

# Evidence for the Involvement of the Posterior Parietal Cortex in Coordination of Fingertip Forces for Grasp Stability in Manipulation

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**Ehrsson, H. Henrik, Anders Fagergren, Roland S. Johansson, and Hans Forssberg.** Evidence for the involvement of the posterior parietal cortex in coordination of fingertip forces for grasp stability in manipulation. *J Neurophysiol* 90: 2978–2986, 2003; 10.1152/jn.00958.2002. Grasp stability during object manipulation is achieved by the grip forces applied normal to the grasped surfaces increasing and decreasing in phase with increases and decreases of destabilizing load forces applied tangential to the grasped surfaces. This force coordination requires that the CNS anticipates the grip forces that match the requirements imposed by the self-generated load forces. Here, we use functional MRI (fMRI) to study neural correlates of the grip-load force coordination in a grip-load force task in which six healthy humans attempted to lift an immovable test object held between the tips of the right index finger and thumb. The recorded brain activity was compared with the brain activity obtained in two control tasks in which the same pair of digits generated forces with similar time courses and magnitudes; i.e., a grip force task where the subjects only pinched the object and did not apply load forces, and a load force task, in which the subjects applied vertical forces to the object without generating grip forces. Thus neither the load force task nor the grip force task involved coordinated grip-load forces, but together they involved the same grip force and load force output. We found that the grip-load force task was specifically associated with activation of a section of the right intraparietal cortex, which is the first evidence for involvement of the posterior parietal cortex in the sensorimotor control of coordinated grip and load forces in manipulation. We suggest that this area might represent a node in the network of cortical and subcortical regions that implement anticipatory control of fingertip forces for grasp stability.

## INTRODUCTION

One critical control issue in most skillful object manipulations is to maintain grasp stability, which entails the prevention of both accidental slips and excessive fingertip forces. Object manipulation generally requires the application of fingertip forces tangential to the contact surfaces. Such tangential forces (load forces) tend to destabilize the grasp. To stabilize the grasp, humans automatically produce grip forces normal to the contact surfaces that increase and decrease in phase with increases and decreases in the self-generated load forces. This coordination of grip and tangential load forces was originally demonstrated in tasks where humans use a precision grip to lift objects with vertical grasp surfaces against mass and spring

loads (Johansson and Westling 1984; Westling and Johansson 1984). This coordination of grip and load forces is observed during various types of manipulatory tasks (e.g., Flanagan and Wing 1993; Flanagan et al. 1993; Johansson and Westling 1988; Johansson et al. 1999) and grasp configurations (Burstedt et al. 1997; Flanagan and Tresilian 1994; Flanagan et al. 1999). The same coordination is also used when humans apply load forces to a fixed object in an attempt to move it (Johansson et al. 1992). This force coordination depends on an anticipatory control strategy in which the CNS predicts the consequences of the self-generated load forces and anticipates the grip forces required to maintain grasp stability (Blakemore et al. 1998a; Flanagan and Wing 1997; Johansson 1998; Johansson and Westling 1984, 1988; Jordan and Wolpert 1999; Kawato 1999). This anticipatory coordination of the fingertip forces is not innate but develops gradually during ontogeny. The mature pattern of force coordination is not developed until approximately 8 yr of age (Forssberg et al. 1991, 1992).

Primary motor and somatosensory cortical areas are involved in the control of object oriented fingertip actions in man and monkey (e.g., Ehrsson et al. 2000, 2001; Hikosaka et al. 1985; Jeannerod et al. 1984; Kinoshita et al. 2000; Kruger and Porter 1958; Lemon et al. 1995; Passingham et al. 1983; Peele 1944; Porter and Lemon 1993; Schieber and Poliakov 1998). However, skilled object manipulation is also associated with activation of bilateral fronto-parietal cortical areas, including the dorsal and ventral premotor cortex, the supplementary motor area, the cingulate motor area and the posterior parietal lobe (intraparietal and supramarginal cortices; Ehrsson et al. 2000, 2001; Kuhtz-Buschbeck et al. 2001). It is reasonable to expect that the neural processes controlling the coordination of fingertip forces to some degree engage the bilateral cortical network explored in earlier studies. To test this hypothesis and to identify cortical areas of specific importance for the anticipatory coordination of grip and load forces for grasp stability, we used functional MRI (fMRI) to register the blood oxygenation level-dependent (BOLD) signal as a measure of regional increases in synaptic activity when humans performed a grip-load force task that automatically invoked coordinated changes in the load and grip forces. In two control tasks subjects either applied only grip forces (grip force task) or only vertical load forces to the test object (load force task). By contrasting the

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grip-load force task with the other two tasks, we sought to detect cortical activation specifically related to the application of coordinated grip and load forces to an object.

## METHODS

### Subjects, general procedure, and apparatus

Six healthy male subjects with no history of neurological disease participated in the study. Their ages ranged from 24 to 29 yr. All subjects were right-handed (Oldfield 1971). They were naive as far as the specific purposes of the experiments were concerned. The subjects had given their written consent and the Ethical Committee of the Karolinska Hospital approved the study, which was performed in accordance with the guidelines of the Declaration of Helsinki (1975). During the experiments, the subjects rested in a supine position in the MR scanner. The arms were extended and were oriented parallel to the trunk and supported from the elbow to the radial side of the hand. The subjects used the tips of the thumb and the index finger of the right hand to manipulate a nonmagnetic immovable test object (Fig. 1). The right wrist was supported so that the subjects could employ lift forces to the test object by attempting a radial deviation of the wrist without any movements of the arm. The test object had vertical flat and parallel contact surfaces (spaced 30 mm apart) covered with sandpaper (grit: 180). The top of the object could be equipped with a horizontally oriented yoke as shown in Fig. 1C. The object was equipped with optometric transducers that measured the forces normal to the contact surfaces (grip force) and the vertical (load) force. The grip force was measured as the mean of the normal forces recorded at the two grasped surfaces. The vector sum of the grip force and the vertical load force represented the resultant fingertip force. The subjects were blindfolded throughout the experiments and instructed to keep their eyes closed. They wore headphones to reduce the noise from the MR scanner and to receive auditory cues (from a metronome).

### Tasks

When an object is lifted from a support surface with a precision grip, the grip and load forces are coordinated to increase in parallel to maintain grasp stability during the "load phase" when the load force increases before lift off to overcome the weight of the object (Johansson and Westling 1984). Similarly, during the "unloading phase," when an object is being put down, the grip force and the load force decrease in parallel after the object is replaced on the support surface until it is released. Thus during the loading and unloading phases, subjects generate coordinated changes in fingertip forces with no overt movement of the hand (and of the object). Subjects indeed also coordinate the fingertip forces for grasp stability even when only applying forces to fixed objects (Johansson et al. 1992). Thus to examine the neural correlates of the grip-load force coordination, we designed a task where the subjects applied forces to an immovable test object akin to those forces generated during the loading and unloading phases of lifting tasks.

Using the right hand, each subject performed three tasks in which they repeatedly applied increases and decreases of fingertip forces to the test object following similar time courses and with similar magnitudes. 1) In the grip-load force task, the subjects held the object between the pulps of the index finger and thumb and applied vertical load forces to the object as if intending to lift it vertically (Fig. 1A). In this task, the subjects automatically controlled for grasp stability by changing the grip force in-phase with the load force, i.e., with the load force applied tangentially to the contact surfaces. 2) In the grip force task, the subjects were asked to pinch the object held between the pulps of the index finger and thumb to apply grip forces only, i.e., forces normal to the grasp surfaces (Fig. 1B). 3) In the load force task, the subjects applied vertical load forces without gripping the object.

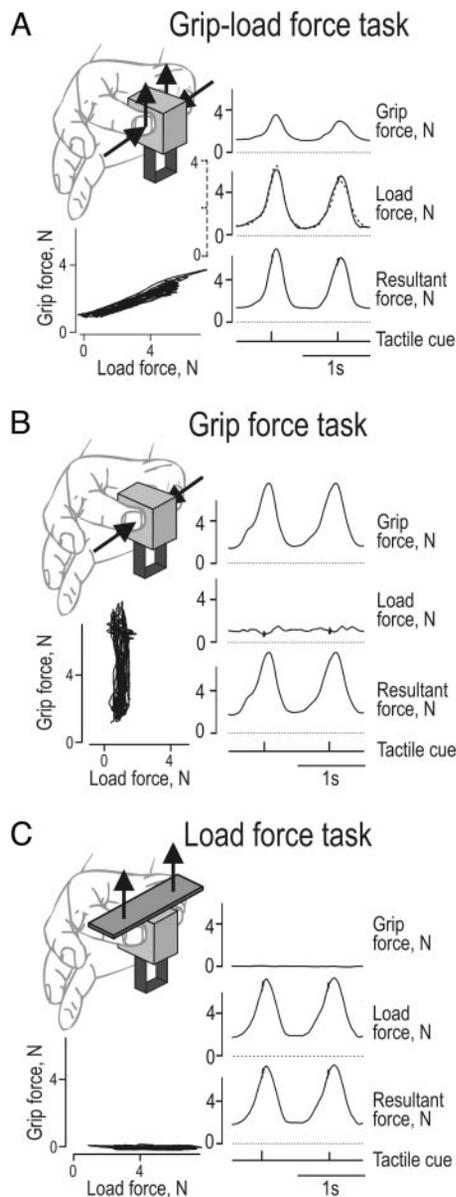


FIG. 1. Hand posture, configuration of the test object, and fingertip forces applied in the grip-load force task (A), grip force task (B), and the load force task (C). The right hand rested at a stable support and the thumb and index finger were in contact with a force sensor (data not shown). A–C: fingertip forces shown as the mean of the grip forces applied normal to the 2 grasp surfaces and as the total load force (load force is being defined as the vertical force in this study). Time traces show representative grip and load force recordings from 1 subject performing the tasks in the MR scanner (data shown from an arbitrarily chosen 2-s period to represent 2 consecutive force pulses). Time traces below show the vector sum of the grip and load forces (resultant force) and the occurrences of the brief weak tactile signals that provided feedback about the target force (6-N resultant force). Note especially the parallel coordination of grip and load forces in the grip-load force task (A). To illustrate the tight coupling of the grip and load forces in this task, we superimposed the grip force (dashed line) on the load force recording (black line). Also note that the time course of the resultant force pulses were similar in the three tasks. Because the subjects did not release the object between the force pulses, the grip and load force typically did not return to 0 N. Graph below the hand shows recordings of the fingertip forces during all trials by the same subject by plotting the grip force against the load force. (In B, a small force oscillation is visible in the plot of the grip force against the load force; this corresponds to the weak mechanical pulse that provided the feedback about the target force.)

That is, with the radial side of the index finger and the ulnar side of the thumb in unbroken contact with the object, they attempted to lift the object by applying vertical forces to a horizontally oriented yoke at the top of the object (Fig. 1C). (In the present paper we will refer to these vertical forces as “load forces,” although traditionally, in precision grip-lift tasks, load forces are defined as the forces that are applied tangential to the grasp surfaces). Since the digits were spaced sufficiently to avoid contact with the object’s grasp surfaces, no grip forces were applied.

In each task, subjects generated a force every second (a force pulse), paced by a metronome that produced click sounds at 1 Hz. The resultant forces were unimodal and of similar shape in all tasks (Fig. 1, A–C, right). To help the subjects generate force of constant amplitude, a brief weak mechanical vertical load force (of 10-ms duration and <0.5-N peak force) was delivered by the object when the resultant fingertip force reached 6 N (this is the “tactile cue” in Fig. 1). The subjects were instructed to just reach this target force for each force pulse and to generate the same force in all force pulses. Force pulses where the subjects reached the target force were defined as correct. In a baseline condition, we collected data while the subjects gently held the object between right index finger and thumb. In addition, the subjects heard the metronome and received brief mechanical pulses to the digits just as they had in the three force production tasks. Before the brain scanning, the subjects practiced each task for about 5 min. All subjects quickly learned the tasks and found them simple. Indeed, after a short period of training, they could keep up a conversation while performing the tasks adequately, which shows that the exercises were very simple.

During the practice as well as during the scanning, the force signals were digitized, displayed on-line, and stored at 400 samples/s using the SC/ZOOM data acquisition and analysis system (Physiology Section, IMB, University of Umeå, Sweden). For each force production task, we measured the peak forces for each force cycle off-line.

To assess possible involvement of proximal muscles in the right arm and in the muscles of the nonoperating left hand and arm during the tasks, electromyograms (EMGs; using Myo115 surface electrodes with 2,000 $\times$  amplifiers, Liberty Technology, Hopkinton, MA) were recorded in separate experiments outside the MR scanner in four subjects. The biceps brachii and anterior deltoid muscles of the operating right arm showed no EMG signals related to force production cycles during the grip force task, but did so during the lift and grip-lift force tasks. We also recorded activity in the first dorsal interosseous, abductor pollicis brevis, biceps brachii, and anterior deltoid muscles of the left arm. None of the tasks was associated with EMG signals in the muscles of the left arm and hand.

### Brain scanning

fMRI was conducted on a 1.5-T scanner (Signa Horizon EchoSpeed, General Electric Medical Systems) equipped with a head-coil. We collected gradient-echo, echo-planar (EPI) T2\*-weighted image volumes with BOLD contrast (Kwong et al. 1992; Logothetis et al. 2001; Ogawa et al. 1992). The imaging parameters were echo time (TE) = 60 ms; field of view (FOV) = 22 cm; matrix size = 64  $\times$  64; pixel size = 3.4 by 3.4 mm; and flip angle = 90°. Twenty-four contiguous axial slices of 4 mm thickness were collected in each volume. This volume covered the whole brain in all subjects, except the caudal two-thirds of the cerebellum ( $z > -22$  in the MNI standard space).

Functional-image volumes were collected in six separate runs. In each run, 114 volumes were acquired continuously, with one volume being collected every 6,000 ms (TR = 6 s). The subjects performed the different tasks for periods of 36 s (6 image volumes). Periods where the force production tasks were performed were alternated with periods of the baseline condition in a classical blocked design. In each run, we alternated the order of the tasks to reduce possible time dependent trends and sequential effects. To allow for T1 equilibration

effects, we started each experiment by recording four “dummy” volumes that were not stored. A total number of 684 volumes were collected for each participant; the same number of volumes was collected for each subject and task.

### Data analysis and image processing

We used SPM-97 to process and analyze the images (Friston et al. <http://www.fil.ion.ucl.ac.uk/spm>). The volumes were realigned, coregistered to each individual anatomical T1-weighted image (3D-SPGR), and normalized to the stereotactic coordinate system defined by Talarach and Tournoux (1988) using the reference brain of the Montreal Neurological Institute (MNI; Evans et al. 1994). The image volumes were subsequently spatially smoothed with an isotropic Gaussian filter of 8-mm full width at half-maximum (FWHM), and smoothed temporally with a Gaussian kernel of 4 s width to increase the signal to noise ratio and conform to the Gaussian assumptions of SPM97. The data were modeled using the General Linear Model (GLM; Friston et al. 1995a; Worsley and Friston 1995). We used the standard SPM hemodynamic response function to filter the boxcar waveform that defined the different experimental conditions. A high pass filter (with cut-off frequency of 2.3 mHz) was used to remove low frequency drifts and fluctuations in the signal (Holms et al. 1997). Proportional scaling was applied to compensate for global changes in the signal. To increase the sensitivity of the analysis, we analyzed the time series of the images obtained from the six subjects as one group. Thus the statistical analyses used in the present study are fixed-effect analyses, and as such, our inferences pertain only to the group of subjects studied. However, to confirm that the results obtained in the group analysis were representative for all subjects in the group and thus highly likely to generalize, we also examined the activation maps from individual subjects (see RESULTS).

For every voxel, the activity was modeled as a linear sum of factors in a design matrix. The design matrix had each of the four experimental conditions (the three force production tasks and the baseline condition) and the mean value of the data from each run as factors (this is the standard model implemented in SPM97). By estimating the task specific effects using linear contrasts in the GLM, we created statistical images [i.e., statistical parametric maps (SPMs)] with a *t*-distribution (SPM *t*) that we transformed subsequently to the Z-distribution (SPM Z). A threshold at  $Z > 3.09$  at each voxel was used for each of the images. These statistical images (SPM Z) have many clustered voxels (clusters) with high Z-values in regions where there was a large difference in activity between the contrasted conditions. The activations were then characterized in terms of peak height and spatial extent. We report clusters of active voxels that corresponded to a  $P < 0.05$  from a combined test for peak height and spatial extent (Poline et al. 1997b) after correction for the number of multiple comparisons within the whole brain space (omnibus  $P < 0.05$ ). Some large clusters engaging engaged multiple regions were distinguished as separate local maxima of activity. We report such local maxima within a cluster if they corresponded to a  $P < 0.05$  after correction for the number of multiple comparisons using a test for peak height (Friston et al. 1995b). The tests described above to address the problem of making multiple comparisons are based on the theory of random Gaussian fields, which have been described in detail elsewhere (e.g., Poline et al. 1997a).

We defined linear contrasts in the GLM to test our hypotheses. First, we identified brain regions with stronger BOLD contrast signals during the grip-load force task than during the baseline condition. Second, to localize brain activity specifically associated with the application of coordinated grip and load forces, the activity in the grip-load force task was compared with the activities in the load force and grip force tasks, respectively (thus the comparisons were grip-load force task – grip force task; grip-load force task – load force task). Thereby any brain areas specifically activated during the grip-load force coordination should appear in both contrasts. We also

employed conjunction analyses to test for common activation across these two contrasts. This analysis examines whether an area shows increased activity in two pairwise contrasts. The SPM  $t$  resulting from the two contrasts are combined to generate a new SPM  $t_{\min}$  that describes the minimum  $t$ -value detected in the contrasts. To ensure that the contrasts were independent, as required in the SPM99 conjunction analysis, each functional image volume was only used in one of the two contrasts (and the orthogonalization procedure was employed). Voxels that show a minimum  $t$ -value corresponding to  $P < 0.05$  were then reported (Worsley and Friston 2000). The conjunction analysis represents a more sensitive approach than the simple contrasts: active voxels corresponding to  $t$ -values of 2.9 are detected, while a  $t$ -value of 4.5 is required in the pairwise contrasts (corresponding to  $P < 0.05$  after correction for multiple comparisons). We have adopted a conservative approach, and only present areas that are significantly activated in the conjunction analysis as well as being significantly active in at least one of the pairwise contrasts. Furthermore, we only report voxels that showed increased activity when compared with the baseline condition (by applying an inclusive masking procedure;  $Z > 1.66$  at each voxel; corresponding to  $P < 0.05$ ). By this means we focused on sensorimotor related areas that were activated during the grip-load force task but not at rest, rather than on brain areas that did not show any BOLD signal increases during these tasks and were possibly subjected to task related deactivation.

#### Anatomical localizations

The anatomical localization of the activation was related to the major sulci and gyri distinguishable in a mean standardized anatomical MRI obtained from the six subjects (Duvernoy 2000). We use the terminology of Roland and Zilles (1996) for the cortical motor areas.

## RESULTS

#### Task performance

Figure 1 illustrates the grip and the load force profiles together with the resultant fingertip force obtained from a representative subject while performing the three tasks: the grip-load force task, the grip force task, and the load force task. In all tasks, the subjects generated the requested forces in  $>99\%$  of the force pulses while the fMRI scanning was being conducted. As expected, in the grip-load force task, the grip force and load force changed in-phase and without a time delay during both the increase and the decrease of the load force; no slips between the digits and the test object were ever observed. The grip-load force coordination is illustrated by the approximately straight line relationship in the graph of Fig. 1A, which plots the grip force against the load force for all force cycles performed by a subject during the scanning period (1 run). To further illustrate the tight temporal coordination between grip and load forces, the dashed line superimposed on the time trace of the load force in Fig. 1A shows the corresponding grip force trace after it had been scaled and aligned to match the amplitude of the load force. Since the subjects were instructed to maintain finger-object contact throughout the experiments, the grip force did not fully reach zero when the object was unloaded and the load force approached zero in the grip-load force and in the grip tasks. Likewise, since contact was maintained throughout the test sequence, prior to the load increase there was no period of initial grip force increase without a load force change in the grip-load force task, in contrast to what is typically observed after the initial contact with an object in

lifting tasks (see “preload” phase in Johansson and Westling 1984).

For data pooled across all subjects, the peak resultant force was  $7.8 \pm 0.96$  (SD) N in the grip force task,  $7.7 \pm 1.0$  N during the load force task, and  $6.6 \pm 1.2$  N in the grip-load force task.

#### Brain activation

GRIP-LOAD FORCE TASK COMPARED WITH THE BASELINE CONDITION. The brain regions that showed stronger BOLD contrast signals during the grip-load force task than during the baseline condition are displayed in Fig. 2 and Table 1. Several areas in the left hemisphere were activated. These areas in-

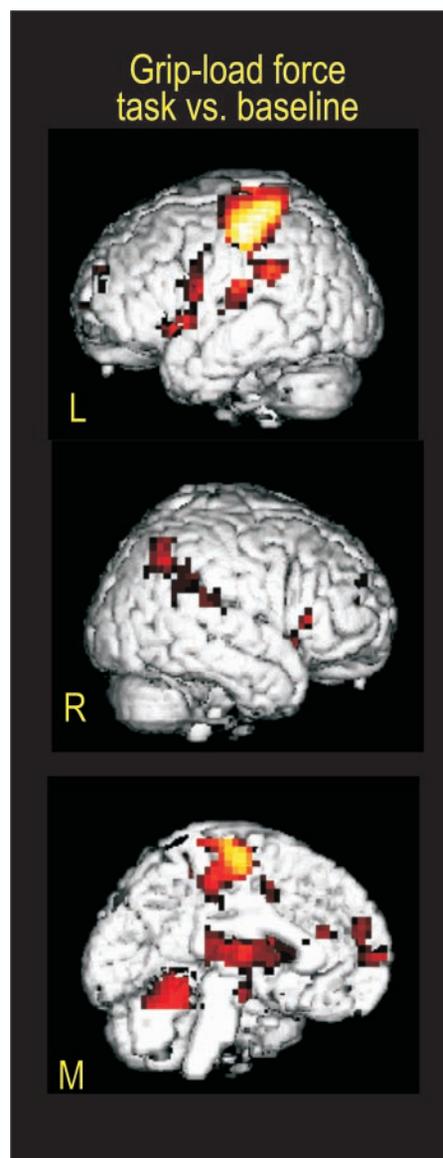


FIG. 2. Brain regions with stronger activity during the grip-load force task in comparison with the baseline condition. The significant activations (i.e.,  $P < 0.05$  after a correction for multiple comparisons) are superimposed on 3D-representations of the standard brain (MNI). *Top*: left hemisphere (L). *Middle*: right hemisphere (R). *Bottom*: medial wall (M) of the left hemisphere. Activation maps were thresholded at each voxel at  $Z > 3.09$  for display purposes. For further details, see Table 1. (Note that the lower part of the cerebellum was outside the field of view of the MR scanner.)

TABLE 1. Grip-load force task compared to the baseline condition

Talarach Coordinates (MNI)				
Anatomical Region (Functional/Cytoarchitectural Area)	X	Y	Z	Peak Z-Score
Left hemisphere				
Left central sulcus, (M1/S1)	-40	-36	60	9.54
Left medial superior frontal gyrus (SMA)	-8	-24	56	8.45
Left medial superior frontal gyrus (SMA)	-8	-16	64	8.38
Left thalamus	-16	-12	8	7.89
Left putamen	-32	8	0	8.13
Left posterior lateral fissure/supramarginal gyrus†	-56	-40	24	7.35
Left parietal operculum (SII region)	-56	-20	16	7.29
Left superior frontal gyrus	-8	68	8	6.47
Left frontal operculum	-56	8	-4	5.54
Left precentral gyrus, PMV	-60	0	16	5.81
Left superior frontal gyrus	-4	64	8	4.90
Left superior frontal gyrus	-12	56	24	4.88
Left thalamus	-12	4	8	4.87
Right hemisphere				
Right anterior cerebellar hemisphere	8	-48	-20	8.71
Right intraparietal sulcus‡	52	-56	52	5.68
Right thalamus	16	0	16	6.00
Right putamen	24	12	8	7.03
Right posterior inferior frontal gyrus (pars opercularis, area 45)	52	24	8	5.53
Right thalamus	12	4	4	5.30
Right putamen	24	8	-8	5.26
Right supramarginal cortex	64	-52	20	5.13

Significant increases in BOLD contrast signal ( $P < 0.05$  corrected for multiple comparisons). The Z-scores of the peak activations correspond to the following  $P$  values after correction for the number of multiple comparisons in the whole brain space:  $Z = 4.68$  ( $P = 0.05$ ),  $Z = 5.05$  ( $P = 0.01$ ),  $Z = 5.18$  ( $P = 0.005$ ),  $Z = 5.54$  ( $P = 0.001$ ). Anatomical locations were related to the mean standardized anatomical EPT.

† It was difficult to distinguish between these two structures on the mean EPI (or mean anatomical T1).

‡ Located on the lateral upper bank of the sulcus. It was difficult to distinguish between the IPS and the angular gyrus using the mean EPI.

cluded the cortex of the central sulcus (i.e., M1 and S1) with a cluster that extended rostrally into the dorsal premotor cortex (PMD). Increased activity was also observed in the ventral premotor cortex (PMV; the inferior part of the precentral gyrus posterior to area 44), area 44, the supplementary motor area (SMA; with the clusters of active voxels extending into the cingulate sulcus, CMA), the parietal operculum (the SII region), the postcentral sulcus, and the supramarginal cortex (with the clusters of active voxels extending into the anterior part of the intraparietal sulcus). In addition, the grip-lift force task was associated with increased activity in areas of the right (ipsilateral) hemisphere. These were located in a right-sided section of the intraparietal cortex, in the right supramarginal cortex, and in a part of the right inferior prefrontal cortex. Subcortically, we observed bilateral activation of the motor sections of the putamen and the bilateral anterior cerebellar hemispheres (with the strongest cerebellar activation being observed on the right side).

**BRAIN ACTIVITY ASSOCIATED WITH COORDINATED GRIP AND LOAD FORCES.** To reveal brain activity specifically associated with the coordination of grip and load forces for grasp stability,

we compared the activity associated with the grip-load force task with the activities observed during the grip force task and the load force task. The rationale for this was that neither the lift force task nor the grip force task involved coordinated grip-load forces, but they included the generation of fingertip forces (grip forces and load forces). A posterior section of the cortex lining the IPS and the cortex of the angular gyrus of the right posterior parietal lobe, and the right prefrontal cortex, showed stronger activity when the grip-load force task was compared with the load force task (Fig. 3, *A* and *B*; Table 2). When we contrasted the grip-load force task with the grip force task, virtually the same part of the right posterior IPS was activated (Fig. 3, *C* and *D*; Table 2). Consistent with these observations, the same section of the posterior IPS was also significantly activated when the conjunction analysis was performed to compare the grip-load task with the other two tasks ( $x = 44$ ,  $y = -64$ ,  $z = 40$ ,  $t_{\min} = 3.07$ ;  $P < 0.05$  corrected). Likewise, the intraparietal cortex showed stronger activity when the subject performed the grip-load force task compared with the sum of the activities observed during the grip force task and the load force task [ $P < 0.0001$  uncorrected; (grip-load force task – load force task) – (load force task – rest)]. Importantly, this right-sided intraparietal area was active when the grip-load task was compared with the baseline condition (cf. Fig. 2), but not when the grip force and load force tasks were compared with the baseline condition, even when we

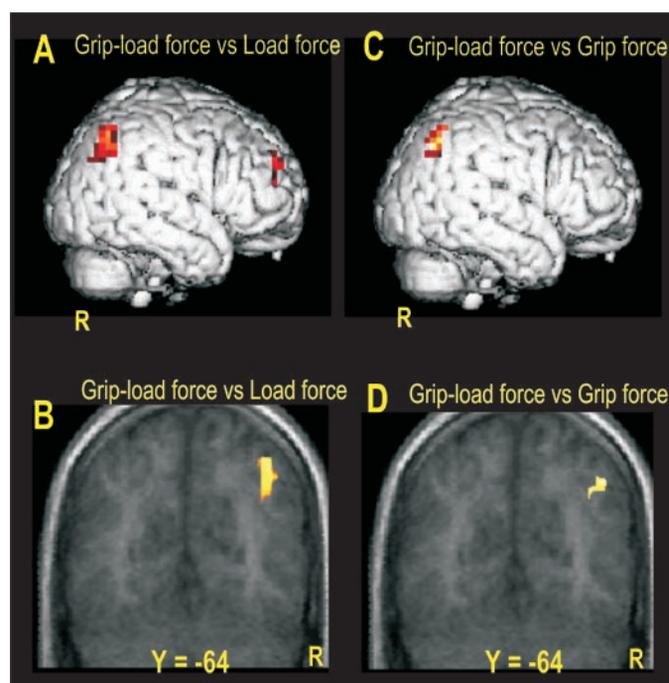


FIG. 3. Posterior parietal activation associated with the coordination of grip and load forces assessed by contrasting the different force production tasks. The significant activation is superimposed on 3D reconstructions (*A* and *C*) or a coronal slice (*B* and *D*) of the standard brain (MNI). *A* and *B*: significant blood oxygenation level-dependent (BOLD) contrast signals in a posterior section of the right intraparietal cortex when the subjects performed the grip-load force task compared with the load force task. *C* and *D*: activation of the same intraparietal area when the subjects performed the grip-load force task compared with the grip task. Activation maps were thresholded at each voxel at  $Z > 3.09$ ; only activations significant at  $P < 0.05$  after a correction for multiple comparisons are shown. For further details, see Table 2. L and R refers to the laterality of the hemispheres (L, left; R, right). The Talaraich coordinate is indicated for the coronal slice in *B*.

TABLE 2. Activation related to the coordination of grip and load forces

Anatomical Region	Talarach Coordinates (MNI)			Peak Z-Score	Cluster Size (mm <sup>3</sup> )	P Value (Corrected)
	X	Y	Z			
Grip-load force task vs. load force task						
Right posterior intraparietal sulcus	48	-60	48	5.73	2,820	0.003
Right angular gyrus	40	-68	36	5.14	Same cluster	0.0066
Right inferior frontal gyrus	48	44	-4	5.73	4,350	<0.001
Right inferior frontal gyrus (anterior area 45)	48	36	8	5.31	Same cluster	0.003
Right middle frontal gyrus (anterior area 45)	52	40	20	5.31	Same cluster	0.003
Right superior frontal gyrus	24	48	12	5.30	4,600	<0.001
Right superior frontal gyrus	24	52	28	4.75	Same cluster	0.037
Grip-load force task vs. grip force task						
Right posterior intraparietal sulcus	48	-64	44	4.20	1,280	0.050

Significant increases in BOLD contrast signal ( $P < 0.05$  corrected for multiple comparisons). All regions were also active ( $Z > 1.66$  at the voxel) compared with the baseline condition. Anatomical locations were related to the mean standardized anatomical EPI. We used cytoarchitectural population maps to define areas 44 and 45 (Amunts et al. 1999; see METHODS).

used a more liberal statistical criterion ( $P > 0.001$  uncorrected; data not shown). We conclude that the grip-load force task that involved coordinated grip and load forces specifically activated the right IPS.

To make sure that the intraparietal activation detected in the group analysis represented a consistent result for all six subjects, we examined the activation maps of the subjects individually. In a purely descriptive approach, we searched for peaks of activity in individual brains ( $P < 0.01$  uncorrected) in a sphere of radius 12 mm around the peak voxel from the group analysis (48, -64, 44). We observed that five of six subjects showed intraparietal activation at this site when we contrasted the grip-load force task and the load force task. The sixth subject also showed some intraparietal activation, although this cluster of active voxels was located slightly more medially in the standard anatomical space ( $x = 32, -56, 44$ ). We conclude that our main finding is a consistent observation across the individual subjects.

## DISCUSSION

By measuring BOLD contrast signals, we have demonstrated increased activation of a right-sided section of the intraparietal cortex in association with coordinated grip and load force changes in a precision grip task. This suggests that the right intraparietal cortex participates in the anticipatory coordination of fingertip forces providing grasp stability in the performed grip-load task.

We employed three isometric tasks, all of which involved the generation of fingertip forces with similar time courses and amplitudes. We ensured that the auditory and tactile cues that guided the subjects were the same in all tasks to eliminate potential confounders. By using a nonmovable object, we could study the coordination of fingertip forces without confounding movements of the digits and hand. However, the parallel increase and decrease of the grip and load forces (Fig. 1A) corresponded to the characteristic force coordination during the isometric loading and unloading phases in tasks when an object is lifted up from a surface and put down again (Johansson and Westling 1984). By requiring the subjects to maintain contact with the object throughout the test sequences of all tasks, we avoided confounding activities related to finger movements, somatosensory inputs and control actions associ-

ated with making and breaking contact with the object (Lemon et al. 1995; Westling and Johansson 1987).

The grip-load force task, which involved applying coordinated grip and load forces, activated a set of areas related to sensorimotor neural processes (Table 1). This included the right intraparietal cortex and bilateral supramarginal cortex, the left PMV/area 44, the SMA, the CMA, and the M1/S1 cortex, i.e., cortical areas observed active in earlier fMRI studies concerning precision grip tasks (Ehrsson et al. 2000, 2001; Kuhtz-Buschbeck et al. 2001) and object manipulation (Binkofski et al. 1999). Thus our new data supports the notion that fronto-parietal areas located in both hemispheres and subcortical motor structures are working in concert in the control of skillful manipulatory actions.

To detect activity specifically related to the control of the coordination of grip and load forces we contrasted 1) the grip-load force task with the grip force task and 2) the grip-load force task with the load force task. Areas active in both of these contrasts should be associated with the coordination of the fingertip forces since the overall force output is matched. The fact that different hand and arm muscles were recruited in the three tasks could not influence our results since they are matched in the contrasts.

The cortex lining a section of the right (ipsilateral) posterior intraparietal sulcus showed specific activity during these contrasts, thus indicating a special role, within the fronto-parietal network, in the anticipatory coupling of fingertip forces for grasp stability. This right-sided parietal region is also active in fMRI studies when subjects explore objects with complex shapes using either their right or left hand (Binkofski et al. 1999). Indeed, control of grasp stability should be crucial in such tasks to prevent slippage and object loss. Interestingly, this area is not activated when subjects simply move their digits without touching anything (Ehrsson et al. 2002) or when subjects statically hold an object in the air using a precision grip (Kuhtz-Buschbeck et al. 2001). Thus in humans, the IPS seems to have an important role in dynamic object manipulation requiring anticipatory coordination of grip and load forces.

The grip-load task differed from the other two tasks in that the fingertip forces included a force component applied tangentially to the contact area, i.e., shear forces. Such tangential force components are known to influence the spatiotemporal patterns of somatosensory afferent signals from fingertips (Bir-

zniaks et al. 2001). Hence, the intraparietal activation could be related to the central processing of the somatosensory afferent signals caused by the shear forces. However, there are several facts that suggests that shear forces cannot explain the activation of the right intraparietal cortex during the grip-load task. First, the fingertip forces had similar magnitudes and rates of changes in the three force production tasks in the present study. Therefore the shear component did probably only have a modest influence on the overall firing rates of the afferents (cf. Birznieks et al. 2001). Second, we did not observe increased activity in the S1 and SII during the grip-lift task. This suggests that possible quantitative or qualitative differences in the somatosensory afferent signals in our experiment were not large enough to cause detectable activation. The primary and secondary somatosensory areas are known to show the strongest brain responses to somatosensory stimulation (e.g., Roland 1993) and they should therefore have been activated if the sensory afferent signals from the fingertips had been much larger in the grip-load force task than in the other tasks. Third, somatosensory stimulation of the hand or fingers in passive subjects does not activate the part of the intraparietal cortex that was activated in the present study (e.g., Bodegard et al. 2001; Naito et al. 2002; Roland 1993). Fourth, in a recent fMRI study we observed no activation of IPS during unpredictable load perturbations when subject held an object with a precision grip ( $P < 0.01$  uncorrected; Ehrsson et al., unpublished data). These load perturbations caused shear forces at the fingertips, which triggered reactive grip force responses to maintain grasp stability. In conclusion, although the grip-load task included shear forces at the fingertips, it is unlikely that the altered sensory information, alone, explains the specific activation of the IPS. Having concluded this, it is still a plausible scenario that the intraparietal cortex is involved in the central processing of somatosensory signals used to guide the control of the coordinated grip and load forces (sensorimotor integration) during active manipulative tasks.

The parallel coordination of grip and load forces depends on anticipatory control mechanisms. Closed-loop feedback adjustment of grip forces based on load force information provided by digital afferents would result in too long delays to provide grasp stability because of the large time delays in the sensorimotor feedback loop (Johansson 1998; Johansson et al. 1992). To predict the destabilising forces that will be generated when an object is lifted and program accurate compensatory motor commands, the brain needs to integrate information from an internal memory representation of the physical properties of the object, the programmed motor commands and the sensory signals related to the action (Flanagan and Wing 1997; Johansson 1996, 1998; Kawato 1999). The posterior parietal cortex is receiving information from both sensory signals the different sensory modalities (visual, tactile, kinesthetic, vestibular and auditory) and efferent copy signals from frontal motor structures and would be a plausible area integrating this information to be used in programming the motor commands (e.g., Andersen et al. 1997; Bremmer et al. 2001; Mountcastle et al. 1975; Snyder et al. 1997, 1998).

That the human intraparietal cortex supports sensorimotor integration during fine finger actions area is compatible with the physiology and anatomy of the PPC as described in humans and monkey (Andersen et al. 1997; Bremmer et al. 2000; Culham and Kanwisher 2001; Rizzolatti and Arbib 1998; Ro-

land 1993; Simon et al. 2002) and in the macaque, the intraparietal sulcus is composed of several functionally distinct areas (e.g., AIP, LIP, VIP, MIP, and PIP or CIP; e.g., Colby and Duhamel 1996; Jeannerod et al. 1995; Taira et al. 1990). Several areas in which neurons respond during tactile stimulation and voluntary movement are located in the intraparietal sulcus (Andersen et al. 1997; Colby and Duhamel 1996; Hyvarinen 1982; Mountcastle et al. 1975). The anterior intraparietal area (AIP), which is located in the anterior part of the lateral bank of the intra-parietal sulcus, is of particular interest since neurons in this area are activated when the hand is preshaped during object-directed reaching and when making hand contact with the object (Sakata et al. 1995; Taira et al. 1990). However, we are of the opinion that it is somewhat unlikely that the intraparietal activation associated with the present grip-lift force task was located in a human homologue of the AIP. This activation was sited some 20 mm posterior to the peaks of activation of the anterior part of the intraparietal cortex during precision grip tasks (Ehrsson et al. 2000, 2001) and hand preshaping during visually guided reach-to-grasp actions (Binkofski et al. 1998). However, because the anatomic correspondence between human and nonhuman primate parietal lobes is not fully established, it is not possible to relate the intraparietal activation discovered in the present study to any specific area in the monkey brain. However, there is an overall correspondence that neurons in this part of the posterior parietal cortex are involved in the control of fine manipulative skills in both humans and monkeys.

It is unlikely that only one cortical area is involved in the anticipatory control of grip forces for grasp stability, and our results should not be interpreted as favoring such a view. First, anticipatory control mechanisms are fundamental in most purposeful actions and their neural correlates are likely to be present at many levels of the neural organization (Bernstein 1967; Grillner 1985; Ito 1984; Jordan and Wolpert 1999; Kawato 1999; Sperry 1943, 1950; Von Holst and Mittelstaedt 1950; Wolpert and Ghahramani 2000). Second, the anticipatory control mechanisms supporting grasp stability in manipulation are likely to depend on task and context, such that different neural networks are engaged depending on which type of sensory and memory information is primarily used (e.g., see Gordon et al. 1993; Jenmalm and Johansson 1997). Furthermore, other brain structures, such as the cerebellum, have been implicated in functions related to anticipatory control mechanisms, including the prediction of sensory consequences of self-generated movements (Blakemore et al. 1998b, 1999, 2001) and the implementation of other types of forward and/or inverse kinematic 'internal models' for control of motor skills (Imamizu et al. 2000; Kawato 1999; Miall et al. 2001). There is also direct evidence that neural mechanisms supporting grasp stability can be organized at subcortical levels (Harrison et al. 2000).

In conclusion, previous studies indicate that the human posterior parietal cortex is involved in coordination of arm and finger movements when moved to visual targets (Ramnani et al. 2001), hand-eye coordination during prism-adaptation (Clower et al. 1996) and learning advantageous arm trajectories when reaching in novel artificial force-fields (Shadmehr and Holcomb 1997). The present findings indicate that the human posterior parietal cortex is also involved in the antici-

patory coordination of grip and load forces to maintain grasp stability during object manipulation.

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#### DISCLOSURES

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