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Brain activity is similar during precision and power gripping with light force: An fMRI study

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Handgrips can be broadly classified into precision and power grips. To compare central neuronal control of these tasks, functional magnetic resonance imaging was used in 14 healthy right-handed volunteers, who repetitively squeezed non-flexible force transducers with a precision grip and a power grip of the dominant hand. The relative grip force levels and movement rates (0.45 Hertz) of both tasks were comparable. Peak isometric grip forces ranged between 1% and 10% of the maximum voluntary force. Reflecting the additional recruitment of extrinsic hand muscles and the higher absolute force, activation of the contralateral primary sensorimotor cortex (M1/S1) and ipsilateral cerebellum was significantly stronger during power than during precision grip. No brain areas exhibited stronger activity during the precision grip than during the power grip. The left M1/S1 and right cerebellum showed a positive linear relationship with the grip force, while the right angular gyrus and left superior frontal gyrus showed a gradual increase in activity when less force was applied. However, these force-dependent modulations of brain activity were similar for the precision and power grip tasks. No brain region was specifically activated during one task but not during the other. Activity during precision gripping did not exceed the activity associated with power gripping possibly because the precision grip task was not challenging enough to call on dexterous fine motor control.

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Introduction

Handgrips of humans and nonhuman primates can be classified into two fundamental categories, the power grip and the precision grip (Napier, 1956). During power grip, all fingers participate in grasping an object against the palm, and extrinsic muscles of the hand provide the major grip force (Long et al., 1970). The precision grip (or pincer grip) involves smaller forces and is

confined to the pulps of the index finger and thumb. It is used for the manipulation of small objects (e.g., needles, beads), which requires fine tuning of the applied forces. Single-cell recording experiments in nonhuman primates suggest that both grips are controlled by different neural mechanisms (Lemon, 1993). Neurons of the primary motor cortex (M1), which project monosynaptically to spinal motoneurons innervating intrinsic hand muscles, were more active during precision grip than during power grip (Muir and Lemon 1983). Lawrence and Kuypers (1968) reported that macaque monkeys can still grasp objects with a power grip after pyramidotomy, while the ability to perform manipulations with a precision grip and independent finger movements are severely impaired.

In humans, transcranial magnetic stimulation (TMS) was used to probe changes in corticospinal excitability during these tasks. Recordings of the motor-evoked potentials (MEPs) from intrinsic hand muscles showed that MEP amplitudes were higher during precision gripping than power gripping, indicating greater motor cortical excitability and possibly stronger involvement of direct corticomotoneuronal connections (Flament et al., 1993; Schieppati et al., 1996; Hasegawa et al., 2001; Huesler et al., 1998; Tinazzi et al., 2003). The first dorsal interosseus muscle (FDI) was typically chosen as a target muscle. However, besides the FDI, contractions of at least eleven other extrinsic and intrinsic hand muscles contribute to the generation of precision and power grip forces (Hepp-Reymond et al., 1996; Long et al., 1970). Neuroimaging studies of grip tasks do not focus on specific target muscles. Instead, they outline brain regions involved in control of all muscles participating in a given task and can detect task-dependent variations of the cortical activation patterns.

Up to now, only two studies directly compared regional patterns of brain activity during precision and power grip tasks. Ehrsson et al. (2000) used functional magnetic resonance imaging (fMRI) in five male subjects, who repetitively squeezed a cylindrical object with a power grip, and a force transducer with a precision grip of the dominant right hand at approximately 5% of the respective maximum voluntary force (MVF). Fixed-effects analyses revealed that the precision grip task resulted in a stronger activity of ipsilateral

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ventral premotor cortex, rostral cingulate motor area, and several posterior parietal and prefrontal regions, while the power grip task led to a stronger activation of the left primary sensorimotor cortex (M1/S1) relative to the precision grip task. Takasawa et al. (2003) used positron emission tomography (PET) to study cerebral and cerebellar activation in seven volunteers. In a first condition, subjects lightly and repetitively pressed and released the tips of the right thumb and index finger (precision grip). In a second condition, participants were asked to repetitively close and open the fist (power grip). No real objects were grasped, nor were the grip forces measured. Takasawa et al. (2003) concluded that there are no significant differences in brain activity between power grip and precision grip without a target object.

These discordant findings prompted the present fMRI study, which tests for regional differences in neuronal activity during isometric power and precision grip tasks in a larger sample of normal volunteers ($n=14$) by using a random effects analysis. Two MR-compatible force transducers were compressed rhythmically either between the pads of the thumb and index finger (precision grip) or by clenching the fist (power grip). We included two target force levels, namely 4% and 1% of the individual MVF. Three issues are addressed. First, patterns of brain activity during repetitive precision and power gripping per se are contrasted. Second, force-related changes in brain activation are identified and compared for both tasks. Third, the factorial study design enabled us to test whether differences in neuronal activity between precision and power grip are modified by the force level and/or the presence of visual feedback.

Methods

Participants

Fourteen healthy volunteers (7 women, 7 men) with no history of neurological or psychiatric disease participated in the study, which had been approved by the local ethics committee. All subjects gave their informed written consent. The age of the participants was 26 ± 5 years (mean \pm SD), ranging from 21 to 38 years. All subjects were consistent right-handers according to a questionnaire and a square marking test (Annett, 1992). Before the experiments, maximum voluntary grip force (MVF, three trials) of the dominant hand was determined in each subject with a hand dynamometer. The posture of the hand during these MVF recordings was the same as during the subsequent fMRI experiments (see Supplementary data). Average MVF values were 65 ± 14 N for the precision grip and 435 ± 130 N for the power grip (mean \pm SD).

Experimental procedure

Participants lay supine in the MR scanner with the arms extended comfortably. The right hand rested in a relaxed semiprone posture on a platform next to the right hip joint. Two custom-made non-metallic force transducers (Dasch Instruments, Kiel, Germany) were used to measure the power and precision grip forces under nearly isometric conditions. They were connected to the computer-based SC/ZOOM data acquisition and analysis system (Dept. of Physiology, Umeå University, Sweden). The power grip force transducer (length 11 cm, width 6×3.5 cm) was shaped like two parallel adjacent cylinders and had an accuracy of 0.3 N (range 0–120 N, sampling rate 50 Hz). With increasing force, light trans-

mission between two optical cables was progressively dimmed by a shutter (spring excursion <1 mm). The precision grip force transducer, which had two flat vertical grip surfaces (40×40 mm) spaced 28 mm apart, measured the isometric pinch force exerted between the pads of thumb and index finger (spring excursion <0.5 mm). The grip surfaces were covered with thin felt. Power and precision grip force transducers were exchanged during practice and between fMRI sessions according to the task. The respective device was placed into the volunteer's right hand by the examiner and was then attached to the platform. This ensured that the participants were able to grasp and squeeze the force transducer without any effort or arm movement. Because the transducer was attached to the platform, there was no need for the subjects to hold the device or to actively stabilize its position.

During each grip task, participants repetitively squeezed the respective force transducer at a rate of 0.45 Hz. Blocks of eleven compression–release cycles were performed. The target force was either set to 4% (L, light grip force) or to 1% (VL, very light grip force) of the individual MVF, but it was kept constant within blocks (Figs. 1A, B). A grip force of $\sim 4\%$ of MVF is representative of the fingertip forces that are applied when small objects are manipulated in everyday situations (Ehrsson et al., 2001). The grip force of 1% MVF represents an exceptionally light force that is used when very fragile and delicate items are handled.

In a visual feedback condition, subjects saw their actual grip force as a red line and the required target force as a horizontal yellow line on a display. A video hood with a 7-in. LCD monitor and a 15° field of view was used (IFIS-SA, Intermagnetics, New York). Click sounds of a metronome (54/min) paced the compression–release cycles. The subjects were instructed to swiftly increase the grip force after one click in order to match the target line and to release the grip after the next click, which followed ~ 1 s later. The fingers stayed in light touch with the felt of the grip surfaces also between the compressions. This avoided “exaggerated” movements, such as complete finger extensions between squeezes. In the no-vision condition, the monitor was switched off and the participants kept their eyes closed all the time. They reproduced the VL and L target grip forces (announced at the start of each block) as best as possible from memory and prior practice. All tasks were practiced extensively with and without visual feedback for about 20 min before MR scanning started.

MR imaging

A 3.0-T Philips Achieva tomograph with a phased array head coil (Philips, Best, The Netherlands) was used for blood oxygen level-dependent (BOLD) sensitive fMRI. The subjects wore headphones for noise protection, and foam pads restricted head motion. Functional imaging was performed using a T2*-weighted echo planar imaging technique (EPI, echo time 35 ms, field of view 230×230 mm, pixel size 2.9×2.9 mm). Each EPI volume was obtained within 3000 ms (repetition time) and comprised 36 axial slices that covered the brain from the vertex to the cerebellum (3-mm slice thickness, 0.3-mm inter-slice gaps).

Each participant underwent four fMRI sessions, corresponding to the conditions: precision grip with visual feedback (PREC_{VIS}), precision grip without visual feedback (PREC_{NO-VIS}), power grip with visual feedback (POW_{VIS}), power grip without vision (POW_{NO-VIS}). These conditions were scanned in separate sessions to ensure a constant cognitive set. Each session lasted 408 s and comprised 136 EPI volumes. Half of the subjects started with the

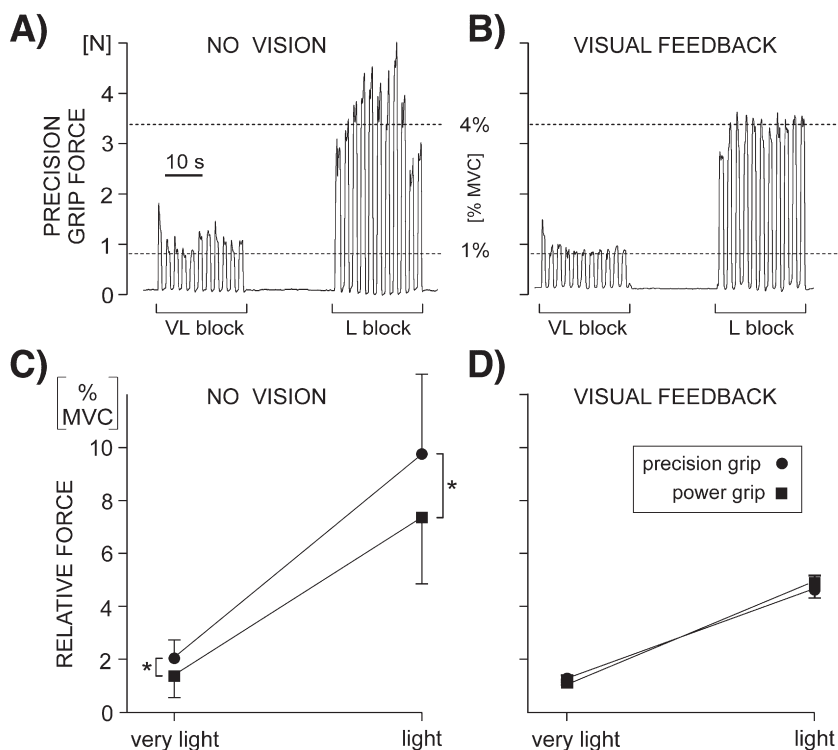


Fig. 1. Grip forces. Original force curves of a typical volunteer during precision gripping without (A) and with visual feedback (B). Blocks of repetitive squeezing with very light (VL) and light (L) grip force alternated. Dotted lines indicate the target force levels (1% and 4% of the MVF). (C, D) Grip force maxima of the VL and L blocks (one average of eleven force maxima per block) of all subjects in the no-vision and visual feedback conditions. Asterisks indicate significant (paired *t*-test, $P < 0.05$) differences between precision (circles) and power grip forces (squares). Error bars indicate inter-individual SD.

two power grip sessions, the other half with the two precision grip sessions. Sessions with visual feedback always preceded sessions without visual feedback of the same grip task to match the amount of prior practice in the no-feedback condition.

During each fMRI session, eight blocks (duration, 24 s each) of repetitive squeezing alternated with periods of rest (24 s). We alternated between blocks of light (L=4% MVF) and very light (VL=1% MVF) target grip forces. Short verbal commands (start, stop, force level) and the metronome sounds, which were audible during both the resting and gripping periods, were given via headphones. We furthermore acquired high-resolution anatomical images of the whole brain in each subject with a three-dimensional

T1-TFE sequence (repetition time 7.7 ms, field of view 230 mm, 160 slices, voxel size $1 \times 1 \times 1$ mm).

Image processing and analysis

Pre-processing and analyses of the MR data were performed using SPM2 (available at <http://www.fil.ion.ac.uk/spm>) and Matlab (Mathworks, Sherborn, MA). For each subject, image volumes were realigned spatially using a least squares approach and six-parameter rigid body spatial transformations. The T1 anatomical images and the EPI image volumes were normalized to the Montreal Neurological Institute (MNI) brain template. The fMRI images were re-

Table 1
Forces of precision and power gripping

	Very light force (VL)		Light force (L)	
	Precision grip	Power grip	Precision grip	Power grip
<i>Squeezing with visual feedback</i>				
Relative grip force [% MVF]	1.28±0.13	1.15±0.10	4.61±0.28	4.82±0.36
Variability of relative grip force ^a	0.22±0.07	0.18±0.04	0.57±0.25	0.49±0.14
Absolute grip force [N]	0.83±0.19 ^b	4.99±1.62	2.99±0.64 ^b	21.23±7.32
<i>Squeezing without vision</i>				
Relative grip force [% MVF]	2.05±0.69 ^b	1.38±0.81	9.77±3.04 ^b	7.36±2.51
Variability of relative grip force ^a	0.56±0.21	0.47±0.13	1.39±0.89	1.21±0.56
Absolute grip force [N]	1.32±0.59 ^b	6.43±5.66	6.07±2.11 ^b	31.36±13.30

Grip force peaks of the repetitive squeezes (see Fig. 1) with mean values±inter-individual SD of the 14 subjects.

N, Newton; MVF, maximum voluntary grip force.

^a Intra-individual variability (SD) of the peak grip forces of each block of repetitive squeezing.

^b Significant differences between precision and power grip forces (paired *t*-test, $P < 0.05$).

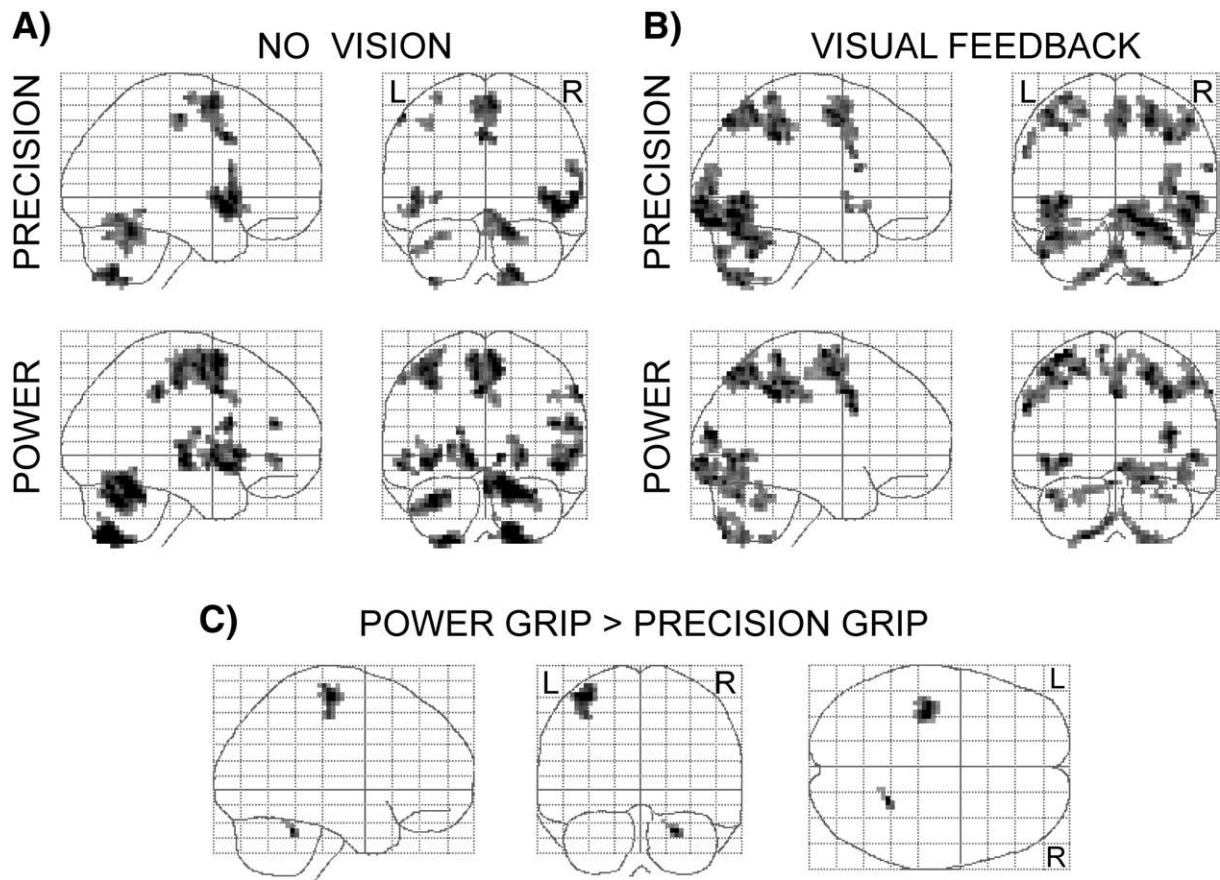


Fig. 2. Brain activity during gripping movements per se (irrespective of the force). (A, B) Lateral and frontal view of activations in a “glass brain” during precision and power gripping without feedback (A) and with (B) visual feedback. (C) Regions that were more active during power than precision gripping (lateral, frontal, and axial view). Significance is $P < 0.05$ (corrected) at the cluster level in panels A–C. L, left; R, right brain hemisphere.

sampled with a voxel size of $3 \times 3 \times 3$ mm and smoothed with a 7-mm full-width-at-half-maximum Gaussian kernel. They were high-pass filtered to remove low-frequency drifts of the signal (cutoff period, 128 s). Serial correlations were accounted for with an autoregressive model (SPM model AR(1)). Proportional scaling was applied to eliminate the effects of global signal changes.

A two-level data analysis procedure was performed. At the first level, activation maps were calculated for each individual subject. A general linear model was applied to the time-course of the signal of each voxel (Friston et al., 1995). Since the grip forces (L, VL) were not constant especially in the no-vision sessions, we chose an epoch-related parametric study design which included the actual grip force as a regressor (“parametric modulation” in SPM; Buechel et al., 1998) instead of a categorical design. The resulting design matrix had two regressors per session, which allowed us to distinguish between regions that were active during gripping (squeezing) per se (irrespective of the grip force) and regions whose activity covaried with the force. A similar approach has been used in previous studies of force-related brain activation (Dettmers et al., 1995; van Duinen et al., 2007a,b; Ward and Frackowiak, 2003).

The first regressor, a boxcar function convolved with the hemodynamic response function, modeled the onset and duration of each block of repetitive squeezing, irrespective of the actual grip force. Appropriate contrasts identified brain activity associated with gripping per se for each condition ($PREC_{VIS}$, $PREC_{NO-VIS}$, POW_{VIS} , POW_{NO-VIS}). Precision and power grip-related brain ac-

tivity was compared [$(PREC_{VIS} + PREC_{NO-VIS})$ minus $(POW_{VIS} + POW_{NO-VIS})$, and vice versa]. It was also examined whether differences depended on visual feedback (interaction). The second regressor, which parametrically modeled grip force, was

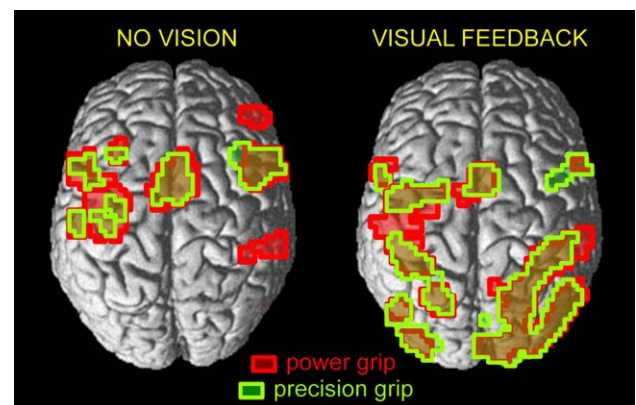


Fig. 3. Brain activity during precision gripping (green) and power gripping (red), superimposed on a normalized template brain. Activations occur during movements per se (disregarding force-dependent modulations) and are based on data of all 14 subjects (random effects analysis). Views from above; left in images is left in subjects. Significance is $P < 0.05$ (corrected) at the cluster level.

Table 2
Brain activity during precision and power gripping without visual feedback

Cluster level		Voxel level				Coordinates (MNI) of foci (mm)				
<i>P</i> (cor)	KE	<i>P</i> (FWE)	<i>P</i> (FDR)	<i>T</i>	<i>Z</i>	<i>x</i>	<i>y</i>	<i>z</i>	Anatomical region	BA
<i>Precision gripping</i>										
0.000	185	0.002	0.001	10.99	5.42	51	6	-6	R insula	
		0.005	0.001	10.05	5.23	60	15	0	R Rolandic operculum	44 (50%)
0.000	137	0.030	0.001	8.63	4.90	6	0	60	R SMA	6 (80%)
		0.059	0.002	8.12	4.76	-3	9	39	L middle cingulate gyrus	
		0.211	0.002	7.21	4.50	-3	-6	60	L SMA	6 (90%)
0.000	79	0.035	0.002	8.51	4.87	21	-66	-51	R cerebellum (lbl. VIII)	
0.000	174	0.051	0.002	8.22	4.79	15	-54	-21	R cerebellum (lbl. IV,V)	
0.034	11	0.090	0.002	7.80	4.68	-54	-21	54	L postcentral gyrus	1 (80%)
0.000	55	0.111	0.002	7.66	4.63	-48	0	0	L frontal operculum	44 (10%)
0.009	16	0.134	0.002	7.52	4.59	-36	-57	-54	L cerebellum (lbl. VIII)	
0.046	10	0.445	0.003	6.71	4.34	-33	18	0	L insula	
0.000	47	0.452	0.003	6.70	4.33	-39	-57	-30	L cerebellum (crus 1)	
0.019	13	0.612	0.003	6.49	4.26	-30	-15	66	L precentral gyrus	6 (80%)
0.011	15	0.808	0.004	6.00	4.08	-36	-24	48	L central sulcus	3 (60%)
<i>Power gripping</i>										
0.000	81	0.002	0.000	10.98	5.42	-27	-75	-57	L cerebellum (lbl. VII)	
0.000	162	0.003	0.000	10.45	5.31	48	9	-9	R insula	
		0.052	0.000	8.21	4.79	57	12	21	R inf. frontal operculum	44 (70%)
0.000	306	0.003	0.000	10.45	5.31	21	-51	-24	R cerebellum (lbl. V)	
0.000	151	0.003	0.000	10.44	5.31	18	-66	-51	R cerebellum (lbl. VIII)	
0.000	238	0.005	0.000	10.17	5.26	-3	3	42	L middle cingulate gyrus	6 (10%)
		0.007	0.000	9.77	5.17	6	3	63	R SMA	6 (80%)
		0.039	0.000	8.42	4.84	-6	-6	51	L SMA	6 (80%)
0.000	76	0.005	0.000	10.01	5.22	-9	-18	-3	L thalamus	
0.012	12	0.007	0.000	9.82	5.18	9	-18	0	R thalamus	
0.000	109	0.009	0.000	9.61	5.13	-33	-63	-30	L cerebellum (crus 1)	
0.000	39	0.014	0.000	9.22	5.04	63	-36	42	R supramarginal gyrus	
0.000	34	0.020	0.000	8.94	4.97	-39	6	-6	L insula	
0.003	16	0.045	0.000	8.31	4.81	48	42	21	R middle frontal gyrus	
0.000	54	0.050	0.000	8.23	4.79	24	0	0	R globus pallidus	
0.000	218	0.057	0.000	8.13	4.77	-39	-6	57	L precentral gyrus	6 (40%)
		0.064	0.000	8.05	4.75	-36	-24	48	L postcentral gyrus	3 (60%)
0.000	72	0.059	0.000	8.11	4.76	-33	18	0	L insula	
		0.167	0.001	7.37	4.55	-51	3	0	L frontal operculum	44 (20%)
0.000	31	0.144	0.001	7.47	4.58	-24	3	6	L putamen	
0.000	23	0.247	0.001	7.10	4.46	48	45	-3	R inf. frontal gyrus	
0.003	16	0.771	0.001	6.32	4.20	6	15	36	R middle cingulate gyrus	6 (10%)

Regions activated ($P < 0.05$, corrected for multiple comparisons at the cluster level) during precision and power-gripping movements per se (irrespective of force) in the no-vision condition. Foci which were significant with $P < 0.05$ (FWE correction) at the voxel level are shown in bold. Percentages in the right column give the probabilities for the activation foci of belonging to the respective Brodmann areas (BA) according to cytoarchitectonic probability maps (Eickhoff et al., 2005). KE, cluster size; L, left; lbl., Larsell lobulus; R, right; *T*, *T*-value; *Z*, *Z*-score.

orthogonalized with respect to the first regressor which modeled the task per se (Andrade et al., 1999). This allows to identify brain regions where task-related BOLD signals covary with the grip force, rather than showing just a general increase relative to baseline during the blocks of repetitive squeezing. For the second regressor, the grip force peaks of the eleven squeezes of each block (see Fig. 1) were extracted and averaged, and entered as covariates into the statistical design matrix (one force value per block). Force-related changes in activity occurring during precision and power gripping were compared and interactions with the visual condition were examined. To assess stable and regular motor performance, we also calculated the cycle-to-cycle (intra-individual) variability as the SD of the grip force peaks in each block.

The contrast images of all 14 participants obtained at the first level were entered into a random effects second level ana-

lysis. This approach accounts for the inter-individual variability of the BOLD responses and therefore permits inferences at the population level (Friston et al., 1996, 1999). One-sample *t*-tests were calculated for each effect of interest to obtain statistical parametric maps. Significance level was set at a corrected $P < 0.05$. Correction for multiple comparisons was performed at the cluster level. We used a height threshold of $P < 0.0001$, corresponding to $T = 5.11$. At this height level, clusters were considered significant if they consisted of more than eight contiguous voxels. The locations of regional maxima are given as MNI spatial coordinates. We used the definitions of functional areas in the cortical motor system (M1/S1, primary sensorimotor cortex; SMA, supplementary, CMA, cingulate motor area) as given by Roland and Zilles (1996). Anatomical landmarks (e.g., central sulcus) from averaged images, probabilistic cytoarchitectonic maps (Eickhoff et al., 2005), and the labeling tool of

Table 3
Brain activity during precision- and power gripping with visual feedback

Cluster level		Voxel level				Coordinates (MNI) of foci (mm)				
<i>P</i> (cor)	KE	<i>P</i> (FWE)	<i>P</i> (FDR)	<i>T</i>	<i>Z</i>	<i>x</i>	<i>y</i>	<i>z</i>	Anatomical region	BA
<i>Precision gripping</i>										
0.000	767	0.001	0.001	12.24	5.65	24	-84	-18	R cerebellum (crus 1)	
		0.001	0.001	11.24	5.47	48	-72	-12	R inferior occipital gyrus	
		0.005	0.001	10.01	5.22	6	-96	-9	L calcarine sulcus	
0.000	215	0.002	0.001	11.02	5.43	-42	-63	-27	L cerebellum crus 1	
		0.005	0.001	10.15	5.25	-45	-72	-3	L inf. occipital gyrus	
0.000	86	0.004	0.001	10.33	5.29	-36	-93	-3	L middle occipital gyrus	18 (10%)
0.000	255	0.006	0.001	9.91	5.20	21	-75	51	R superior parietal lobe	
		0.016	0.001	9.11	5.02	48	-39	51	R inferior parietal lobe	2 (20%)
0.000	69	0.029	0.001	8.65	4.90	27	-66	-57	R cerebellum (Ibl. VIII)	
0.000	69	0.040	0.001	8.41	4.84	-45	-9	57	L precentral gyrus	6 (70%)
0.000	100	0.045	0.001	8.31	4.81	3	0	51	R SMA	6 (60%)
0.000	82	0.075	0.001	7.94	4.71	-33	-45	48	L inf. parietal cortex	2 (20%)
0.016	10	0.102	0.001	7.71	4.65	63	9	18	R frontal operculum	44 (30%)
0.000	37	0.149	0.001	7.45	4.57	-24	-66	57	L superior parietal lobe	
0.000	21	0.209	0.001	7.22	4.50	-60	6	33	L precentral gyrus	6 (60%)
0.000	35	0.229	0.001	7.15	4.48	45	3	-6	R insula	
<i>Power gripping</i>										
0.000	34	0.001	0.001	12.03	5.61	-36	-93	-3	L middle occipital gyrus	18 (10%)
0.000	122	0.002	0.001	10.98	5.42	-39	-42	63	L postcentral gyrus	2 (50%)
		0.036	0.001	8.49	4.86	-33	-45	48	L inferior parietal lobe	2 (20%)
0.000	298	0.002	0.001	10.79	5.38	33	-48	42	R inferior parietal lobe	
		0.015	0.001	9.17	5.03	24	-60	57	R superior parietal lobe	
0.000	51	0.007	0.001	9.80	5.17	36	-87	15	R middle occipital gyrus	
0.000	253	0.012	0.001	9.38	5.08	51	-66	0	R middle temporal gyrus	
		0.019	0.001	8.99	4.99	24	-84	-15	R fusiform gyrus	18 (40%)
		0.039	0.001	8.43	4.85	3	-96	-9	L calcarine sulcus	17 (70%)
0.000	102	0.012	0.001	9.38	5.08	0	6	42	L middle cingulate gyrus	6 (20%)
		0.092	0.001	7.79	4.67	-9	-3	69	L SMA	6 (80%)
		0.167	0.002	7.37	4.55	3	0	57	R SMA	6 (90%)
0.000	22	0.012	0.001	9.35	5.07	-57	6	33	L precentral sulcus	6 (50%)
0.000	121	0.025	0.001	8.78	4.94	-33	-12	69	L precentral gyrus	
		0.025	0.001	8.76	4.93	-42	-3	54	L precentral gyrus	6 (40%)
0.000	31	0.028	0.001	8.69	4.91	-45	-72	-3	L middle occipital gyrus	
0.000	42	0.030	0.001	8.62	4.90	-27	-69	57	L superior parietal lobe	
0.000	112	0.030	0.001	8.62	4.90	-21	-78	-54	L cerebellum (Ibl. VII)	
0.000	21	0.048	0.001	8.27	4.80	-42	-69	-27	L cerebellum (crus 1)	
0.000	34	0.072	0.001	7.97	4.72	-3	-78	-18	Vermis cerebelli	
0.000	21	0.282	0.002	7.01	4.44	-36	-54	-33	L cerebellum (crus 1)	
0.000	25	0.317	0.002	6.93	4.41	30	-48	-27	R cerebellum (Ibl. VI)	
0.001	18	0.344	0.002	6.88	4.39	27	-48	-57	R cerebellum (Ibl. VIII)	
0.013	11	0.763	0.002	6.36	4.22	12	-54	-21	R cerebellum (Ibl. IV,V)	
0.029	9	0.830	0.002	6.23	4.17	60	12	21	R frontal operculum	44 (50%)
0.002	17	0.892	0.003	6.03	4.09	-27	-69	-24	L cerebellum (Ibl. VI)	

Activated regions during precision and power gripping movements per se (irrespective of force) with visual feedback. Statistical thresholds, abbreviations, and labeling of regions as in Table 2.

Tzourio-Mazoyer et al. (2002) were to identify the anatomical location of each given cluster.

Results

Precision and power grip forces

Analysis of variance revealed significant main effects of the force level, task, and visual condition, and a significant interaction between these factors ($F_{1,13}=61.3$; $P<0.05$). With on-line visual feedback, all subjects were able to closely match the required target force levels (1% and 4% MVF). The grip force peaks had a slight tendency to

overshoot the target line, so 1–1.5% MVF were reached during very light (VL) and 4–5% MVF during light (L) squeezing with visual feedback (Table 1, Fig. 1). There were no significant differences between the relative forces of precision and power gripping in the visual condition (paired *t*-tests, n.s.). Without visual feedback, the grip force maxima exceeded the target lines more frequently, resulting in average values of ~2% MVF for very light and ~9% MVF for light squeezing. The relative precision grip forces were significantly higher (paired *t*-tests, $P<0.05$) than the respective power grip forces in the no-vision condition (Fig. 1). All subjects confirmed that they could differentiate between the VL and L tasks. The intra-individual variability of the force peaks, measured in %MVF (Table 1), was

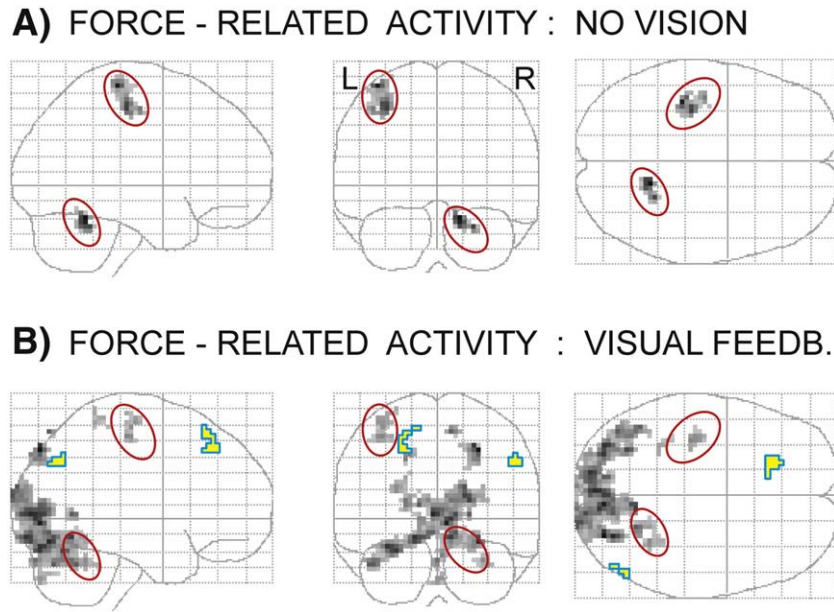


Fig. 4. Brain regions whose activity covaried with the grip force in the no-vision (A) and in the visual feedback condition (B). Grey voxels exhibited positive correlations between local BOLD signals and force. Red ellipsoids denote force-dependent signal changes in left primary sensorimotor cortex and right cerebellum. Yellow regions (blue outline) were more active when the force was less (i.e., correlation is negative). View of activations and statistical thresholds are the same as in Fig. 2.

comparable for power and precision gripping (ANOVA, no significant task effect).

Brain activity during the squeezing tasks per se

Figs. 2 and 3 illustrate the brain activity associated with repetitive squeezing per se, irrespective of the force level (i.e., squeezing vs.

rest). In the no-vision condition, the precision grip task activated the left primary sensorimotor cortex (M1/S1), left dorsolateral premotor cortex, the SMA, bilateral cerebellum, and bilateral foci in the insular and opercular cortex (Table 2). During the power grip task without visual feedback, the thalamus, basal ganglia, and the right supramarginal gyrus were activated bilaterally, and in addition to the aforementioned regions (Figs. 2A, 3).

Table 4
Brain areas whose activity correlates with the force of gripping

Cluster level		Voxel level				Coordinates (MNI) of foci (mm)				
<i>P</i> (cor)	KE	<i>P</i> (FWE)	<i>P</i> (FDR)	<i>T</i>	<i>Z</i>	<i>x</i>	<i>y</i>	<i>z</i>	Anatomical region	BA
<i>No vision: positive correlation with force</i>										
0.000	39	0.063	0.025	8.06	4.75	15	-51	-21	R cerebellum (lbl. IV,V)	
0.000	83	0.096	0.025	7.76	4.66	-39	-30	66	L central sulcus	4 (60%)
<i>Visual feedback: positive correlation with force</i>										
0.000	50	0.008	0.002	9.64	5.14	27	-81	45	R parieto-occipital sulcus	
0.000	645	0.015	0.002	9.18	5.03	6	-81	-3	R calcarine gyrus	17 (100%)
0.000	34	0.021	0.002	8.89	4.96	27	-75	-15	R fusiform gyrus	18 (20%)
0.030	10	0.110	0.002	7.66	4.63	9	-75	57	R precuneus	
0.030	10	0.123	0.002	7.58	4.61	21	-60	3	R lingual gyrus	17 (100%)
0.000	30	0.213	0.003	7.20	4.50	-3	-84	-27	L cerebellum (crus 2)	
0.003	18	0.274	0.003	7.03	4.44	-21	-99	12	L middle occipital gyrus	18 (60%)
0.016	12	0.354	0.003	6.86	4.39	-21	-84	39	L superior occipital gyrus	
0.000	34	0.447	0.003	6.71	4.34	24	-60	-15	R cerebellum (lbl. VI)	
0.000	34	0.506	0.003	6.63	4.31	-36	-24	54	L central sulcus	4 (40%)
0.001	21	0.591	0.003	6.53	4.27	30	-51	-27	R cerebellum (lbl. VI)	
0.001	24	0.641	0.003	6.47	4.26	-27	-90	21	L middle occipital gyrus	17 (10%)
0.008	14	0.852	0.004	6.02	4.09	-33	-45	63	L postcentral sulcus	2 (40%)
<i>Visual feedback: negative correlation with force</i>										
0.043	9	0.183	0.080	7.31	4.35	51	-69	39	R angular gyrus	
0.001	21	0.742	0.080	6.33	4.20	-21	33	45	L superior frontal gyrus	

Regions whose activity covaried with the grip force of squeezing were the same during precision and power gripping (interaction, n.s.). Negative correlations (deactivation with increasing force) were only found in the visual feedback condition. Statistical thresholds, abbreviations, and anatomical labeling method as in Tables 2 and 3.

The same regions were also active when visual feedback of grip force was provided. Visual processing led to bilateral activations of occipital and bilateral posterior parietal areas that were absent in the no-vision condition (Figs. 2B, 3; Table 3). Brain areas involved in precision and power gripping showed considerable overlap, with a more widespread activity during the power grip task (Fig. 3, compare red and green areas). A statistical comparison of both tasks revealed stronger activity in the left precentral gyrus (peak difference at coordinates $x=-33, y=-24, z=63$) and in Larsell lobule VI of the right cerebellum (peak difference at $x=24, y=-48, z=-27$) during the power grip task (Fig. 2C). This difference was independent of the visual condition as there was no interaction between grip task and feedback. Despite the significantly higher relative force levels in the no-vision condition (see above), no brain region was more active during precision gripping than during power gripping in any condition.

Force-related activations

Fig. 4 depicts the brain areas where activity during squeezing showed a linear increase with grip force. Force-related modulations of the cortical activity were comparable for the precision and the power grip tasks (Table 4). Regardless of visual feedback, activity along the left central sulcus and of the right cerebellum increased in parallel with force (ellipsoids in Figs. 4A, B). In posterior brain regions, a modulation of neuronal activity occurred only in the presence of visual feedback (Fig. 4B). BOLD signals in the bilateral occipital gyri, fusiform and calcarine gyri, and the right precuneus

showed a linear increase with force when on-line visual feedback of the actual grip force was provided. In the visual feedback condition, activity of two brain regions exhibited a negative linear relationship with force: clusters in the right angular gyrus and left superior frontal gyrus showed a gradual increase in BOLD signal when the grip force decreased, i.e., these areas were more active during very light than during light squeezing (Table 4; Fig. 4B, yellow regions).

Discussion

Using fMRI in 14 normal right-handed volunteers, we found a striking congruence in the patterns of activations when repetitive precision and power gripping movements were performed with light grip force of the dominant hand (see Fig. 3). No brain region was specifically activated during one task but not during the other. Confirming two previous studies (Ehrsson et al., 2000; Takasawa et al., 2003), there was a relative increase in task-related activation in left M1/S1 and right cerebellar hemisphere during power grip relative to precision grip (Fig. 2C). However, in contrast to Ehrsson et al. (2000), we found no brain regions that were significantly more active during the precision grip than during the power grip task. We had not expected such a high overlap of the regions implicated in the control of precision and power gripping.

Methodological differences between PET/fMRI and TMS studies

More than twelve different intrinsic and extrinsic hand muscles, whose EMG activity changes in parallel with grip force, contract

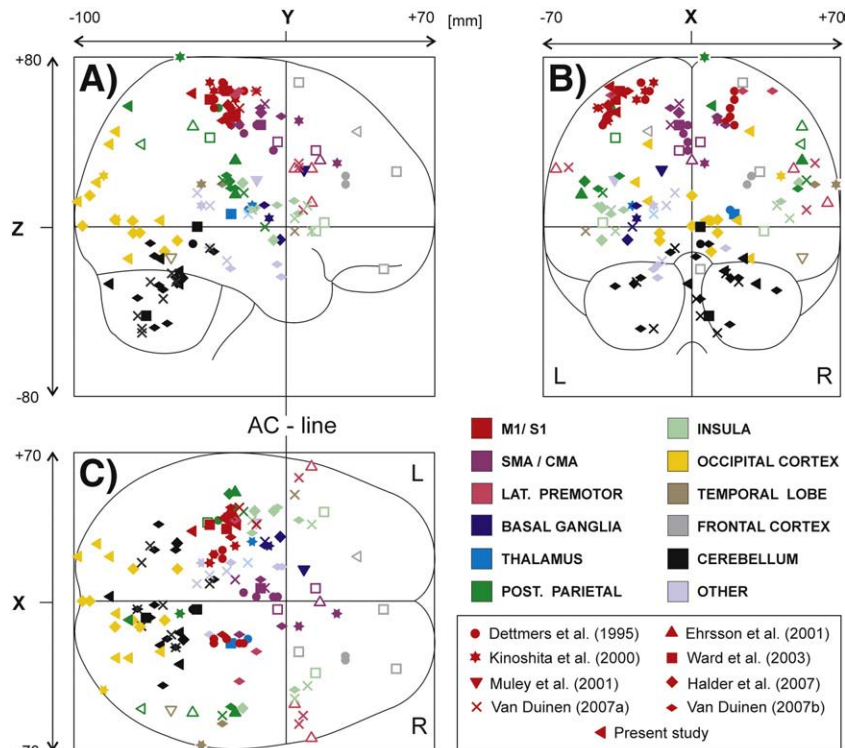


Fig. 5. Published coordinates of brain regions with force-dependent activity. (A–C) Lateral, frontal, axial view of the foci, projected onto the contours of a template brain. Different symbols denote data of different studies (inset), colors indicate brain regions. AC-line: plane of the anterior commissure. All x, y, z values denote MNI coordinates. Closed symbols indicate force-related increases of activity (i.e., positive correlations), and open symbols denote negative correlations and nonlinear relations (as reported by Ward and Frackowiak, 2003) that involve deactivations and activations. The underlying different studies are summarized in Table 5, lines 1–8.

during precision grip tasks (Hepp-Reymond et al., 1996). During power gripping, most of these muscles are active as well, and additional forearm muscles are recruited (Anson et al., 2002; Long et al., 1970). Neuroimaging studies of precision and power grip tasks therefore delineate cortical regions involved in the control of large and partially overlapping groups of muscles (see Supplementary EMG data). By contrast, TMS studies focus on selected target muscles, keep the background EMG level constant, and often use confined cortical stimulation sites (point of highest excitability). The FDI muscle, a prime force generator of the precision grip, is a typical target muscle. A series of TMS studies found higher MEPs of this muscle during precision than power grip tasks (Flament et al., 1993; Hasegawa et al., 2001; Huesler et al., 1998; Schieppati et al., 1996; Tinazzi et al., 2003). The larger MEP amplitudes reflect a focal increase in excitability of cortical neurons innervating FDI motoneurons, possibly involving direct

monosynaptic cortico-motoneuronal connections. An even more focal approach was used by Muir and Lemon (1983), who recorded task-dependent variations of single M1 neurons with microelectrodes. Cortical neurons (CM cells), which monosynaptically innervated FDI motoneurons, were more active during a precision grip than a power grip task, although the latter involved higher absolute forces and stronger EMG signals of the FDI (their Fig. 2).

PET and fMRI lack the spatial resolution to selectively detect changes in activity of cortical neurons innervating specific muscles (e.g., FDI) or of CM cells. Furthermore, the hand region of M1 does not contain well-ordered demarcated point-to-point representations of the muscles of the thumb, index, middle, ring, little finger, wrist and so on (Schieber, 2001). Instead, each finger has multiple representations, with a somatotopic gradient superimposed on these scattered zones (Schieber and Santello, 2004). This explains why BOLD signal changes measured in a given voxel

Table 5
Summary of studies of force-related changes of brain activity during dominant (right) hand motor tasks

#	Study	Method	n	Task	Force range	Feedback	Deactivate ^a	Coordinates	Data evaluation, statistical threshold
1	Dettmers et al. (1995) ^b	PET	6	Key press, index finger (1 Hz)	5–60% MVF	AUD	Yes ^b	Yes	SPM correlation analysis, $Z > 4$
2	Kinoshita et al. (2000) ^c	PET	10	Precision grip-lift task (0.29 Hz)	4 g, 200 g, 600 g	TAC ^c	No	Yes	SPM; categ. comp.; $Z > 3.1$
3	Muley et al. (2001) ^d	PET	20 ^d	precision grip (static, for 60 s)	2–10 N	VIS	Yes	Yes	Canonical variates analysis
4	Ehrsson et al. (2001)	fMRI	6	precision grip (0.67 Hz)	3.8 N vs. 16.6 N	TAC	Yes	Yes	SPM fixed eff.; categ. comp.; $Z > 4.35$
5	Ward and Frackowiak (2003) ^e	fMRI	26	Power grip (0.33 and 0.67 Hz)	10–60% MVF	VIS	Yes ^e	Yes	SPM rand. eff.; par. mod.; $Z > 3.6$
6	Halder et al. (2007) ^f	fMRI	51 ^f	power grip (~0.25 Hz, irregular)	20–75% MVF	VIS	No	Yes	SPM rand. eff.; par. mod.; $Z > 4.85$
7	van Duinen et al. (2007a)	fMRI	15	Index finger abduction (for 15 s)	10%, 30%, 70% MVF	VIS	No	Yes	SPM rand. eff.; par. mod.; $Z > 3.1$
8	van Duinen et al. (2007b) ^g	fMRI	10	Index finger abduction (for 20 s)	5–70% MVF	VIS	Yes ^g	Yes	SPM rand. eff.; par. mod.; $Z > 3.1$
9	Ludman et al. (1996)	fMRI	16	Power grip (1.3–1.7 Hz)	2.4 N vs. 13.7 N	No	No	No	AFNI cross-correlation analysis
10	Wexler et al. (1997)	fMRI	11	Index finger tapping (0.75–1.5 Hz)	Low–high resistance	No	No	No	Signal change and voxel count in 10 ROIs
11	Thickbroom et al. (1998)	fMRI	10	Power grip (static, for 18 s)	5–50% MVF	VIS	No	No	Signal change and voxel count in M1/S1
12	Thickbroom et al. (1999)	fMRI	6	Power grip (static vs. dynamic)	5 vs. 10% MVF	VIS	No	No	Signal change and voxel count in M1/S1
13	Dai et al. (2001)	fMRI	10	Power grip (static, for 30 s)	20–80% MVF	VIS	No	No	Signal change and voxel count in 12 ROIs
14	Peck et al. (2001)	fMRI	6	Wrist extension (for 19 s)	5–40% MVF	VIS	No	No	Signal change and voxel count in M1 and SMA
15	Cramer et al. (2002)	fMRI	8	Power grip (1 Hz)	27 vs. 83 vs. 183 N	No	No	No	Signal change and voxel count in M1/S1, SMA
16	Present study	fMRI	14	Precision and power grip (0.45 Hz)	1% vs. 5% MVF	VIS/No	Yes	Yes	SPM rand. eff.; par. mod.; $Z > 3.7$

Abbreviations: AUD, auditory feedback; categ. comp., categorical comparison; FWE, family-wise error correction; Hz, Hertz; MVF, maximum voluntary force; n, number of subjects studied; N, Newton; par. mod., parametric modulation; ROI, region of interest; s, second; SPM fixed eff., fixed effects model; SPM rand. eff., random effects model; TAC, tactile feedback; VIS, visual feedback.

^a Deactivate: negative correlations between brain activity and force (deactivations) are reported.

^b Dettmers et al. (1995) observed deactivation of the right (ipsilateral) M1/S1 only at the lowest force level (5% MVF), their Fig. 6.

^c Kinoshita et al. (2000): Subjects repetitively grasped, lifted, and released objects of 3 different weights, with the eyes closed.

^d Muley et al. (2001): 20 of 40 subjects were included in the analysis of linear force related effects (their Table 2).

^e Ward and Frackowiak (2003) found linear and non-linear relationships (2nd and 3rd order) between BOLD signal and force (their Tables 3, 4).

^f Halder et al. (2007) studied three developmental age groups (9–11; 15–17 years; adults).

^g van Duinen (2007b) found negative correlations between EMG activity (force) and the inferior right precentral sulcus in 3 subjects (their Fig. 5).

within the hand area cannot be attributed unequivocally to the activity of neurons targeting a specific hand muscle. The recruitment of additional extrinsic hand muscles (Long et al., 1970), the high absolute force, and the stronger proprioceptive and cutaneous afferent feedback during power gripping will generally enhance the BOLD signal in contralateral M1/S1, as shown previously (Ehrsson et al., 2000; Takasawa et al., 2003). Taking into account the distributed representation of hand muscles, a recent TMS study mapped the entire cortical representation of the FDI (Reilly and Mercier, 2007). Healthy subjects grasped the same object between their thumb and index finger (precision grip) or between their thumb and all four fingers (power grip). Interestingly, no task-related changes in the topography of the cortical FDI map were found.

Precision grip tasks are of different complexity

The similar activation patterns during power and precision grip may be due to the fact that we employed a rather simple precision grip task. As in the experiments of Ehrsson et al. (2000), a stationary nonflexible object was compressed between the pulps of the thumb and index finger. Neither stabilization nor active tilting/turning of this object was required, so that it was not necessary to carefully control the direction of the grip force vectors. The three ulnar long fingers were in a more extended posture than the index finger (see Fig. 1A in Ehrsson et al., 2000), but they did not move independently. The precision grip task of Takasawa et al. (2003) was even less difficult as the tips of the thumb and index finger were just opposed and released repetitively. This is certainly less demanding than dexterous object manipulations, which are known to elicit pronounced frontoparietal brain activity (Binkofski et al., 1999; Ehrsson et al., 2003; Stoeckel et al., 2003).

The precision grip task investigated in the pioneering studies of the corticospinal system in rhesus monkeys was more demanding, too (Lawrence and Kuypers, 1968). Morsels of food were winkled out of small food wells by movements of the index finger, aided by the thumb, and then grasped by these two digits (Lawrence and Hopkins, 1976). These dexterous and independent finger movements were abolished by complete pyramidal lesions, while the ability to grasp objects by closure of the fingers all together (power grip) recovered gradually (Passingham et al., 1983). Studies of human patients confirm that skilful and fractionated digit movements are impaired after damage to the motor cortex or corticospinal tract (Lang and Schieber, 2004; Raghavan et al., 2006). It is generally accepted that the capacity to perform such movements depends on the intactness of direct cortico-motoneuronal connections (Lemon 1993; Lemon and Griffiths, 2005). Nevertheless, even after interruption of the monosynaptic corticospinal pathway at the level of the cervical spinal cord, monkeys can learn to grasp morsels of food with a precision grip, suggesting that indirect oligosynaptic pathways are relevant for recovery (Sasaki et al., 2004). Yet the grip force was reduced and the grasping was slower than preoperatively in these animals (see also Hepp-Reymond et al., 1974).

Hence, it is important to distinguish between the ability to use a precision grip per se and the ability to optimally control the movements and forces of the different digits (Johansson, 1996). Increasing demands on accurate force control, e.g., during a force-tracking task performed with the thumb and index finger, are known to increase corticospinal excitability to intrinsic hand muscles and to enhance the BOLD signal in contralateral M1, SMA, and premotor areas (Bonnard et al., 2007). Although not

varied systematically, accuracy demands and regularity of grip force production (intra-individual variability) were comparable for the two tasks that we compared, i.e., precision and power gripping.

The role of feedback signals

Activity of ventral premotor, cingulate, posterior parietal and prefrontal regions was stronger during precision than power grip in the fMRI study of Ehrsson et al. (2000), but not in the present one. At first glance, this discrepancy is surprising as the grip tasks and forces were nearly identical in both studies. Differences in the external feedback signals may provide a clue: in the experiments of Ehrsson et al. (2000), subjects kept their eyes closed. In the precision grip task, a weak tactile stimulus was given by an external device as soon as the grip force reached 2 N. This feedback cue indicated that the force level should be maintained until a metronome click gave the signal to release the grip. It is conceivable that the subjects paid particular attention to this cue in order to match and then hold the target force level appropriately. This may have resulted in an increased activity of frontoparietal and cingulate regions implicated in transferring sensory feedback information into appropriate motor output (Johansen-Berg and Matthews, 2002). Gaining awareness of the produced force may also have contributed (de Graaf et al., 2004). Of note, feedback was different during the power grip task in the study by Ehrsson et al. (2000). Here subjects compressed a plastic tube with a longitudinal split, whose edges closed at about 20 N as a mechanical cue for the target force. Hence, no external signal was provided, as this cue was generated directly by the clenching fist and was maintained as long as the force exceeded 20 N (self-generated feedback). This probably required less attention and less precise adjustment of the contractile force than the precision grip task. In the present study, the force-related feedback signals were identical during precision and power gripping. The subjects either saw the self-generated grip force curves, which had the same size during both tasks, or they received no external feedback at all.

Brain activity and force

An actual range of about 1–10% MVF was examined in the present study, because the subjects overshot the target force levels especially in the no-vision condition. Such low grip forces do not induce fatigue (van Duinen et al., 2007a) nor do they involve contractions of more proximal arm muscles (Detmers et al., 1995). Linear force-related increases of the BOLD signal involved the same regions during precision and power gripping. In good agreement with published data (Fig. 5), neuronal activity of the left M1/S1 and right cerebellum increased with the applied force level in the no-vision and visual feedback conditions. When visual feedback was provided, additional BOLD signal increases were detected in the left cerebellum, right precuneus, and occipital regions, reflecting additional processing of visual feedback and visually guided adjustments of the grip force (Vaillancourt et al., 2003).

Parts of the superior frontal gyrus and right (ipsilateral) angular gyrus were more active during very light (VL) than light (L) gripping in the visual feedback condition. Increased attention was necessary to keep the force of the very gentle contractions below the target line. Enhanced processing of somatosensory signals from the fingertips and/or active suppression of motor output may be relevant when fine forces are applied (Ehrsson et al., 2001). Accordingly, premotor and posterior parietal cortex were found to be particularly active when subjects carefully reduced their

precision grip force to a low level while holding an object (Kuitz-Buschbeck et al., 2001). Single-cell recordings in monkeys detected neurons in M1/S1 and premotor areas whose activity is negatively correlated with grip force, which may be relevant for the control of low forces (Hepp-Reymond et al., 1994; Maier et al., 1993).

Previous fMRI and PET studies of force-related modulations of brain activity during dominant (right) hand movements in normal subjects are summarized in Table 5. Mostly power grip tasks were examined. The movement frequency ranged from static contractions to fast repetitive movements, with stronger M1/S1 activity in dynamic tasks (Thickbroom et al., 1999). Forces covered the range between 5% and 80% of the MVF; lower forces, such as in the present study, have not been investigated previously. Eight studies (# 1–8, Table 5) published coordinates of foci whose activity covaried with force, which are summarized together with the present data in Fig. 5. Force-related increases of local brain activity were consistently present in the left M1/S1 (red symbols, Fig. 5), lateral premotor cortex (pink), and SMA/CMA (lilac), right cerebellum (black), but occurred in posterior parietal (green) and other regions, too. The ipsilateral posterior cerebellum controls predictive adaptations of the grip force (Boecker et al., 2005; Nowak et al., 2002). Two studies observed force-related signal increases in the ipsilateral right M1/S1 (Dettmers et al., 1995; van Duinen et al., 2007b), indicating that interhemispheric inhibition does not suppress the signals of this region (Foltys et al., 2003). Congruent with our results, a study of power gripping with visual feedback (Halder et al., 2007) reported conspicuous force-related modulations of the occipital activity (yellow symbols, Fig. 5). Signals of the ipsilateral basal ganglia (dark blue symbols) correlate positively with the amplitude of force changes (Halder et al., 2007; Kinoshita et al., 2000; Muley et al., 2001; van Duinen et al., 2007a,b) but are also influenced by the change rate (Vaillancourt et al., 2004). Negative correlations between brain activity and force of (right) hand movements were reported in five studies (Dettmers et al., 1995; Ehrsson et al., 2001; Muley et al., 2001; van Duinen et al., 2007b; Ward and Frackowiak, 2003). Bilateral ventral premotor areas, anterior portions of the SMA/CMA, and ipsilateral posterior parietal regions were involved (open symbols, Fig. 5). In summary, the activity of multiple brain regions has been shown to covary with the force of hand movements, with most consistent signal changes in M1/S1, the cerebellum, and the SMA. The other published coordinates diverge considerably (note the scatter in Fig. 5), possibly due to the differences of the tasks, force ranges, and statistical models.

Conclusions

Patterns of brain activity were very similar when normal subjects performed repetitive squeezing movements with either a power grip or a precision grip of the right dominant hand, applying peak grip forces ranging between 1% and 10% of the maximum voluntary force. Reflecting the additional recruitment of extrinsic hand muscles and the higher absolute force, BOLD signals of the contralateral primary sensorimotor cortex and ipsilateral cerebellum were significantly stronger during power than during precision gripping. However, no brain areas exhibited stronger activity during the precision grip than the power grip task. The force-related modulations of the brain activity were similar for both tasks, too. A “simple” precision grip task may not be challenging enough to evoke the cortical activity that is representative for dexterous manipulations.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2008.01.037.

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