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Report

Neural Correlates of Internal-Model Loading

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Summary

Skilled object manipulation requires knowledge, or internal models, of object dynamics relating applied force to motion [1–4], and our ability to handle myriad objects [5–6] indicates that the brain maintains multiple models [7–9]. Recent behavioral studies have shown that once learned, an internal model of an object with novel dynamics can be rapidly recruited and derecruited as the object is grasped and released [10–12]. We used event-related fMRI to investigate neural activity linked to grasping an object with recently learned dynamics in preparation for moving it after a delay. Subjects also performed two control tasks in which they either moved without the object in hand or applied isometric forces to the object. In all trials, subjects received a cue indicating which task to perform in response to a go signal delivered 5–10 s later. We examined BOLD responses during the interval between the cue and go and assessed the conjunction of the two contrasts formed by comparing the primary task to each control. The analysis revealed significant activity in the ipsilateral cerebellum and the contralateral and supplementary motor areas. We propose that these regions are involved in internal-model recruitment in preparation for movement execution.

Results

While in the MRI scanner, subjects performed a random sequence of three tasks. In the primary MOVE task, subjects moved an object (cylindrical handle), attached to a one-degree-of-freedom MR-compatible manipulandum [13], from a start position to a target by flexing the wrist (Figure 1A). The FREE task involved the same hand movement but without the object. There were two variations of the isometric force task, each performed by half the subjects. In the ISO-GRIP task, subjects simply squeezed the object. In the ISO-TORQUE task, they used their wrist to generate a phasic torque that was similar, in both magnitude and duration, to that observed in the MOVE task. In all trials, simultaneous visual and haptic cues indicated the task to be performed, and these cues were followed by a random 5–10 s delay before the presentation of a go signal (Figure 1B). All tasks were practiced before scanning took place so that accurate performance could be ensured.

In order to control the object in the MOVE task, subjects first generated a small and brief wrist flexor torque to overcome the initial inertia of the object, then a large extensor torque to brake the movement, and finally a gradually decreasing extensor torque to maintain the object on target after the movement terminated (Figure 2). Overall, the six subjects who performed the ISO-TORQUE task generated similar time-varying torque profiles in the MOVE and ISO tasks (Figure 2B). Repeated measures ANOVAs, based on these subjects, revealed no reliable differences between tasks in terms of peak torque ($F_{1,5} = 017$; $p = 0.69$) or the SD of peak torques computed for each subject ($F_{1,5} = 3.87$; $p = 0.11$). In addition, there was a strong positive correlation across subjects between average peak torques in the ISO and MOVE tasks ($r = 0.97$; $p < 0.001$), indicating that subjects who exerted a large force during the MOVE task also exerted a large force during the ISO task. However, it may be noted that the brief flexion torque, characteristic of the MOVE task, was not produced in the ISO task.

The time period of interest for imaging was the interval between the presentation of visual and haptic cues and the go signal. The data were analyzed as an event occurring at the moment of the cue onset. This approach was based on our assumption that recruiting or loading an internal model is a discrete event that, in our task, occurs as soon as the appropriate cue is provided so that the subject is ready to act when the go signal is presented. By comparing the MOVE task with the FREE and ISO tasks, we thought to isolate loading of the internal model of the object dynamics. The control tasks were designed to include all major events in the MOVE task except for loading of the internal model. The FREE task controlled for the displacement of the hand during the movement, the two ISO tasks controlled for the tactile cue, and all three tasks controlled for the visual cue, posture of the hand, and preparatory attention-related activity before the onset of motor output. Whereas the ISO-GRIP task provided a general control for grip force applied to the object, the ISO-TORQUE task provided additional control for wrist torque production and tactile sensation closely resembling the MOVE condition. Importantly, there was no significant difference in neural activity

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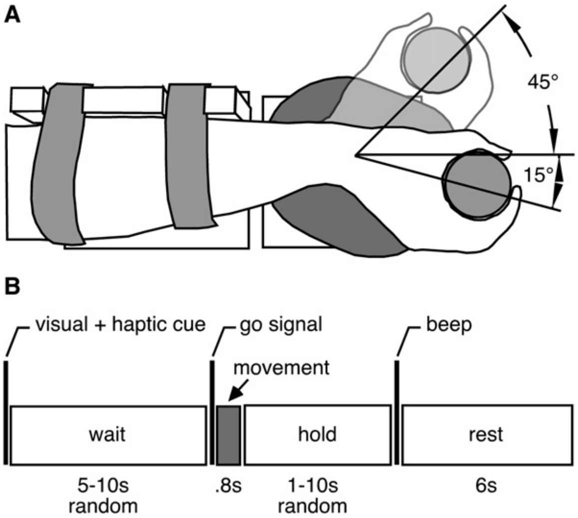

Figure 1. Tasks and Timeline

(A) In the MOVE task, subjects grasped the handle of a MR compatible robotic manipulandum and made 60° wrist flexion movements. In the ISO task, the handle was fixed at the start (15 wrist extension) and subjects either squeezed the handle or generated an isometric extensor torque. In the FREE task, subjects made the same 60° movement but without the handle in hand.

(B) All three tasks followed the same time course. To initiate each trial, simultaneous visual and haptic cues were presented indicating the task to be performed. After a random delay of 5–10 s, a visual go signal was given. Subjects were required to complete the movement within 800 ms and remain at the end position for a random interval of 1–10 s before a beep indicated they should return to the start position.

between the two ISO tasks even at a low threshold ($p < 0.001$, uncorrected), and we therefore combined the subject groups together for analysis. Theoretically, the conjunction of MOVE–FREE with MOVE–ISO should leave only the HRF related to loading the internal model. This conjunction analysis revealed significant BOLD activity ($p < 0.05$ corrected) in the contralateral primary sensory-motor region including Brodmann area 4 (M1) and Brodmann area 3 (S1), bilateral supplementary motor area (SMA), cingulate sulcus, and the ipsilateral cerebellum (Figure 3 and Table 1).

Discussion

Our ability to skillfully manipulate familiar objects as soon as we grasp them indicates that the brain stores internal models of their dynamics and can rapidly recruit them as needed [2, 5, 6, 10–12, 14]. Evidence from imaging, neurophysiological, and lesion studies suggests that the cerebellum plays an important role in storing internal models [4, 15–17]. Shadmehr and Holcomb [18] examined a task in which subjects, by using their right hand, first learned to move an object with complex dynamics and then, after a 6 hr delay, performed the task again. By using PET, they compared changes in rCBF from late learning to recall (where performance levels were similar) and found increased rCBF in the right anterior cerebellar cortex as well as the left dorsal premotor and posterior parietal cortices. They suggested that, shortly after initial learning, the internal model is stored in the cerebellum and that premotor and parietal structures are involved in linking the internal model to contextual cues during recall. From a computational perspective, the cerebellum is well suited for internal-model storage because it contains the required inputs and outputs to support supervised or error-feedback learning, which is the most effective means of learning internal models [4, 19].

Precentral gyrus (M1), postcentral gyrus (S1), SMA, and the cingulate sulcus were also preferentially activated by the cue onset in the MOVE task. Studies in human and nonhuman primates have demonstrated that the motor cortex is involved in early motor learning as well as consolidation (e.g., [20]). The SMA, along with the putamen body and caudate nucleus, has been identified as part of the motor loop for well-learned movements ([21], see [22] for a review). Furthermore, SMA, S1, and cingulate regions have been shown to be involved in precision grip tasks involving object manipulation [23]. The activity in these regions was found to be significantly less in the ISO tasks even though the hand posture and forces applied by the hand were similar. This argues against the possibility that the greater activity in the MOVE task compared to the ISO condition is related to higher muscle activity or a difference in tactile and kinesthetic sensory feedback. The activation pattern thus seems to suggest that loading of an internal model, possibly in the cerebellum, is accompanied by interactions with M1 and S1 for sensory-motor preparation and with SMA and cingulate regions for grasp control. All of these interactions may be required for a successful completion of the MOVE task.

Imamizu et al. [24] studied switching between internal models by using a task in which subjects performed right-handed reaches by using one normal computer mouse and two with novel visuomotor mappings. At the moment of transition between mouse type, signaled by visual feedback, neural activity related to switching was observed in the anterior parietal region, left insula, right cerebellum, and right prefrontal region. This activity was sustained throughout the use of a novel mouse in the cerebellum and parietal regions, suggesting an association with the use, rather than the switching, of internal models. The lack of anterior parietal cortex involvement in the current study could presumably be explained by the difference in tasks between the two studies. Whereas the above study involved the learning of kinematics, the current study involves the learning of novel dynamics.

In all three of our tasks, we might expect to observe neural activity related to what has been termed the readiness potential: cortical activity that ramps up as movement onset approaches and that occurs prior to and linked to voluntary movement [25]. If there are differences in movement parameters across tasks, it is possible that there may be differences in the readiness potential that could contribute to the effects we observed in our conjunction analysis. We have two arguments against this possibility. First, when we modeled the neural response either as a ramp from the cue signal to the go signal or from the cue signal to 5 s later and used these models as regressors in the SPM conjunction analysis, we failed to observe significant activation ($p < 0.1$, FDR corrected, 0 voxel threshold). This

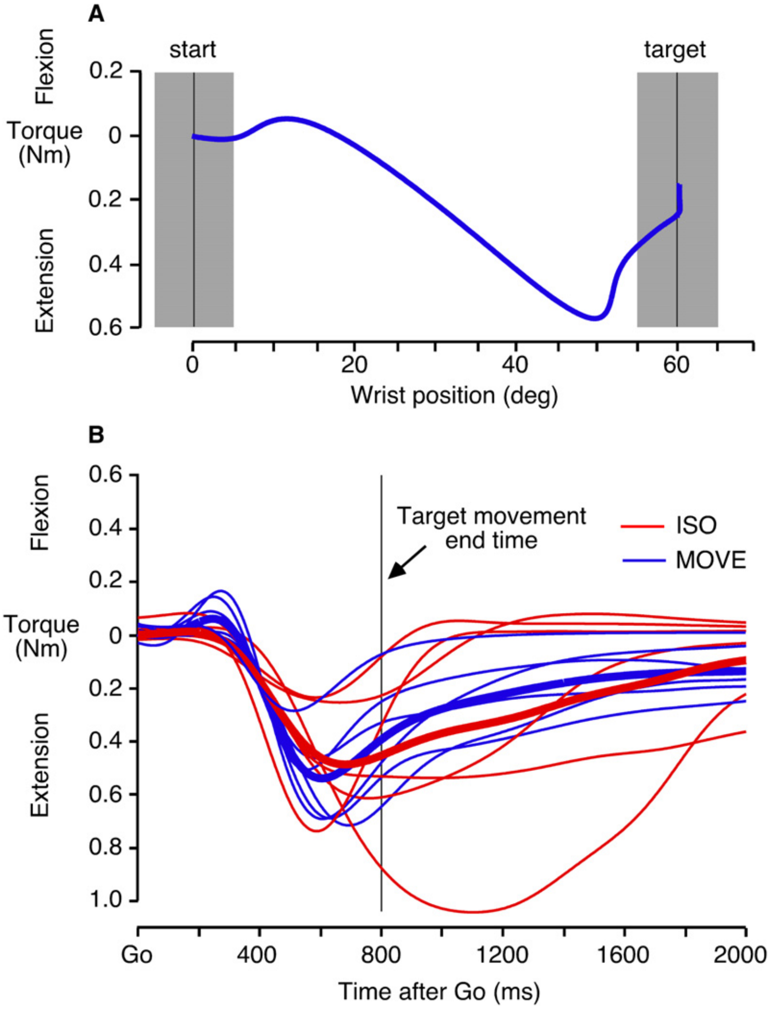

Figure 2. Movement Torque Profiles

(A) Average torque from all trials plotted against wrist angular position from the go signal to the end of movement (800 ms).

(B) Mean torque profiles for the MOVE and ISO-TORQUE tasks. Each thin curve represents the average of 40 trials from a single subject, aligned at the go signal. The thick curves represent the means of these average curves, also aligned at the go signal.

indicates that any activity related to the readiness potential was similar in the MOVE and control tasks. Second, we attempted to preempt this issue in our experimental design by equating movement parameters in the different tasks. Specifically, we sought to equate extensor torques in the MOVE and ISO-TORQUE tasks and movement amplitude and duration in the MOVE and FREE tasks. Although no visual feedback was provided about torque in the ISO-TORQUE task, subjects successfully generated torque profiles that were similar to those observed in the MOVE tasks.

We have suggested that the activation yielded by our conjunction analysis is due to recruitment or recall of an internal model of the object in the MOVE task. An alternative possibility is that subjects recall a representation of the kinematics or kinetics of the task [26–28]. However, if the areas we have identified are active in relation to kinematics or kinetics, they would show vast differences between our two control tasks. The ISO-TORQUE task involved relatively large torque but no hand motion, whereas the FREE task involved low torque and significant hand motion. Both contrasts of ISO–FREE and FREE–ISO at the cue onset show no activity ($p > 0.1$, FDR corrected), suggesting that no systematic planning for either torque production or hand movement occurs in response to the cue presentation. (Recall that there were no activity differences between the two ISO tasks and that these were therefore grouped together.)

We have previously argued that moving a hand-held load requires internal models of the dynamics of both the object and arm [2, 4]. Although an internal model of the arm is presumably recruited during the FREE task, such recruitment would also occur during the MOVE and ISO tasks, and therefore differences between the MOVE and FREE tasks could only be due to recruitment of an internal model of the object and not the arm. One could also argue that generating a torque against a rigid object (as in our ISO task) also involves recruiting an internal model of the load. It is not clear whether the mechanics of rigid objects (described by statics rather than dynamics) are represented in the same way as objects that move when forces are applied. However, assuming that people do maintain internal models of rigid loads, the mechanical properties of rigid objects are both highly familiar and simple, unlike the complex and novel dynamics of the object used in the MOVE condition. Thus, it is possible that an internal model of the rigid object is recruited during the ISO condition but, because the load is familiar and simple, far less activation is seen. If so, our results suggest that the activation we observed is linked to the recruitment of an internal model of an object with complex and relatively unfamiliar (i.e., recently

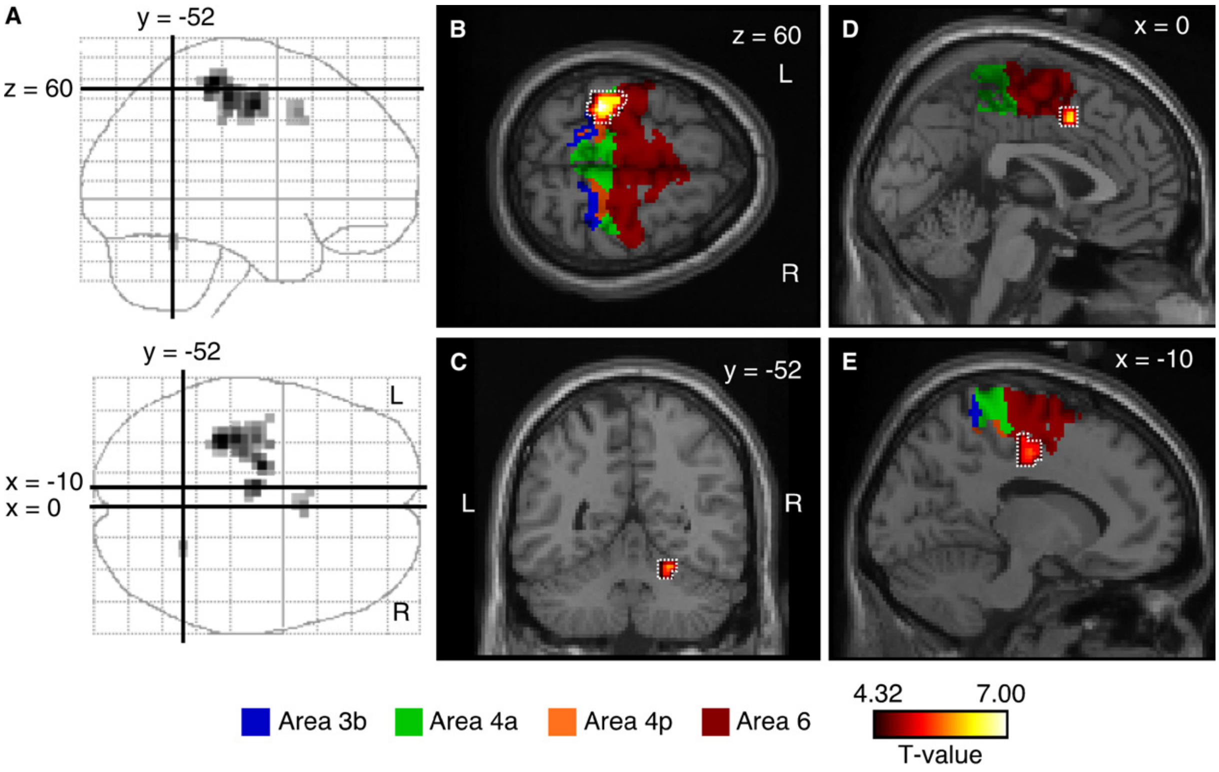

Figure 3. Conjunction of MOVE–ISO and MOVE–FREE

(A) The second level conjunction at $p < 0.05$, FDR corrected, gave activity in sensory-motor regions including (B) area 3 (postcentral gyrus) and area 4 (precentral gyrus), (C) the cerebellum, (D) the rostral cluster involving the cingulate and the pre-SMA, and (E) the caudal cluster involving the cingulate and the SMA. The maximum probability maps [33] of Area 3b (blue), Area 4a (green), Area 4p (orange), and Area 6 (red) have been overlaid in (B), (D), and (E) for showing possible anatomic locations of the observed activations in the sensory-motor cortex.

learned) dynamics. This activation was elicited in the time period between the cue presentation and the go signal, suggesting that the model was recruited in response to the haptic and visual cues and was not simply maintained throughout the entire experiment. We therefore suggest that the observed activity is related to the recruitment of an internal model associated with the MOVE task. This internal model may contain information both about the dynamics of the manipulated object as well as the target obtainment task to be

Table 1. Location of Significant Clusters of Activation

	Cluster			Peak				
				MNI Coordinates				
Brain Region	Size[a]	Cytoarchitectonic Composition (voxels)[b]		x	y	z	T Value	Cytoarchitectonic Probabilities[c]
Primary sensory-motor cluster	110			−35	−32	60	6.30	
		33	Left area 4p					Area 4p 40%
		18	Left area 6					—
		17	Left area 4a					Area 4a 50%
		9	Left area 3b					Area 3b 40%
Caudal cingulate/SMA cluster	17			−11	−14	48	5.74	
		10	Left area 6					Area 6 50%
Rostral cingulate/pre-SMA cluster	10			0	11	44	4.77	
		2	Left area 6					Area 6 10%
		1	Right area 6					Area 6 10%
Cerebellum cluster (lobule 4–5)	3			21	−53	−20	4.56	

[a] Number of 3 mm isotropic voxels in cluster.

[b] Number of voxels assigned to cytoarchitectonic areas in the maximum probability maps [33]. Note that the summation is not equal to the cluster size because the maps do not cover the entire cortical surfaces.

[c] Probability of peak location belonging to each area. Note that the summation can be over 100% because a probability map for each area was independently determined.

performed. This putative recruitment is associated with clear activity in contralateral M1, S1, SMA, and the cingulate and ipsilateral anterior cerebellar cortex.

Experimental Procedures

Subjects

Twelve healthy right-handed subjects (nine males and three females) between 22 and 35 years old participated in the experiment after giving informed consent. The procedure was approved by a local ethics committee. All subjects performed three different trial conditions: MOVE, ISO, and FREE.

Apparatus and Procedure

All experiments were performed with the one-degree-of-freedom MR-compatible manipulandum [13] mounted outside an MRI scanner. To minimize head motion caused by arm movement, we fitted each subject with a bite bar to stabilize his or her head. In the MOVE task, subjects held an object (or handle) attached to the robot during movement. Visual feedback of the positions of the object, start location, and target were displayed on a screen in the scanner. The MOVE task involved a 60° ± 5° wrist flexion for moving the object from the start position (5° wide). The following equation describes the nonlinear dynamics of the object controlled by the manipulandum [29]:

$$I_m\ddot{w} + D\dot{w} + K\left(\frac{1}{\sqrt{|w - w_{kr}|} + 0.01}\right) + F_r|w - w_{fr}|sign(\dot{w}) + \psi_w = T$$

where $I_m = 0.009$ Kgm^2 represents the inertia of the manipulandum handle and $w, \dot{w}$, and $\ddot{w}$ represent the angular position, velocity, and acceleration of the object in radians. The damping constant ($D = 0.246$ Nms/rad), nonlinear inverse spring stiffness ($K = -0.283$ Nm$\sqrt{}$rad), and the spring resting length ($w_{kr} = 0.2$ rad) were tuned for achieving a difficult but learnable task. The system was observed to have a residual position-dependent static friction approximated by a piecewise linear function with the constant $F_r = 0.036$ Nm/rad, position of minimum friction $w_{fr} = 0.2$ rad, and the $sign(\dot{w})$function coding the direction of motion. Finally, ψ_w represents the natural wrist dynamics of the subject, and T is the joint torque applied by the subject.

All subjects completed an initial training on the MOVE task in a mock setup of the fMRI apparatus in advance of scanning. Subjects had to initiate the movement within 400 ms of the go signal and complete the movement to the target, without overshooting or undershooting, within 800 ms of the go signal. Feedback for a success or a specific error message (too slow, too short, and too long) was given after each trial. Subjects practiced the task (in blocks of 50 trials) until they achieved at least eight successes within a moving window of ten trials. Thereafter, subjects practiced the sequence of tasks they would perform in the scanner.

The ISO task involved either squeezing the handle (ISO-GRIP; six subjects) or isometric torque production in the wrist extension direction while holding the handle (ISO-TORQUE; six subjects). In the ISO-TORQUE task, subjects were asked to produce a maximum torque similar to that observed during training in the MOVE task and were given several practice trials just before scanning, in which they received visual feedback of their torque and a target they were asked to match. The target was the mean maximum torque they had applied during training on the MOVE task. Grip force was not measured in the ISO-GRIP task. In both ISO tasks, the duration of torque production was matched to the duration of hand movement in the MOVE (and FREE) tasks.

In the FREE task, subjects made the same motion and used the same hand posture as in the MOVE task but without grasping and moving the object. The start position was the same as in the other two conditions (15° wrist extension) but with the object positioned at the endpoint (45° wrist flexion) and covered in soft padding that contacted the knuckles at the completion of the movement.

Twenty repetitions of each task were randomly interspersed within a session. Each condition had the same time course, shown in Figure 1B, whereby subjects were simultaneously presented with a visual color cue (color of the target circle) and a haptic cue (hand touches object or not). At the start position, the hand was open with the fingers extended and the back of the hand contacting a block of foam. As subjects waited in this position, the object was either moved toward the hand to gently rest on the palm (MOVE and ISO tasks), or away from the hand to mark the endpoint (FREE task). After a random interval between 5 and 10 s, a go signal (blue ring around the start circle) appeared, indicating to the subjects that they should begin the task specified by the preceding cues. After the movement in the MOVE and FREE tasks, subjects kept the cursor (and hand) at the end position for a random interval between 1 and 10 s until a beep indicated they should return their hand to the start position. Toni et al. [30] have demonstrated that the neural signals from sensory and motor events occurring close together can be distinguished by randomly varying the time period between them. Similarly, the random delays between the cue, go, and return signals allowed us to distinguish the hemodynamic response function (HRF) associated with the cue signal from the actual movement.

fMRI Acquisition

A 1.5 T MRI scanner (Shimadzu-Marconi) was used for obtaining blood-oxygen-level-dependent (BOLD) contrast functional images. Images weighted with the apparent transverse relaxation time were obtained with an echoplanar imaging sequence (repetition time: 3.5 s; echo time: 50 ms; flip angle: 90°). Two sessions were conducted where 330 sequential whole-brain volumes (64 × 64 × 35 voxels of 3.5 × 3.5 × 4 mm resolution and 224 mm field of view) were acquired in each session.

fMRI Analysis

We used SPM2 software (http://www.fil.ion.ucl.ac.uk/spm/) for image processing and analysis. We discarded the first four volumes of images to allow for T1 equilibration. The remaining 326 image volumes were realigned to the first volume so that head motion over time could be corrected; the volumes were spatially normalized to the Montreal Neurological Institute (MNI; Montreal, Canada) reference brain and resliced to 3 mm isotropic voxel size. The data were smoothed spatially with a Gaussian kernel with an 8 mm full-width at half maximum (FWHM).

Statistical analyses were performed in two stages of a mixed-effects model. In the first stage (fixed effect) individual analysis, six types of events were defined: cue and go events in the MOVE, ISO, and FREE conditions. Each event was modeled by an impulse function locked at the onset of the cue or the go signal. The impulse functions were convolved with the canonical hemodynamic response function in SPM2 for yielding regressors in a general linear model. A parameter was estimated for each regressor for each voxel by the least-squares method. The two images of particular interest were derived from pair-wise contrasts between the estimated parameters for the cue events MOVE-FREE and MOVE-ISO. In the second stage (random effect) group analysis, we applied a one-sample t test to contrast images from each individual to obtain t static maps for MOVE-FREE and MOVE-ISO at the onset of the cue. To examine activation common to both contrasts, we calculated a minimum t statistic conjunction map by taking the minimum t statistic from the two maps. A threshold was applied to the conjunction map such that both contrasts were individually significant (testing the conjunction null hypothesis as described in [31]). We used a height threshold of $T_n > 4.15$ ($p < 0.05$, corrected for multiple comparisons based on the false discovery rate) and an extent threshold of three voxels. The Automated Anatomical Labeling [32] toolbox for SPM2 was used for identifying global anatomical regions, and the SPM Anatomy toolbox [33] was used for identifying fine cytoarchitectonic regions near the central sulcus.

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