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Central control of grasp: Manipulation of objects with complex and simple dynamics

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We performed whole-brain fMRI to explore the neural mechanisms that contribute to the ability to manipulate an object with complex dynamics. Subjects grasped a weighted flexible ruler and balanced it in an unstable equilibrium position as an archetype of grasping an object with complex dynamics. This was contrasted with squeezing a soft foam ball as an archetype of grasping an object with simple dynamics. We hypothesized that changes in activity in primary motor cortex (MI) would be similar under the two conditions, since muscle activation was matched, which was confirmed. We hypothesized further that the cerebellum would be selectively activated when manipulating the flexible ruler because the ability to make the adjustments necessary to balance the ruler would require an internal dynamics model, represented in the cerebellum. As predicted, the ipsilateral cerebellum was strongly activated when balancing the weighted ruler whereas only moderate activation was found when squeezing the foam ball. We also found evidence for selective activation of areas, previously implicated in tactile object recognition, when holding the flexible ruler. We speculate that these areas, which include secondary somatosensory cortex (SII), Brodmann area 40 and insula, integrate tactile and proprioceptive information in the context of controlling the orientation of the flexible ruler and provide appropriate feedback to MI. We speculate that the failure to find activation of these areas when squeezing the ball was due to the fact that tactile stimulation was entirely self-produced, resulting in the attenuation of cortical sensory activity (Blakemore, S.-J., Wolpert, D.M., Frith, C.D., 1998. Central cancellation of self-produced tickle sensation. Nat. Neurosci. 1, 635–640, Blakemore, S.-J., Frith, C.D., Wolpert, D.M., 2001. The cerebellum is involved in predicting the sensory consequences of action. NeuroReport 12, 1879–1884).

Keywords: Cerebellum; Hand; Internal model; fMRI; Motor cortex; Insula

Introduction

The complexity of dynamic interactions between humans and common implements which we employ as tools and instruments can vary widely. Our ability to use implements effectively requires that we be able to hold them despite differences in dynamics. With experience we can quickly change patterns of muscle activation to adjust our grasp for differences in mass, moment of inertia, rigidity or other mechanical properties. This ability is thought to depend on a central representation (internal model) of the dynamics of the interaction between the human subject and the manipulated object (Flanagan and Wing, 1997; Kawato, 1999). By internal dynamics model we mean the neural networks that compute the neural commands to control the movement of the handheld object and compensate for its dynamics.

The cerebellum and primary motor cortex appear to be the regions of the brain most directly implicated in the formation and implementation of internal dynamics models. In particular, the ipsilateral cerebellum shows changes in regional cerebral blood flow during adaptation to novel environmental dynamics that appear to be related to changes in motor error (Nezafat et al., 2001). Other evidence from fMRI studies suggests that the cerebellum is involved in forming and implementing representations of novel transformations between hand and cursor motion (Imamizu et al., 2000, 2003), forward models of grip force–load force coupling (Kawato et al., 2003) and dynamics of object manipulation (Milner et al., 2006). Evidence for involvement of primary motor cortex is based primarily on single unit recordings from non-human primates. Studies of changes in manipulation dynamics with non-human primates have reported shifts in the preferred directions of neurons in MI (Li et al., 2001) and to a lesser extent in SMA (Padoa-Schioppa et al., 2004) that develop during adaptation and are retained after washout. However, there are major outputs from the cerebellum to M1 and minor outputs to SMA (Sakai et al., 2002; Kelly and Strick, 2003) so it is possible that underlying changes in cerebellar activity may be responsible for the observed changes in MI and SMA.

To test the hypothesis that cerebellar activity more closely represents implementation of an internal model than does activity

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in primary motor cortex, we designed an fMRI study which compared brain activity when subjects held an object with simple dynamics and an object with complex dynamics. The former required no internal model to control grasp while the latter required an internal model to adjust the finger forces used in grasping the object for the moment-to-moment control of the object's orientation. From earlier studies, we expected that activity in both primary motor cortex and cerebellum, relative to resting baseline, would increase in proportion to muscle activation (Dettmers et al., 1996; Thickbroom et al., 1998; Ehrsson et al., 2001; Kuhtz-Buschbeck et al., 2001; Dai et al., 2001). However, we predicted that for similar levels of muscle activation we would find little or no difference in primary motor cortex activity, but marked differences in activation of the cerebellum because of its involvement in internal model-based control.

Methods

Seventeen neurologically normal subjects participated in the first experiment. Five of these subjects and five additional subjects participated in the second experiment. Four of these subjects and six additional subjects participated in the third experiment. All subjects gave informed consent to the procedures which were approved by the institutional ethics board and conformed to the Declaration of Helsinki. There were three conditions, corresponding to three tasks performed while lying in the supine position. All subjects performed the tasks with the right hand. The tasks consisted of squeezing a foam ball (simple), balancing a weighted flexible ruler (complex) and resting. Each task was performed for 30 s.

In the fMRI experiment (first experiment), there was a 6-s interval between conditions during which the experimenter prepared the subject for the next condition. The subject went through the conditions 10 times in one order and then 10 times in the reverse order. The condition order was varied randomly among subjects. The experimenter stood at the subject's side throughout the recording session and placed the object in the subject's hand prior to the start of each 30-s scan. At the end of the scan, the current object was removed from the subject's hand or replaced another object, according to the condition order.

Because of the position of the subject's head in the gantry of the scanner the subject could not see the objects. Therefore, the task was performed using only somatosensory feedback. When holding an object, subjects rested their forearm on a soft support surface, although the wrist remained unsupported. The object with complex dynamics was an inverted pendulum created by attaching two 130 g weights to a thin plastic ruler at a distance of 25 cm from the center of the grip position (Fig. 1). Subjects held the ruler in a pinch grip between the thumb and two or three fingers. They were instructed to keep the weights directly above the hand, i.e., not to allow the inverted pendulum to deviate from vertical. The object with simple dynamics was a foam ball, which was held with the same pinch grip. Subjects were instructed to compress the foam ball to a point where the force was approximately equal to the force applied to the inverted pendulum. This amounted to compressing the ball until the thumb was felt to contact the fingers. Extensive training was not required to perform the tasks successfully. All subjects were given sufficient practice with each condition prior to the experiment to master the control of each object.

In the second experiment, ten subjects performed the same tasks in the Neuromuscular Control Laboratory at Simon Fraser University. They reclined on a hospital stretcher raised to approximately the same height as the gantry and adopted the same posture as during the brain imaging. Their right arm was similarly supported. Acceleration was recorded with a single-axis accelerometer (IC Sensors) fixed at the center of the dorsum of the hand. The bandwidth of the accelerometer was 0 Hz (DC) to 1000 Hz with an output of 2.5 V/g. The DC offset varied as the sensitive axis of the accelerometer rotated with respect to the gravitational axis. Consequently, the accelerometer registered both translation and rotation of the hand. EMG was recorded from the first dorsal interosseus, flexor pollicis brevis, flexor digitorum superficialis, extensor carpi radialis longus and biceps muscles of the right arm. The EMG was recorded using custom-built active bipolar electrodes (13-mm contact spacing), which amplified and bandpass filtered the signals between 20 Hz (high pass) and 500 Hz (low pass). EMG signals were then sampled at 2 kHz and stored for later analysis. Each of the 3 tasks was again performed for 30 s, but this time the conditions were performed 10 times in one order, randomly chosen for each subject, but not in reverse. As before, subjects performed the task without visual feedback. Acceleration and rms EMG were compared for the simple and complex tasks using repeated measures ANOVA. Data collected during the first 5 s of each task were not included in the analysis to eliminate transient effects during the transition between tasks.

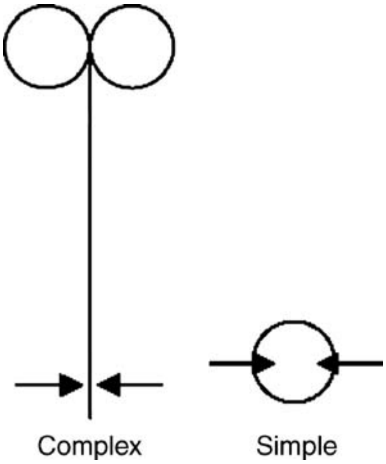

Fig. 1. The objects chosen as archetypes of complex and simple dynamics are schematically illustrated. Arrows illustrate where the objects were gripped.

In the third experiment, a miniature load cell (LM-2KA-P, Kyowa) was sandwiched between two thin plastic surfaces and used to measure subjects' grip force. Maximum grip force was first measured. Subjects then performed the simple and complex task for 30 s as in the fMRI experiment. The load cell was placed between the subject's thumb and the object. Because of the width of the load cell it was not possible to reproduce identical conditions to the fMRI experiment. However, subjects were still instructed to match the grip force under the two conditions. The mean grip force during each 30-s interval was expressed as a percentage of each subject's maximum grip force. Grip force under the two conditions was compared using a paired *t*-test. For 5 of these subjects we recorded both the grip force and the position of the top of the flexible ruler using an OPTOTRAK system (Northern Digital) under the complex condition and computed the cross-correlation function to determine whether grip force adjustments were predictive or reactive.

The 1.5-T MRI scanner (Shimadzu-Marconi) in the ATR Brain Activity Imaging Center was used to obtain blood-oxygenation level-dependent (BOLD) contrast functional images. High-resolution anatomical (structural) images were obtained with a T_1-weighted sequence for each subject. Functional images weighted with the apparent transverse relaxation time (T_2^*) were obtained with an echo-planar imaging sequence (repetition time = 5.4 s, echo time = 65 ms, flip angle = 90°). 92 Sequential whole-brain volumes ($64 \times 64 \times 50$ voxels at 3-mm isotropic resolution) were acquired in each session.

We used SPM2 software (http://www.fil.ion.ucl.ac.uk/spm/) to analyze the images. The first two image volumes were discarded to allow for T_1 equilibration. The remaining 90 image volumes were realigned to the first volume and normalized to the Montreal Neurological Institute (MNI; Montreal, Canada) reference brain. The data were spatially smoothed with a Gaussian kernel with a 7-mm full width at half maximum (FWHM). Voxels outside of the brain and in the ventricles were masked. The voxel time series were temporally smoothed with a Gaussian filter (FWHM of 4 s). Anatomical regions were identified from normalized T_1 structural images averaged across subjects, using the automated anatomical labeling method of Tzourio-Mazoyer et al. (2002), and functional anatomy was determined from the Brodmann map as implemented in the FWU pick atlas (Maldjian et al., 2003, 2004). We used the SPM Anatomy toolbox (Eickhoff et al., 2005) to identify fine cytoarchitechtonic regions near the central sulcus.

Statistical analysis was performed in two stages using a mixed effects model. In a first-stage (fixed effect) individual analysis, conditions were modeled by boxcar functions that had been convolved with the standard SPM hemodynamic response. They were used as covariates in a general linear model as implemented in SPM2 yielding parameter estimates for the conditions for each voxel. Images of parameter estimates for the contrasts of interest (complex-simple, simple-rest and complex-rest) were created for each subject. In the second-stage (random effects) group analysis, the images were entered into a one-sample t-test across subjects (Penny and Holmes, 2003; Schmitz et al., 2005), and maps of t-statistics for the contrast of interest were derived.

A significance threshold of $p < 0.05$ ($T(16) > 8.14$ in the random effect model, corrected for multiple comparisons) was applied to determine which brain areas reliably showed significant activity for complex-simple, complex-rest and simple-rest contrasts. Although relatively large regions of activation were found for the complex-rest and simple-rest contrasts, which were noticeably different, little evidence of these differences appeared in the complex-simple contrast. We attribute this to the relatively high significance threshold. Since we were particularly interested in activation differences in motor areas, we defined motor regions of interest (ROI) based on the union of motor regions activated in the complex-rest and simple-rest contrasts. Thus, these motor ROIs included all motor regions where significant activation was observed in either the complex-rest or simple-rest contrast. We then computed the percentage change in the BOLD signal under the complex condition relative to rest and under the simple condition relative to rest. t-tests, corrected for multiple comparisons, were then performed to determine whether the change in BOLD signal was greater under the complex than the simple condition.

Results

We report regions where activation in clusters of 5 or more voxels (40 mm^3) reached the significance threshold, using the random effects model, corrected for multiple comparisons ($p < 0.05$). For the complex-simple contrast, we found small regions of significant activation in two regions normally associated with processing of somatosensory activity, namely contralateral somatosensory cortex (SI, area 2) and ipsilateral (right) Brodmann area 40. We found significant activation of the contralateral primary motor cortex (MI), primary somatosensory cortex (SI, area 3) and ipsilateral anterior cerebellum for both the simple-rest and complex-rest contrasts. In addition, the ipsilateral posterior cerebellum, dorsal premotor cortex (area 6), contralateral thalamus, contralateral insula and contralateral SII were significantly activated in the complex-rest contrast (Fig. 2, Table 1). Note that the contiguous region identified as MI in the Table 1, is primarily MI, but also includes about 40 voxels that fall in area 3 for both complex-rest and simple-rest contrasts and about 30 voxels that fall in area 6 for the complex-rest contrast only.

The most striking finding was the difference in the size of the clusters of significant activation in the cerebellum. In the simple-rest contrast, there was only a 15-voxel cluster in the anterior cerebellum where activity reached the significance threshold ($p = 0.021$ at the focus) and none in the posterior cerebellum. On the other hand, in the complex-rest contrast, the cluster in the posterior cerebellum alone was 73 voxels ($p = 0.001$ at the activation maximum) while the cluster in the anterior cerebellum was about four times larger still ($p < 0.0001$ at the focus). Thus, not only was the cerebellum much more strongly activated under the complex condition, but there were two very distinct, widely separated activation foci (Table 1).

Since we did not find any motor region where activation reached the significance threshold for the complex-simple contrast, despite the large differences in the size of the activated regions of the cerebellum, we decided to compare the percentage change in BOLD signal intensity in motor regions activated under the two conditions. Three motor regions were identified as being significantly activated in either the complex-rest or simple-rest contrasts. These were MI, cerebellum and area 6. Because activated regions in the anterior and posterior cerebellum were unconnected and widely separated, we treated them as separate ROIs in the analysis. The mean intensity of the BOLD signal over the defined ROIs for all subjects combined was compared between complex and simple conditions (Fig. 3). We tested the null hypothesis that the percentage signal change would not be greater, relative to rest, for the complex than the simple condition. Because there were four ROIs, we used t-tests corrected for multiple comparisons ($p < 0.01$). We found that only for the cerebellar regions was the null hypothesis rejected, i.e., activity was significantly greater under the complex than the simple condition ($p = 0.0016$ for the anterior region and $p < 0.0001$ for the posterior region). The null hypothesis could not be rejected for MI ($p = 0.16$) or area 6 ($p = 0.017$).

We were able to demonstrate that muscle activation was well matched under the two conditions. No significant difference in the rms EMG was found for any of the five muscles ($p > 0.4$; Fig 4A). The acceleration was analyzed by determining the signal power in 3 specific frequency bands, 0–1.5 Hz, 1.5–6 Hz and 8–14 Hz, where distinct peaks were identified under the simple condition (Fig. 4B). There was no significant difference in the signal power under the simple and complex conditions in the 0–1.5 Hz ($p > 0.4$) and 8- to 14-Hz bands ($p > 0.1$). However, there was significantly more signal power in the 1.5- to 6-Hz band under the simple than the complex condition ($p = 0.022$). This band was then separated into three bands of equal width and reanalyzed. Only in the 3- to 4.5-Hz

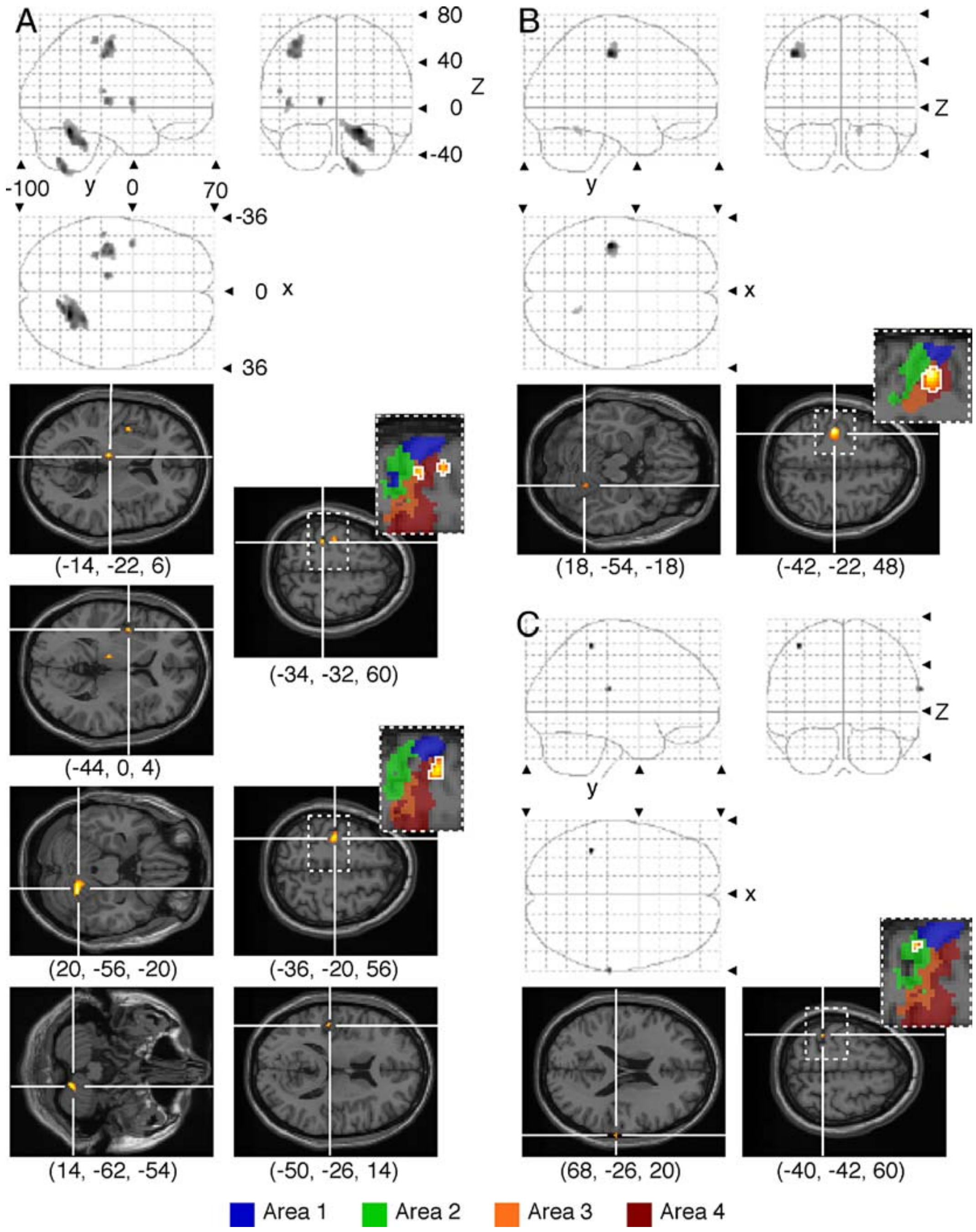

Fig. 2. (A) Complex-rest contrast. Statistical parametrical maps (SPM*t*) illustrate activated regions ($p < 0.05$, random effect model, corrected for multiple comparisons). Slices containing activity peaks listed in Table 1 are shown with crosshairs indicating the coordinates shown under each panel. Insets identify areas of sensorimotor cortex according to the maximum probability maps based on cytoarchitectonic studies (SPM anatomy tool box; Eickhoff et al., 2005). (B) Simple-rest contrast. (C) Complex-simple contrast.

band was there a significant difference, with more signal power under the simple than the complex condition ($p = 0.014$). This indicates that motion in the 3- to 4.5-Hz frequency band was suppressed under the complex condition. It may be somewhat surprising that there was not more motion of the hand under the complex than the simple condition. However, it should be noted that the orientation of the inverted pendulum was controlled principally by a rolling action between the thumb and fingers (rather than rotation of the wrist), which was not detected by the accelerometer.

The mean grip force of the 10 subjects measured under the complex condition was 13% (SD 5.8) of maximum grip force whereas that measured under the simple condition was 15% (SD 6.7) of maximum grip force. The two were not significantly different ($p = 0.34$). We computed the cross-correlation function of grip force versus position of the tip of the ruler under the complex condition. The mean of the cross-correlation peak was 0.44 (SD 0.20), indicating that grip force and ruler motion were moderately correlated. The peak occurred at a mean of −6.8 ms (SD 20), i.e.,

Table 1
Manipulation task contrasts

Anatomical region	MNI coordinates			Peak z-score	Cluster size[a]	P value
	x	y	z			
Simple-rest						
Left MI	−42	−22	48	6.27	104	< 0.0001
Right anterior cerebellum (lobule V/VI)	18	−54	−18	5.21	15	0.021
Complex-rest						
Left MI	−36	−20	56	5.82	166	0.001
Right anterior cerebellum (lobule V/VI)	20	−56	−20	6.27	288	< 0.0001
Right posterior cerebellum (lobule VIII)	14	−62	−54	5.83	73	0.001
Left thalamus	−14	−22	6	5.77	22	0.001
Left anterior insula	−44	0	4	5.58	22	0.003
Left SI (area 3)	−34	−32	60	5.56	14	0.003
Left SII	−50	−26	14	5.45	6	0.006
Complex-simple						
Left SI (area 2)	−40	−42	60	5.55	6	0.003
Right Brodmann area 40	68	−26	20	5.34	6	0.01

[a] Number of 8-mm^3 voxels in cluster.

grip force adjustments occurred before motion of the tip of the ruler, indicating that they were predictive rather than reactive. We also computed the cross-correlation function of both grip force versus velocity and grip force versus acceleration of the tip of the ruler. In neither case did we find that the peak grip force lagged motion, indicating that the grip force responses could not be attributed to velocity or acceleration dependent reflex activity. Furthermore, the mean values of the cross-correlation peaks were 0.07 and 0.02 for velocity and acceleration, respectively, indicating that the anticipatory changes in grip force were related to maintaining the position of the ruler rather than controlling its motion.

Discussion

The complex-simple contrast revealed significant activation only in areas normally associated with processing of somatosensory information. Regions such as SI and thalamus, which were found to have significant activity in the complex-rest contrast, have been previously shown to be activated during control of precision grasp. Somatosensory association areas such as SII, Brodmann area 40 and insula, which were found to have significant activation in the complex-rest or complex-simple contrast, are likely involved in the integration of somatosensory information when grasping and stabilizing the inverted pendulum. Comparison of the complex-rest and simple-rest contrasts and analysis of the change in BOLD signal intensity, relative to rest, indicate that the ipsilateral cerebellum was also selectively activated when dynamic control of grasp was needed to balance a flexible inverted pendulum compared to the static grasp needed to squeeze a foam ball. Based on the studies of Blakemore et al. (1998, 2001), it is likely that the selective activation of somatosensory areas and cerebellum are related to the ability of the cerebellum to predict the sensory consequences of motor commands under the two conditions. The similarity in the size of the activated regions in MI in the complex-rest and simple-rest contrasts and the failure to find a significant difference in the change in BOLD signal intensity, suggest that MI was activated to the same extent under both conditions and is, therefore, less implicated in representation of the task dynamics than the cerebellum.

The significant activation of area 2 in the complex-simple contrast underlines the importance of the integration of tactile and proprioceptive information in successfully dealing with the complex dynamics of the flexible ruler. Ehrsson et al. (2001, 2003) and Kuhtz-Buschbeck et al. (2001) identified a number of regions in frontal and parietal cortex which were activated in relation to different aspects of manipulation with precision grip. The study by Kuhtz-Buschbeck et al. (2001) was the most similar to our study in that subjects continuously maintained the same grip force for about 40 s, although grip initiation, lifting of the object, setting the object down and releasing the grip were also part of the task. When subjects used a firm grip the contralateral primary sensorimotor areas, premotor areas (PMd and PMv) and Brodmann area 7 were activated along with Brodmann area 40 bilaterally. The cerebellum, however, was outside their scanning range. We did not find significant activation in premotor areas or area 7. The main reason for this may be that their task would have involved decision and planning phases for initiating and releasing the grip, which were absent in our task.

Bilateral activation of SII together with insula, Brodmann area 40 and parietal association areas has been shown to be important in tactile object recognition (Reed et al., 2004). These regions are believed to integrate somatosensory information to provide a coherent image of an object appropriate for cognitive action. SII receives both cutaneous and proprioceptive input from peripheral sensory receptors (Fitzgerald et al., 2004) and projects to MI, among other regions (Friedman et al., 1986). Thus, SII and the adjacent connected areas (insula and area 40) likely provide integrated feedback to MI. These areas may perform higher level processing than SI, for example, integrating proprioceptive and tactile information in the context of the flexibility of the ruler to produce awareness of the direction in which the ruler is leaning and its direction of motion.

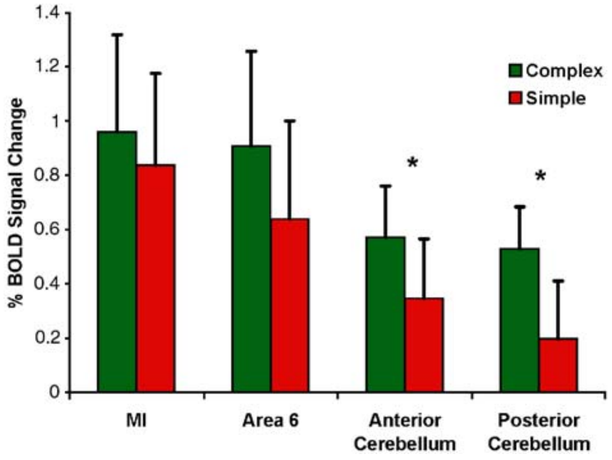

Fig. 3. Inter-subject means for percentage change in BOLD signal intensity, relative to rest, recorded in motor areas (MI, area 6, anterior cerebellum and posterior cerebellum) for complex-rest (green) and simple-rest (red) conditions. The significance level is corrected for multiple comparisons ($p < 0.01$). Significant differences are indicated by asterisks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

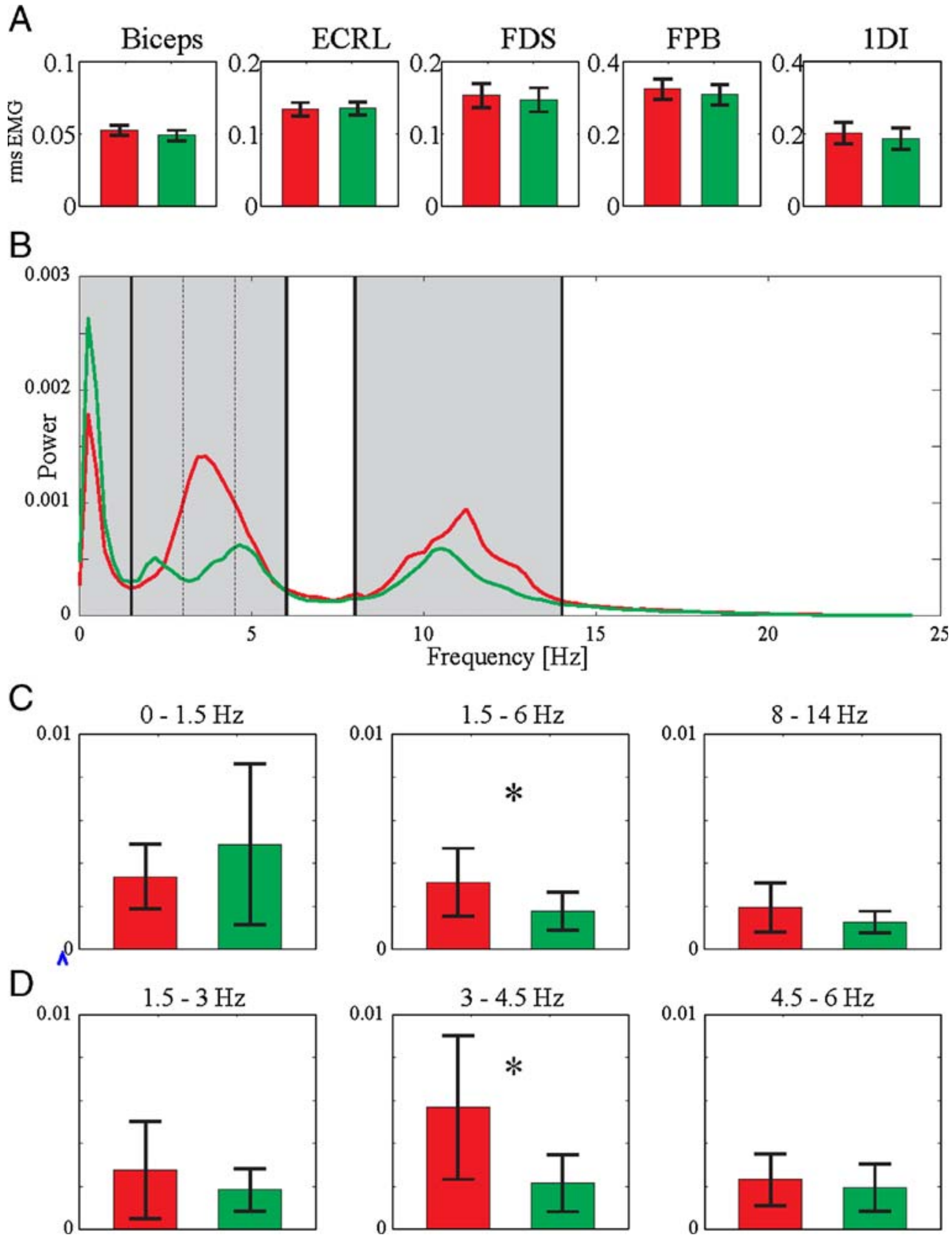

Fig. 4. (A) Mean rms EMG for simple (red) and complex (green) tasks for biceps, extensor carpi radialis longus (ECRL), flexor digitorum superficialis (FDS), flexor pollicis brevis (FPB) and first dorsal interosseus (1DI) muscles of the 10 subjects. (B) Mean power spectral density function from 0 to 25 Hz for simple (red) and complex (green) tasks for the 10 subjects. (C) Mean integrated power of the 10 subjects for the frequency bands delimited by solid vertical lines in panel B. (D) Mean integrated power of the 10 subjects for the frequency bands delimited by dashed-dotted vertical lines in panel B. Error bars represent standard deviations in all plots. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The regions of activity in the anterior and posterior cerebellum, identified in the complex-rest contrast, closely matched those described in fMRI studies of cerebellar somatotopy for movements of the fingers (Rijntjes et al., 1999; Grodd et al., 2001) and tactile stimulation of the fingers (Bushara et al., 2001). These regions were activated under the complex condition, but much less under the simple condition. The anterior region matches the location of common activation found in our previous studies of tasks involving manipulation of a grasped object (Kawato et al., 2003; Milner et al., 2006). Bilateral activation in this region of the cerebellum has previously been shown to be associated with tracking error, as well as acquisition of an internal model of the kinematics of a visuomotor task (Imamizu et al., 2000, 2003). Our task did not involve vision, which likely accounts for ipsilateral rather than bilateral activation of this region. Activation of the posterior cerebellum, exclusively on the ipsilateral side, has not been reported previously in studies of tasks involving manipulation of objects in the absence of vision, although deactivation has been reported in a contralateral region (Kawato et al., 2003), but with a focus slightly more lateral and posterior to the region which we identified. Because both of these regions of the cerebellum have been shown to receive strong somatosensory inputs (Bushara et al., 2001) their activation under the complex condition may be due to proprioceptive perception of error in the position of the flexible inverted pendulum or neural representation of the task dynamics.

The difference in cerebellar activation between the complex and simple conditions could not be attributed to differences in the mean level of muscle activation, i.e., differences in effort, since the rms EMG of finger, wrist and elbow muscles did not differ. A likely explanation is that a larger network of cerebellar neurons was needed to transform somatosensory information about the orientation of the inverted pendulum into motor commands to keep it upright than to apply a constant force to the foam ball. Cutaneous information about contact between the thumb and fingers would have been sufficient to compute the necessary levels of muscle activation when squeezing the ball. To balance the flexible inverted pendulum a much more complex transformation of sensory input to motor output would have been needed. The torque applied by the inverted pendulum to the hand would provide information about its orientation. This information would then be transformed into commands to the hand and wrist muscles, where the change in activation of specific muscles would be determined by the direction and magnitude of the sensed torque. The object was moved principally by “rolling” action of the thumb and fingers. Consequently the activity of thumb and finger muscles served both to grasp and apply torque to the object. To keep the wrist stationary, the activity of wrist muscles had to be modulated to balance torque arising from thumb and finger muscles crossing the wrist and to increase joint stiffness for stability. Because subjects were instructed to hold the inverted pendulum in a position of unstable equilibrium, moment-to-moment changes in muscle activation were needed to control its orientation. The cerebellum has been implicated in both feedback and feedforward control of movement. In the former case, it regulates feedback gains (MacKay and Murphy, 1979; Kawato et al., 1987) and in the latter it represents the system dynamics (Nezafat et al., 2001). Subjects reduced involuntary movement in the 3- to 4.5-Hz range under the complex condition compared to the simple condition. The natural frequency of the elbow in flexion/extension under the conditions of our experiment would be approximately 3 Hz. Although the natural frequency of the inverted pendulum was an order of magnitude lower than the natural frequency of the elbow, any movement of the elbow would have been transferred to the inverted pendulum, acting to destabilize it. Therefore, attenuation of the 3- to 4.5-Hz movement can be considered as an active control process important to stabilizing the inverted pendulum. The finding that changes in grip force are correlated with the position of the inverted pendulum and that they are predictive, is consistent with the idea that increased activation of the cerebellum under the complex condition was related to feedforward control of the position of the tip of the flexible ruler. This suggests the use of an internal model of the object’s interaction dynamics to control its position. Overall, our results are consistent with the view that considerably more computational resources were devoted to the transformation of afferent input to motor output to grasp the object with complex dynamics than the object with simple dynamics and that the neural substrates for the representation of the task dynamics are localized in the cerebellum. Since we found little difference in the size of the activated regions in MI and no significant difference in the change in BOLD signal intensity under the complex and simple conditions, it is unlikely that differences in task dynamics were represented in MI.

The finding that somatosensory regions were significantly activated only under the complex condition cannot be attributed to differences in the amount of somatosensory input. The input from cutaneous mechanoreceptors should have been similar under the two conditions, given that the grip force was not significantly different under the two conditions and that the texture of the foam ball was rougher than that of plastic ruler. Instead, we interpret this finding in the light of recent work by Blakemore et al. (1998, 2001) who showed that activation of somatosensory areas is reduced when tactile stimulation is self-produced than when it is externally produced. They proposed that the cerebellum generates a forward model of the sensory consequences of motor commands, which produces gating of somatosensory activity. Under the simple condition, we can consider squeezing the foam ball to result in tactile stimulation that is self-produced. Under the complex condition, tactile stimulation originated from gripping the ruler (self-produced) and from bending of the ruler by the weights (externally produced). Thus, under the simple condition we could expect significant attenuation of sensory activity in somatosensory areas. In contrast, under the complex condition, stimulation of cutaneous and muscle mechanoreceptors produced by bending of the ruler could not have been attenuated to the same extent unless subjects had a very accurate forward model of the complex dynamics of the flexible ruler. This would explain why significant activation of somatosensory areas was found in the complex-rest and complex-simple contrasts.

Our results suggest that the cerebellum is differentially activated to control grasp while holding an object with complex dynamics compared to one with simple dynamics. We propose that the cerebellar activity represented the implementation of feedback processes used to stabilize the arm and control the fingers so as to keep an inverted pendulum in a vertical orientation. Because of the similarity in the activation of MI under the simple and complex conditions, it is unlikely that the neural representation of the task dynamics is localized in MI. Somatosensory association areas such as SII, Brodmann area 40 and insula, which were selectively activated under the complex condition, are likely involved in the integration of somatosensory information in the context of physical attributes of the object, which in this case might include its flexibility. Under the simple condition, somatosensory activity was likely attenuated because tactile stimulation was self-produced rather than externally produced (Blakemore et al., 1998, 2001).

Acknowledgments

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