

Cortical Activity in Precision- Versus Power-Grip Tasks: An fMRI Study

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Ehrsson, H. Henrik, Anders Fagergren, Tomas Jonsson, Göran Westling, Roland S. Johansson, and Hans Forssberg. Cortical activity in precision- versus power-grip tasks: an fMRI study. *J. Neurophysiol.* 83: 528–536, 2000. Most manual grips can be divided in precision and power grips on the basis of phylogenetic and functional considerations. We used functional magnetic resonance imaging to compare human brain activity during force production by the right hand when subjects used a precision grip and a power grip. During the precision-grip task, subjects applied fine grip forces between the tips of the index finger and the thumb. During the power-grip task, subjects squeezed a cylindrical object using all digits in a palmar opposition grasp. The activity recorded in the primary sensory and motor cortex contralateral to the operating hand was higher when the power grip was applied than when subjects applied force with a precision grip. In contrast, the activity in the ipsilateral ventral premotor area, the rostral cingulate motor area, and at several locations in the posterior parietal and prefrontal cortices was stronger while making the precision grip than during the power grip. The power grip was associated predominately with contralateral left-sided activity, whereas the precision-grip task involved extensive activations in both hemispheres. Thus our findings indicate that in addition to the primary motor cortex, premotor and parietal areas are important for control of fingertip forces during precision grip. Moreover, the ipsilateral hemisphere appears to be strongly engaged in the control of precision-grip tasks performed with the right hand.

INTRODUCTION

Napier (1956) divided handgrips into precision and power grips from a functional and a phylogenetic perspective. The power grip is a palmar opposition grasp in which all digits are flexed around the object to provide high stability. The precision grip has developed in primates for the manipulation of small objects with the tips of the thumb and fingers. It requires for stability independent finger movements that involve fine control of the directions and magnitudes of fingertip forces (Flanagan et al. 1999; Johansson 1996).

In nonhuman primates, the primary motor cortex (M1) plays a fundamental role in the execution of skilled manipulatory tasks, especially those that involve a precision grip (Kuypers 1981; Porter and Lemon 1993). Lesions of the pyramidal tract abolish independent finger movements while the capacity to flex all fingers together remains (Lawrence and Kuypers 1968).

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Interestingly, subpopulations of neurons in M1 that project to motoneurons that innervate hand muscles are active while conducting a precision grip but not during power grip although their target muscles may be activated in either grasp (Muir and Lemon 1983). As such, this indicates that the control of fingertip actions with a precision grip engages neural circuits that are different to those engaged during the phylogenetically older power grip. However, results from neuroimaging studies in humans have shown that M1 is active during many types of voluntary hand movement (Roland and Zilles 1996). Furthermore the M1, the supplementary motor area (SMA) and the premotor area (PM) are all active while making individual finger movements and when opening and closing the whole hand (Colbatch et al. 1991). However, in none of these brain-imaging studies has the task of the subjects been to grasp real objects using different grip configurations. Here we explore the possibility that healthy human subjects engage different cortical areas when they apply forces under practically isometric conditions using a precision grip between index finger and thumb and during a power grip that engages all digits. We use functional magnetic resonance imaging (fMRI) to measure brain activity. By contrasting the activity recorded during the two tasks, we attempted to localize those regions of the brain that were involved selectively in one grasp configuration or the other. Preliminary results from this study have been reported (Ehrsson et al. 1998).

METHODS

Subjects

Five healthy male subjects (21–27 yr) participated in the study. All subjects were right-handed (Oldfield 1971) and had given their informed consent. The Ethical Committee of the Karolinska Hospital had approved the study.

Tasks

The subjects performed two different grip tasks with the right hand and two matching rest tasks. The grip tasks involved the production of force under almost isometric conditions. During the tasks, the subjects rested comfortably in a supine position in the MR scanner. The extended right arm was oriented parallel to the trunk in a relaxed position. We used appropriate supports to minimize movements of the arm and hand during the force production. The room was dark and the subjects kept their eyes closed. The subjects wore headphones to reduce the noise from the scanner and to present auditory cues.

To perform the precision-grip task, the subjects used the tips of the thumb and the index finger to grasp a nonmagnetic instrumented handle with vertical flat parallel contact surfaces spaced 30 mm apart (Fig. 1A). The handle was connected by a beam to a force motor (not shown). We used a nonmagnetic optic transducer system to record the grip force (the force applied perpendicular to the contact surfaces). The data were stored and analyzed using the SC/ZOOM data-acquisition system (Department of Physiology, University of Umeå). The subjects changed the grip force cyclically, being paced by a metronome that generated click sounds at 0.67 Hz through the headphones. When they squeezed the handle, at a target force of 2 N, they received a weak tactile cue through the handle. This was a brief force pulse delivered tangential to the contact surfaces (10-ms duration and <0.5 N peak force). The subjects then held the force until the click sound, which indicated that they should relax the grip and then squeeze the handle again. Figure 1C illustrates the resultant grip force profile together with the occurrence of the auditory and tactile cues; note the plateaus in the force during each grip cycle. For the matching rest condition, the subjects held the thumb and index finger in weak contact with the grip surface while they received tactile pulses as they had during the precision-grip task (Fig. 1D). The pulses were delivered at 0.67 Hz, and again the subjects heard the metronome sound (0.67 Hz) through the headphones. In this task, the subjects applied virtually no force to the handle.

During the power-grip task, the subjects clenched a cylindrical plastic-tube in a palmar opposition grasp that engaged all digits (Fig. 1B). Paced by the metronome, they generated a time-varying grip force like that applied for the precision-grip task, but the overall force

output was much higher. The diameter of the vertically oriented tube was 40 mm, and it had a 10-mm longitudinal gap. When the overall grip force reached some 20 N, the edges of this gap closed. This provided a mechanical cue for the target force. This mechanical event resembled the tactile cue received by the subjects when performing the precision-grip task. During the matching rest condition, the subject held the cylinder in the palm without applying a noticeable force and heard the metronome sound through the headphones.

Before the scanning commenced, the subjects practiced the grip tasks until they produced the requested time-varying grip forces. During the precision-grip task, we recorded the grip force during the scanning by the nonmagnetic transducer system. Technical limitations meant that the force could not be recorded during the power-grip task in the MR environment. Instead, the experimenter followed the performance of the subjects by visual inspection.

After the scanning, we measured the grip force during maximal voluntary contraction (MVC) as subjects grasped a standard dynamometer (cylindrical handle, 30 mm diam) with a precision or a power grip. We also recorded surface electromyograms (EMGs; Myo115-electrodes with in-built 2,000 × preamplifiers, Liberty Technology, Hopkinton, MA) in four subjects while they performed the precision- and power-grip tasks outside the MR scanner. We recorded from the right first dorsal interosseous (1DI), abductor pollicis brevis (AbPB), flexor digitorum superficialis, biceps-brachii, and deltoid muscles. We also recorded from the left 1DI and AbPB to check for possible nonvoluntary synergistic movements of the nonoperating hand. The electromyographic signals were sampled, stored and analyzed (root-mean-squared value) off-line on a portable PC using the Visual Designer and ZOOM software packages.

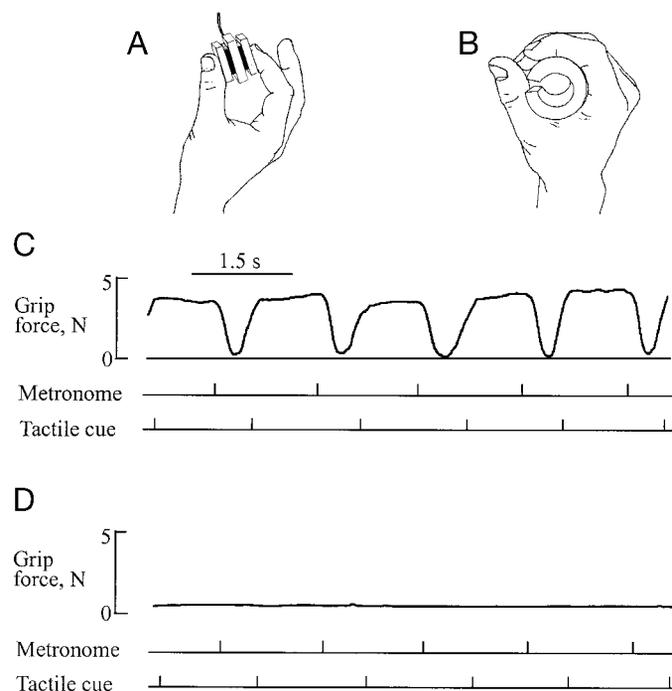


FIG. 1. Precision-grip task (A), the power-grip task (B), the grip force generated during the precision grip task by a single subject (C), and the matching rest condition (D). To perform the precision- and power-grip tasks, the subjects had to generate the same pattern of time variant grip force. Grip force changed rhythmically. Force plateau followed by a brief period of relaxation characterized each cycle. Click sound of a metronome (0.67 Hz) paced the relaxation phases, and a tactile pulse delivered through the object provided a cue for the target force (2 N in the precision-grip task and 20 N in the power-grip task). During the matching rest conditions, the subjects relaxed, and the digits were kept in weak contact with the grip surface. In the reference condition for the precision grip, the subjects heard the metronome and received the tactile pulses, and in the reference condition for power grip, they heard the metronome. For details, see METHODS.

Brain imaging

fMRI was conducted on a clinical 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 blood oxygenation level-dependent (BOLD) contrast (Kwong et al. 1992; Ogawa et al. 1992). [The parameters were: echo time (TE) = 50 ms; field of view (FOV) = 22 cm; matrix size = 64 × 64; pixel size = 3.4 mm by 3.4 mm; flip angle = 90°]. Twenty contiguous axial slices of 3.4-mm thickness were collected in each volume. We selected slices from the dorsal surface of the brain to cover the frontal and parietal lobes. The cerebellum and part of the basal ganglia were outside the field of view. A plastic bite bar restricted head movements. A high-resolution, three-dimensional gradient echo T1-weighted anatomic image volume of the whole brain was collected [3D-SPGR, echo time (TE) = 13 ms; field of view (FOV) = 24 cm; matrix size 128 × 256; 124 2-mm coronal slices; flip angle = 10°; 2 NEX].

Functional-image volumes were collected in separate runs, each of which either included the precision-grip task and the matching rest condition or the power-grip task and the matching rest condition. These runs were conducted in alternate order to reduce possible time effects. During each run, functional-image volumes were acquired continuously every 5,000 ms (TR = 5s) while the subjects performed the different tasks; for each run, a total of 104 volumes was collected (a time series). The tasks were performed in epochs that lasted 25 s (5 volumes being collected in this time), and the epochs of movement (precision-grip task or power-grip task) were alternated with the epochs of the matching rest condition. To allow for T1 equilibration effects, we started each run by recording four "dummy" volumes that we subsequently discarded. A total number of 954 volumes were collected for each participant; 780 were used in the analysis (some data were not used for technical reasons). Each task consisted of an equal number of image-volumes.

Data analysis and image processing

We used SPM-96 to analyze the functional images (Friston et al. <http://www.fil.ion.ucl.ac.uk/spm>). The volumes were realigned, coregistered to each individual's anatomic T1-weighted image (3D-SPGR), and normalized to the stereotactic space of Talaraich and Tournoux (Friston et al. 1995a; Talaraich and Tournoux 1988). The time series were smoothed spatially with an isotropic Gaussian filter of 8 mm full width at half-maximum, and temporally smoothed with a Gaussian kernel of width 2.83 s. We estimated the task-specific effects using the general linear model (GLM) with a delayed boxcar wave form (Friston et al. 1995b; Worsley and Friston 1995). Each of the time series was modeled with regressors for the tasks and the mean value using the standard model implemented in SPM-96. The significance of the effects was assessed using *Z* statistics for every voxel from the brain, and these sets of *Z* values were used to create statistical parametric maps (SPMs). A high-pass filter was used to remove low-frequency drifts and fluctuations of the signal (Holms et al. 1997), and proportional scaling was applied to remove global changes in the signal. To disclose activity that was robust across subjects and to increase the sensitivity of the analysis, we analyzed time series from the five subjects as a group. Linear contrasts between the different tasks were used to create SPMs, and these were arbitrarily thresholded at a *Z* value of 3.09. From these SPMs we report peaks (local maxima) of activity which, when corrected for multiple comparisons for the whole brain volume, corresponded to $P < 0.05$ on the basis on a test of peak height (Friston et al. 1995b). We also confirmed the consistency of the activity by examining statistical contrasts for individual subjects. The precision- and power-grip tasks were compared with the matching rest tasks with the contrasts (precision-grip—matching rest) and (power-grip—matching rest). Because the precision- and power-grip tasks were acquired in different runs (and the contrasts should have weights which sum to 0 over the task effects within each run), we compared the grip tasks with the two contrasts: [(precision-grip task—matching rest) - (power-grip task—matching rest)] and [(power-grip task—matching rest) - (precision-grip task—matching rest)], respectively.

In the present analysis, we compared data acquired in different runs, this might be inappropriate if the data had been collected under nonstationary conditions. However, there was no reason to believe that this was a problem because there was no obvious variability among corresponding runs in the manner in which subjects performed the task, because the different runs were conducted alternately to reduce any eventual time effects, because we modeled each time series as a regressor in the GLM remove variability between series, because we found similar activity for a given task when examining the equivalent series separately, and finally because we found no relevant task-by-series interactions when we contrasted the same tasks using subsets of time series.

Anatomic localizations of the activated regions were determined from an average image made from normalized (and intensity standardized) T2*-weighted images from each of the five subjects. In this average image, most of the major gyri and sulci were clearly identifiable. We use the terminology of Roland and Zilles (1996) for the cortical motor areas with the exception of the cortex in the depth of the central sulcus, which we termed SMC (primary sensori-motor cortex).

RESULTS

General task performance

The performance during the precision-grip task was consistent across the force cycles, and subjects generated the requested grip force profiles in >99% of the cycles. The mean

grip force during the plateau phases was 3.61 ± 1.06 N (mean \pm SD for data pooled across subjects). During the power-grip task, we observed no errors that indicated that the performance deviated from the requested pattern of force generation.

The mean grip-force across subjects during MVC was 80 N (range: 62–96 N) for the precision grip and 416 N (range: 355–456 N) for the power grip. Thus the mean grip force in the precision-grip task corresponded to 4.5% of that of the MVC, and the target force in the power-grip task (20 N) corresponded to 4.8% of that of the MVC.

The surface EMG of the right 1DI, AbPB, and flexor

TABLE 1. Activations associated with the grip tasks

Anatomic Location	Talaraich Coordinates (MNI Template)			Peak Z score
	X	Y	Z	
Precision-grip task minus matching rest condition				
Superior frontal gyrus (SMA)	0	0	52	8.62
L. central sulcus (SMC, MI/SI)	-40	-16	44	8.48
L. precentral gyrus (PMD)	-36	-12	60	8.43
Superior frontal gyrus (SMA)	-8	-8	60	8.18
L. precentral gyrus (PMV)	-60	0	16	7.64
L. lateral parietal operculum	-48	-36	20	6.98
L. thalamus	-12	-8	12	6.61
L. postcentral sulcus	-60	-24	44	6.43
L. inferior frontal gyrus	-44	56	8	5.47
L. angular gyrus	-60	-44	44	5.32
R. intraparietal sulcus	52	-44	48	7.87
R. intraparietal sulcus	48	-52	52	7.77
R. inferior precentral sulcus (PMV)	56	8	32	7.53
R. middle frontal sulcus	44	32	24	7.53
R. inferior precentral sulcus (PMV)	56	4	8	7.46
R. supramarginal gyrus	60	-36	20	7.45
R. supramarginal gyrus	64	-32	36	7.39
R. supramarginal gyrus	40	-40	36	7.23
R. inferior precentral sulcus (PMV)	48	4	28	7.23
R. precentral gyrus (PMD)	52	-4	44	6.93
R. inferior frontal sulcus	48	44	-4	6.85
R. superior precentral sulcus (PMD)	36	-4	40	6.81
R. anterior insula	32	20	0	6.43
R. middle frontal gyrus	36	8	48	6.01
R. middle frontal gyrus	40	0	52	5.79
R. supramarginal gyrus	36	-64	44	5.10
R. superior parietal gyrus	28	-68	60	5.03
Power-grip task minus matching rest condition				
L. post central gyrus (SMC, SI)	-40	-20	48	9.69
L. central sulcus, upper anterior bank (SMC, MI/PMD)	-28	-24	68	9.18
Superior frontal gyrus (SMA)	0	0	48	7.83
L. lateral parietal operculum	-56	-20	16	7.53
Superior frontal gyrus (SMA)	-8	-8	60	7.46
L. thalamus	-12	-12	8	5.51
Cingulate sulcus (CMAc)	-8	-20	40	4.60
L. precentral gyrus (PMV)	-64	4	24	4.40
R. precentral gyrus (PMV)	56	-4	36	5.86
R. postcentral sulcus	60	-28	36	5.77
R. lateral parietal operculum	56	-40	20	5.22

Significant increases in the BOLD contrast signal ($P < 0.05$ corrected for multiple comparisons).

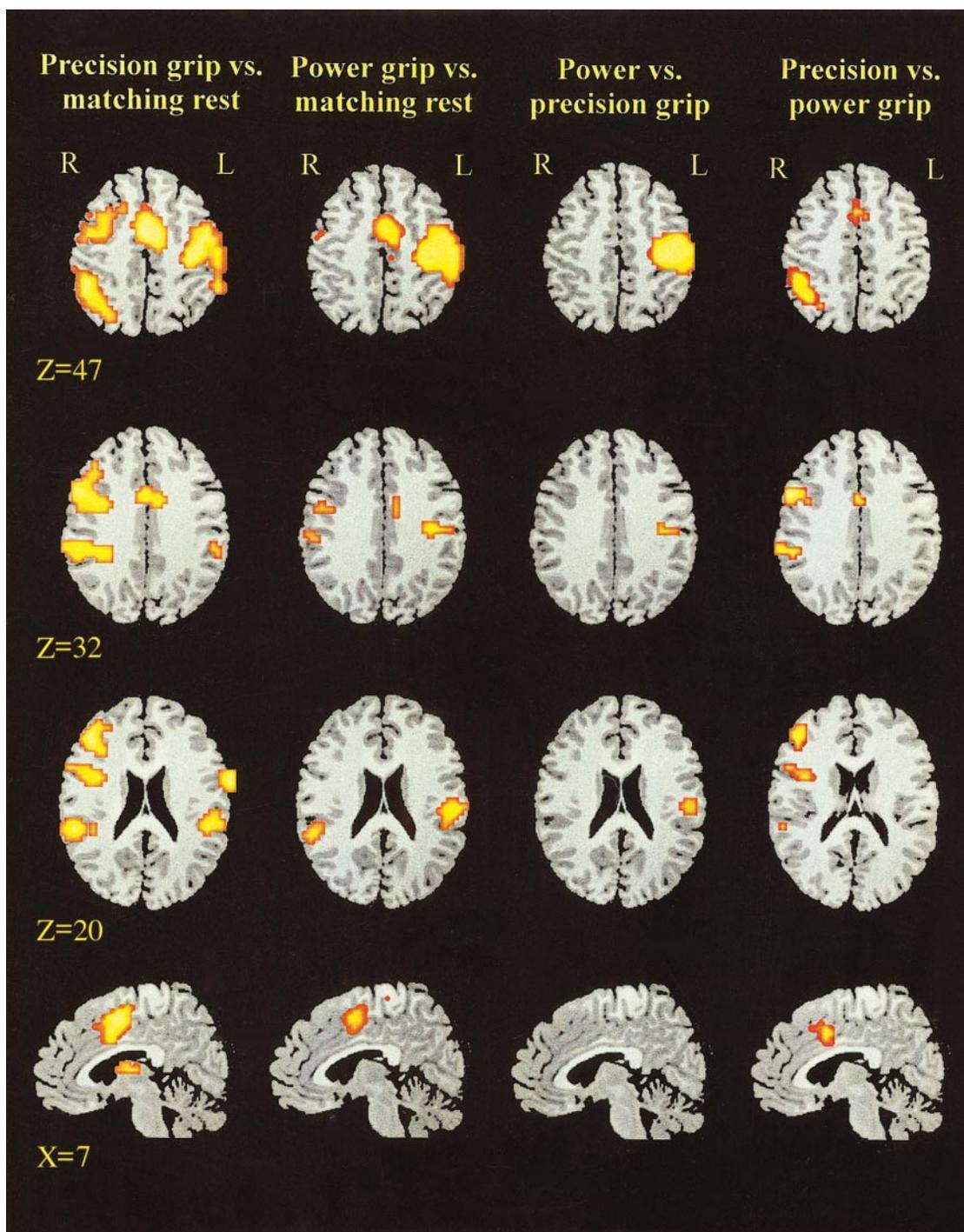


FIG. 2. Activation maps showing significant task-related increases in the BOLD contrast signal ($P < 0.05$, corrected for multiple comparisons). Data correspond to a group analysis (of 5 subjects) and each column represents 1 of the 4 contrasts analyzed. Results are displayed on a reference brain (MNI) for 3 axial slices and 1 sagittal slice with the Talarach coordinates indicated. *Top*: strong hemodynamic response in primary sensori-motor cortex (SMC) associated with the power-grip task and the selective activation of right intraparietal cortex and rostral cingulate motor area (CMAr) during the precision-grip task. *Second row*: strong activity demonstrated in right ventral premotor cortex (PMV), CMAr, and right supramarginal cortex while performing the precision-grip task. *Third row*: stronger activity indicated in the contralateral parietal operculum (PO) during the power-grip task as well as higher activity in the right PMV and the right inferior frontal sulcus (activity extending into the middle frontal gyrus) associated with the precision-grip task. *Bottom*: stronger response in rCMA emphasized during the precision-grip task. Left supramarginal and left inferior frontal activations are not shown on these slices.

digitorum superficialis showed stronger activity during the power-grip task than during the precision-grip task ($P < 0.05$, paired t -tests). Neither the proximal muscles of the

right arm (biceps and deltoid) nor the 1DI and AbPB muscles of the left hand showed reliable EMG activity in any of the tasks.

TABLE 2. Differences in activity between the grip tasks

Anatomic Location	Talarach Coordinates (MNI Template)			Peak Z score
	X	Y	Z	
Power grip compared to precision grip				
L. postcentral gyrus (SMC, SI)	-40	-20	52	8.88
L. central sulcus, anterior upper bank (SMC, M1/PMD)	-28	-24	68	8.28
L. lateral parietal operculum	-52	-20	20	4.62
Precision grip compared to power grip				
L. inferior frontal sulcus	-44	48	4	4.72
L. supramarginal gyrus	-64	-40	24	4.71
R. inferior frontal sulcus	44	40	0	5.63
R. inferior precentral sulcus (PMV)	56	12	32	5.41
R. intraparietal sulcus	44	-56	48	5.34
R. intraparietal sulcus	52	-44	48	4.85
R. middle frontal gyrus	48	36	16	4.84
Cingulate sulcus (CMAr)	4	8	40	4.76
R. supramarginal gyrus	64	-36	32	4.66

Significant increases in the BOLD contrast signal ($P < 0.05$ corrected for multiple comparisons).

Regions active during both grip tasks

Table 1 shows brain regions with significantly stronger BOLD contrast signal while performing the grip tasks than during the matching rest conditions ($P < 0.05$, corrected for multiple comparisons) (see also Fig. 2). Because the cerebellum was outside and the basal ganglia was only partially within the field of view, we do not report activity in these structures.

Both the precision- and power-grip tasks activated the SMC contralateral to the grasping hand. The activations extended into the dorsal premotor cortex (PMD) and the postcentral sulcus. Furthermore the ventral premotor cortex (PMV) showed bilateral activation with peaks of activity in the inferior part of the precentral gyrus. The SMA was active with an anterior and a posterior peak with activity extending into the cingulate sulcus (rostral cingulate motor area). We also observed activity in the contralateral parietal operculum (PO) and in the left thalamus. The activation extended into the right thalamus in the precision-grip task.

Regions differentially activated by the two grip tasks

Table 2 and Fig. 2 indicate regions that showed a significant difference in the BOLD contrast signal when the precision- and power-grip tasks were compared ($P < 0.05$, after correction for multiple comparisons). The left primary sensory cortex (SI) showed stronger activity during the power-grip task with a peak of activation located in the postcentral gyrus. Similarly we observed a stronger response in the anterior bank of the left central sulcus during the power-grip task. It is likely that this corresponds to the border between M1 (area 4a) and PMD (area 6) (Geyer et al. 1996). The cluster extended deeply into the central sulcus and, anteriorly, to the precentral gyrus and the superior precentral sulcus (PMD). During the power-grip task, we also observed stronger activity in the left PO.

Several regions showed significantly stronger activity during

the precision-grip task than during the power-grip task (Table 2 and Fig. 2; $P < 0.05$ corrected for multiple comparisons). Many of these were located in the right hemisphere, i.e., in cortical areas ipsilateral to the operating hand. We observed higher activity in the upper part of the right intraparietal sulcus (IPS) at two locations, and bilaterally in the supramarginal gyrus. In the prefrontal cortex, there were peaks of activity bilaterally in the inferior frontal sulcus with the activations extending to the middle frontal gyrus (more extensive in the right hemisphere). We also found stronger BOLD contrast signal in the inferior part of the right precentral sulcus, i.e., in the PMV. The cluster extended into the opercular cortex. Activation of the left inferior precentral sulcus ($Z = 4.08$, $P = 0.28$ corrected for multiple comparisons) did not reach the significance criterion. However, we descriptively report this finding to illustrate the tendency for a bilateral response in the PMV region. Furthermore an activation was found 8 mm rostral from the anterior commissural line (vertical line passing through the anterior commissure) in the cingulate sulcus, i.e., in the rostral cingulate motor area (CMAr) (Roland and Zilles 1996). This location corresponds to the "posterior portion of the rostral cingulate zone" in the classification of mesial areas by Picard and Strick (1996). The activity appeared to extend into the cingulate sulcus bilaterally, but the resolution of the statistical images did not allow reliable separation into two peaks.

We confirmed the consistency of the main findings in the group analysis by descriptively examining contrasts in individual subjects. At $Z > 1.66$, all subjects showed extensive ($> 600 \text{ mm}^3$) activations of the right PMV, right IPS, right supramarginal cortex, right inferior frontal sulcus and the CMAr when the precision-grip task was compared with the power-grip task. Furthermore four of five subjects showed activity in the left supramarginal cortex and three in the left inferior frontal sulcus. When power grip was compared with precision grip, we observed stronger activity in the contralateral SMC in all subjects and in the contralateral PO in four of our five subjects. We concluded that the results acquired from the group analysis was representative of the observations made for individual subjects.

DISCUSSION

The generation of grip forces by a precision grip between the index finger and thumb was associated with a different pattern of brain activity than that observed when making a power grip that engaged all digits. Our power-grip task was associated with stronger activity in the contralateral SI, M1 and PO, whereas the precision-grip task was associated with stronger activity in the right PMV, CMAr and the prefrontal and posterior parietal cortex bilaterally. Many of the regions that were more active in the precision-grip task were right-sided, i.e., they were located in the hemisphere ipsilateral to the operating hand.

During both grip tasks, the subjects rhythmically changed the grip force under virtually isometric conditions. A metronome paced the force production and a tactile signal provided feedback from the target force. Thus auditory and somatosensory information was used to guide the motor acts. In this respect, the two grip tasks were thought to be well balanced.

In addition to the grip configuration, the precision- and

power-grip tasks differed in terms of the overall force exerted. The higher force output applied while conducting the power-grip task might explain the higher activity observed in the SMC because the hemodynamic response in this and other posterior motor regions [i.e., SMA and the caudal motor field of the cingulate sulcus (CMAc)] increases with increased manual force (Dettmers et al. 1995; Thickbroom et al. 1998). Likewise the involvement of more digits in the power-grip task may have contributed to the stronger responses in these areas. Furthermore the higher activity in the PO may have been caused by a more spatially distributed tactile sensory input because this region also is activated by tactile stimuli (Burton et al. 1997; Coghill et al. 1994; Ledberg et al. 1995). A possible confounding factor may be differences in the general level of effort during the two grip tasks. However, relative to the corresponding MVC forces the forces applied during the two tasks were similar, which suggest that this factor is of little importance. It is also noteworthy that two of the prime movers (1DI and AbPB) in the precision-grip task were more active when performing the power grip. These results indicate that the hemodynamic responses exclusively associated with the precision-grip task were specific for this task and not related to additional activity of the intrinsic hand muscles.

A difference in the tactile input in the two reference conditions (matching rest) is another factor that may have influenced the results of the comparisons of the precision- and power-grip tasks: the reference condition for the precision-grip task involved the subjects receiving weak tactile pulses at 0.67 Hz, whereas the reference condition for the power-grip task did not include this tactile stimuli. Although the tactile pulses were brief and weak and did not evoke any grip force responses, we cannot exclude that their absence in the reference condition could have augmented the hemodynamic response estimated during the power-grip task. This primarily would have concerned regions that tactile stimulation would activate in passive subjects, i.e., SMC and PO. Another concern is whether the neural signals evoked by the auditory and tactile signals when present in the rest conditions were processed differently than when they guided the motor acts. Indeed, data obtained using evoked potential methods in man and single-cell recordings in monkey at the level of the primary somatosensory cortex have shown that voluntary movements attenuate the overall transmission of cutaneous signals from the distal forelimb (Chapman et al. 1996; Knecht et al. 1993). However, if present such "gating effect" could probably not explain the *increases* in the hemodynamic response during the grip tasks because previous positron emission tomography (PET) and fMRI studies have failed to record increased activity specifically related to tactile or auditory triggering of movements (Jasanshahi et al. 1995; Naito et al. 1999) or to self-produced tactile stimuli generated by movements of the hand (Blakemore et al. 1998).

Regions selectively activated during the precision-grip task

Studies in nonhuman primates indicate that M1 and other posterior motor areas that send direct projections to the spinal cord (i.e., SMA, CMAc) are of utmost importance for the control of force output during precision-grip tasks (Cadoret and Smith 1995, 1997; Hepp-Reymond 1988; Maier et al. 1993; Picard and Smith 1992; Porter and Lemon 1993; Wannier et al. 1991). The results in the present study indicate that the rostral

part of the right PMV, CMAr, and bilateral parietal and prefrontal regions also are engaged in skilled force production by an isometric precision grip but not by a power grip. Presumably this difference between grips reflects the need for additional sensory-motor control mechanisms to control force during pulp-to-pulp opposition engaging pairs of individual digits. Because two-fingered precision grips are inherently less stable than multidigit grips, the control of direction and magnitude of the applied finger forces needs to be more constrained at the level of individual digits (Flanagan et al. 1999). Thus the precision grip therefore may be more demanding in terms of neural control. Indeed a refined use of cutaneous afferent information is required to control fingertip force vectors during precision-grip tasks (Johansson 1996).

Frontal regions

We observed higher activity in the two nonprimary motor areas PMV and CMAr during the precision-grip task. By virtue of their projections to the cervical spinal enlargement (Dum and Strick 1991; Galea and Darian-Smith 1994; He et al. 1993, 1995) and to the primary motor cortex (Mukkasa and Strick 1979; Tokuno and Tanji 1993), both areas are likely to contribute to the control of the hand. The activation of PMV agrees with recent studies on object grasping in the macaque (Jeanerod et al. 1995; Rizzolatti et al. 1988, 1998). Interestingly, in our precision-grip task we specifically observed activity in the inferior part of the precentral sulcus. This activity was located some 10 mm rostral to that reported in previous PET studies during more general movements of individual digits (Fink et al. 1997; Kawashima et al. 1998; Matsumura et al. 1996; Sadato et al. 1996). Likewise it was located 16 mm rostral to the activity that we found in the right inferior precentral gyrus when we contrasted the power-grip tasks to the matching rest condition. The rostral border of the human PMV is not known (Roland and Zilles 1996), but it has been proposed that the human inferior precentral sulcus corresponds to the PMV in the macaque (Petrides and Pandya 1994; Rizzolatti et al. 1998). Indeed there are neurons in the rostral PMV (area F5) in the macaque that show activity that is specific for precision-grip configurations used to pick up small objects. Such neurons are more common than neurons related to whole-hand grips (Rizzolatti et al. 1988).

The CMAr was more active in the precision-grip task than in the power-grip task. Importantly, this region is separate from the CMAc (Dum and Strick 1991; Matelli et al. 1991; Roland and Zilles 1996; Shima et al. 1991) that was active when the power-grip task was contrasted to the matching rest condition (see Table 1). The location of the CMAr activity in the present study (8 mm rostral from the anterior commissural line) corresponded to a site predominately activated by movements of individual digits in previous human brain imaging studies (Fink et al. 1997; Grafton et al. 1993; Jahanshahi et al. 1995; Kawashima et al. 1996; Larsson et al. 1996; Picard and Strick 1996). Furthermore movements of individual digits activate neuronal populations in macaque CMAr (Shima et al. 1991). Hence our findings in humans, combined with previous observations in monkeys, strongly indicate that PMV and CMAr play an important role in the control of precision grips.

Overall, the activity we observed in the frontal lobes during the precision-grip task was located more anteriorly than that

during the power-grip task. As such, this novel finding supports the notion of Fuster (1995) that phylogenetically old motor skills are represented in posterior parts of the frontal lobes, whereas more skilled movements also involve more anterior regions. Previously, prefrontal activity has been observed in several PET studies during execution of simple movements when a rest condition was used as the control. (e.g., Jasanshahi et al. 1995; Larsson et al. 1996; Sadato et al. 1997). Activation of the prefrontal cortex also has been associated with several other behavioral factors relevant for motor control such as spatial attention (Jonides et al. 1993; Pardo et al. 1991), short-term retention of tactile information (Klingberg et al. 1996), selection of motor responses (Frith et al. 1991), and attentive self-monitoring of ongoing motor performance (Fink et al. 1999; Jueptner et al. 1997). The novel finding in the present study was that the activity in the lateral prefrontal cortex differed depending on the particular grasp-configuration used in a simple force production task. Specifically the inferior frontal sulcus was engaged only when force was applied using the precision grip. In the macaque monkey, the ventrolateral prefrontal cortex (ventral area 46) has strong reciprocal connections with the PMV and the parietal operculum (Preuss et al. 1989), and similarly, the dorsolateral prefrontal cortex (area 46) has connections with the PMV, CMAr, and the posterior parietal cortex (Cavada and Goldman-Rakic 1989; Lu et al. 1994). Thus given the existence of these pathways in the monkey and the activity recorded in the present study, it is interesting to speculate that the prefrontal cortex could be involved in skilled force production with a precision grip.

Parietal regions

Another interesting result from the present study was the selective involvement of the right intraparietal and bilateral supramarginal cortex during the precision-grip task. The posterior parietal cortex is a heterogeneous region with little information available concerning the possible anatomic correspondence between the human and monkey brain (Eidelberg and Galaburda 1984; Milner 1997). In the nonhuman primate, numerous studies have shown that populations of neurons in the intraparietal sulcus are likely to be involved in visuomotor transformations during reach and grasp (Jeannerod et al. 1995; Sakata et al. 1997). Of special interest is a region within the macaque anterior intraparietal sulcus that contains neurons that show activity specific to the grasping of small objects (Sakata et al. 1995, 1997; Taira et al. 1990). In addition, neurons in area 7 increase the discharge rates during voluntary hand movements and in response to visual and tactile stimuli (Hyvärinen et al. 1981). The anatomic connections between these parietal regions and the premotor fields, including the ventral premotor area, are considered of particular importance for the sensory control of the hand (Rizzolatti et al. 1998). In humans, lesions in the posterior parietal cortex, involving intraparietal cortex cause disorders of grip formation (Jeannerod 1986; Pause et al. 1989). Indeed previous PET and fMRI studies have reported right- and left-sided activity in the intraparietal and supramarginal regions during visually guided reach, grasp, and graphomotor movements performed with the right hand (Binkofski et al. 1998; Grafton et al. 1998; Inue et al. 1998; Matsumura et al. 1996; Seitz et al. 1997). Similar regions also are activated in sensorimotor manipulatory tasks performed

without vision, i.e., when subjects rotate two small cylindrical objects held in the right hand (Kawashima et al. 1998) and somatosensory discrimination of objects shape with exploratory finger movements (O'Sullivan et al. 1994; Roland et al. 1998; Seitz et al. 1991). However, our precision-grip task differed from all these previous studies in that neither vision nor overt arm or finger movements were involved. Instead somatosensory input was used to control isometric grip force. Hence our findings suggests that the control of fingertip forces in the precision-grip task might require processing of somatosensory signals in the posterior parietal cortex in addition to the processing required for the control of force during the power-grip task.

Activity in the ipsilateral hemisphere during the precision-grip task

The two grip configurations exhibited differences in the hemispheric lateralization of the activation patterns. The power grip was associated predominately with contralateral left-sided activations, whereas the precision-grip task involved extensive activity in both hemispheres. As such, the ipsilateral activity in the precision-grip task agrees with previous findings that many motor regions are activated bilaterally during unimanual motor tasks (Kawashima et al. 1998; Rao et al. 1993; Roland and Zilles 1996). Furthermore brain-damaged patients often have contralateral but not ipsilateral deficits in simple movements tasks, whereas more complex sensory-motor tasks requires the integrity of both hemispheres (Haaland and Harrington 1996). Lesions of the right hemisphere have been associated with ipsilateral impairment of skilled finger movements and of motor tasks that depend on movement-to-movement sensory feedback (Arrigoni and DeRenzi 1964; Haaland and Harrington 1996; Warrington et al. 1966; Winstein and Pohl 1995). Thus the right-sided activity in the precision-grip task may reflect additional demands in terms of somatosensory control and sensory-motor processing compared with the power-grip task. During the precision-grip task, we observed a preponderance of activity in the right PMV and the right intraparietal cortex. However, we also measured an increased hemodynamic response in the contralateral left inferior precentral sulcus (PMV), which was close to being statistically significant.

In conclusion, in addition to previously well-recognized sensorimotor areas, our results reveal novel premotor and association areas that are activated in the control of precision grip but less so in power grip. Our findings also indicate that the right hemisphere is engaged in important control mechanisms during precision-grip tasks executed by the right hand.

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