objects used. The wide variety of stimuli meant that we could be confident that the results revealed a general neural representation of outcomes, rather than being a quirk of one particular stimulus set. All movie stimuli created by filming intentional natural, right-handed actions on an object to cause a particular outcome. In 50% of movies, the left hand stabilised an object in the scene but remained still for the duration of the clip. Care was taken to ensure that that only the outcome or action varied between clips, all other cues were constant. Clip durations ranged from 2.5 to 9 seconds, according to the natural duration of the event depicted, but were constant within a set.

20 right-handed participants (7 male, mean age 20.8 years) gave their informed consent to take part in the study in accordance with the requirements of the local ethics board. Participants watched the twelve sets of movies presented in a pseudorandom order during fMRI scanning. They were instructed to watch carefully and press a key if the movie froze in the middle of the action (stop trials, 12% of total). Each stop trial ended a set, and was followed by a rest of 4-8 seconds before the next set of movies began. Intertrial interval was 500 msec. All stimuli were presented with Cogent running under Matlab 6.5, which provides accurate trial timing and synchronisation with the scanner.

Within each set of movies, the movies were presented in a pseudorandom order according to a one-back repetition suppression design (Figure 1). A different pseudorandom trial order was used for every set of movies and every participant, to ensure that the results reflect only the desired one-back RS effects and are not contaminated with any second or higher order effects. For the purposes of analysis, each movie was classified relative to the previous movie as either novel Outcome – novel Kinematics (nOnK), novel Outcome – repeated Kinematics (nOrK), repeated Outcome –

novel Kinematics (rOnK) or repeated Outcome – repeated Kinematics (rOrK). Participants saw 11 RS trials for each set of movies, so conditions were not precisely balanced within set but were balanced over sets. That is, over the 12 sets of movies, each participant saw 132 RS trials falling evenly into the 2x2 factorial design for Outcomes and Kinematics. A post-hoc analysis of the actual trial order was conducted to check for any possible artefacts due to the randomization algorithm. This analysis showed that the probability that an nO trial was preceded by an nK trial was equal to the probability that it was preceded by an rK trial, and similarly for all other combinations of trial types. Thus, we can be confident that the reported results are not due to artefacts of the trial sequence.

The experiment was carried out in a 3T Philips Achieva Quasar Dual 8 channel scanner using an eight channel phased array coil and 30 slices per TR (4 mm thickness, 0.5 mm gap); TR: 1975 ms; TE: 35 ms; flip angle:90^o; field of view: 24cm; matrix 80x80. For each of 4 functional runs, the first two brain images were discarded, then 240 images were collected and stored. Data were realigned, unwarped and normalized to the MNI template with a resolution of 2x2x2mm in SPM2. A design matrix was fitted for each subject with one regressor for each movie type (nOnK, nOrK, rOnK, rOrK) in each set of movies, plus a regressor each for New and Stop movies in each run, giving a total of 56 regressors. Each movie was modeled as a boxcar with the duration of that movie, convolved with the standard haemodynamic response function. Every design matrix was tested for the efficiency of the outcome and kinematic contrasts, and for the orthogonality of the regressors (Price et al., 2004), in order to be sure that the conditions were fully independent. The design matrix weighted each raw image according to its overall variability to reduce the impact of movement artifacts (Diedrichsen and Shadmehr, 2005). After estimation, 9mm smoothing was applied to the beta images.

To identify brain regions showing repetition suppression for outcomes, we calculated a contrast for the main effect of Outcome (novel > repeated) over all movies. Contrast images for all twenty participants were taken to the second level for a random effects analysis. We report regions which survive a threshold of $p<0.001$ uncorrected and 10 voxels over the whole brain in Table 1. Our discussion of the results focuses on the regions within this set which passed correction for multiple comparisons at this threshold ($t>3.58$ and 10 voxels) and the cluster corrected level, searching over the whole brain. In addition, we tested for RS for outcome in a region of interest in the left aIPS (10mm radius, centred on -52,-32, 44), defined by our previous work on object-goals (Hamilton and Grafton, 2006).

A region of interest (ROI) analysis was used to test for differences in the magnitude of the RS effect between the left and right IPL and IFG. We used a voxel counting approach with large ROIs because we do not have localiser scans or precise ‘a priori’ predictions. Four ROIs were generated, covering the left and right IFG and left and right IPL as defined in previous studies of the MNS (Iacoboni et al., 2005; Iacoboni et al., 1999; Johnson-Frey et al., 2003; Johnson-Frey et al., 2005). Each ROI contained over 3000 voxels, providing an inclusive definition of the frontal and parietal components associated with the putative human mirror neuron system. For each participant, we localised the strongest RS effect by examining the magnitude of the main effect of Outcome in every voxel over all four ROIs, and defining the voxels which were in the top 5% for effect size as ‘strong RS voxels’. If the outcome effect was equally distributed between all four ROIs, we would expect 5% of the voxels in each ROI to be ‘strong RS voxels’ by chance. For each participant and each ROI, the total number of ‘strong RS voxels’ was calculated. This gives a measure of the extent of the RS effect in each ROI, regardless of individual differences in the global level of the BOLD signal. A repeated-measures ANOVA with factors lateralisation (left – right) and site (IFG – IPL) was then used to test if ‘strong RS voxels’ were preferentially located in one of the four ROIs. The same analysis was repeated with thresholds of 20% and 1% to ensure generality.

To identify brain regions showing repetition suppression for the kinematic features of an action, we calculated a contrast for the main effect of Kinematics (novel > repeated), regardless of the outcome of the observed action. We report regions which survive a threshold of $p<0.001$ uncorrected and 10 voxels over the whole brain in the lower part of Table 1. An analysis of the distribution of the top 5% of voxels for the kinematics contrast (strong RS voxels) was also carried out to determine if the left or right inferior frontal or parietal regions preferentially encoded kinematic features, and to check that this method of analysis was not systematically biased by physiological factors.

Results

A stronger response to novel outcomes than to repeated outcomes was found in regions throughout the expected fronto-parietal action circuits (Table 1). Two of these regions, the right inferior parietal lobule (IPL) and the right inferior frontal gyrus (IFG) extending to the inferior frontal sulcus, survived the whole brain cluster-corrected threshold, and are illustrated in Figure 2A&B. In both these clusters, the robust response to novel outcomes was suppressed when the same outcome was repeated on a second trial, regardless of the hand action. This pattern of data signifies that outcomes rather than motor parameters are encoded in neuronal populations within these regions (Grill-Spector and Malach, 2001; Hamilton and Grafton, 2006). Because of previous evidence for an RS effect for the goal of a simple grasping action in left aIPS (Hamilton and Grafton, 2006), a region of interest analysis was performed in this area to test for RS for the more complex outcomes. Significant suppression for repeated outcomes was seen in this region (Figure 2), as part of a larger cluster extending into the post-central sulcus.

The plots of parameter estimates shown in Figure 2 also hint at an interaction between RS for outcome and for kinematics, but an analysis of interactions over the whole brain did not reveal any effect in this region even at the weaker $p<0.001$ threshold. This further supports the conclusion that these areas are primarily sensitive to novelty for outcome irrespective of the kinematic parameters. Analysis of the responses of right IPL to each individual set of movies indicates that these effects are not driven by a single stimulus, but generalise across a wide variety of actions (Supplementary Figure 1). A plot of a post-stimulus time histogram in this region confirms that activity started near zero in all conditions (Supplementary Figure 3).

A further analysis was used to determine if the RS effect for outcomes differentially recruited inferior parietal or inferior frontal cortex, and if there was an interaction with hemisphere. Descriptively, the peak RS effect in the right IPL region was 50% greater than the next largest peak RS effect in the right IFG region, and the right IPL cluster contains over four times the number of voxels found in the right IFG cluster (Table 1). A t-test directly comparing the magnitude of the RS effect in the peak voxel of right IPL to the peak voxel of right IFG revealed a significantly stronger effect size in the parietal region ($t=1.77$, $df = 19$, $p=0.046$). An 2x2 factorial repeated measures ANOVA comparing the number of strongly activated voxels in each participant and each ROI revealed a main effect of side (F = 9.01, df = 1,19, p=0.007) with a stronger RS effect on the right compared to the left. There were no effects of lobe (F=0.19) but there was a interaction between lobe and hemisphere (F=4.44, df = 1,19, p=0.049), with the more voxels activated in the right IPL compared to other regions. This effect is illustrated in Figure 3 (dark bars). Two secondary analyses using harsher (top 1%) and weaker (top 20%) thresholds to define the number of strongly activated voxels gave a similar pattern of results for the main effect of side (p<0.025 for both thresholds) but a mixed result for the interaction (p<0.014 for the 20% threshold but not significant for the 1% threshold). This is likely due to floor effects on the number of voxels in the 1% case.

These results demonstrate a clear lateralisation of the RS effect for outcomes to the right hemisphere. Though both the right IFG and right IPL showed robust RS effects for outcomes, the ANOVA analysis also revealed a stronger effect in the right IPL ROI, leading to the conclusion that this is the dominant region for outcome representations in the brain.

An analysis of novel kinematic features compared to repeated kinematic features did not yield any regions with significance exceeding the corrected statistical thresholds accounting for a whole brain search volume. In an exploratory analysis, RS for kinematics passed an uncorrected threshold (p<0.001 and 10 voxels) in left middle intraparietal sulcus, left lateral occipital cortex and left superior temporal sulcus (Supplementary Figure 2). These results are consistent with previous data showing RS in left lateral occipital cortex for hand trajectory (Hamilton and Grafton, 2006) and grasp (Hamilton and Grafton, in press).

The analysis of the distribution of the 5% of voxels with the strongest RS effect (strong RS voxels) was also conducted using data from the Kinematics contrast in order to check the generality of the method, and results are illustrated in Figure 3 (light bars). An ANOVA on the number of voxels strongly activated for the kinematics contrast in each ROI of each participant revealed a significant lobe by hemisphere interaction (F=5.97, df = 1,19, p=0.024) driven by the large number of voxels in left IFG. There were no significant main effects (all p>0.3). The finding of excess ‘kinematic’ voxels in left IFG is in line with other results from our lab showing RS for grasps in the left IFG (Hamilton and Grafton, in press). The apparent discrepancy between this result and the lack of a main effect of kinematics in left IFG could be due to inter-subject variability in IFG, but further studies will be required to examine this issue fully. Importantly, the distribution of highly active voxels in the Kinematics contrast demonstrates that this method of examining voxel distribution is not systematically biased towards any one brain region by physiological factors, but rather provides a valuable assessment of effect sizes in the different lobes of the brain.

In addition to these analyses, the data was examined at the single subject level as described in the supplementary information. The results broadly support our contention that the right inferior parietal lobule shows repetition suppression for the outcomes of human actions, but also emphasis the need for further studies of individual differences in the localisation of high level action representations in the brain.

Discussion

Our data demonstrate a robust repetition suppression effect for outcomes in right IPL and right IFG, regardless of the kinematic features of the observed action generating the outcome. Repetition suppression occurs when a population of neurons encoding a particular stimulus characteristic gives a weaker response when that characteristic is repeated (Grill-Spector and Malach, 2001). Thus, our data demonstrate that human IPL and IFG contain populations of neurons which encode the outcome of an observed action. These results are concordant with previous data implicating IPL and IFG in goals (Hamilton and Grafton, 2006) and intentions (Fogassi et al., 2005; Iacoboni et al., 2005).

The present results have important repercussions for models of human action understanding in relation to the brain. In particular, our data provide some preliminary evidence against the claim that the inferior frontal and inferior parietal brain regions commonly termed the mirror neuron system represent only the kinematic parameters, such as the shape of the hand during observed grasping and cannot reflect higher order intentions (Jacob and Jeannerod, 2005). Before addressing the issue of intention representations in the brain, we first consider possible confounds in our data and summarise how our results fit into an emerging hierarchical model of human action understanding.

Limitations

There are three possible confounds which might affect our interpretation of these data. First, there is evidence that the kinematics of performed hand actions are altered by the goal of the action (Ansuini et al., 2006), so it could be argued that our outcome RS reflects a subtle sensitivity to kinematic parameters. However, if this were the case, we would expect to see similar RS for both the subtle kinematic effects when repeating particular outcomes and the more dramatic kinematic differences in the kinematics contrast. This was not the case, and similar results were obtained in other RS studies of high level action representations (Hamilton and Grafton, 2006; Hamilton and Grafton, in press). Thus it is implausible to suggest that kinematic representations rather than outcome representations underlie the observed effects.

The second question which arises from this result is the possibility of an attentional or task switching confound. The right parietal cortex is associated with spatial attention (Corbetta and Shulman, 2002) and the right inferior frontal sulcus with task switching (Brass et al., 2005) – could the sequence of repeated and novel stimuli have engaged these more general processes? We suggest that the data do not support this interpretation. fMRI (Corbetta and Shulman, 2002), TMS (Mevorach et al., 2006) and lesion (Husain and Rorden, 2003) studies of attention and salience all demonstrate a role for posterior inferior parietal cortex in this function. The locus of the RS for outcome we report is in the anterior inferior parietal lobule, which does not have a specific role in attention. Furthermore, our experiment used a one-back RS design, where every movie functions as both ‘prime’ and ‘target’. Participants have no awareness of the sequence and performed the same cognitive task (detect the stop movies) throughout the experiment, which rules out a switching account. There were no systematic differences in the use of space between the video clips, and all clips within a set showed the same objects in contact with the actor’s hands. This rules out spatial or object-based attentional explanations of our data. Any brain mechanism which detects the sequence of repeated or changing action outcomes and motor parameters is the subject of our study, and we suggest that it would be a tautology to label such a mechanism ‘attention’ or ‘switching’ without specifying how and why it detects these changes.

A third limitation arises from our incomplete knowledge of the neural mechanisms underlying RS effects and their link to behaviour. Several different mechanisms have been proposed (Grill-Spector et al., 2006; James and Gauthier, 2006; Krekelberg et al., 2006). These differ in their attitude to general neural suppression versus more rapid responses versus the sharpening of neuronal tuning curves, but agree that a population-code explanation for suppression of the BOLD signal and the release from suppression is plausible. Neurophysiological recordings from visual processing regions support this conclusion (Desimone, 1996; Van Wezel and Britten, 2002). Though single cell recordings have not yet been made in parietal or premotor regions to test for RS, fMRI evidence suggests that RS occurs throughout the brain in domains as varied as number, object and syntax (Buckner et al., 1998; Noppeney and Price, 2004; Piazza et al., 2004).

Some RS studies go further than ours and make links between RS in the brain and behavioural priming (Wig et al., 2005), but this was not possible in the present experiment. Normal participants perform perfectly in tasks requiring psychophysical judgments about the intentions and actions present in the simple video clips, and reaction times cannot be measured for video stimuli with a duration of several seconds. Thus, behavioural measures were not available in the present task. This means that we are able to avoid the complex debate over the precise links between RS and behavioural priming, and focus on the most general and parsimonious interpretation of our RS effects. This is the proposal that suppression of the BOLD signal reflects the repeated engagement of the same neuronal population, and release from suppression reflects the engagement of a different neuronal population within the same brain region (Grill-Spector and Malach, 2001; Hamilton and Grafton, in press). Therefore, we suggest that the observed RS effects for outcome mean that right IPL and right IFG contains populations of neurons which encode the physical outcomes of other people's actions.

A hierarchy for observed actions

The results presented here demonstrate that the outcomes of observed actions are encoded in a right lateralised, fronto-parietal circuit. Specifically, evidence for outcome representations was found in the right IFG, the right IPL and in a cluster extending from the left post central sulcus to the left anterior intraparietal sulcus. Previous work has associated an inferior parietal – inferior frontal network with the performance and observation of complex, goal directed hand actions (Ehrsson et al., 2000; Grafton et al., 1996). In particular, some studies implicate the left intraparietal sulcus in performing grasps (Culham et al., 2003; Frey et al., 2005) and in the observation of grasps (Shmuelof and Zohary, 2006) while others implicate the IFG in the observation (Iacoboni et al., 2005) and imitation of goals (Koski et al., 2002). As these studies indicate, the question of the representation of goals, grasps and other kinematic parameters in the fronto-parietal motor circuit is a complex one which is unlikely to have a straightforward answer. Furthermore, these studies did not use repetition suppression methods and did not systematically aim to distinguish between different levels of the motor hierarchy.

We suggest that our data can best be interpreted in the context of previous studies which used repetition suppression to examine object-goal, trajectory and grasp representations (Hamilton and Grafton, 2006; Hamilton and Grafton, in press; Shmuelof and Zohary, 2005). The study by Shmuelof and colleagues revealed encoding of different types of grasp in anterior intraparietal sulcus, post-central sulcus and precentral sulcus, as well as encoding object identity (goal) in the left anterior intraparietal sulcus and in visual regions. Congruent with these results, the studies from our own lab demonstrate that the left anterior intraparietal sulcus encodes the object-goal of an action, while inferior frontal and lateral occipital regions encode kinematic features of an observed action such as trajectory and hand shape. The data from the previous studies were used to develop a hierarchical model of action understanding, in which goal representations in the inferior parietal regions sit at the top of the hierarchy, while visual kinematic representations in lateral occipital regions and motor kinematic representations in inferior frontal regions form provide a lower level analysis of action (Hamilton and Grafton, in press). The new data demonstrating a particular role for the right IPL and, to a lesser extent, right IFG in encoding the outcomes of observed actions complements and extends the previous model. It also reinforces our argument that, despite the widespread assumption that abstract and complex entities must be linked to the frontal cortex, in fact the parietal cortex is also important for higher level action representations of goals and outcomes.

There are also some key differences between the present results and the prior studies of goal representation, which can help us understand the brain systems for action understanding in more detail. Our two previous studies examined object-goals, defined by the identity of a grasped object. In contrast, the current study examined the more complex case of outcomes, defined by the physical consequences of the action of a person. In parallel with this distinction in the precise nature of the action understanding, we found a striking difference in brain lateralisation. While both studies of object-goals reported robust left parietal effects, the outcomes studied here induced strong right parietal effects. This means that for the brain, object-goals are not the same as outcomes. Instead, these two different representations may fall at different levels in the motor hierarchy, or have different functions in understanding the intentions of others. To gain some insight into the reasons for this pattern of lateralisation, we must turn to studies characterizing lateralisation of motor control in the human brain.

A hierarchy for performed actions

Few studies distinguish between different hierarchical levels of action representation, in particular for complex, goal oriented behaviour. Beginning at the lower levels, primary motor cortex clearly provides the most primitive cortical motor representation. Slightly more complex representations of different grasp configurations and kinematic parameters can be found in the inferior frontal and premotor cortex (Ehrsson et al., 2000; Rizzolatti et al., 1988). These regions are intimately connected with the primary motor cortex and even the spinal cord (Dum and Strick, 2002), and are likely to provide a kinematic representation of action. For example, inferior frontal gyrus is robustly activated during imitation of simple finger movements (Iacoboni et al., 1999).

Moving to higher levels of the hierarchy, many studies report the activation of both inferior frontal and inferior parietal cortex in a variety of planning tasks (Johnson-Frey et al., 2005) and action tasks (Rizzolatti et al., 1996), and it is clear that these regions function as a closely integrated network. Inferior parietal cortex and the cerebellum also seem to have a role in using and switching between internal models for the control of tools (Imamizu et al., 2004). However, there is some evidence for more abstract, goal representations in the inferior parietal cortex, in particular from studies of patients with apraxia (Buxbaum et al., 2005; Haaland et al., 2000) and in studies which use transcranial magnetic stimulation to disrupt goal processing in typical participants

(Tunik et al., 2005). Similarly, neurophysiological recordings from the monkey IPL report mirror neurons for complex action sequences in this region (Fogassi et al., 2005).

All these data suggest a hierarchy for performed actions, from kinematic representations in IFG to more complex goal representations in IPL, which matches the hierarchy for observed actions described above. However, there is also a distinct lateralisation of observed action representations in the parietal cortex, with observed object-goals represented in the left IPL (Hamilton and Grafton, 2006) and observed outcomes represented in the right IPL. Can this distinction also be made for performed actions?

Many studies of high level action planning and execution report a left lateralisation. For example, planning of grasping actions activates the left IFG and IPL regardless of the hand used (Johnson-Frey et al., 2005) and the left IPL is activated for hand-object interactions of either hand (Naito and Ehrsson, 2006). Similarly, patients with damage to left IPL have difficulty pantomiming or performing tool-use actions (Haaland et al., 2000). These data point to a role for the left IPL in planning goal-directed reaching and grasping actions. However, there is also increasing evidence for a role for right IPL in complex action planning. Patients with right IPL damage have particular difficulties with multi-step actions (Hartmann et al., 2005) and with imagined action (Sirigu et al., 1996). Right IPL is robustly activated in tasks requiring multi-step planning such as the Tower of London task (Baker et al., 1996; Newman et al., 2003), and when participants must plan and remember future actions (den Ouden et al., 2005). This region may also be particularly important for assessing feedback on performed actions (Blakemore et al., 1998; Farrer et al., 2003; Ogawa et al., 2006), which is essential in multi-step and goal oriented behaviours.

Together, all these data on action planning and execution support the idea that there is a hierarchy for performed action representations, with kinematic parameters found in the IFG, planning of goals such as taking a tool in the left IPL, and monitoring of action sequences and action outcomes in right IPL. Taken together, the joint hierarchical models of action execution and action observation have important implications for our understanding of mirroring and intention representation in the brain.

Mirroring in the action hierarchy

The two hierarchical systems described above, for action observation and for action performance, can be mapped together. That is, it seems that the right inferior parietal cortex contributes more to the representation of the outcomes of complex actions for the self and for others, while the left inferior parietal cortex is related more to motor plans and goals for the self and for others. This result implies that a strong principle of mirroring may exist within fronto-parietal cortex, and that there is a tight locking between the neural activations for self and other. However, this tight locking need not imply a unitary 'direct-matching' mechanism acting in a single step over the whole mirror neuron system (Gallese, 2003). Rather, the application of the principle of mirroring at each level of a complex action hierarchy supports more sophisticated, multi-stage models of goal and intention understanding (Csibra, in press).

The suggestion of mirroring for outcomes and intentions also has important implications for Jacob's challenge to the mirror neuron theory of intention understanding (Jacob and Jeannerod, 2005). Jacob argued that the mirror neuron system represents only kinematic properties of actions (motor intentions) and not prior intentions. The data presented here demonstrate that the right IPL and right IFG encode outcomes, which are independent of the kinematic parameters of the action. The outcomes in our study, such as turning on a light or opening a box, meet Jacob's definition of a prior intention (Jacob and Jeannerod, 2005). Thus, our data demonstrate that other people's prior intentions are represented in parts of the human mirror neuron system, contradicting part of Jacob's hypothesis. In addition, a series of papers demonstrate a role for the right IPL in controlling and planning one's own intentional actions (Baker et al., 1996; Blakemore et al., 1998; den Ouden et al., 2005; Farrer et al., 2003; Hartmann et al., 2005; Newman et al., 2003; Ogawa et al., 2006). Thus, it seems possible that the principle of mirroring applies at the level of intentions and outcomes. We note that this does not mean that the mirror neuron system must also represent mental states such as beliefs (Gallese and Goldman, 1998), which are likely encoded elsewhere (Saxe, 2005).

As a neuroimaging study, the current paper cannot demonstrate that individual neurons which encode the outcomes of other people's actions also encode the outcomes of one's own actions, but our data is congruent with single unit recordings in the macaque inferior parietal lobule (Fogassi et al., 2005). Further experiments, in both humans and non-human primates, will be required to fully explore the overlap of outcome and intention representations for self and other, and to provide a definitive test of whether mirroring applies to prior intentions. Our data provide some initial evidence that Jacob's challenge may fail, and that mirror neuron regions of the human brain are not restricted to kinematic parameters but represent complex action outcomes.

Conclusion

This paper demonstrates that repetition suppression for the outcomes of complex actions is found in the right inferior parietal lobule and right inferior frontal gyrus. Therefore, these brain regions contain populations of neurons which encode observed action outcomes, regardless of the kinematic parameters of the action. These results support a hierarchical model of action understanding (Hamilton and Grafton, in press) in which a cascade of visuomotor processing in parietal and frontal regions allows us to understand the goals and outcomes of other people's actions. The principle of mirroring may apply at each level of this hierarchy, providing a common code for both planning our own intentional actions and understanding the intentions of other people.

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Table 1. Regions showing significant repetition suppression for outcome and action over the whole brain at a threshold of p<0.001 uncorrected and 10 voxels. Bold indicates regions which meet the whole brain cluster corrected threshold at p<0.05 or the ROI corrected threshold at p<0.05. Subpeaks more than 8mm from the main peak in each cluster are also listed.

Region	**Number of voxels**	**T**	**p cluster corrected**	**MNI coordinates**		
				x	**y**	**z**
Outcome contrast						
right inferior parietal lobule	**892**	**7.40**	**<0.001**	**58**	**-30**	**32**
				62	-20	20
				42	-38	36
right lateral occipital	199	5.76	0.053	44	-56	-8
left post-central sulcus extending to anterior intraparietal sulcus	**105**	**4.64**	**0.294**	**-56**	**-26**	**46**
left superior parietal lobe	26	4.51	0.942	-34	-46	70
left lateral occipital	72	4.49	0.529	-46	-60	-6
right inferior frontal gyrus extending towards the inferior frontal sulcus	**204**	**4.41**	**0.049**	**42**	**12**	**18**
				50	14	20
				36	6	28
left inferior parietal lobule	54	4.40	0.701	-58	-34	30
left inferior frontal gyrus	31	4.21	0.909	-46	4	18
left premotor cortex	24	3.99	0.953	-18	-4	72
right lateral occipital	12	3.83	0.993	38	-60	12
Actions Contrast						
left lateral occipital	80	4.93	0.444	-56	-60	-2
left superior parietal lobe	46	4.73	0.772	-22	-62	68
left fusiform	12	3.98	0.993	-48	-64	-22
left superior temporal sulcus	15	3.97	0.988	-50	-62	12

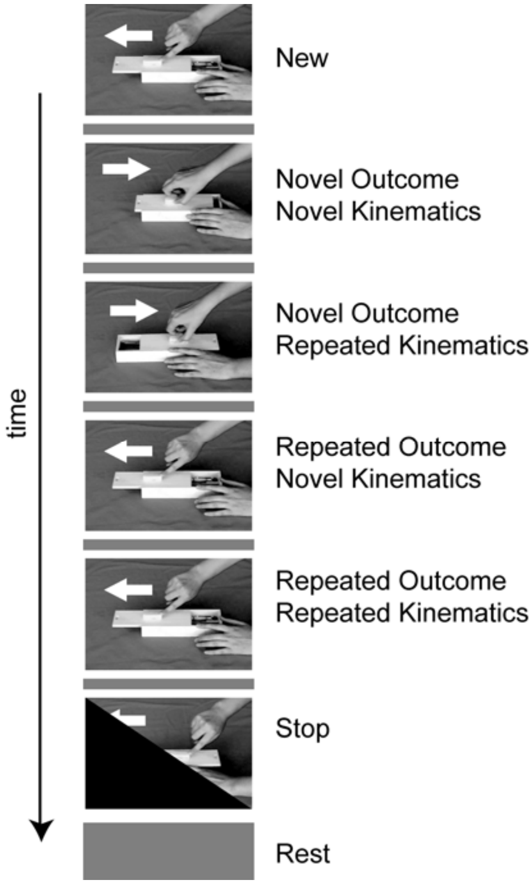

Figure 1. A set of stimuli for inducing repetition suppression. Movies of a hand opening or closing a box were shown in a pseudo-random sequence. In this illustration, each movie is represented by one picture and the white arrows indicate the direction of hand motion in the movie, but were not present in the actual stimuli. Classifications of each movie are given on the right. For example, the first movie (New) depicts a hand opening a box with a leftward finger action. Relative to this, the second movie where the hand closes the box with a rightward precision grip depicts a novel outcome and a novel kinematics pattern. In the third movie, the hand opens the box with a rightward precision grip, which is a novel outcome and a repeated kinematic pattern, relative to the second movie. Thus, every movie functions as both a ‘prime’ for the next movie and a ‘target’ in the analysis. Twelve distinct sets of movies were used, and in every set the physical outcome of the action and the kinematic parameters of the action varied independently.

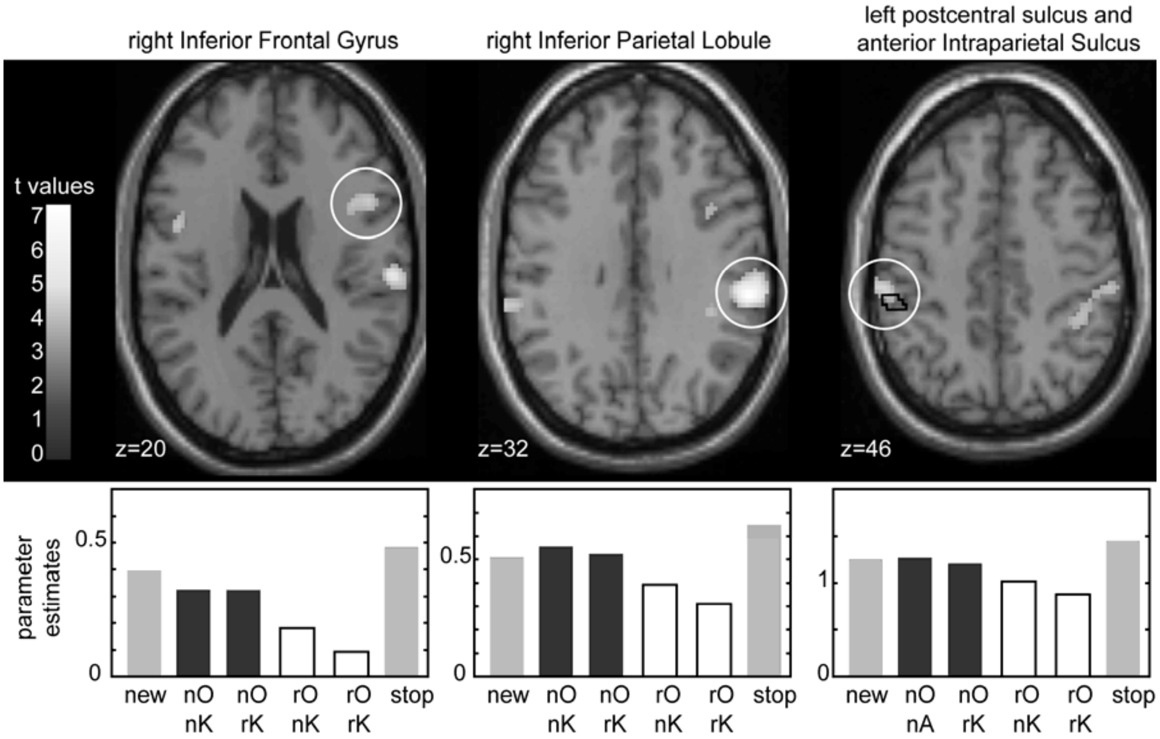

Figure 2. Brain regions showing repetition suppression for outcome. Significant suppression ($p<0.05$ corrected, $t<3.58$) for repeated outcomes (white bars) compared to novel outcomes (dark barks) was seen in the right IFG extending towards inferior frontal sulcus, right IPL and left post-central sulcus extending to aIPS, as highlighted with white circles. Parameter estimates (SPM betas) for each region are plotted below and are labelled as: n=novel, r = repeated, O = Outcome, K = Kinematics. Responses to new and stop trials are shown as mid-grey bars. The region outlined in black in the right brain slice is the part of aIPS which represents action goals (Hamilton and Grafton, 2006), which overlaps with the outcome representation reported here.

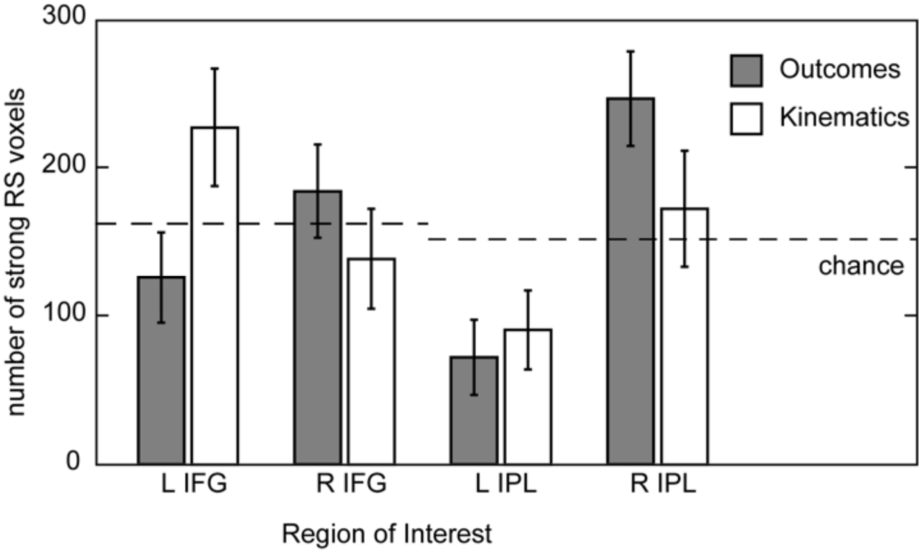

Figure 3. Number of strongly activated Outcome and Kinematic voxels in each lobe The distribution of the top 5% of RS voxels for the Outcome contrast and for the Kinematics contrast between the left and right IPL and IFG ROIs is illustrated. By chance, each ROI should contain approximately 160 strong RS voxels (dashed line). Error bars are standard error.