The Cerebellum Contributes to Somatosensory Cortical Activity during Self-Produced Tactile Stimulation

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We used fMRI to examine neural responses when subjects experienced a tactile stimulus that was either self-produced or externally produced. The somatosensory cortex showed increased levels of activity when the stimulus was externally produced. In the cerebellum there was less activity associated with a movement that generated a tactile stimulus than with a movement that did not. This difference suggests that the cerebellum is involved in predicting the specific sensory consequences of movements and providing the signal that is used to attenuate the sensory response to self-generated stimulation. In this paper, we use regression analyses to test this hypothesis explicitly. Specifically, we predicted that activity in the cerebellum contributes to the decrease in somatosensory cortex activity during self-produced tactile stimulation. Evidence in favor of this hypothesis was obtained by demonstrating that activity in the thalamus and primary and secondary somatosensory cortices significantly regressed on activity in the cerebellum when tactile stimuli were self-produced but not when they were externally produced. This supports the proposal that the cerebellum is involved in predicting the sensory consequences of movements. In the present study, this prediction is accurate when tactile stimuli are self-produced relative to when they are externally produced, and is therefore used to attenuate the somatosensory response to the former type of tactile stimulation but not the latter. © 1999 Academic Press

Key Words: self-monitoring; forward models; tactile sensation; efference copy; psychophysiological interaction.

INTRODUCTION

It is proposed that knowledge of our intentions or motor commands is used to distinguish the sensory consequences of our own actions from externally produced sensory stimuli (Jeannerod, 1988; Frith, 1992; Wolpert *et al.,* 1995; Decety, 1996; Jeannerod, 1997; Wolpert, 1997). In order to achieve this, some kind of

central monitor (Frith, 1992) or internal "forward model" (Wolpert *et al.,* 1995; Wolpert, 1997) has been postulated. These models capture the forward or causal relationship between actions, as signalled by an *efference copy* of the motor command (Von Holst, 1954), and the predicted sensory outcome, originally termed *corollary discharge* (Sperry, 1950). By comparing this prediction with the actual sensory feedback it is possible to distinguish the sensory consequences of our movements from sensory signals due to changes in the outside world.

The ability to predict the consequences of our own actions may underlie the differential perception of identical sensory inputs when self-generated compared to when externally generated. An example of such differential perception is the phenomenon that people cannot tickle themselves (Weiskrantz *et al.,* 1971). Using a robotic interface we have demonstrated that self-produced and externally produced tactile sensations are perceived differently (Blakemore *et al.,* 1999). Subjects consistently rated a self-produced tactile sensation on their right palm as being significantly less "tickly," "intense," and "pleasant" than an identical stimulus produced by a robot. Furthermore, by using two robots so that the motion of the left hand on one robot determined the tactile sensation (a piece of soft foam) on the right hand, computer controlled delays of 0, 100, 200, and 300 ms were introduced between the action of the left hand and the tactile sensation on the right. We found a progressive increase in the "tickly" rating as the delay was increased between 0 ms (corresponding to the normal situation in which subjects use their left hand to move a physical rod across the palm of their right hand) and 200 ms. In a second condition trajectory perturbations (rotations of 30, 60, and 90°) were introduced between the direction of the left hand movement and the direction of the tactile sensation on the right hand. Again there was a progressive increase in the "tickly" rating as the trajectory perturbation was increased between 0 and 90°. Under all delays and trajectory perturbations the left hand made the same

movement and the right hand experienced the same stimulus. Only the temporal or spatial relationship between the action of the left hand and the sensory effect on the right hand was altered. These results suggest that the perceptual attenuation of self-produced tactile stimulation is due to a precise central attenuation of the sensory perception, based on specific spatiotemporal sensory predictions, rather than a non-specific attenuation of all sensory signals.

This perceptual attenuation of self-produced tactile sensations could be due to gating of activity in somatosensory cortex. Neurophysiological data demonstrate that neuronal responses in somatosensory cortex are indeed attenuated by self-generated movement. For example, active touch is "gated" in SI of rats (Chapin & Woodward, 1982) and monkeys (Jiang *et al.*, 1991; Chapman & Ageranioti-Belanger, 1991; Chapman, 1994) compared to passive and external touch of an identical tactile stimulus. In order for somatosensory cortex activity to be attenuated to self-produced sensory stimuli, these stimuli need to be predicted accurately. The cerebellum is a likely site for a "forward model" of the motor apparatus that provides predictions of the sensory consequences of motor commands, which are then compared with the actual sensory feedback from the movement. Evidence for this supposition comes from computational (Ito, 1970; Paulin, 1989; Miall *et al.*, 1993; Wolpert *et al.*, 1998) and neurophysiological data (Oscarsson, 1980; Gellman *et al.*, 1985; Andersson & Armstrong, 1985; Andersson & Armstrong, 1987; Simpson *et al.*, 1995). The error signals from this comparison may be used to modify motor commands during performance, to modulate neural responses to the sensory consequences of the movement, and to update the forward model. This proposed role of the cerebellum is supported by Jueptner & Weiller (1998) who conclude that, based on the results of three PET studies, the cerebellum may be concerned with monitoring the sensory outcome of movements.

Using fMRI we have examined the neural basis of the differential perception of self- and externally produced tactile stimuli (Blakemore *et al.*, 1998). A tactile stimulation device (see Materials and Methods and the legend of Fig. 1 for details) allowed a sinusoidal tactile stimulus to be applied to the subject's left palm either by the subject's right hand or by the experimenter. To examine the neural correlates of self-produced tactile stimuli we employed a factorial design with the factors of self-generated movement of the right hand vs rest and tactile stimulation on the left hand vs no stimulation (Fig. 2). Using this design we were able to assess what brain activity is unique to the self-generated tactile stimulation condition by factoring out activity associated with self-generated movement or tactile stimulation alone.

We found an increase in activity of bilateral second-ary somatosensory cortex when subjects experienced an externally produced tactile stimulus on their palm relative to a self-produced tactile stimulus (Fig. 4a). We propose that this inhibition of somatosensory cortex activity by self-generated movements could result from an attenuation of the actual sensory feedback based on prediction—accurate prediction occurs when a tactile stimulus is self-produced. In the cerebellum there was less activity associated with a movement that generated a tactile stimulus than with a movement that did not (Fig. 4b). We suggest that the cerebellum is involved in predicting the specific sensory consequences of movements and providing the signal that is used to attenuate the somatosensory response to self-produced tactile stimulation.

In this paper we use regression analysis to test this hypothesis, based on the following principles. If the activity in one region (area A) predicts the activity in another region (area B) then the strength of the prediction reflects the influence area A could be exerting on area B. If the strength of the prediction (measured by regression analysis) varies with the psychological context in which the physiological activity is measured then this is evidence for a "psychophysiological interaction" (Friston *et al.*, 1997). Using linear regression we tested an anatomically constrained prediction (see Fig. 3) that the influence of the cerebellum on the thalamus and somatosensory cortex would be strong in conditions where sensation could be predicted from movement (self-generated tactile stimuli), but weak when sensation could not be predicted (externally generated tactile stimuli).

MATERIALS AND METHODS

Subjects

Six normal right-handed volunteers (four females and two males; mean age 33 years) gave informed consent and participated in the study, which was approved by the National Hospital for Neurology and Neurosurgery Ethics Committee.

Design

The experiment was split into two 12-min sessions. Each subject underwent 200 fMRI scans in each session. Within each session the subject lay supine on the MRI bed with their right arm fixed over their chest to limit movement to the fingers. Their left arm was secured to a perspex sheet with the left hand perpendicular to the scanning bed about 5 cm from the fingers of the right hand. A tactile stimulus device (Fig. 1) consisted of a piece of soft foam attached to a plastic rod (length 70 cm) which could pivot about its center. The rotation of the rod was mechanically limited to vertical movements of amplitude 1.5 cm. The rod could be
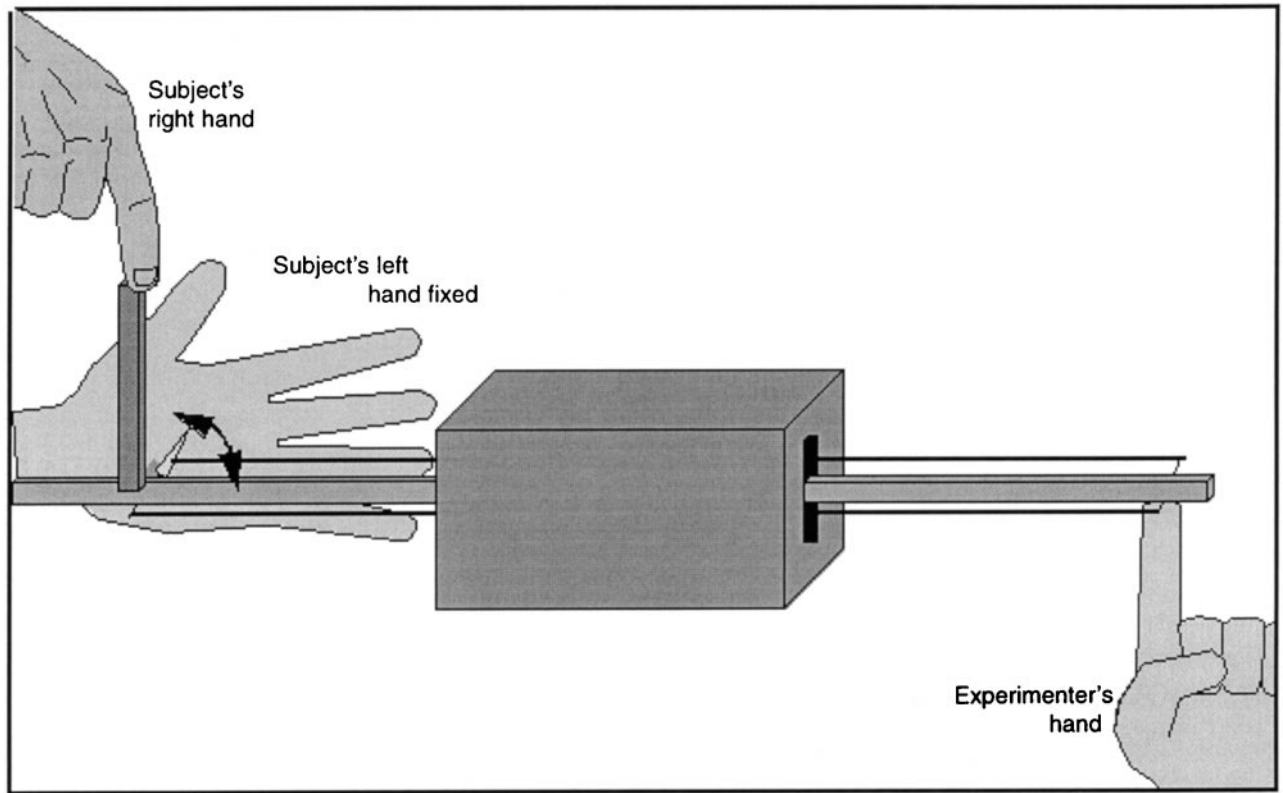
FIG. 1. Diagram of experimental set-up. A tactile stimulus device consisted of a piece of soft foam attached to a plastic rod (length 70 cm), which could pivot about its center. The rotation of the rod was mechanically limited to vertical movements of amplitude 1.5 cm. The rod could be moved either by the subject using their right hand or from the other end of the rod, which was outside the scanner, by the experimenter. A pulley system allowed the foam stimulus to be retracted or exposed, under the experimenters control, during scanning. When exposed the foam made light contact with the subjects left palm. See text for details.

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There were two experimentally manipulated variables: whether a tactile stimulus occurred and whether the subjects were required to make movements. In the movement conditions movements of the rod were always made with the index and third fingers of the right hand. Subjects were instructed to move the rod up and down to its full extent (amplitude 1.5 cm) at a frequency of 2 Hz and were practiced beforehand to ensure that they could reliably generate the desired movements. The tactile stimulus was identical in force, amplitude, and frequency throughout the experiment. Each condition lasted 30 s and was followed immediately by the next condition. There were four conditions using a within-subject factorial design, with a total of 12 replications of each condition per subject (Fig. 2). Subjects were told which condition to perform through ear-

phones (corresponding to the words in parenthesis following each condition name).

Condition A—Self-generated movements producing tactile stimulation ("touch"). Subjects made vertical sinusoidal movements of the rod with the right hand. This movement produced a tactile stimulation on the palm of the left hand.

Condition B—Self-generated movements without tactile stimulation ("move"). Subjects made vertical sinusoidal movements of the rod with the right hand. The tactile stimulus was removed from the subject's left palm so no tactile stimulation was experienced.

Condition C—Externally produced tactile stimulation ("feel"). No subject movement occurred. The experimenter moved the tactile stimulus sinusoidally across the subject's left palm.

Condition D—No movement, no tactile stimulation ("rest"). No movement or tactile sensation occurred. The experimenter moved the rod sinusoidally at a frequency of 2 Hz, but the tactile stimulus did not touch the subject's palm.

The order of conditions was randomized and counter-

	Tactile stimuli	**No tactile stimuli**
Self-generated movement	A: Self-produced tactile stimuli	B: Self-produced movement without tactile stimuli
No self-generated movement	C: Externally-produced tactile stimuli	D: Rest

FIG. 2. Table illustrating 2 × 2 factorial design. There were four conditions: In condition A subjects made vertical sinusoidal movements of the rod with their right hand, which produced a tactile stimulation on the palm on their left hand; in condition B subjects made vertical sinusoidal movements of the rod with their right hand, and no tactile stimulation was experienced; in condition C the experimenter moved the tactile stimulus sinusoidally across the subject's left palm; in condition D no movement or tactile sensation occurred. There were 12 replications of each condition per subject.

balanced within and between subjects. Scanning took place in a darkened room and subjects were asked to keep their eyes closed during the experiment. The total number of movements made was counted by the experimenter: the average frequency of movements of the rod in conditions 1, 2, and 3 was 2.25 Hz.

Data Acquisition

A Siemens VISION system (Siemens, Erlangen) operating at 2 T was used to acquire both axial gradient-echo, echoplanar T2*-weighted image volumes with blood oxygenation level-dependent (BOLD) contrast and axial T1-weighted structural images for anatomical coregistration. The experiment began with the acquisition of a T1-weighted anatomical image from each participant. Functional imaging was then performed in two separate runs with a 3-min break in between sessions. Each functional-image volume comprised 48 3-mm axial slices with in-plane resolution of 3 × 3 mm positioned to cover the whole brain. During each run, volumes were acquired continuously every 4.1 s, while participants performed either epochs of the experimental task lasting 32.8 s (8 vol) or epochs of rest (lasting 32.8 s or 8 vol). Each run began with 8 "dummy" vol, which were subsequently discarded to allow for T1 equilibration effects. Periods of no movement (conditions 3 and 4) then alternated with the

movement conditions (1 and 2) as described above for the duration of each run. The total duration of the experiment was thus around 35 min, during which time 400 functional-image volumes were acquired, of which 384 were subsequently analyzed.

Statistical Analysis

Functional imaging analysis used the technique of statistical parametric mapping, implemented in SPM97
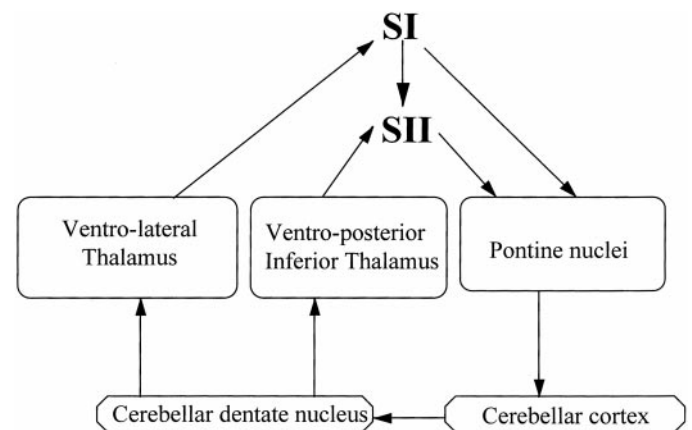

FIG. 3. Diagram of anatomical pathways between the cerebellum and somatosensory cortex in the monkey, taken from Waxman and deGroot (1995).
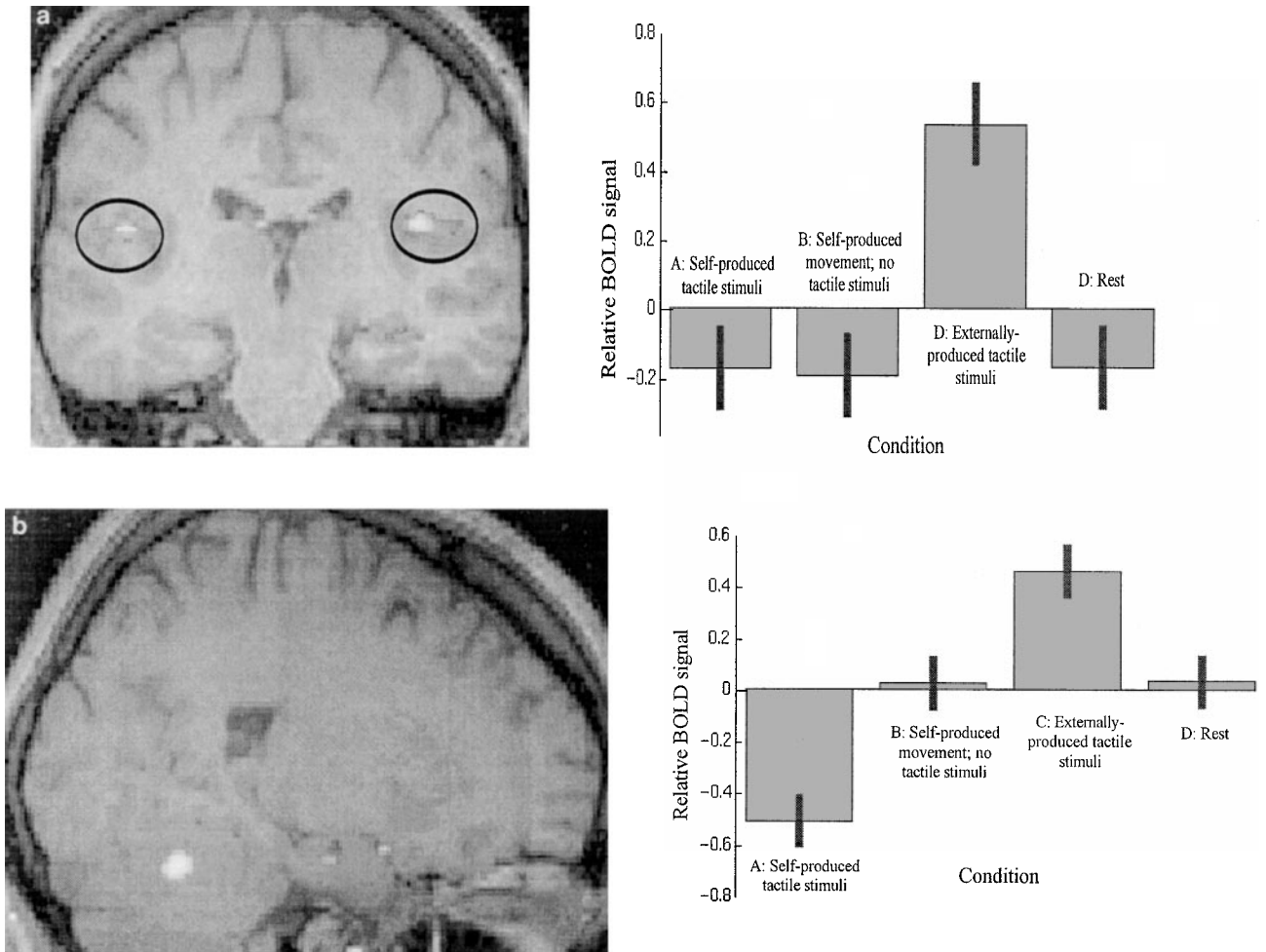
FIG. 4. (a) Shows significant ($P < 0.05$ corrected for multiple comparisons) decreased activity in bilateral secondary somatosensory cortex associated with the interaction between the effects of self-generated movement and tactile stimulation. (b) Shows significant ($P < 0.05$ corrected for multiple comparisons) decreased activity in right anterior cerebellar cortex associated with the interaction between the effects of self-generated movement and tactile stimulation. In the right hand of (a and b), the condition-specific parameter estimates, which reflect the adjusted BOLD contrast signal relative to the fitted mean and expressed as a percentage of whole brain mean activity, are shown. In both cases the effects at the voxel of highest intensity are shown, for illustration, in a single subject. Similar parameter estimates were obtained for the remaining subjects in this statistical model. The labeling of the conditions corresponds to A, self-generated tactile stimulation; B, self-generated movement without tactile stimulation; C, externally generated tactile stimulation; D, rest. In (a), the effects at voxels in the right ($42 - 24\ 18$) parietal operculum are shown. In (b), the effects at the voxel $22 - 58 - 22$ are shown. The right anterior cerebellar cortex was the only area of the brain that resulted from the contrast A–B.

[Wellcome Department of Cognitive Neurology, UK, http://www.fil.ion.ucl.ac.uk/spm]. For each subject, the imaging time series was realigned with sinc interpolation (Friston *et al.,* 1995b). The data were adjusted to remove any signal correlated with head rotation and motion. The scans were then stereotactically normalized using affine registration followed by nonlinear registration. The data were resampled using sinc interpolation into the space of Talairach & Tournoux (1988). The scans were then smoothed with a Gaussian kernel of 6 mm full-width half maximum.

The analysis of functional imaging data entails the creation of statistical parametric maps that represent a statistical assessment of condition-specific effects corresponding to the experimental hypotheses (Friston *et al.,* 1990, 1995a; Friston, 1997). Condition-specific effects were estimated with the General Linear Model with a delayed boxcar wave form. Low-frequency sine and cosine waves modeled and removed participant-specific low-frequency drifts in signal, while global changes in activity were removed by proportional scaling. Areas of significant change in brain activity were specified by appropriately weighted linear contrasts of the condition-specific effects and determined using the *t* statistic on a voxel to voxel basis.

Statistical analysis was performed to examine the

TABLE 1

Regions Showing an Enhanced Contribution from the Cerebellum Voxel Used as the Regressor during the Administration of Self-Produced Relative to Externally Produced Tactile Stimuli, in Two Representative Subjects, for Illustration

	Coordinates (x, y, z)	Z value (P < 0.001)
Subject 1		
Cerebellum voxel (regressor)	34, −56, −24	4.62
Postcentral gyrus (R)	42, −12, 60	3.96
Parietal operculum (R)	38 −16 10	3.99
Parietal operculum (L)	−40 −16 2	3.75
Lateral thalamus (R)	26, −16, −2	3.92
Medial thalamus (R)	4, −18, 6	5.02
Subject 2		
Cerebellum voxel (regressor)	38, −42, −44	2.62 (P < 0.005)
Postcentral gyrus (R)	−40, −6, 46	3.63
Parietal operculum (R)	46, −20, 16	4.09
Parietal operculum (L)	−46, −26, 10	3.88
Lateral thalamus (R)	38, 2, 4	4.02
Lateral thalamus (L)	−12, −19, 0	3.90

main effects of movement $((A + B) − (C + D)$ in Fig. 2) and tactile stimulation $(A + C) − (B + D)$, the interaction of these two factors $(A − B) − (C − D)$, and the simple main effect of movement with tactile stimulation compared to movement with no tactile stimulation $(A − B)$. Examination of the interaction reflects the statistically significant differential effects of self- vs externally produced tactile stimuli while factoring out activity due to movement or tactile stimuli alone. These statistical contrasts were used to create an SPM[*t*], which was transformed into an SPM[*Z*] and thresholded at $P < 0.001$. Resultant areas of activation were characterized in terms of their peak heights.

Regression Analysis Testing for Psychophysiological Interactions

Our hypothesis concerning psychophysiological interactions was constrained on the basis of established anatomical pathways between the cerebellum and somatosensory cortex in the monkey (Waxman & DeGroot, 1995; see Fig. 3). We first identified a target area in the cerebellum which showed a significant interaction between self-generated movement and tactile stimulation. In three subjects this was in the anterior lobe of the cerebellum; in the other three subjects, the voxel of maximum intensity was in Crus I of the cerebellum. We then used SPM to identify brain areas within the subset shown in Fig. 3 where activity was predicted by activity in the target area (the cerebellum) during self-generated tactile stimulation, but not during externally generated simulation. To do this a covariate (or regressor) of interest was constructed by taking

BOLD signal values for the target voxel in the cerebellum over the time course of the experiment (384 scans) for each subject and multiplying these by the contrast vector for the interaction term in the experimental design. Having removed the confounding effects of physiological component (the activity in the cerebellum) and the psychological component (the contrast vector for the interaction between movement and touch), any region in which activity can be predicted from the covariate of interest shows a psychophysiological interaction of the kind we have hypothesized. Regression with the covariate of interest after taking account of the two confounding covariates was calculated for every voxel in the relevant brain regions. The significance of the regression in all these voxels was displayed in a SPM[*t*] map. A significant value implies a difference in the regression slopes linking cerebellar activity to activity in other brain areas in different psychological contexts. Where significant effects were found the two regression slopes were plotted in order to visualize the effects revealed by the psychophysiological interaction. We predicted that activity in the cerebellum would covary with activity in the thalamus and somatosensory cortex during the experience of self-generated tactile stimuli, but not during the experience of externally generated tactile stimuli.

RESULTS

Examination of the interaction $((A − B) − (C − D)$ in Fig. 2) reflects the differential effects of self- vs externally produced tactile stimuli, while factoring out activity due to movement or tactile stimuli alone (Fig. 4a). This analysis demonstrated that there was significantly less activity in bilateral secondary somatosensory cortex, the anterior cingulate gyrus (ACG) and the anterior lobe of the right cerebellum when the tactile stimulation was self-produced relative to when it was externally produced (Fig. 4b). The location of the secondary somatosensory cortex activation was very similar to the results of a meta-analysis of functional imaging studies that have found SII activations (Paulesu *et al.*, 1997). Self-generated movements that did not touch the hand, and movements that did, resulted in equal activation of somatosensory cortex (there was no activity in this area in the subtraction of conditions A − B in Fig. 2). In contrast, the right anterior cerebellar cortex was selectively deactivated by self-produced movement, which resulted in a tactile stimulus, but not by movement alone, and significantly activated by externally produced tactile stimuli relative to rest (Fig. 4b). Detailed discussion of these results are reported in Blakemore *et al.* (1998).

To test the hypothesis that the cerebellum can influence neural activity in other brain regions, regression analyses were performed to test for the presence of
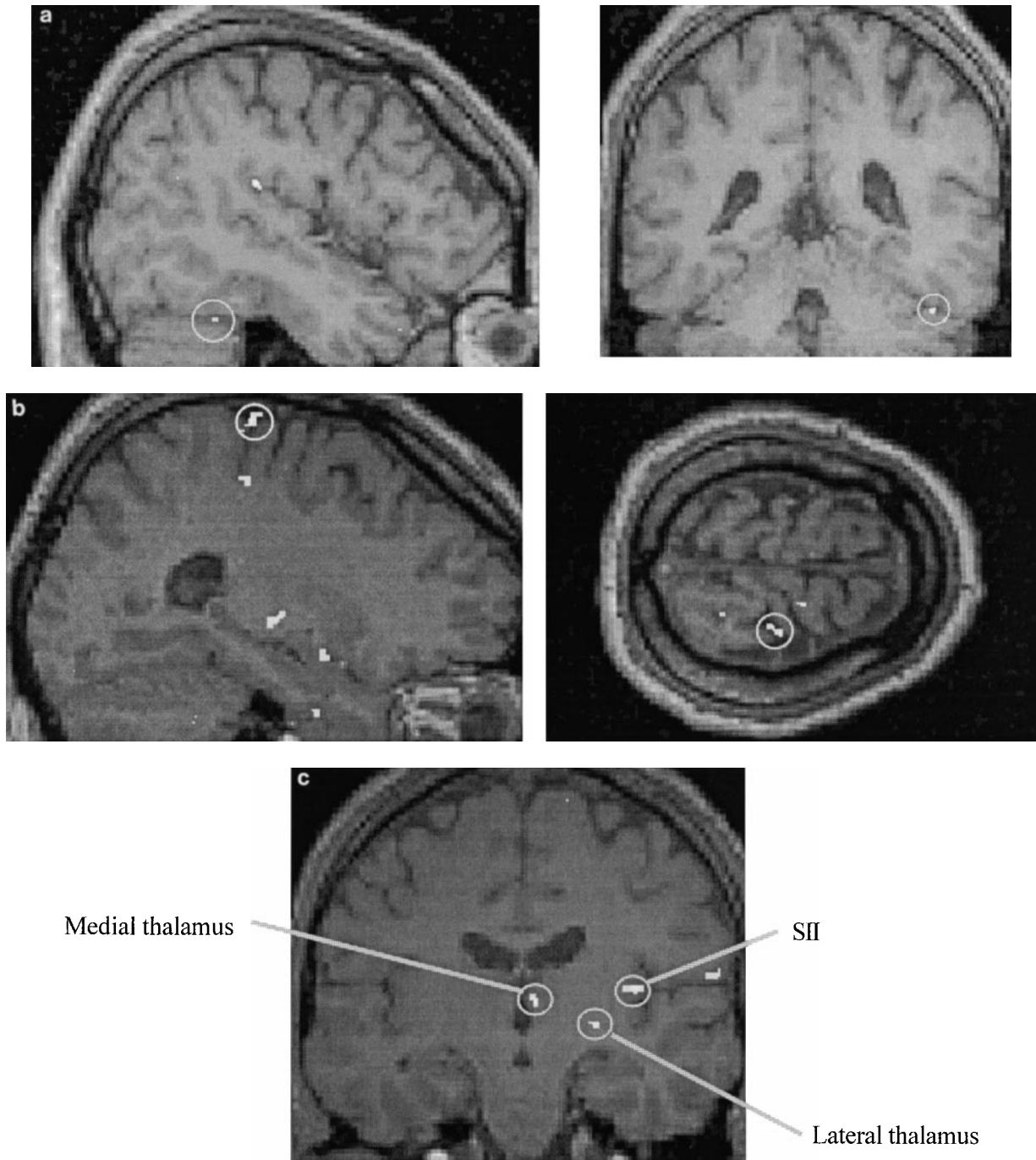
FIG. 5. The cerebellum voxel (circled) as the regressor in the psychophysiological interaction analysis and brain regions (circled) with an increased contribution from the cerebellum during the self-produced tactile stimuli are shown, for illustration, in a single typical subject (subject 1). (a) Shows the voxel of maximum intensity in the cerebellum showing a significant interaction between the effects of self-generated movement and tactile stimulation, which was used as the regressor in the psychophysiological interaction analysis. (b and c) Show brain regions with an increased contribution from the cerebellum during the self-produced tactile stimuli. The primary somatosensory cortex (b), the secondary somatosensory cortex (c), and the thalamus (c) are shown.

psychophysiological interactions (see Materials and Methods). Brain regions of interest demonstrating significant ($P < 0.001$) condition-specific changes in the influence of the cerebellum in two subjects are shown in Table 1. The data from these two subjects are represen-

tative of those from all six subjects and are shown for illustration purposes.

We demonstrate here that, as predicted, activity in the thalamus (Fig. 5b), right SI, and bilateral SII (Fig. 5c) showed a significant regression on activity in
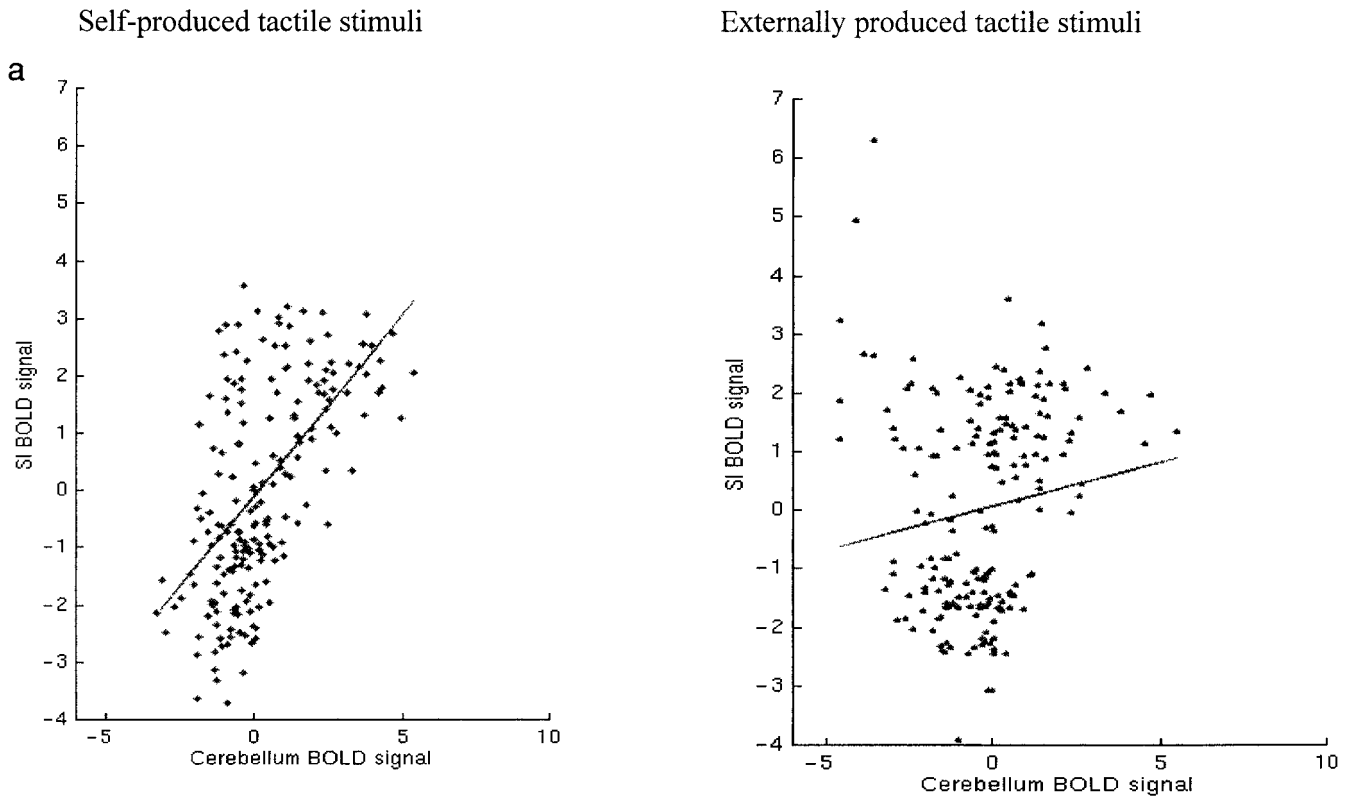
Self-produced tactile stimuli

Externally produced tactile stimuli

a

FIG. 6. Graphical displays illustrating the psychophysiological interaction between the cerebellum and the thalamus and somatosensory cortices in a single typical subject (subject 1). The BOLD values for the voxels ($x = 34$, $y = -56$, $z = -24$) in the right cerebellum and ($x = 42$, $y = -12$, $z = 60$) in the right primary somatosensory cortex (a); ($x = 38$, $y = -16$, $z = 10$) in the right secondary somatosensory cortex (b); and ($x = 26$, $y = -16$, $z = -2$) in the lateral thalamus (c) are plotted against each other in the self-produced tactile stimuli and externally produced tactile stimuli conditions (see Fig. 2). Regression lines have been fitted to the data, demonstrating a positive gradient in the self-produced tactile stimuli condition and a negative gradient in the externally produced tactile stimuli condition. The correlation coefficients (r) between cerebellum and SI, SII and thalamic activity are 0.58, 0.42, and 0.47, respectively, for the self-produced tactile stimuli condition, and 0.14, −0.02, and −0.06, respectively, for the externally produced tactile stimuli condition. See Materials and Methods for details of the regression analysis.

the cerebellum (Fig. 5a) during self-produced tactile stimuli conditions and not in conditions where tactile stimuli were externally produced. The context-specific nature of the inferred connectivity between the cerebellum and other brain areas is illustrated graphically in Fig. 6. These plots show a positive regression slope between cerebellum BOLD signal and the thalamus (Fig. 6a), right primary (Fig. 6b), and secondary (Fig. 6c) somatosensory cortex BOLD signal in the self-produced condition and a flat slope in the externally produced condition. The difference between these slopes was significant at $P < 0.001$ in all six subjects. The maximum intensity projection images in Fig. 5 and the graphical displays in Fig. 6 illustrate the psychophysiological interaction between the cerebellum and the thalamus and somatosensory cortices in a single representative subject (subject 1), for illustration.

It is possible that the positive correlation between activity in the cerebellum and activity in the thalamus and somatosensory cortex is caused by activity in a third area. The only other area that was activated by

externally produced but not by self-produced tactile stimulation was the ACG. Activity in the cerebellum and the somatosensory cortices did not significantly regress on activity in the voxel of maximum intensity in the ACG when this was used as the regressor. Therefore the hypothesis that activity in the ACG influenced activity in the cerebellum and the somatosensory cortices was not supported.

DISCUSSION

The finding that somatosensory cortex is activated more by externally produced than by self-produced tactile stimulation is likely to be the physiological correlate of the reduced perception associated with the latter type of stimulation (Weiskrantz *et al.*, 1971; Blakemore *et al.*, 1999). The reduction in somatosensory cortex activity to self-produced tactile stimuli is in accord with neurophysiological experiments demonstrating that active touch results in less neuronal firing in SI than passive and external touch of the same
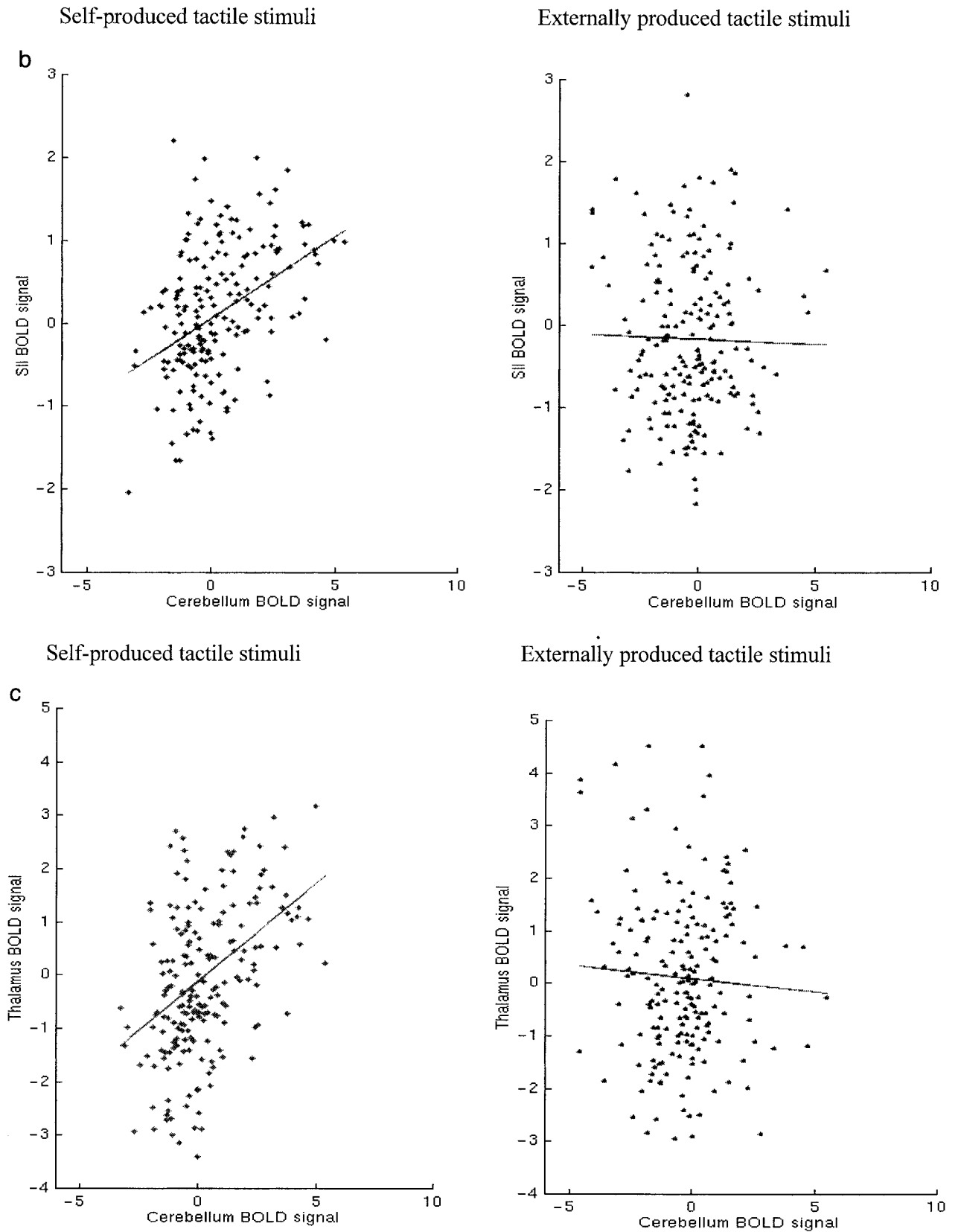
Self-produced tactile stimuli

Externally produced tactile stimuli

Self-produced tactile stimuli

Externally produced tactile stimuli

FIG. 6—*Continued*

surface (see Chapman, 1994). The pattern of brain activity we observed in the cerebellum suggests that this area might be a source of the somatosensory modulation. As discussed in a previous paper (Blakemore *et al.*, 1998) in somatosensory areas activity was attenuated by all movement: these areas were equally activated by movement that did and that did not result in tactile stimulation, a finding that is in line with a recent fMRI experiment by Jansma *et al.* (1998). In other words this movement-related somatosensory gating does not seem to depend on the specific sensory consequences of a movement, but instead is associated with all self-generated movements. However, our psychophysical experiment described above suggests that sensory gating is very sensitive to the consequences of the movement since very small delays modulated the perception of the tactile stimulus (Blakemore *et al.*, 1999).

We previously found that in contrast to activity in somatosensory cortex, the right anterior cerebellar cortex activity was not attenuated as a general consequence of all movement. Instead this area was selectively deactivated by self-produced movement, which resulted in a tactile stimulus (condition A), but not by movement alone (condition B), and significantly activated by externally produced tactile stimuli (condition C) relative to rest (condition 4; Fig. 4b; Blakemore *et al.*, 1998). This pattern suggests that the cerebellum makes use of a forward model of the motor apparatus, which provides a prediction of the specific sensory consequences of motor commands and therefore differentiates between movements depending on their specific sensory feedback. In our previous study, when the actual sensory feedback of a movement matched the predicted sensory feedback (when tactile stimuli were self-produced), cerebellar activity decreased and the somatosensory cortex was not activated. In contrast, when tactile stimuli were externally produced they could not be predicted based on efference copy so the predicted and actual sensory feedback did not match. We propose that this discrepancy is signalled by the cerebellum in the form of increased activity, and activity in somatosensory cortex cannot be predictively gated.

In the present study, to test explicitly the hypothesis that the cerebellum might be a source of the somatosensory modulation we used regression analyses to investigate the contribution of cerebellum to the thalamus and somatosensory cortex when stimuli were self-produced relative to when they were externally produced. The resulting regression slope suggests an influence of cerebellum on the thalamus and right primary and bilateral secondary somatosensory cortex. As can be seen in Fig. 6, each regression slope changed when tactile stimuli were self-produced compared to when they were externally produced, thus constituting a

psychophysiological interaction (Friston *et al.*, 1997). These results suggest that the cerebellum output might modulate activity in somatosensory cortex via the thalamus when, and only when, the predicted and actual sensory information are matched, i.e., when tactile stimuli are self-generated not when they are externally generated.

This reasoning is consistent with the theory that the cerebellum is a component of a system that provides precise predictions of the sensory consequences of motor commands (Ito, 1970; Paulin, 1989; Miall *et al.*, 1993; Wolpert *et al.*, 1998). The forward model of the arm's dynamics has, as inputs, the current state of the arm and an efference copy of the motor commands being issued and produces a new state of the arm. This model therefore captures the state changes in the arm in response to the motor outflow. In addition, a forward sensory output model of the arm predicts the sensory reafferent signals that are consequent on a particular change in state. By linking a forward dynamic and forward sensory output model an estimate of the sensory consequences of a motor command can be achieved. In the case of the current experiment, an estimate of the tactile feedback from the hand movement is made and, when congruent with the actual sensory consequences, this estimate is used predictively to attenuate the percept of the tactile stimulus.

Empirical research supports the proposal that the cerebellum is implicated in making sensory predictions in the sensorimotor system. The main input to the cerebellum, the climbing fibers from the inferior olive, has been proposed to act as a comparator between intended and achieved movement, signalling errors in motor performance (Simpson *et al.*, 1995). Evidence for this comes from electrophysiological studies, demonstrating that neurons in the inferior olive of cats respond to passively applied cutaneous stimuli but not to similar stimuli produced by a voluntary movement of the cat (except when stimuli were unexpectedly encountered during movement; Gellman *et al.*, 1985). Similarly, Andersson & Armstrong (1985, 1987) demonstrated that inferior olive neurons fire when a cat walking on a horizontal ladder encounters a rung that unexpectedly gives way. Therefore inferior olivary neurons have been proposed to act as somatic "event detectors" responding particularly reliably to unexpected stimuli (Gellman *et al.*, 1985; Simpson *et al.*, 1995). The proposal that the cerebellum provides predictions of the sensory consequences of motor commands is also consistent with research demonstrating the role of the cerebellum in processing sensory information on line. Our data lend support to theories proposing that the cerebellum is involved in the acquisition and discrimination of sensory data (Leiner *et al.*, 1995; Gao *et al.*, 1996; Bower, 1997a, 1997b), a function that would

be necessary for the comparison between the actual and predicted sensory consequences of the movement.

SUMMARY

Our study demonstrates that self-produced tactile stimuli result in less activation of somatosensory cortex than identical tactile stimuli when externally produced. Differential sensory responses to a self-generated movement do not occur at the level of somatosensory cortex. Instead, our results suggest that specific sensory predictions occur at the level of the cerebellum. We propose that the decrease of activity in somatosensory cortex to self-produced tactile stimuli occurs because these match the predicted sensory feedback of the movement. Our regression analyses suggest that this prediction might take place in the cerebellum since activity in the thalamus and somatosensory cortex significantly regressed on activity in the cerebellum when tactile stimuli were self-produced but not when they were externally produced.

ACKNOWLEDGMENTS

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