

VISUAL AND TACTILE GUIDANCE OF DEXTEROUS MANIPULATION TASKS: AN fMRI STUDY^{1,2}

ARDESHEER TALATI

*Department of Psychiatry
Columbia University*

FRANCISCO J. VALERO-CUEVAS

*Sibley School of Mechanical and Aerospace Engineering
Cornell University*

*Musculoskeletal Integrity Program
The Hospital for Special Surgery, New York*

JOY HIRSCH

*Departments of Radiology and Psychology
Center for Neurobiology and Behavior
Columbia University*

Summary.—Models of motor guidance that dynamically adjust to the availability and quality of sensory information are based on the observation that dexterous tasks are routinely performed using various combinations of visual and tactile inputs. However, a dynamic neural system that acquires and processes relevant visual and tactile information remains relatively uncharacterized in humans. In this study, whole-brain functional magnetic resonance images were acquired during a dexterous manipulation task, compression of the end caps of a slender spring prone to buckling, to investigate the neural systems associated with motor guidance under four visual and tactile guidance conditions: (1) eyes closed (no visual input), smooth end caps, (2) eyes closed, rough end caps, (3) eyes open and watching hand, smooth end caps, and (4) eyes open and watching hand, rough end caps. Performance of the dexterous task remained constant in all conditions. Variations in the two levels of visual input resulted in modulation of activity in the middle and inferior occipital gyri and inferior parietal lobule, and variation in the two levels of tactile input during the task resulted in modulation of activity in the precentral (primary motor) gyrus. Although significantly active in all conditions, cingulate gyrus, medial frontal gyrus, postcentral gyrus, and cerebellum activities were not modulated by levels of either visual or somatosensory input, and no interaction effects were observed. Together, these data indicate that a fine-tuned motor task guided by varying visual and tactile information engages a distributed and integrated neural complex consisting of control and executive functions and regions that process dynamic sensory information related to guidance functions.

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²Address correspondence to Joy Hirsch, Ph.D., Professor of Psychology and Functional Neuro-radiology, Director, fMRI Research Center, Department of Radiology, Center for Neurobiology and Behavior, Columbia University, Neurological Institute-B41, Box 108, 710 West 168th Street, New York, NY 10032 or e-mail (jh2155@columbia.edu).

Dexterous motor tasks are performed under a variety of sensory input conditions. For example, a musical instrument can be played with or without visual, auditory or tactile feedback. However, there is abundant biomechanical evidence that the occlusion or alteration of the sensory input degrades the performance of many dexterity tasks such as somersaults (Davlin, Sands, & Shultz, 2001), balance (Barin, Jefferson, Sparto, & Parnianpour, 1997; Vuillerme, Teasdale, & Nougier, 2001), gait (Spaulding, Patla, Elliott, Flanagan, Rietdyk, & Brown, 1994; Varraine, Bonnard, & Pailhous, 2002), arm pointing (Tremblay, Welsh, & Elliott, 2001), and grip precision (Johansson & Cole, 1994; Cole, Rotella, & Harper, 1998). This raises the fundamental question of how the brain adapts its strategies based on the particular sensory inputs that guide a task. In this study, we focus on characterizing brain activity involved in one dexterous manipulation task—controlling a helical compression spring prone to buckling (Fig. 1; Valero-Cuevas, Smaby, Venkadesan, Peterson, & Wright, 2003), performed at a constant rate with varied visual and tactile input.

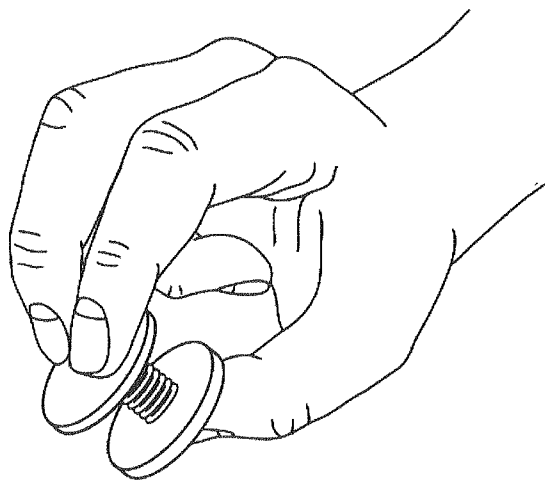


FIG. 1. Diagram of the helical coiled spring, demonstrating the correct hand configuration for the three-point pinch

The spring compression task employed for this study requires the simultaneous regulation of three well described biomechanical aspects of digit motor output: fingertip force magnitude, fingertip force direction, and 3-D digit kinematics (Valero-Cuevas, *et al.*, 2003), and thus challenges the neural guidance system in all three domains. Previous imaging studies of finger motor output have used tasks that emphasize only a subset of these aspects of

digit motor output. For example, isometric fingertip force production (Ehrsson, Fagergren, Jonsson, Westling, Johansson, & Forssberg, 2000; Ehrsson, Fagergren, & Forssberg, 2001) emphasizes the regulation of fingertip force magnitude, as finger pad friction allows much latitude in fingertip force direction (Valero-Cuevas, Zajac, & Bugar, 1998; Valero-Cuevas, 2000), and finger posture is constant. Finger tapping emphasizes the regulation of three-dimensional digit kinematics (Allison, Meador, Loring, Figueroa, & Wright, 2000). More complex manipulation tasks such as object twirling (Binkofski, Buccino, Posse, Seitz, Rizzolatti, & Freund, 1999) are mechanically ill-defined because of the latitude in how subjects distribute their digits about the object, which in turn affects the requirements on fingertip force magnitude, fingertip force direction, and three-dimensional digit kinematics.

We aimed to identify the neuro-anatomical system of cortical regions associated with visual and tactile guidance of this dexterous manipulation task. Based on the known pathways for sensorimotor processes, we hypothesized the existence of two broad categories of brain regions within this system: those that directly mediate the sensory input and those that mediate putative integrative and executive aspects of motor guidance. Whole-brain functional Magnetic Resonance Imaging (fMRI) and a factorial (2×2) experimental design was employed, wherein the dexterous manipulation task was performed under four combinations of visual and tactile sensory input: (a) eyes closed, no visual input, and smooth (minimal) tactile sensation, (b) eyes closed and rough (maximal) tactile sensation, (c) eyes open, watching hand, and smooth tactile sensation, or (d) eyes open, watching hand, with rough tactile sensation. For the tactile sensation, sandpaper was adhered to the spring end caps of the end caps to roughen the surface and enhance tactile sensation. Subjects were instructed to keep the same pace for the repetitive movements, and performance was visually monitored by the primary investigator to monitor task performance and measure the rate of compression.

METHOD

Imaging

A 1.5 Tesla Magnetic Resonance Scanner with a standard head coil (GE Twinspeed, General Electric, Inc.) was employed to obtain T_2^* -weighted images with a gradient echo pulse sequence (echo time 60 msec., repetition time 4,000 msec., flip angle 60°). This sequence is known to be sensitive to variations in magnetic resonance susceptibility due to alteration in the proportion of deoxyhemoglobin in the local vasculature accompanying neuronal activation (Ogawa, Lee, Nayak, & Glynn, 1990). The cubic size of each volume element [voxel] was 10 mm^3 , where the in-plane resolution was $1.5 \text{ mm} \times 1.5 \text{ mm}$, and slice thickness was 4.5 mm. Twenty-one contiguous slices were acquired parallel to the "AC/PC line," a standard reference line that

intersects the superior edge of the Anterior Commissure and the inferior edge of the Posterior Commissure. This orientation allowed direct comparison of acquired images with the Talairach and Tournoux Human Brain Atlas (Talairach & Tournoux, 1988) according to standard practice. In each subject, the 21 slices covered the entire cortex. Conventional high resolution T_1 weighted images were also acquired along the same plane locations as the T_2^* weighted images for anatomical reference. Seventy-two images were acquired for each condition, which lasted 4 min., 48 sec. Ten images were acquired during each resting baseline block, in which the subject held the spring stationary in the relaxed configuration while staring at a fixed cross-hair, and 10 images were acquired during each of two performance blocks. Each performance block was preceded and followed by a baseline block, and the sequence of stimulus presentation was baseline-task-baseline, baseline-task-baseline.

Prior to statistical analysis, all images were reconstructed, aligned, and corrected in the x and y dimensions for movement artifacts (Woods, Mazziotta, & Cherry, 1983). Data were analyzed using an analysis package developed for neurosurgical planning procedures and previously validated by conventional mapping techniques such as direct cortical stimulation, somatosensory evoked potentials, and surgical outcome studies (Hirsch, Ruge, Kim, Correa, Victor, Relkin, Labar, Krol, Bilsky, Souweidane, DeAngelis, & Guttin, 2000). A strength of this package is that all data are analyzed on the original T_2^* weighted images on which they are acquired, resulting in high fidelity and spatial resolution. This method does not make assumptions about the Hemodynamic Response Function but rather assumes an underlying T-distribution, and confidence levels are based on signal reproducibility across multiple trials (Hirsch, Rodriguez-Moreno, & Kim, 2001; Nichols, Brett, Andersson, Wager, Poline, 2005).

A two-dimensional Gaussian filter (3 mm at half-height) was applied to each voxel to enhance signal to noise. For each condition, signal changes were identified using a "block design" that compared average signal amplitude acquired during the activity epochs with average signals acquired during baseline epochs. According to a general linear model, an active voxel was defined as one in which the average magnetic resonance signal acquired during the stimulation periods was significantly different from the average baseline levels, on each performance epoch, at a threshold of $p < .0005$. This threshold was based on Bonferroni corrections for multiple comparisons (using a voxel size of $1.5 \times 1.5 \times 4.5$ mm and an activation requirement of five contiguous voxels; Huettel, Song, & McCarthy, 2004) and was also empirically validated by rates of false-positive activation calculated on images acquired using either a resting human brain or a copper sulfate ball (General Electric, Inc.) (Hirsch, *et al.*, 2000; Hirsch, *et al.*, 2001). An Active Area was

defined for each subject by a cluster of at least 5 Active contiguous voxels at $p < .0005$ during each of all four conditions. Group-based statistics required that reported observations were present for each subject.

A modified “forward transform” method was employed to assign labels to the Active Areas where the brain topology for each subject was employed as an index to labels of the Human Brain Atlas (Lancaster, Woldorff, Parsons, Liotti, Freitas, Rainey, Kochunov, Nickerson, Mikiten, & Fox, 2000). The stages of assignment included (1) identification of the brain slice passing through the AC/PC line and location of respective commissures of the axial view, (2) assignment of an atlas plate to each brain slice, (3) location of the vertical AC/PC plane on all brain slices, (4) location of the central sulcus on all T_2^* weighted images where it was represented and confirmation of those landmarks on all T_1 weighted images, (5) assignment of the anatomical labels, Brodmann’s areas and atlas sectors for each Active Area, and (6) determination of the Active Area volume based on the voxel count for each Active Area. Active Areas reported in this study were observed individually in all subjects. The group analysis yielded the average locations of activity in x , y , and z coordinates based on the normalized Talairach and Tournoux brain atlas (Talairach & Tournoux, 1988). All labels of brain activity were externally verified by 8 independent investigators, and consistency across labelers was greater than .95.

Dexterous Manipulation Task

The task is a subset of the Strength-Dexterity test (Valero-Cuevas, *et al.*, 2003) which consists of compressing a collection of compression springs of varying strength and dexterity requirements. For this study, a slender helical compression spring made of a magnetically inert metal was flanked by two smooth plastic end caps (see Fig. 1). Its strength requirement is defined as the pinch force necessary to compress the spring to its solid length, i.e., when the coils are all in contact with one another, whereas the dexterity requirement is defined as the ability to compress the slender spring fully without buckling it. To prevent buckling, the posture of the fingers and the magnitude and direction of fingertip forces need to be dynamically regulated to maintain the end caps parallel and aligned. The greater the propensity of a spring to buckle, the more precisely the end caps need to be held parallel and aligned, the more accurately the fingertip forces need to be directed, and the faster the perturbations need to be corrected. The Dexterity Index quantifies the dexterity requirement of the spring, and is quantified as

$$[1/(D^*C_1)] * \sqrt{[2*y_{\max} * C_1 * (L_0 - y_{\max}^2)/C_2]}$$

where D is the mean diameter of the spring, C_1 and C_2 are constants that depend on the spring material, L_0 is the free length of the spring, and y_{\max}

is the maximum shortening of the spring. Note that this index depends only on geometric and material properties and is independent of the strength requirement (Valero-Cuevas, *et al.*, 2003). The choice of strength and dexterity characteristics of the spring allowed repeated full compression for 40 sec. without fatigue, while requiring that subjects actively control the alignment of the two discs to compress the spring fully and avoid buckling. Springs of varying strength and dexterity indices were tested on subjects outside of the scanner, and based on the requirements above, the stainless steel spring chosen had the following characteristics: Free Length: 2.5 cm, Diameter: 4 cm, Solid Length: 1 cm, Force at Solid Length: 1.5 N, Dexterity Index: 1.59.

A three-point pinch configuration was used, which required opposing the first to the second and third digits. The pads at the anterior distal point of the second and third digits are directly opposite and face the pad of the first digit. This pinch is a position of function that normal performance in many activities require, e.g., needlework, game of darts. A successful three-point pinch compression required four components: (1) absence of joint hyperextension at any digit, (2) consistent curling of the fourth and fifth digits, (3) compressing the spring without buckling, and (4) full compression to solid length.

Prior to the start of each trial, subjects positioned the right hand in the three-point pinch relaxed configuration and placed their arm above their abdomen, within the field of view. During the 40-sec. stimulation periods, subjects were instructed to compress and relax the spring repeatedly, while maintaining a self-determined constant rate of compression (average rate = 22.5 compression cycles per minute, where one cycle included one complete compression and one complete relaxation of the spring). Spring compression rates were measured for each epoch. During the initial and recovery baselines, they were instructed to hold the stationary spring in the relaxed configuration. A light tap by the investigator on alternate legs indicated the commencement and conclusion of each stimulation epoch. Because the analysis scheme required BOLD signal increases in active voxels to be sustained across a 40-sec. block, any cortical stimulation resulting from a brief tap was not expected to result in image activation. The order of the conditions was randomly varied, both within and across subjects.

Subjects

Subjects (5 men, 5 women) participated in this study. All were right handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971) with mean Edinburgh Quotient = +96%. Subjects' mean age was 27 yr. ($SD = 5$). All subjects were healthy adult volunteers and were recruited according to institutional guidelines for informed consent. Spring compressions were monitored throughout all experiments to obtain counts of the number of spring compressions and to confirm accuracy of the performance.

RESULTS

Spring Compression Performance

The average number of spring compressions across all subjects for each experimental condition is shown in Fig. 2. Bars represent Means \pm SEM ($N=10$) spring compression cycles (where one cycle is one complete compression and relaxation). Each of the four conditions was performed twice, yielding a total of eight trials per subject. The average number of spring compressions

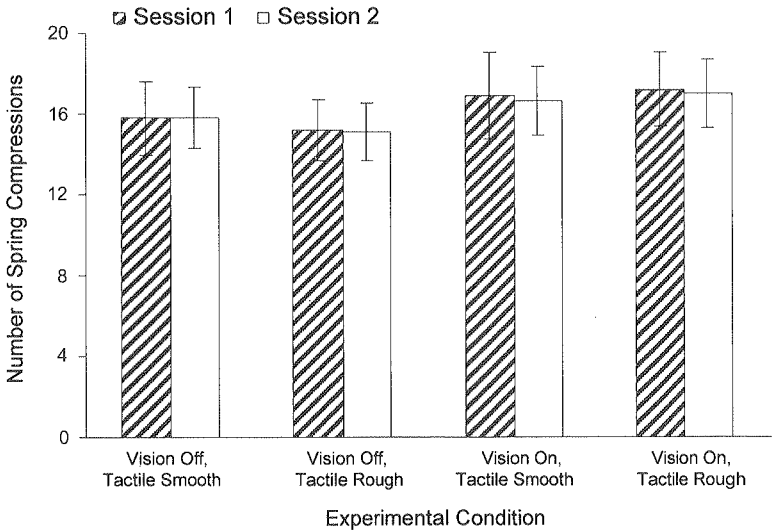


Fig. 2. The average number of spring compressions (y axis) for each experimental condition (x axis). Bars represent mean \pm SEM ($N=10$) of the total number of spring compression cycles (where one cycle is one complete compression and relaxation). Each of the four conditions was performed twice (striped bars, Session 1; white bars, Session 2), yielding a total of 8 trials per subject. A repeated-measures analysis of variance (Statistical Package for the Social Sciences; General Linear Model) comparing the four conditions across all subjects did not confirm significant differences in spring compression rates between experimental conditions or sessions.

was slightly higher for the experimental conditions in which visual input was present. However, a within-subject repeated-measures analysis of variance (General Linear Model; Statistical Package for the Social Sciences [SPSS]) across the four conditions did not yield any significant differences in rates of spring compression across different levels of the visual factor (on versus off; $p=.1$), the tactile factor (rough versus smooth; $p=.5$) or across the experimental sessions ($p=.6$), and there were no interaction effects between any factors.

Further comparison of global volumes of brain activation for each ex-

perimental session and subject with the corresponding number of spring compressions provided no evidence for a correlation between the performance measures and the volume of activity ($R = -.02$), indicating that magnitude of brain activation was not driven by spring compression rates. However, the total volume of active cortex was dependent on the type of sensory input (visual versus tactile, $p = .0003$). These findings collectively suggest that distribution of observed cortical activity is not driven by the number of spring compressions but is dependent on the experimental condition (visual versus tactile stimulation).

Distributed Brain Regions

Eight anatomical regions met the criteria for an Active Area (5 continuous voxels, $p < .0005$, during all four conditions by subject; see Method): medial frontal gyrus Brodmann's Area (BA) 6; cingulate gyrus, BA 24; precentral (primary motor; M1) gyrus BA 4; postcentral (primary sensory, S1) gyrus, BA 3, 1, 2; inferior parietal lobule, BA 40; middle occipital gyrus, BA 19; inferior occipital gyrus, BA 18; and cerebellum. The average coordinate locations are listed in Fig. 3 (Talairach & Tournoux, 1988) and illustrated on a mid-sagittal schematic. All regions were bilaterally active except for the pre- and postcentral gyrii (left hemispheres), and the cerebellum (right hemisphere), as expected for a motor task performed using the right hand.

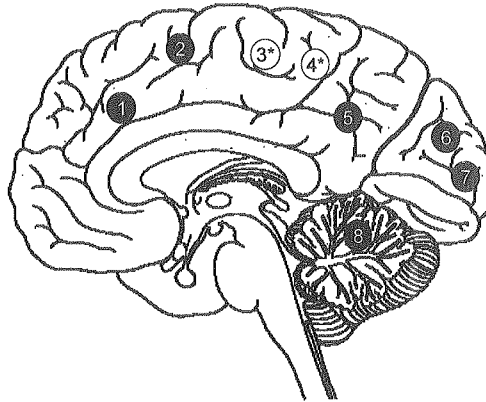
Modulation by Level of Visual and Tactile Input

Changes in the volumes of the active brain regions that correspond to levels of sensory input are taken as responsiveness to visual and tactile stimulation. Fig. 4 illustrates visual modulation of the middle occipital gyrus for one subject (DR) during eyes-closed and eyes-open conditions (left panel) and of precentral gyrus during tactile modulation, i.e., "smooth" and "rough" conditions. Specifically, the middle occipital gyrus (BA 19) was more active when eyes were open (volume of activation = 500 mm^3) than when eyes were closed (70 mm^3), whereas the precentral gyrus was more active when spring caps were smooth (330 mm^3) than when they were enhanced by sandpaper (130 mm^3). Locations of these regions in normalized space are illustrated on the adjacent atlas plates.

Group Analysis

The average Active Volumes across all subjects, based on the number of Active voxels where each voxel was $1.5 \times 1.5 \times 4.5 \text{ mm}$ within each experimental condition and brain area, are shown in Fig. 5. Anatomical labels are based on the human brain atlas of Talairach and Tournoux (1988) and Active Volumes within the areas are based on contiguous voxels at a consistent statistical criterion ($p \leq .0005$) applied across all conditions and subjects. Black and white bars represent average Active Volumes within each region

Neural Guidance System for Dexterous Manipulation



Areas modulated by visual input

| No. | Anatomical Area | BA | Hemisphere | Average Coordinates (x,y,z) |
|-----|--------------------|----|------------|-----------------------------|
| 5 | Inferior Parietal | 40 | L/R | ± 42, +11, +55 |
| 6 | Middle Occipital | 19 | L/R | ± 25, +92, +12 |
| 7 | Inferior Occipital | 18 | L/R | ± 25, +92, -4 |

Areas modulated by visual input

| No. | Anatomical Area | BA | Hemisphere | Average Coordinates (x,y,z) |
|-----|-----------------|----|------------|-----------------------------|
| 3 | Pre Central | 4 | L | +45, +11, +50 |

Areas modulated by visual input

| No. | Anatomical Area | BA | Hemisphere | Average Coordinates (x,y,z) |
|-----|-----------------|-------|------------|-----------------------------|
| 1 | Cingulate | 24 | L/R | ±8, +11, +35 |
| 2 | Medial Frontal | 6 | L/R | ±8, +11, +55 |
| 4 | Post Central | 3,1,2 | L | +45, +11, +40 |
| 8 | Cerebellum | - | R | -25, +52, -12 |

FIG. 3. The midsagittal schematic displays the conserved brain areas observed in all subjects. Regions modulated by visual and tactile input, as well as regions not modulated by either sensory input, are indicated in the table at the bottom. The Brodmann's regions, active hemispheres, average locations (x, y, z Talairach coordinates), and modulation by visual and tactile input are indicated in the panel. Neural guidance system for Dexterous manipulation: BA = Brodmann's Areas. Talairach coordinates: positive x = left hemisphere, Negative x = right hemisphere. Positive Y = posterior to Anterior Commissure (AC); Negative Y = anterior to AC. Positive Z = superior to the plane connecting the AC and the posterior commissure (PC). Negative Z = inferior to the plane connecting the AC-PC plane.

of interest, for the "eyes-closed" and "eyes-open" conditions, respectively, whereas the checkered and striped bars represent average Active Volume of brain activity for the "smooth tactile" and "rough tactile" conditions, respectively. Differences in average voxel counts were observed in the middle occipital gyrus ($p \leq .02$), inferior occipital gyrus ($p \leq .02$), and inferior parietal lobule ($p \leq .02$) when the eyes were open and closed, and in the precentral gyrus when the tactile input was either a smooth or rough surface ($p \leq .05$). Otherwise, there were no significant differences between the sensory conditions for the regions.

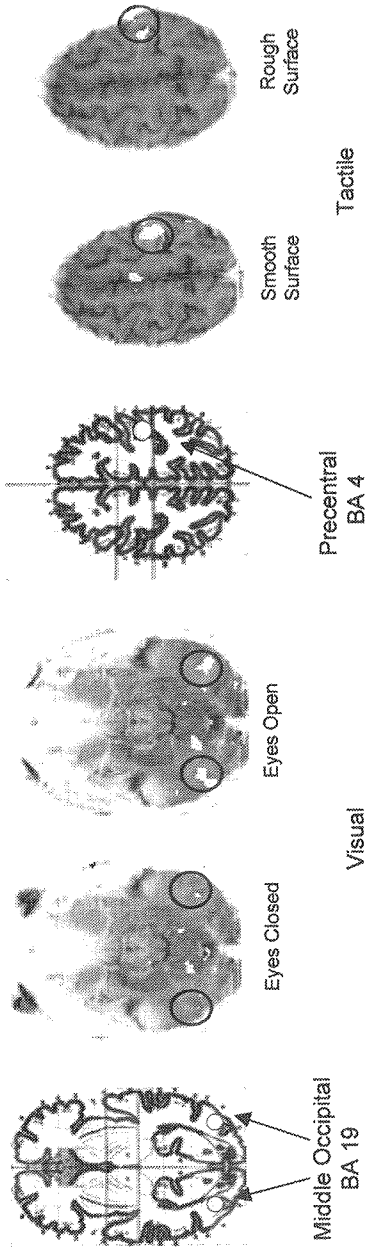


FIG. 4. Regions modulated by visual and tactile input. Sensory modulation (Subject DR) during a single experimental session. Activity is shown on the original T_2^* -weighted axial slices on which they were acquired (block panels). The left panel illustrates activity during the "eyes closed" and "eyes open" states, and the right panel illustrates activity during the "smooth tactile" and "rough tactile" conditions. Atlas plates indicate locations of the activity. Middle occipital gyrus (BA 19) was more active (increased cluster size) when eyes were open (right), and the precentral gyrus was most active (larger cluster size) when tactile input was minimized (left). Activity within the middle occipital gyrus is bilateral, whereas activity within the precentral gyrus is restricted to the left hemisphere, reflecting the right-handed nature of the task and the contralateral projections of the sensory motor system.

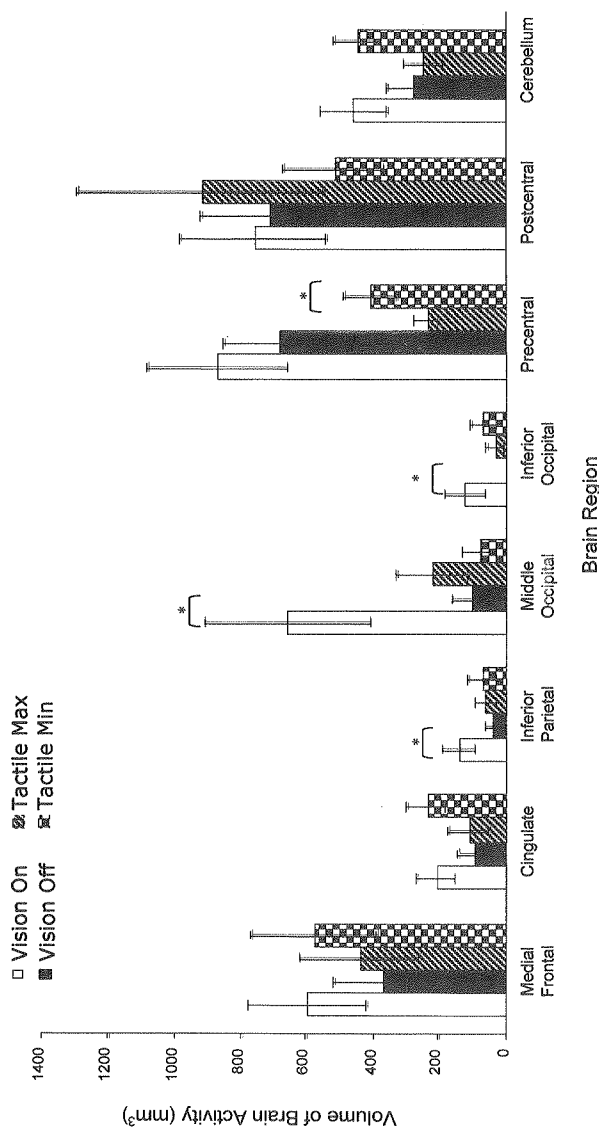


FIG. 5. Average volumes of brain activity elicited by visual and tactile conditions within each region. Bar graphs represent the group average (\pm SEM) Active Volumes elicited within each region, for each experimental condition. Black and white bars represent activity for the "eyes open" and "eyes closed" conditions, respectively; checkered and striped bars represent activity for the "smooth tactile" and "rough tactile" conditions, respectively. Significant differences in volumes are indicated with an asterisk. For brain regions in which both hemispheres were active (middle occipital, medial frontal, and cingulate), columns include activity in both hemispheres. For regions in which only one hemisphere was conserved (precentral [left], postcentral gyrus [right], and cerebellum [right]), only activity within one hemisphere is included. Note that in the middle occipital gyrus (BA 19), having eyes open and watching the task significantly increased ($t=2.3, p=.02$) Active Volume compared to the eyes-closed condition. A similar effect was noted in the inferior parietal lobule ($t=2.0, p=.04$) and the inferior occipital gyrus ($t=1.9, p=.08$). In each of these regions, the level of tactile input did not significantly change the Active Volume. In the precentral gyrus, the opposite effect was observed: having eyes open did not significantly alter the percentage of total Active Volume, but rough tactile input was associated with altered total Active Volume ($t=2.3, p=.02$). Within the remaining regions (cerebellum, postcentral, medial frontal, and cingulate gyrus), no modulation was detectable.

These findings were also confirmed by a two-factor analysis of variance that compared Active Volume associated with the visual and tactile conditions for each brain region (Table 1). Consistent with the data shown in Fig. 5, Active Volume within the inferior and middle occipital gyrii, and inferior parietal lobule was modulated by changes in visual input but not tactile input, whereas in the precentral gyrus, activity was modulated by changes in the tactile input but not visual input. There were no interaction effects, and no other significant comparisons within other areas were observed.

TABLE 1
ANALYSIS OF VARIANCE FOR EACH BRAIN REGION

| Brain Region | Effect | SS | MS | F |
|--------------------|-------------|--------|--------|--------|
| Medial Frontal | Visual | 0.22 | 0.22 | 0.15 |
| | Tactile | 0.63 | 0.63 | 0.29 |
| | Interaction | 31.63 | 3.51 | 1.62 |
| Cingulate | Visual | 0.08 | 0.08 | 0.34 |
| | Tactile | 0.26 | 0.26 | 1.38 |
| | Interaction | 0.97 | 0.11 | 0.58 |
| Inferior Parietal | Visual | 15.30 | 15.30 | 9.20* |
| | Tactile | 0.20 | 0.21 | 0.00 |
| | Interaction | 0.90 | 0.18 | 0.42 |
| Middle Occipital | Visual | 22.50 | 22.50 | 36.25† |
| | Tactile | 0.01 | 0.01 | 0.00 |
| | Interaction | 3.05 | 0.34 | 0.15 |
| Inferior Occipital | Visual | 11.32 | 11.32 | 7.31* |
| | Tactile | 0.01 | 0.01 | 0.01 |
| | Interaction | 2.13 | 0.37 | 0.91 |
| Precentral | Visual | 230.40 | 230.40 | 3.05 |
| | Tactile | 70.22 | 70.22 | 6.58* |
| | Interaction | 21.53 | 2.39 | 0.22 |
| Postcentral | Visual | 0.22 | 0.22 | 0.01 |
| | Tactile | 70.22 | 70.22 | 2.95 |
| | Interaction | 261.53 | 29.06 | 1.22 |

* $p < .05$. † $p < .01$.

Attention-related Effects

Even though the rate of spring compressions did not vary across conditions (Fig. 2), we can not rule out effects related to global attention. This possibility was assessed by comparison of regional activity in the middle and inferior occipital, inferior parietal, and precentral gyrii to global whole brain cortical activity. Putative changes in global responsiveness could possibly indicate the influence of factors such as attention, load, or vigilance on these results. Correlation of global and local changes did not confirm a significant covariation between these two variables in any of the above regions (visual regions: $R = -.02$, tactile regions, $R = +.04$), suggesting that the effects ob-

served are site-specific rather than global, a defining characteristic of visual attention, task difficulty, and spatial selectivity (Ress, Backus, & Heeger, 2000). Finally, the effects of top-down mediated influences such as attention are often observed in V1, the primary visual cortex, an area not included in this motor guidance system. Although attention must play a significant role in hand-eye coordination, it is not likely, for the reasons cited above, that these observations reflect a hidden attention component.

DISCUSSION

Visual and tactile input are transmitted along two distinct sensory channels that are combined within a system that guides dexterous tasks such as repetitive spring compressions. An aim of this study was to identify and model the neural system that acquires and processes varying levels of visual and tactile input during the execution of a dexterous motor task. In this study, the task consisted of compressing a slender spring prone to buckling, where the fingertips had to meet the same strength and dexterity requirements for every compression. It was performed consistently by compressing the spring at a similar rate during all conditions.

Vision-related Areas

In three brain regions Active Volumes were modulated by levels of visual input: middle and inferior occipital gyrii (BA 19 and 18) and inferior parietal lobule (BA 40). The middle and inferior occipital gyrii include peristriate visual association areas that project to parietal cortex and receive inputs from early visual processing, areas including the primary visual cortex (BA 17) (Boussaoud, Ungerleider, & Desimone, 1990). Interestingly, primary visual regions were not among the regions that met our inclusion criteria in this study. This is presumably because the inclusion criteria required an area to be active in all conditions, including conditions in which the eyes were closed. Primary visual areas in this study were not consistently active when the eyes were closed, in contrast to the areas with higher levels of visual processing, i.e., the middle and inferior occipital gyrii and the inferior parietal lobule. This may reflect internal visualization of the task (Klein, Paradis, Poline, Kosslyn, & Le Bihan, 2000; Sparing, Mottaghy, Ganis, Thompson, Topper, Kosslyn, & Pascual-Leone, 2002) or maintenance of visual responsiveness ("vigilance") when vision is occluded (Girard, Salin, & Bullier, 1991).

The dorsal stream connects the visual cortex to the superior and inferior parietal lobules and subsequently to the frontal cortex (Mishkin & Ungerleider, 1982), and connections between the visual, parietal, and frontal cortices during visual control of movement are well documented (Matelli, Luppino, Fogassi, & Rizzolatti, 1989; Marconi, Genovesio, Battaglia-Mayer, Ferraina, Squatrito, Molinari, Lacquaniti, & Caminiti, 2001). The results of our study suggest a specific role for the middle and inferior occipital gyrii in

object-directed action and are consistent with previous studies showing that the activation of the dorsal visual cortex can be affected by not only visual but also tactile components (James, Humphrey, Gati, Menon, & Goodale, 2002).

The posterior areas of the parietal lobe have been implicated in visual information processing, whereas the anterior part of these regions, particularly within the superior parietal lobe, have been implicated in somatosensory information processing (Caminiti, Ferraina, & Johnson, 1996; Hamzei, Dettmers, Rijntjes, Glauche, Kiebel, Weber, & Weiller, 2002). It is not surprising, therefore, that the inferior parietal lobule, an area involved in visuo-motor integration, was not only active during the motor task but also modulated by the presence of visual input. Our data are consistent with other dexterity studies demonstrating a distinct role for the intraparietal cortex in complex manual tasks (Ehrsson, Fagergren, Johansson, & Forssberg, 2003) and also with reports of nonspatial, motor-specific activity demonstrated within the posterior parietal cortex (Calton, Dickinson, & Snyder, 2002).

Tactile-related Areas: Primary Motor Cortex: BA 4

The region of the primary motor cortex (M1) corresponding to the right hand (precentral gyrus, BA 4, coordinates +45, +11, +50) was modulated by level of tactile input. This region is generally associated with motor execution rather than tactile-related functions (Strick, Dum, & Picard, 1998; Ehrsson, *et al.*, 2000, 2001; Rizzolatti & Luppino, 2001). However, it is known to receive inputs from the postcentral (somatosensory) gyrus, and neuroanatomical and electrophysiological evidence (Asanuma & Rosen, 1972; Matelli, *et al.*, 1989; Darian-Smith, Darian-Smith, & Cheema, 1990; Huffman & Krubitzer, 2001) suggests direct somatosensory input to BA 4 from the VLo, VLc, VPLO and VPLm nuclei of the thalamus, especially in the hand area. Our observations are concordant with evidence that BA 4 is also associated with somatosensory processing in addition to its motor-related functions. One possible role for integrated sensory and motor processing is to provide reliable estimates of the task state by combining multiple sensory signals of varying quality and availability.

A further observation is that activity within the primary motor cortex was decreased following enhancement of tactile input with sandpaper, suggesting an inverse relationship between magnitude of sensory input and force of output. One possible explanation for this observation is that the smooth surface puts more demands on precise control of the fingertip forces, either because there is increased likelihood of slipping or because there is decrease in sensory and proprioceptive feedback. Our observations are consistent with previous studies that have shown activity in the primary motor and sensory cortices, as well as in parts of the supplementary and cingulate motor areas,

to increase when subjects lightened their grip approaching the slip threshold, even though the force of muscle contractions was weaker (Ehrsson, *et al.*, 2001; Kuhtz-Buschbeck, Ehrsson, & Forssberg, 2001).

Nonsensory Modulated Regions

Activity did not covary with sensory input in the medial frontal, post-central, and cingulate gyrii, or the cerebellum. The lack of covariance in the postcentral (primary somatosensory) gyrus and cerebellum may be due to the constant pressure of the spring grasp throughout all conditions and potentially masking small tactile gradations between the smooth and rough (sandpaper) surfaces. Failure to observe modulation within the medial frontal gyrus, BA 6, and cingulate gyrus, BA 24, is consistent with the roles of these structures in supramodal planning and attention processes, respectively (Picard & Strick, 1996; Strick, *et al.*, 1998).

Implications for Models of Motor Guidance and Sensory Integration

Previous dexterity studies have suggested a role for multiple specific cortical areas in complex manual tasks (Ehrsson, *et al.*, 2001; Kuhtz-Buschbeck, *et al.*, 2001) and a dynamic model of motor control during planning and regulating complex tasks (Wolpert, Ghahramani, & Jordan, 1995; Kawato & Wolpert, 1998; Wolpert & Ghahramani, 1999). By comparing the predicted current state with actual past states, errors in motor plans can be minimized. Regardless of whether an internal model regulates complex tasks favoring feedback or feed-forward control (Kuo, 2002) or whether the coordinate variables are mechanics-based or somatosensory based (Kawato, Isobe, Maeda, & Suzuki, 1988; Shadmehr & Mussa-Ivaldi, 1994; Ghilardi, Gordon, & Ghez, 1995; Ghahramani, Wolpert, & Jordan, 1996; Krakauer, Ghilardi, & Ghez, 1999; Kuo, 2002), we assume that the nervous system considers all available sensory information to extract the state of the system and preferentially weighs the most reliable sensory channels (Wolpert, *et al.*, 1995; Kuo, 2002; Sparing, *et al.*, 2002).

Our findings differentiate the complementary sensory-invariant and sensory-modulated roles of the motor control system for this manipulation task. However, they do not assume or support any particular type of motor control theory. We assume that every area of the network conserved across conditions played a role in the execution of the motor task and that cortical modulations corresponding to input sensory conditions reflect varying contributions to the processing of the sensory information. Given the strict mechanical definition of the dexterous task, the standardized protocol, and the regularity of execution across subjects and conditions, we further assume that changes across sensory conditions suggest changes in their contributions to the processing of the sensory information. Specifically, changes in activity in associative sensory regions, middle and inferior occipital gyrii, inferior pa-

rietal lobule, and precentral gyrus, may reflect the cortical activity associated with the sensory-tuning necessary to adapt to the availability of vision and tactile sensations during dexterous manipulation.

Potential Limitations

This experiment examined specifically dexterous manipulation and the task employed was not necessarily representative of other visually guided behaviors. The levels of visual and tactile conditions were not strictly equivalent in this study: visual input was either present or not, whereas the tactile stimulation was presented along two levels of a continuous scale and therefore always present. It is possible that gradations in tactile input were not sufficient to elicit detectable changes in cortical activity, and that some possible modulations were not observed. Furthermore, enhancement of the tactile surface with sandpaper may have decreased the slip force (Johansson & Cole, 1994), which may in turn have induced shifts in attention between the two tactile conditions (Binkofski, *et al.*, 1999). Nonetheless, no effect reported in this study covaried with global and possibly attention- and vigilance-related effects, so it is assumed that these factors are small relative to the reported observations. Finally, regions in addition to those reported may be involved in some aspects of visual and tactile dexterous manipulation. In this study, only brain regions consistently active across all conditions and across all 10 subjects were reported. The criteria, that each voxel must be active in (1) all conditions for each subject and (2) the region must meet this criterion in all subjects, shift the error for this study toward exclusion of some real findings and enhanced confidence in those reported.

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