The role of immediate and final goals in action planning: An fMRI study

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To interact effectively with our environment, we need to specify the intended outcomes (goals) of our actions. In this process, immediate goals and final goals can be regarded as different levels within a hierarchically organized system for action planning: immediate goals and movement details are selected to accomplish more remote goals. Behavioral studies support this notion of different levels of action planning, but the neurophysiological basis remains unclear.

Using fMRI, we examined the neural correlates of preparing object manipulations based on either the desired end-state (the final goal) or the initial movement towards a target (the immediate goal). Subjects had to insert an object (consisting of a large and a small cube) into one of two corresponding large and small slots. The subjects were cued on either which slot to fill (FINAL GOAL trials) or which object part to grasp (IMMEDIATE GOAL trials). These actions required similar movements, but different planning.

During FINAL GOAL trials, there was differential preparatory activity along the superior frontal gyrus (bilaterally) and in left inferior parietal cortex. IMMEDIATE GOAL trials evoked differential activity in occipito-parietal and occipito-temporal cortex. These findings support the notion that actions can be planned at different levels. We show that different fronto-parietal circuits plan the same action, by a relative emphasis on either selecting a sequence of movements to achieve a desired end-state, or selecting movements spatially compatible with given object properties.
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Introduction

When we perform actions in daily life, these actions are usually driven by a desired outcome or action goal, rather than being stereotyped responses to environmental stimuli (Hommel et al., 2001; Mechsner et al., 2001). Using the anticipated effects of our actions to guide action planning allows us to execute top down control (including contextual information and previous knowledge) over movement execution, and hence to behave flexibly and purposefully.

Once an action goal has been defined, the movement details to achieve that goal can be selected. Accordingly, a single action goal may be accomplished by multiple action means. For instance, a ball may be thrown either underarm or overarm to hit a certain target. This phenomenon, referred to as motor equivalence (Lashley, 1930), suggests that specifying the intended end-state of an action (the goal) can be functionally distinguished from the processes involved in selecting the contingent movement details (the means) (Dehaene and Changeux, 1997).

The relevance of this distinction is illustrated by studies showing that brain lesions leading to ideational apraxia can impair the patient's conceptual knowledge of the overall goal of an action, leading to spatial and temporal errors in executing the action, although the individual movement elements may be performed accurately in isolation (Luria, 1980). At the behavioral level, imitation studies provide evidence for the dominant role of goals in action planning, showing that children tend to imitate the goal of observed movements and ignore the way in which the goal is accomplished (Meltzoff, 1995; Bekkering et al., 2000).

It should be emphasized that, rather than forming a dichotomy, action goals and individual movements can be considered to represent different levels within a functional hierarchy. The notion that the motor system is organized hierarchically has been proposed already in the first half of the 20th century (e.g., (Sherrington, 1947). This hierarchy implies that the motor system can be viewed as a "system of systems" (Weiss, 1941), in which each level consists of a collection of subsystems, which are themselves composed of smaller units. In such a system, higher-level systems can modulate the activity of lower-level mechanisms. With respect to motor planning, the highest levels of the hierarchy are concerned with generating commands to achieve an action goal, while lower-level mechanisms translate the commands into a movement. Thus, action selection would involve activation of increasingly smaller elements – although it should be noted that

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this does not imply that the elements are activated in sequential order. This hierarchical view of the motor system is paralleled by its phylogenetic development, during which additional layers of control have developed that modify the reflexes of more ancient structures like the spinal cord (Gazzaniga et al., 2002).

Although the central role of action goals is widely recognized, most studies on action goals have focused on one type of goal, typically operationalized as the position or object that is the target of a single reaching or grasping act (Hamilton and Grafton, 2006; Hoshi and Tanji, 2002; Koski et al., 2002). However, in most daily life situations, grasping is just an initial component of a broader action, in which the grasped object is used to achieve a subsequent goal. For instance, to drink milk from a cup, the cup has to be brought to the mouth. This requires grasping and transporting the cup by means of specifying reaching parameters of the arm and selecting the appropriate hand aperture. Thus, multiple immediate goals may be selected to comply with a more remote action outcome. Indeed, behavioural studies have shown that the immediate goal of grasping an object is typically selected in a way that allows the actor to accomplish a comfortable end-position, depending on the overall goal (Rosenbaum et al., 2001; Cohen and Rosenbaum, 2004). These findings indicate that action goals are selected at different levels, with the more final goals guiding the selection of immediate ones. Yet, little is known about the neural implementation of this principle in action planning.

It has been well established that spatially guided action planning involves a fronto-parietal network (Rushworth et al., 2003; Kalaska et al., 1997; Passingham, 1993; Kakei et al., 2001; Passingham et al., 1998). Within this network, basic motor control parameters like movement direction and force are encoded in primary motor cortex (Georgopoulos et al., 1986), premotor cortex (Rizzolatti et al., 1988), and posterior parietal areas (Gallese et al., 1994; Crammond and Kalaska, 1989). However, the same areas appear to be also involved in controlling more complex or goal-related aspects of action (Koski et al., 2002; Mushiake et al., 2006; Thoenissen et al., 2002; Hamilton and Grafton, 2006). Since most studies have typically focused on the lowest and highest levels of the proposed action hierarchy, it remains unclear how portions of the fronto-parietal network contribute to action planning from increasingly remote outcome levels.

In the present study, we assessed how the behavioral distinction between planning actions on different goal levels is realized in the brain. To manipulate these levels, we designed a task in which subjects performed object manipulations that were cued by either the end-state to be accomplished (the *final goal*), or the initial grip on the object (the *immediate goal*). We used fMRI to explore how areas within the fronto-parietal network are involved in planning these tasks. The design allowed us to compare cerebral activity evoked by actions that involved similar movements, but were planned differently.

This is the first study to systematically compare action planning according to different goal levels with fMRI. Manipulating these levels within the action selection hierarchy might enable us to identify which general neural mechanisms are involved when actions have to be planned based on increasingly remote outcomes.

Materials and methods

Subjects

Data were analyzed from sixteen healthy right-handed male volunteers (25±4 years, mean±standard deviation). They all had normal or corrected-to-normal vision, and gave informed consent according to institutional guidelines of the local ethics committee (CMO region Arnhem-Nijmegen, The Netherlands). Data from two other subjects were discarded because of head-movement artifacts during the MR scanning.

Experimental set-up

Subjects had to perform object manipulations while laying supine in the MR scanner. The standard mattress of the scanner bed was removed, allowing the subjects to lie considerably lower within the bore of the scanner. Their head was fitted inside a phased-array receiver head coil. The head-coil was tilted forward by 30° along the subject's sagittal plane (see Supplementary Fig. 1). This set-up allowed the subjects to have a direct line of sight of the objects to be grasped and to visually control their movements. We ensured that subjects performed the task by moving their right forearm only. This was achieved by fitting a plastic splint around the elbow, and by firmly but comfortably strapping the arm to the scanner table. The splint constrained the rotations around the elbow to the plane between the home key and the target object, minimizing the movements around the shoulder. The subject's head was kept in place by using foam wedges.

An optical response button box (MRI Devices, Waukesha, WI), positioned on the upper leg, served as a home key on which subjects had to keep their hand in between trials. This device allowed us to record subjects' reaction times and total movement time.

The subjects were instructed to grasp and manipulate an object consisting of a large red cube and a small green cube, attached to a supporting rail positioned in front of them. The object was held in place through an arc-shaped device positioned over the subject's hips inside the MR scanner (see Supplementary Fig. 1). The object was positioned next to a rectangular box containing two cubic slots of different size and color. The subject could comfortably perform visually guided reaching–grasping movements towards the object, extract the object from the supporting rail, insert the object into one of the slots, and finally re-position the object in the supporting rail. Crucially, the object and the slots were designed such that the object could be placed in the large slot only when it was grasped at the small cube. Analogously, the object could be placed in the small slot only when it was grasped at the large cube (Fig. 1).

The side of the box that was not visible for the subject contained two cubic slots as well, but the combination of size and color was reversed: while on one side of the box, the yellow slot (located above the blue slot) was large, the yellow slot on the other side of the box was small, still located above the blue slot. Which two slots were visible for the subject could be varied by rotating the box by means of a pneumatic mechanism.

An LED was installed in the middle of each of the two sides of the box (Fig. 1). The LED could light up in red, green, blue, and yellow. The color of the LED instructed the subject on the movement required to solve the task (see below).

MR-compatible switches located at various positions on the device recorded the time at which the object was removed from the supporting rail, the time at which the object was inserted into one of the slots, and the time at which the object was put back into the supporting rail. The fact that the subjects had to click the object back into the rail ensured that the starting position of the larger cube did not vary over trials.

Control of the pneumatic rotation mechanism and recording of the movement-related responses was carried out using a PC
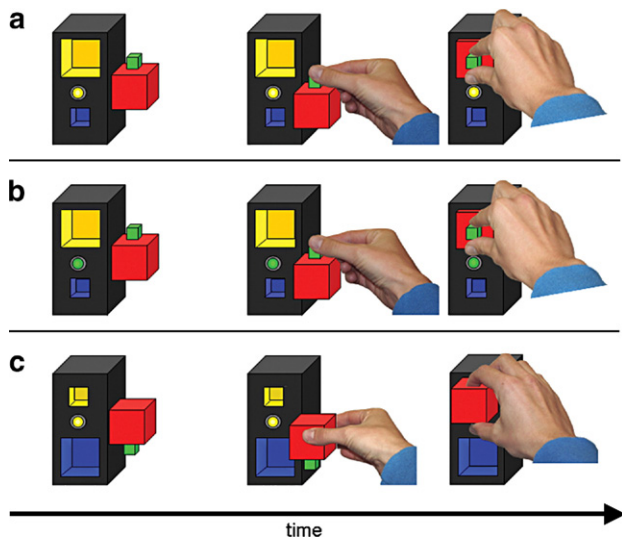
Fig. 1. Object manipulation task. The task involved removing the object from the rail by grasping it at either the small (green) or large (red) part, inserting it into one of the slots, and placing it back into the rail. The size and shape of the object and the slots constrained the manipulation: when the object was grasped at its small part, it could only be fitted into the large slot, and when it was grasped at its large part, it could only be inserted into the small slot. An LED instructed the subjects about the slot to insert the object in (FINAL GOAL trial) or the object part to manipulate (IMMEDIATE GOAL trial). This design allowed us to manipulate the manner in which the action was planned (i.e. based on either the end-state of the action, or the object to be manipulated), while keeping the actual movements constant. Figure shows time course from cue onset until inserting the object into a slot. (a) Time course of a trial in which a FINAL GOAL cue is given: the yellow LED instructs the subject to insert the object into the yellow slot. This requires the subject to grasp object at its small part. (b) Time course of a trial involving an equal object manipulation, but now instructed with an IMMEDIATE GOAL cue. The green LED instructs the subject to grasp the object at its green part. This requires the subject to insert the object into the large slot. (c) Time course of a trial with the grasping device in the alternative orientation. A yellow FINAL GOAL cue is given, but now this refers to the smaller slot. The subject has to grasp the object at its large part to insert it into the yellow slot. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

running Presentation 0.81 (Neurobehavioral Systems, San Francisco, CA).

Experimental time course and procedures

During the task, in each trial subjects had to grasp the object in a certain way, either at the large or the small part, remove the object from the rail to put it into one of the two slots, and re-position object in the supporting rail. These object manipulations could be cued by providing either the required end position of the object (the slot) or the part of the object that had to be grasped. A FINAL GOAL cue typically referred to one of the two slots; it instructed the subject to put the object into either the blue or the yellow slot. Accordingly, subjects had to grasp the object in a way that allowed them to achieve this outcome. An IMMEDIATE GOAL cue referred to the part of the object that had to be grasped; this could be either the red (large) part or the green (small) part. Subjects then had to transport the object to the slot that could be filled up using this grip. In this way, each action could be cued by either its IMMEDIATE

or its FINAL GOAL, allowing us to compare otherwise similar movements that differed in only this respect.

The cues were signaled using a four-colored LED. When the LED turned blue or yellow, it referred to the FINAL GOAL, and the object had to be inserted into the blue or yellow slot, respectively. Conversely, a red or green LED referred to the IMMEDIATE GOAL, and the object had to be grasped at the red (large) or green (small) part.

Crucially, the device was rotated from time to time to ensure that color and location of the FINAL GOAL slot were unrelated to the part of the object to be grasped, as signaled by the IMMEDIATE GOAL cue. This prevented subjects from using any association between IMMEDIATE and FINAL GOAL cues as a strategy. Due to the alternating rotation, the small cube was on top of the large cube (orientation 1) in 50% of the trials, and below the large cube (orientation 2) in the other 50% of the trials, which was balanced over the main conditions (FINAL GOAL, IMMEDIATE GOAL).

When the LED switched on, subjects had to leave the home key as soon as possible, make the appropriate object manipulation, and return to the home key. After 6 s, the LED switched off, and an inter trial interval of variable length (1.5–6 s) followed. Subjects were instructed to complete their action before the LED switched off. The experiment was subdivided into blocks that had alternating orientations of the slotted box. At the beginning of each block, the box rotated, followed by a variable amount of time (2–7 s), so that the subject could not predict cue onset. Each block contained a randomized number of 3 to 9 trials.

Subjects first had a training session outside the scanner (typically 15 min), until error-free and sufficiently fast performance was reached over at least 20 consecutive trials. This could be monitored by the experimenter on a computer screen. After the subject had been positioned into the scanner, another short practice session followed. The experiment consisted of a total of 252 pseudo-randomized trials, subdivided into 42 blocks. Total scanning time was 45 min.

Behavioral analysis

For each trial, the following behavioral measures were obtained: Reaction time (RT; time from cue onset to release of the home key), Reaching time (ReT, time from release of home key to taking off the object from the side), Transport time (TrT, time from taking off the object to putting the object in its end position in the slot), and Return time (time from putting the object into its end position to return of the hand on the home key). In addition, it was recorded whether the object manipulation that was performed was correct.

RTs, ReTs, and TrTs measured during the scanning session were analyzed separately using SPSS Version 14.0 (Chicago, IL, USA), and considered independent variables of a $2 \times 2 \times 2$ repeated measures ANOVA with main effects of Cue [FINAL GOAL, IMMEDIATE GOAL], Object [LARGE, SMALL], and Orientation of the device [1, 2]. The number of trials was balanced over factor levels, although slight variations occurred due to excluded error trials. Subjects were considered a random factor. Alpha-level was set at $p = 0.05$.

Image acquisition

Images were acquired using a Siemens 3 T Trio MRI system (Siemens, Erlangen, Germany), using the body coil for radio-

frequency transmission, and an 8-channel phased array surface head coil for signal reception. BOLD sensitive functional images were acquired using a single shot gradient EPI sequence (TR/TE 2.3 s/40 ms, 31 transversal slices, voxel size 3.5×3.5× 3.5 mm). At the end of the scanning session, anatomical images were acquired using an MP_RAGE sequence (TE/TR 3.93/ 2300 ms, 192 sagittal slices, voxel size 1.0×1.0×1.0 mm, FoV 256 mm).

Image analysis

Functional data were pre-processed and analyzed with SPM2 (Statistical Parametric Mapping, www.fil.ion.ucl.ac.uk/spm). The first five volumes of each participant's data set were discarded to allow for T1 equilibration. The image time series were spatially realigned using a sinc interpolation algorithm that estimates rigid body transformations (translations, rotations) by minimizing head-movements between each image and the reference image (Friston et al., 1995).

The time series for each voxel was realigned temporally to acquisition of the middle slice. Subsequently, images were normalized onto a custom MNI-aligned EPI template (based on 28 male brains acquired on the Siemens Trio at the F.C. Donders Centre) using both linear and nonlinear transformations.

Finally, the normalized images were spatially smoothed using an isotropic 10 mm full-width at half-maximum Gaussian kernel. Each participant's structural image was spatially coregistered to the mean of the functional images (Ashburner and Friston, 1997) and spatially normalized by using the same transformation matrix as applied to the functional images.

The fMRI time series were analyzed using an event-related approach in the context of the general linear model. Single-subject models consisted of separate regressors describing planning stages for the different levels of Cue, Object, and Orientation. Trial-by-trial measures of this planning stage were extracted from the behavioral measurements during the experiment. In addition, we separately modeled movement execution (split into distinct regressors for grasping the large and the small part of the object), rotation of the device, and error trials.

Each effect was modeled on a trial-by-trial basis as a concatenation of square-wave functions, with onsets time-locked to onset of the LED cue, and offsets time-locked to the release of the hand from the home key. Each of these 12 square-wave functions were then convolved with a canonical haemodynamic response function and its temporal derivative, and down-sampled at each scan in order to generate 24 regressors modeling the main effects described above (Friston et al., 1995).

Head movement effects were accounted for as described in Friston et al. (1996) by including a Volterra expansion of the 6 rigid-body motion parameters as nuisance covariates (Worsley and Friston, 1995), which consisted of linear and quadratic effects of the 6 realignment parameters belonging to each volume and also included spin-history effects as linear and quadratic effects of motion parameters in the previous volume, giving a total of 24 regressors (Lund et al., 2005).

Three further regressors, describing intensities in white matter (WM), cerebrospinal fluid (CSF), and residual compartment (section outside the brain and skull, RC) were added. This was done to account for image intensity shifts due to movement of the hand within the main magnetic field of the scanner (Culham et al., 2006; Verhagen et al., 2006).

Statistical inference

The statistical significance of the estimated evoked haemody-namic responses was assessed using t-statistics in the context of a multiple regression analysis. Contrasts of the parameter estimates for planning stages were calculated, and entered into a one-way, within-subjects analysis of variance (ANOVA). We were specifi-cally interested in assessing effects of Cue (FINAL GOAL, IMMEDIATE GOAL) on brain activity during the planning stage before movement onset. For this purpose, SPM$\{t\}$ values for these effects were created, with the degrees of freedom corrected for nonsphericity at each voxel.

We report the results of a random effects analysis, with inferences drawn at the cluster level, corrected for multiple comparisons using family-wise error correction (corrected thresh-old $p<0.05$, corresponding to a cluster extent threshold of 100 contiguous voxels, given an intensity threshold of $t>3.5$ (Friston et al., 1996)).

Results

Behavioral performance

During scanning, the subjects performed the task accurately (average error rate: 1.9±0.5%). As illustrated in Fig. 2, reaction times (RTs) were shorter when subjects were instructed to grasp
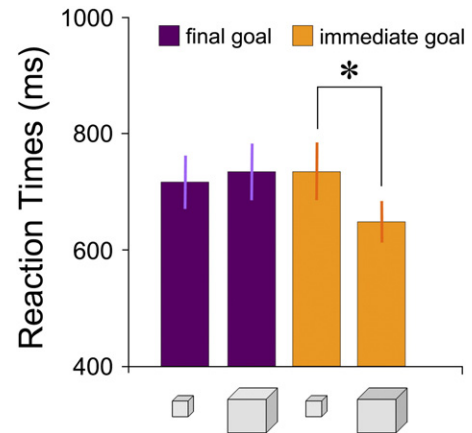
Fig. 2. Reaction times to the LED cue, separate for Cue (FINAL GOAL or IMMEDIATE GOAL), and for the grasped Object part (SMALL or LARGE). FINAL GOAL cues instructed the subject about the required end position of the object (the yellow or the blue slot); IMMEDIATE GOAL cues instructed the subject about the part of the object to be manipulated, which could be either the red (large) or the green (small) cube. In this way, each potential object manipulation could be instructed by either a FINAL GOAL or a IMMEDIATE GOAL cue. RTs were shorter when subjects were instructed to grasp the large part of the object (main effect of Object: $F_{1,15}=21.68$; $P<0.001$). This effect was only observed during IMMEDIATE GOAL trials (Cue×Object interaction: $F_{1,15}=27.41$; $P<0.001$; post-hoc paired T-test of SMALL vs. LARGE (within IMMEDIATE GOAL): $T_{15}=5.19$; $P<0.001$ (orientation 1) and $T_{15}=4.37$; $P=0.001$ (orientation 2); post-hoc paired T-test of SMALL vs. LARGE (within FINAL GOAL): $T_{15}=-0.52$; $P=0.61$ (orientation 1) and $T_{15}=-1.38$; $P=0.19$ (orientation 2)). This indicates that only RTs during IMMEDIATE GOAL, and not during FINAL GOAL trials, were affected by the different accuracy requirements of grasping the small and large part of the object. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
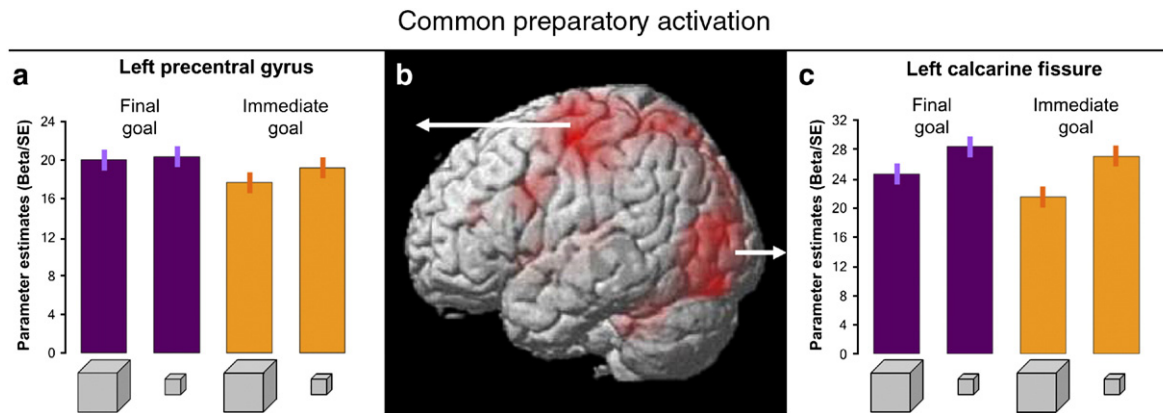
Common preparatory activation

Fig. 3. Common activation in the left hemisphere during preparation of correctly performed trials over all experimental conditions, obtained by conjunction of Cue (Final Goal, Immediate Goal) and Object (Large, Small). (a) Parameter estimates (beta/SE) in Left precentral gyrus [−34 −18 54] for Final Goal (violet) and Immediate Goal (orange) cued actions, separate for Large and Small Object. (b) Statistical parametric maps corrected for multiple comparisons ($P < 0.05$) at the cluster level showing common preparatory activity across conditions, superimposed on a rendered brain. (c) Parameter estimates (beta/SE) in Left calcarine fissure [−4 −78 4] for Final Goal (violet) and Immediate Goal (orange) cued actions, separate for Large and Small Object. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the large part of the object (main effect of Object: $F_{1,15} = 21.68$; $P < 0.001$). Importantly, this effect was different for the two cueing conditions (Cue×Object interaction: $F_{1,15} = 27.41$; $P < 0.001$), being driven by the IMMEDIATE GOAL condition [Post Hoc Paired *T*-test of SMALL vs. LARGE (within IMMEDIATE GOAL): $T_{15} = 5.19$; $P < 0.001$ (orientation 1) and $T_{15} = 4.37$; $P = 0.001$ (orientation 2); Post Hoc Paired *T*-test of SMALL vs. LARGE (within FINAL GOAL): $T_{15} = -0.52$; $P = 0.61$ (orientation 1) and $T_{15} = -1.38$; $P = .19$ (orientation 2)]. This indicates that motor planning was affected by the different spatial accuracy requirements of the small and large object during IMMEDIATE GOAL, but not during FINAL GOAL trials. Both reaching times (ReT) and transport times (TrT) were longer when subjects were instructed to grasp the small part of the object (main effect of Object – ReT: $F_{1,15} = 49.69$; $P < 0.001$; TrT: $F_{1,15} = 9.67$; $P < 0.01$), but these movement parameters did not differ between IMMEDIATE and FINAL GOAL trials (main effect of Cue – ReT: $F_{1,15} = 0.73$; $P = 0.41$; TrT: $F_{1,15} = 2.06$; $P = 0.17$).

Imaging data

On the basis of the behavioral data acquired during scanning, we generated a model of the expected BOLD signal changes evoked during task performance. We considered the planning stage of correctly performed trials in the four conditions determined by Cue (FINAL GOAL, IMMEDIATE GOAL) and Object (SMALL, LARGE). Furthermore, these four independent effects were distinguished from the execution phase of the movements, and from the few incorrect trials. We were able to separately model the planning and execution stages thanks to the fact that the planning stage was modeled according to a 2×2×2 factorial model (i.e., by eight separate regressors), whereas the movement execution was modeled by only two separate regressors, according to the factor that influenced it (i.e., the size of the object to be grasped). This model is justified by the subjects' behavior: the planning stage was influenced not only by the size of the object to be grasped (main effect of Object, $P < 0.001$), but also by the other factors (Cue×Object interaction, $P < 0.001$; Cue×Orientation interaction, $P = 0.018$). Hence, the regressors

describing planning- and movement-related effects were not collinear; their correlations ranged from 4.7% to 26.6%, demonstrating that Planning stage could be distinguished from Movement execution. In this way, we were able to isolate differences and commonalities in cerebral activity evoked during the *planning stage* of actions instructed either based on the end-state to be accomplished (FINAL GOAL), or based on the part of the object to be grasped (IMMEDIATE GOAL).

As can be seen in Supplementary Fig. 2, *execution* of the manipulative movements evoked activity in left precentral gyrus, whereas viewing the device being rotated yielded extensive activity in visual areas. A conjunction analysis on the preparation phase of the experimental conditions showed that preparing the manipulative movements evoked extensive common cerebral activity across experimental conditions, spanning occipital, parietal and frontal regions (Fig. 3). Below we detail our specific findings relative to the *differences* in preparatory activity evoked during the FINAL and the IMMEDIATE GOAL trials (Tables 1 and 2). There was no significant Cue×Object interaction in the whole-brain analysis of the imaging data (*F*-test on Cue×Object; peak voxel $F = 17.05$; $P > 0.7$, FWE-corrected). Direct testing of the main effects of Object (SMALL > LARGE and LARGE > SMALL) revealed no significant effects.

Comparing FINAL and IMMEDIATE GOAL-related preparatory activity

Contrasting FINAL and IMMEDIATE GOAL trials revealed a series of significant clusters bilaterally along the superior frontal gyrus,

Table 1

MNI coordinates of the clusters of activation related to the comparison of FINAL- with IMMEDIATE GOAL-cued action planning

Region	Cluster size	Laterality	x	y	z
Superior frontal sulcus	327	R	14	26	58
Superior frontal sulcus	320	L	−12	38	50
Superior frontopolar gyrus	282	R	16	60	20
Inferior parietal cortex	464	L	−56	−66	26

Cluster size is reported in voxels.

Table 2
MNI coordinates of the clusters of activation related to the comparison of
IMMEDIATE- with FINAL GOAL-cued action planning

Region	Cluster size	Laterality	x	y	z
Occipito-parietal fissure	336	R	18	−72	52
Occipito-temporal sulcus	296	L	−38	−74	−14

Cluster size is reported in voxels.

and in the left supramarginal gyrus (Fig. 4). The clusters along the superior frontal gyrus were anterior to human Brodmann area (BA) 6 (Eickhoff et al., 2005), medial to the dorsal border of BA 46 (Rajkowska and Goldman-Rakic, 1995), and anterior to prefrontal regions involved in maintenance of sensory items over temporal intervals (Rowe et al., 2000). Therefore, the frontal clusters are likely to fall within BA 9/46d or BA 9 (Petrides and Pandya, 2002). The size of the parietal activation prevents a unequivocal attribution of this cluster to the supramarginal gyrus; we cannot exclude the involvement of the angular gyrus.

Comparing IMMEDIATE and FINAL GOAL-related preparatory activity

Contrasting IMMEDIATE and FINAL GOAL trials revealed two significant clusters of activity, one along the dorsal portion of the occipito-parietal fissure, and the other along the occipito-temporal fissure (Fig. 5). The spatial distribution of the occipito-parietal differential increase appears to overlap with the location of human V6A (Simon et al., 2002; de Jong et al., 2001); the cluster within occipito-temporal cortex seems to correspond to LOtv (lateral occipital tactile – visual region), which is part of the lateral occipital complex (LOC) (Amedi et al., 2002).

Discussion

Using fMRI, we examined the cerebral correlates of preparing object manipulations instructed based on either a desired end-state (FINAL GOAL) or an initial grasping component (IMMEDIATE GOAL). The results indicate that the cognitive distinction that can be drawn between immediate and more remote action goals is reflected in both differential brain activity and behavior.

Planning actions guided by immediate goals

Our behavioral data show that while the durations of the planning phase of the IMMEDIATE GOAL trials were influenced by the differential accuracy constraints evoked by the LARGE and SMALL objects, the planning phase of the FINAL GOAL trials was not sensitive to these accuracy constraints (Fig. 2). This indicates that movements planned based on their immediate and final goals were prepared in a different way. More specifically, the disappearance of the effect of object size in the FINAL GOAL condition suggests that in this condition, the action plan is generated on a level that is relatively independent of the spatial properties of the object. Conversely, during planning based on the immediate goal, the action plan might rely more strongly on these spatial properties.

The imaging data show increased preparatory activity for IMMEDIATE GOAL trials in, firstly, the dorsal part of the anterior bank of the occipito-parietal fissure (Fig. 5). In macaques, this region contains area V6A (Galletti et al., 1999; Luppino et al., 2005), a visual area connected with V1 but with neurons modulated by the preparation and execution of reaching-grasping movements (Fattori et al., 2004). Our results confirm the involvement of this region in motor preparatory activity (Battaglia-Mayer et al., 2001), suggesting that contributions of V6A to visuomotor processes might extend beyond the on-line control of fast responses (Rizzolatti and Matelli, 2003). Rather, this region might provide premotor areas with visuospatial information on the shape and location of the to-be-grasped object before the movements unfold. This role appears compatible with the specific requirements of the IMMEDIATE GOAL trials, as compared to the FINAL GOAL trials. That is, organizing a movement based on a given target object (Fig. 1) is likely to evoke a more elaborate analysis of the location and visuospatial features of the object. This putative cerebral effect has a behavioral counterpart in the sensitivity of IMMEDIATE GOAL trials (but not FINAL GOAL trials) to the size of the object to be grasped (Fig. 2).

The second area where we observed IMMEDIATE GOAL-related activity is located within left occipito-temporal cortex. This area appears to correspond to LOtv (Amedi et al., 2002), a portion of
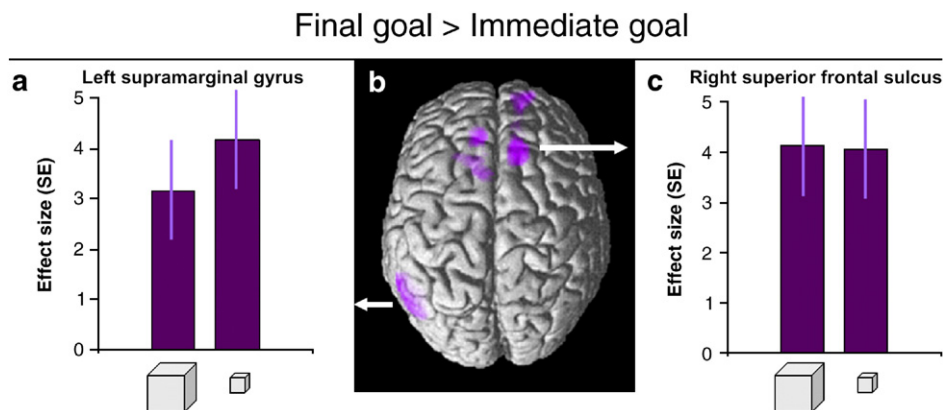

Fig. 4. Imaging data contrasting FINAL GOAL- with IMMEDIATE GOAL-cued action preparation. (a) Effect size (beta/SE) within Left supramarginal gyrus (−56 −66 26) of FINAL GOAL- versus IMMEDIATE GOAL-cued actions, separate for grasping the LARGE and SMALL part of the object. (b) Statistical parametric map corrected for multiple comparisons ($P<0.05$) at the cluster level showing activity that was stronger during preparation of correctly performed FINAL GOAL-cued than IMMEDIATE GOAL-cued trials, superimposed on a rendered brain. (c) Effect size (beta/SE) within right superior frontal sulcus (14 26 58) of FINAL GOAL- versus IMMEDIATE GOAL-cued actions, separate for grasping the LARGE and SMALL part of the object. SE=Standard Error.
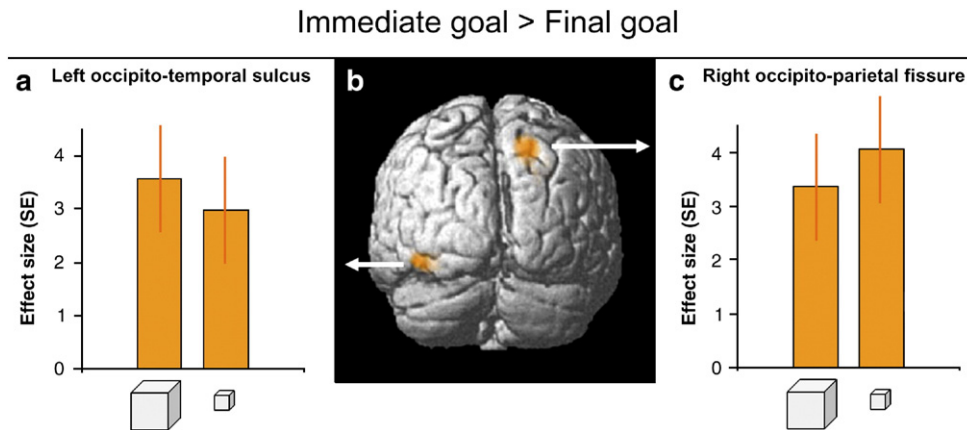
Immediate goal > Final goal

Fig. 5. Imaging data contrasting IMMEDIATE GOAL- with FINAL GOAL-cued action preparation. (a) Effect size (beta/SE) within Left occipito-temporal sulcus (−38 −74 −14) of IMMEDIATE GOAL- versus FINAL GOAL-cued actions, separate for grasping the LARGE and SMALL part of the object. (b) Statistical parametric map corrected for multiple comparisons ($P < 0.05$) at the cluster level showing activity that was stronger during preparation of correctly performed IMMEDIATE GOAL-cued than FINAL GOAL-cued trials, superimposed on a rendered brain. (c) Effect size (beta/SE) within right occipito-parietal fissure (18 −72 52) of IMMEDIATE GOAL- versus FINAL GOAL-cued actions, separate for grasping the LARGE and SMALL part of the object. SE = Standard Error.

the lateral occipital complex (LOC). LOC is part of the ventral visual stream (Milner and Goodale, 1995), and is involved in the perception of geometrical shape and volumetric features of objects (Amedi et al., 2002, 2001; Moore and Engel, 2001). Accordingly, lesions of this area may cause visual form agnosia (James et al., 2003), but no visuomotor deficits (James et al., 2003). LOtv responds not only to visual but also to haptic object information, possibly in relation to the early perceptual processing of the shape of graspable objects (Amedi et al., 2002; Grill-Spector et al., 1999).

These properties of LOtv seem relevant for planning IMMEDIATE GOAL trials. As said, generating a motor plan based on an initial movement towards a target object appears to rely more heavily on visuospatial information. In this process, a comparison between the visuospatial properties of the object to be grasped and of the slot to be filled has to be made. Since this comparison needs to take place before the execution of the movements, it might involve not only sensorimotor information on intrinsic object properties (processed by the anterior intraparietal area (AIP)) (Sakata et al., 1997; Culham et al., 2003; Frey et al., 2005), but also perceptual volumetric information (processed by LOtv). More generally, this finding confirms the notion that planning grasping movements relies not only on visuospatial object features processed within the dorsal visual stream, but also on perceptual information about object identity processed within the ventral visual stream (Jeannerod et al., 1994; Fogassi and Luppino, 2005).

Planning actions guided by final goals

As mentioned before, our behavioral data show that planning times of actions cued by the desired overall outcome were not affected by differences in object size. This suggests that, in this task, action planning takes place on a level that is relatively independent of the spatial properties of the object and slots. The pattern of brain activity related to this planning condition supports this view.

First, we found FINAL GOAL-related activity bilaterally along the mesial and lateral aspects of the superior frontal gyrus. This

frontal region has been associated with planning sequences of multiple movements ahead in time, or more specifically, with generating action sets, defined as superordinate (rather than single) stimulus–response and response–response rules (Rushworth et al., 2004; Rowe et al., 2001; Shima and Tanji, 2000). When left-lateralized, lesions of this area may cause action planning disturbances like ideomotor apraxia (Haaland et al., 2000). More precisely, these lesions may lead to failures in planning when this planning requires combining a number of distinct components and evaluate these prior to responding, or when responses directed towards a final goal have to be inhibited to permit intermediate steps (Morris et al., 1997).

These characteristics appear compatible with the requirements of the FINAL GOAL trials, namely the selection of an appropriate course of action among many possibilities, more precisely a series of movements of which the initial elements are not directly evoked by the instruction cue (Fig. 1).

Second, we found that the left supramarginal gyrus showed stronger activation during FINAL GOAL than during IMMEDIATE GOAL trials (Fig. 4). This area has been associated with several aspects of action planning, including motor attention, defined as covertly preparing movements, independent of their actual execution (Rushworth et al., 2001). Lesions of this region may lead to ideomotor apraxia (Haaland et al., 2000), in particular, to difficulties in disengaging attention from a movement, or in shifting motor attention from one movement in a sequence to the next (Rushworth et al., 1997). This role is in line with the requirements of FINAL GOAL-directed action planning, namely the organization and preparation of a sequence of movements to generate an overall action that has to result in a given end-state (Fig. 1).

Interpretational issues

The design of the present experiment ensured that the subjects could not rely on fixed stimulus–response mappings to solve the task. We varied the configuration of the slots to avoid that a particular color cue would univocally refer to a certain movement

sequence. In other words, the movement sequence required by a particular color cue depended on the momentary, pseudo-randomly determined orientation of the device.

We minimized the possibility that our findings could be driven by motoric differences between FINAL and IMMEDIATE GOAL trials: a crucial feature of the experiment was that the movements required to complete the object manipulations were similar for actions cued by their FINAL and IMMEDIATE GOAL – only the type of instruction varied. This allowed us to separate brain activity that was due to differences in preparation from brain activity related to perceptual processing and movement execution.

Yet, it could be argued that our FINAL and IMMEDIATE GOAL conditions differ in the amount of movement that is prepared during the planning phase. That is, preparation of the entire action has to be completed before movement onset in the FINAL GOAL condition, whereas in the IMMEDIATE GOAL condition, preparation of the transport phase of object towards slot might still go on after movement onset. However, the behavioral data do not support such an interpretation, since movement durations were not affected by the way the movement was instructed.

Conclusions

This experiment examined the cerebral implementation of the cognitive distinction that can be drawn between immediate and final goal levels in action planning. Both behavioral and imaging data support the relevance of this distinction, indicating that different, though complementary, cerebral mechanisms are involved in preparing actions based on their desired overall end-state (final goal) or based on a required initial target movement (immediate goal). Comparing preparatory brain activity during FINAL GOAL and IMMEDIATE GOAL trials showed that FINAL GOAL-cued action planning recruits bilateral frontal and left inferior parietal cortex, whereas IMMEDIATE GOAL-cued planning involves right occipito-parietal and left occipito-temporal cortex.

These outcomes show that areas in both parietal and frontal cortex increase their activation during the preparation of actions based on their desired overall outcome (FINAL GOAL trials). Within parietal cortex, different portions contribute to planning actions based on the given goal: planning based on the FINAL GOAL involves an inferior parietal region (the left supramarginal gyrus), whereas planning based on the IMMEDIATE GOAL involves the right occipito-parietal sulcus. This indicates that there is no clear-cut distinction between frontal and parietal areas in terms of their contributions to planning actions from a final or immediate goal level. Rather, different fronto-parietal circuits are involved in preparing similar actions based on either immediate or final goals. More precisely, the finding that in our experiment, FINAL GOAL-cued preparation involves areas that have been associated with covertly preparing movements and planning motor sequences suggests that when based on a remote end-state, actions are planned by selecting and combining multiple movements into a sequence, a process that is not immediately dictated by visuospatial information. Conversely, the finding that IMMEDIATE GOAL-cued action preparation increases activation in areas associated with visuomotor processing and object perception indicates that here, action planning may depend relatively strongly on visuospatial information about the object and the slots, and involves selecting a movement spatially compatible with these properties. This view is further supported by the finding that the preparation interval of only IMMEDIATE GOAL and not FINAL GOAL trials is sensitive to object size.

The distinction between final and immediate goals should be regarded as an experimental heuristic to manipulate different levels within the proposed hierarchy of action planning. Accordingly, it remains to be seen to what extent our specific activation pattern can be generalized to other experimental manipulations. Yet, our findings might justify the general claim that planning on increasingly higher or "abstract" levels within the goal-means hierarchy may require increasing abilities to represent and temporally organize multiple movement elements in the brain. This capacity is expressed in an increased contribution of dedicated brain areas in superior frontal and supramarginal cortex. Conversely, when actions are aimed at more straightforward goals, the motor system relies more heavily on perceptual and visuomotor areas providing stimulus information.

In sum, our findings confirm the general notion that actions may be planned at different levels, and provide insights into the nature of these differences. Since fMRI was used to obtain the cerebral correlates of these behavioral planning differences, our study provides a link between behavioral studies on the hierarchical nature of action planning on the one hand, and existing knowledge on the anatomical organization of the motor system on the other hand. It would be interesting to see how the notion of differential contributions of specific cortical areas to different levels of action planning can be applied to other research domains, for instance, clinical research on distinctive motor disorders, or studies on analogies of action planning and action observation.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2007.04.071.

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