

# Central cancellation of self-produced tickle sensation

Sarah-J. Blakemore<sup>1,2</sup>, Daniel M. Wolpert<sup>2</sup> and Chris D. Frith<sup>1</sup>

<sup>1</sup> Wellcome Department of Cognitive Neurology, 12 Queen Square, London WC1N 3BG, UK

<sup>2</sup> Sobell Department, Institute of Neurology, Queen Square, London WC1N 3BG, UK

Correspondence should be addressed to S.-J.B. ([s.blakemore@ucl.ac.uk](mailto:s.blakemore@ucl.ac.uk))

A self-produced tactile stimulus is perceived as less ticklish than the same stimulus generated externally. We used fMRI to examine neural responses when subjects experienced a tactile stimulus that was either self-produced or externally produced. More activity was found in somatosensory cortex when the stimulus was externally produced. In the cerebellum, less activity was 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, providing the signal that is used to cancel the sensory response to self-generated stimulation.

Our sensory systems are constantly bombarded by a multitude of sensory stimuli, from which we must extract the few stimuli that correspond to important changes within the environment. One class of stimuli that are in most circumstances unimportant, and therefore can be discarded, are those that arise as a necessary consequence of our own motor actions. Several researchers have proposed that we use knowledge of our intentions or motor commands to distinguish the sensory consequences of our own actions from externally produced sensory stimuli<sup>1–5</sup>. To achieve this, some kind of central monitor<sup>6</sup> or internal ‘forward model’<sup>4,5</sup> has been postulated. These models capture the forward or causal relationship between actions, as signaled by ‘efference copy’, a copy of the motor command<sup>7</sup>, and the predicted sensory outcome, originally termed ‘corollary discharge’<sup>8</sup>. 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. These mechanisms have mainly been studied with reference to eye movements<sup>7,8</sup>. However, it seems that sensory predictions produced in conjunction with the motor command are not restricted to eye movements, but also provide perceptual stability in the context of all self-produced actions; our ability to monitor, and recognize as our own, self-generated limb movements, touch and speech, suggests the existence of a more general mechanism<sup>6</sup>.

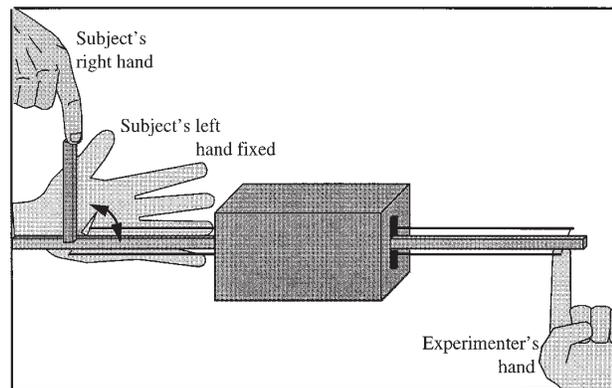
The ability to predict the consequences of our own actions may underlie the differential perception of identical sensory inputs depending on whether they are self-generated or externally generated. An example of such differential perception is the phenomenon that people cannot tickle themselves<sup>9,10</sup>. Using a robotic interface, we have demonstrated that self-produced and externally produced tactile sensations are perceived differently (S.-J.B., D.M.W. & C.D.F. *Neuroimage* 7, 481, 1998; S.-J.B., C.D.F. & D.M.W., unpublished data). 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 tactile stimulus could be delivered under remote control by the subject, we investigated whether tickli-

ness rating is affected by parametrically varied degrees of delay between the movement of the left hand and the tactile stimulus on the right hand. We found a progressive increase in the ‘tickly’ rating as the delay was increased between 0 and 200 ms. Under all delays, the left hand made the same movement, and the right hand experienced the same stimulus. Only the temporal 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 cancellation of the sensory feedback, based on specific sensory predictions, rather than a non-specific attenuation of all sensory signals.

Neurophysiological data demonstrate that neuronal responses in somatosensory cortex are attenuated by self-generated movement. For example, active touch is ‘gated’ in primary somatosensory cortex (SI) of rats<sup>11</sup> and monkeys<sup>12,13</sup> compared to passive and external touch of an identical tactile stimulus. However, it is unknown whether such gating is responsible for the differential perception of self- and externally produced tactile stimuli in humans. Furthermore the neural processes underlying movement-related gating in SI are undetermined.

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, according to computational<sup>14–17</sup> and neurophysiological data<sup>18–27</sup>. 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.

Using fMRI, we have examined the neural basis of the differential perception of self- and externally produced tactile stimuli. A tactile stimulation device (Methods; Fig. 1) allowed a sinusoidal tactile stimulus (amplitude 1.5 cm at 2 Hz) 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



**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 the 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 experimenter's control, during the scanning. When exposed, the foam made light contact with the subject's left palm.

tactile stimuli, we used a factorial design with the factors of self-generated movement of the right hand versus rest, and tactile stimulation on the left hand versus no stimulation. There were four conditions: self-generated tactile stimulation, self-generated movement without tactile stimulation, externally generated tactile stimulation and rest (Table 1). 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. Analysis of the imaging data resulted in the creation of statistical parametric maps reflecting the two main effects, movement and tactile stimulation, and the interaction between these two factors (Methods). Our results demonstrate that self-produced tactile stimuli result in less activation of somatosensory cortex than externally produced tactile stimuli. In addition, activity in the anterior cerebellar cortex is attenuated by self-produced movements that generate tactile stimuli relative to movements that do not. We propose that the cerebellum is involved in predicting the specific sensory consequences of movements, providing the signal that is used to cancel the somatosensory response to self-produced tactile stimulation.

## Results

The main effect of movement of the right hand ((A+B)-(C+D) in Table 1) revealed activity in a number of contralateral motor, premotor, and prefrontal areas and bilateral cerebellar areas (Fig. 2a). The range of activated areas is consistent with previous studies that have examined self-generated movements (for example, refs 28, 29). The main effect of tactile stimulation ((A+C)-(B+D) in Table 1) on the subjects' left palm showed activity in contralateral primary and bilateral secondary somatosensory cortices (Fig. 2b). These areas are consistent with areas activated by tactile stimulation of the hand in previous electrophysiological and functional imaging studies (for example, refs 30, 31).

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 Table 1.) This is in line with the results of an intriguing fMRI experiment<sup>32</sup>, in which subjects were instructed to make finger/thumb opposition movements. Whether subjects did or did not make contact between their fingers and thumb did not affect brain activity, which was equivalent everywhere, including somatosensory cortex, in both conditions.

Examination of the interaction ((A-B)-(C-D) in Table 1) reflects the differential effects of self- versus externally produced tactile stimuli while factoring out activity due to movement or tactile stimuli alone (Fig. 3). This enabled us to investigate the neural correlates of the reduced 'tickliness' of a self-produced tactile stimulus<sup>9,10</sup>. There was significantly less activity in bilateral secondary somatosensory cortex, the anterior lobe of the right cerebellum and the anterior cingulate (area 24/32) when the tactile stimulation was self-produced relative to when it was externally produced (Figs 3-6).

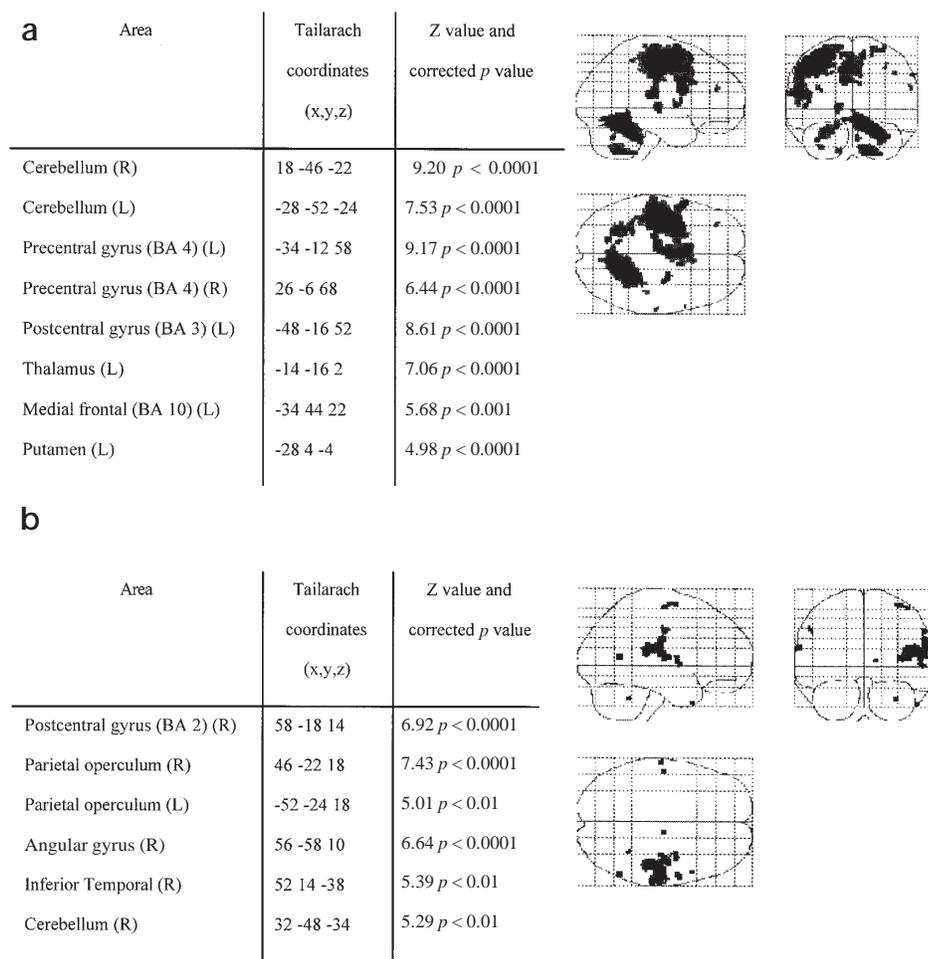
## Discussion

The finding that somatosensory cortex is more activated by externally produced than by self-produced tactile stimulation 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 surface<sup>13</sup>. This reduction in somatosensory cortex activity to self-produced tactile stimuli is likely to be the physiological correlate of the reduced perception associated with this type of stimulation<sup>9,10</sup>. Whereas the changes in somatosensory cortex are likely to underlie perception of tactile stimuli, the pattern of brain activity we observed in the cerebellum suggests that this area is the source of the somatosensory modulation. In somatosensory areas, activity was attenuated by all movement; these areas were equally activated whether or not the movement resulted in tactile stimulation (Fig. 4). In contrast, the right anterior cerebellar cortex was selectively deactivated by self-produced movement that resulted in a tactile stimulus, but not by movement alone, and significantly activated by externally produced tactile stimuli (Fig. 5). This pattern suggests that the cerebellum differentiates between movements depending on their specific sensory consequences. In our 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.

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<sup>14-17</sup> that, when congruent with the actual sensory consequences, are used to cancel the percept of a tactile stimulus. Empirical research supports this account. The main input to the cerebellum, the climbing fibers from the inferior olive, has been proposed to act as a comparator between predicted and actual sensory consequences of movement<sup>18</sup>. Evidence for this comes from electrophysiological studies demonstrating that neurons in the inferior olive of cats respond to passively applied cuta-

**Table 1.** Four experimental conditions in the 2 x 2 factorial design.

	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.** Areas of activation in the main effects of movement and tactile stimuli. **(a)** Regional changes in activity in the comparison between the self-generated movement conditions and those without movement ((A+B)–(C+D) in **Table 1**). Sagittal, coronal and axial views of maximum-intensity projections of statistical parametric maps showing significant activations ( $p < 0.05$ , corrected for multiple comparisons) associated with self-generated movement. **(b)** Regional changes in activity in the comparison between tactile stimulation conditions and those without tactile stimulation ((A+C)–(B+D) in **Table 1**). Sagittal, coronal and axial views of maximum-intensity projections of statistical parametric maps showing significant activations ( $p < 0.05$ , corrected for multiple comparisons) associated with tactile stimulation.

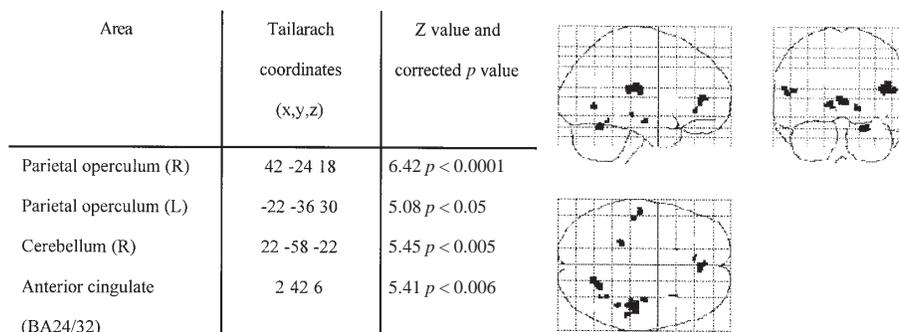
neous stimuli but not to similar stimuli produced by a voluntary movement of the cat (except when unexpectedly encountered during movement)<sup>19</sup>. Similarly, inferior olive neurons fire when a cat walking on a horizontal ladder encounters a rung that unexpectedly gives way<sup>20,21</sup>. Therefore inferior olivary neurons have been proposed to act as somatic ‘event detectors’, responding particularly reliably to unexpected stimuli<sup>18,22</sup>.

The proposal that the cerebellum predicts 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 support theories proposing that the cerebellum is involved in the acquisition and discrimination of sensory data<sup>23–27</sup>, a function that would be necessary for comparison between the actual and predicted sensory consequences of a movement.

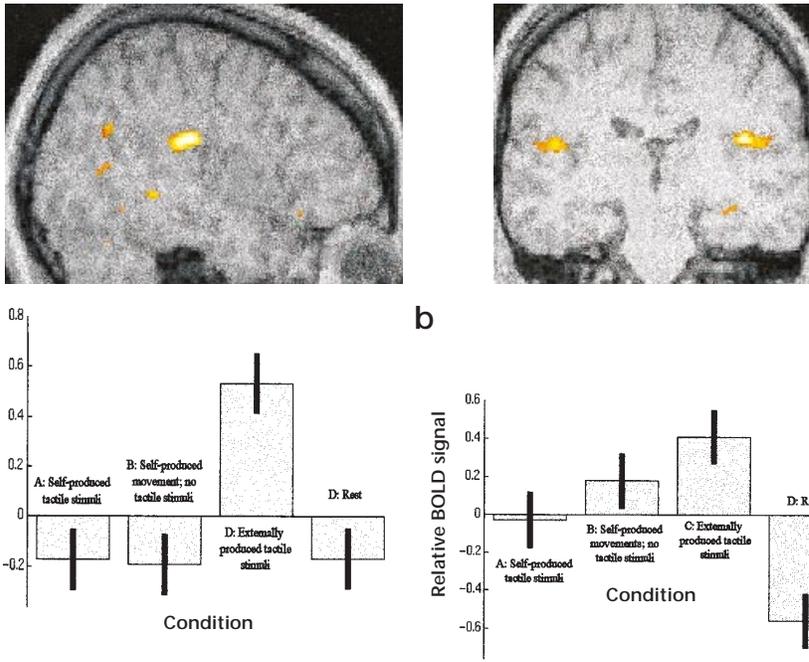
The anterior cingulate (BA 24/32) was significantly more activated by externally produced than by self-produced tactile stimuli (**Fig. 6**). Previous studies have implicated this area in affective behaviour<sup>33,34,35</sup> and have shown that rats will self-stimulate this site, suggesting it is a site of positive

reinforcement<sup>36</sup>. The activity in the anterior cingulate in the present study may have been related to the fact that externally produced tactile stimuli are perceived as more tickly and pleasant than self-produced tactile stimuli (S.-J.B, C.D.F. & D.M.W., unpublished data).

Our study demonstrates that self-produced tactile stimuli cause less activation of somatosensory cortex than do identical tactile stimuli when externally produced. This finding might explain why tactile stimuli are perceived as less tickly when self-produced. We propose that the perception of tickle is associated with increased activity in somatosensory



**Fig. 3.** Areas significantly activated ( $p < 0.05$ , corrected for multiple comparisons) by the interaction of the effects of self-generated movements and tactile stimulation ((C–D)–(A–B) in **Table 1**).



**Fig. 4.** Significantly decreased activity ( $p < 0.05$ , corrected for multiple comparisons) in bilateral secondary somatosensory cortex associated with the interaction between the effects of self-generated movement and tactile stimulation. Shown are condition-specific parameter estimates, which reflect the adjusted BOLD contrast signal relative to the fitted mean and are expressed as a percentage of whole brain mean activity. In the lower panel, the effects at voxels in the right (**a**; 42, -24, 18) and left (**b**; -22, -36, 30) parietal operculum are shown for a single subject. Similar parameter estimates were obtained for the remaining subjects in this statistical model. Conditions are labeled as in Table 1.

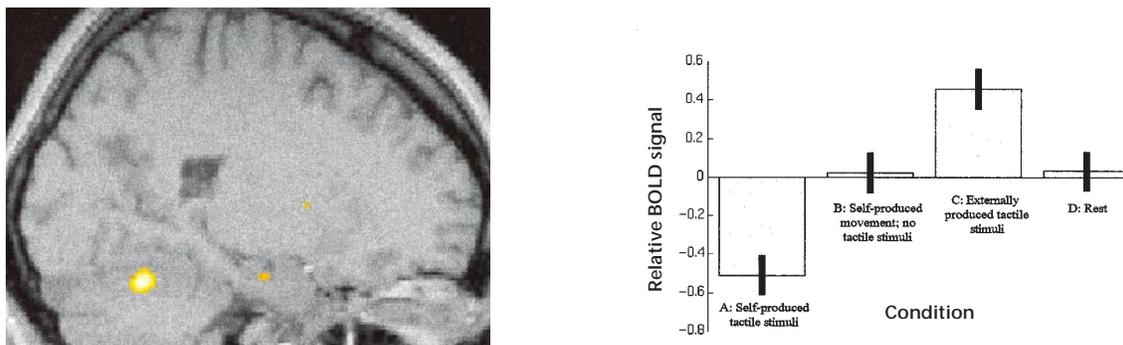
cortex. Differential sensory responses to a self-generated movement do not occur at the level of somatosensory cortex. Instead, our results suggest that specific sensory predictions occur at the level of the anterior cerebellar cortex. We propose that the decrease of activity in somatosensory cortex to self-produced tactile stimuli occurs because these match the predicted sensory feedback of the movement and that this prediction occurs in the cerebellum.

**Methods**

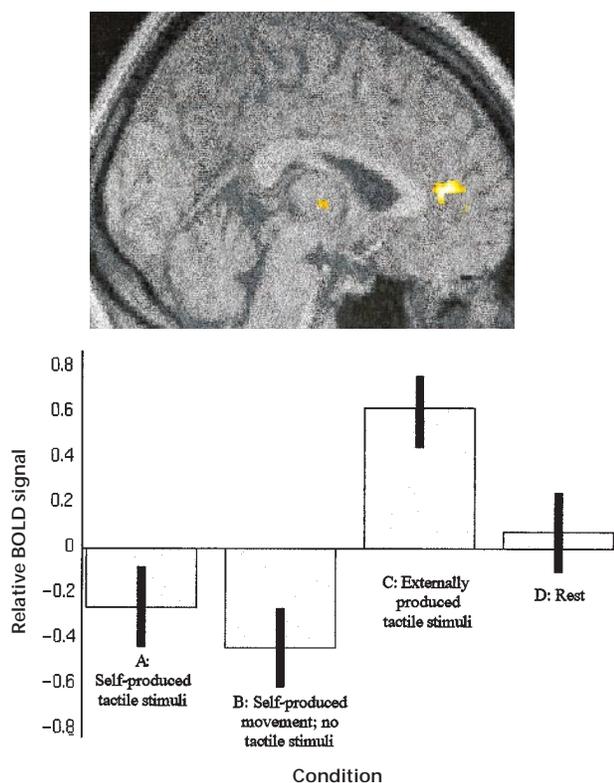
**SUBJECTS AND DESIGN.** Six normal right-handed volunteers (4 females and 2 males; mean age 33 years) gave informed consent and participated in the study, which was approved by the National Hospital for Neurology and Neurosurgery Ethics Committee. The experiment was split into two 12-minute sessions. Each subject underwent 200 fMRI scans in each session. Within each session, the subject lay supine on the MRI bed with the right arm fixed over the chest to limit movement

to the fingers. The 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. The 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 moved either by the subject using the 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 experimenter's control, during the scanning. When exposed, the foam made light contact with the subject's left palm.

There were two experimentally manipulated variables: whether or not 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 at a frequency of 2 Hz and practiced beforehand to ensure that they



**Fig. 5.** Significantly decreased activity ( $p < 0.05$ , corrected for multiple comparisons) in right anterior cerebellar cortex associated with the interaction between the effects of self-generated movement and tactile stimulation. Shown are condition-specific parameter estimates, which reflect the adjusted BOLD contrast signal relative to the fitted mean and are expressed as a percentage of whole brain mean activity. The effects at the voxel 22, -58, -22 are shown, for illustration, for a single subject in the lower panel. Similar parameter estimates were obtained for the remaining subjects in this statistical model. Conditions are labeled as in Table 1. The right anterior cerebellar cortex was the only area of the brain activated in the contrast A–B.



**Fig. 6.** Significantly decreased activity ( $p < 0.05$  corrected for multiple comparisons) in anterior cingulate cortex associated with the interaction between the effects of self-generated movement and tactile stimulation. Shown are condition-specific parameter estimates, which reflect the adjusted BOLD contrast signal relative to the fitted mean and are expressed as a percentage of whole brain mean activity. The effects at the voxel 2, 42, 6 are shown, for illustration, for a single subject in the lower panel. Similar parameter estimates were obtained for the remaining subjects in this statistical model. Conditions are labeled as in Table 1.

could reliably generate the desired movements. The tactile stimulus was identical in force, amplitude and frequency throughout the experiment. Each condition lasted 30 seconds and was followed in immediate succession 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 (Table 2). Subjects were told which task to perform through earphones (corresponding to the word in parentheses following each condition name).

In 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 on their left hand. Subjects were explicitly told that in the 'touch' condition, their right hand movements would produce tactile stimulation on their left palm. In 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. Subjects were told that in the 'move' condition, their right hand movements would not produce any tactile sensation. In Condition C, externally produced tactile stimulation (feel), subjects did not move. The experimenter moved the tactile stimulus sinusoidally across the subject's left palm. Subjects were told that in the 'feel' condition, they would receive tactile stimulation on their left palm. In Condition D, no movement, no tactile stimulation (rest), neither movement nor 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 counterbalanced 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 produced by all subjects in conditions A, B and C was 2.25 Hz.

**DATA ACQUISITION.** A Siemens VISION system (Siemens, Erlangen) operating at 2 T was used to acquire both axial gradient-echo, echo-planar T2\* weighted image volumes with blood oxygenation level dependent (BOLD) contrast and axial T1 weighted structural images for anatomical co-registration. 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 three-minute break between sessions. Each functional-image volume comprised 48 3-mm axial slices with in-plane resolution of 3 x 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 (eight volumes) or epochs of rest (lasting 32.8 s, eight volumes). Each run began with eight 'dummy' volumes, which were subsequently discarded to allow for T1 equilibration effects. Periods of no movement (conditions C and D) then alternated with the movement conditions (A and B) 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 [Wellcome Department of Cognitive Neurology, UK, <http://www.fil.ion.ucl.ac.uk/spm/>]. For each subject, the imaging time series was realigned using sinc interpolation with an 11 x 11 x 11 kernel<sup>37</sup>. 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 non-linear registration using 1196 parameters. The data were resampled using sinc interpolation into the space of Talairach and Tournoux<sup>38</sup>. 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 hypothesized by the experimenter<sup>39-41</sup>. Condition-specific effects were estimated with the general linear model with a delayed box-car wave form. Low-frequency sine and cosine waves modeled and removed participant-specific, low-frequency drifts in signal, and 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 examined the main effects of movement ((A+B)-(C+D)) in Table 1 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- versus 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  $p < 0.05$  (corrected on the basis of the theory of random Gaussian fields for multiple comparisons across the whole brain volume examined). Resultant areas of activation were characterized in terms of their peak heights.

## Acknowledgements

We thank Richard Perry and Richard Frackowiak for comments, and the radiographers at the Wellcome Department for Cognitive Neurology for their help. This work was supported by the Wellcome Trust. S.-J.B. is supported by a Wellcome Trust four-year Ph.D. Programme in Neuroscience at University College London.

RECEIVED 26 MAY; ACCEPTED 4 SEPTEMBER 1998

1. Decety, J. Neural representation for action. *Rev. Neurosci.* 7, 285–297 (1996).
2. Jeannerod, M. *The Neural and Behavioural Organisation of Goal-Directed Movements* (Oxford Univ. Press, 1988).
3. Spenser, M. *The Cognitive Neuroscience of Action* (Blackwell, Cambridge, 1997).
4. Wolpert, D. M., Ghahramani, Z. & Jordan, M. I. An internal model for sensorimotor integration. *Science* 269, 1880–1882 (1995).
5. Wolpert, D. M. Computational approaches to motor control. *Trends Cog. Sci.* 1, 209–216 (1997).
6. Frith, C. D. *The Cognitive Neuropsychology of Schizophrenia* (Lawrence Erlbaum, Hove, UK, 1992).
7. Von Holst, E. Relations between the central nervous system and the peripheral organs. *Brit. J. Anim. Behav.* 2, 89–94 (1954).
8. Sperry, R. W. Neural basis of spontaneous optokinetic responses produced by visual inversion. *J. Comp. Physiol. Psychol.* 43, 482–489 (1950).
9. Weiskrantz, L., Elliot, J. & Darlington, C. Preliminary observations of tickling oneself. *Nature* 230, 598–599 (1971).
10. Claxton, G. Why can't we tickle ourselves? *Percept. Motor Skills* 41, 335–338 (1975).
11. Chapin, J. K. & Woodward, D. J. Somatic sensory transmission to the cortex during movement: gating of single cell responses to touch. *Exp. Neurol.* 78, 654–669 (1982).
12. Jiang, W., Chapman, C. E. & Lamarre, Y. Modulation of the cutaneous responsiveness of neurones in the primary somatosensory cortex during conditioned arm movements in the monkey. *Exp. Brain Res.* 84, 342–354 (1991).
13. Chapman, C. E. Active versus passive touch: factors influencing the transmission of somatosensory signals to primary somatosensory cortex. *Can. J. Physiol. Pharmacol.* 72, 558–570 (1994).
14. Ito, M. Neurophysiological aspects of the cerebellar motor control system. *Int. J. Neurol.* 7, 162–176 (1970).
15. Paulin, M. G. in *Dynamic Interactions in Neural Networks: Models and Data* (eds Arbib, E. M. A. & Amari, E. S.) 241–259 (Springer, 1989).
16. Miall, R. C., Weir, D. J., Wolpert, D. M. & Stein, J. F. Is the cerebellum a Smith predictor? *J. Motor Behav.* 25, 203–216 (1993).
17. Wolpert, D. M., Miall, R. C. & Kawato, M. Internal models in the cerebellum. *Trends Cog. Sci.* 2, 338–347 (1998).
18. Oscarsson, O. in *The Inferior Olivary Nucleus: Anatomy and Physiology* (eds Courville, J., DeMontigny, C. & Lamarre, Y.) 279–289 (Raven, New York, 1980).
19. Gellman, R., Gibson, A. R. & Houk, J. C. Inferior olivary neurons in the awake cat: detection of contact and passive body displacement. *J. Neurophysiol.* 54, 40–60 (1985).
20. Andersson, G. & Armstrong, D. M. Climbing fibre input to b zone Purkinje cells during locomotor perturbation in the cat. *Neurosci. Lett. Supp.* 22, S27 (1985).
21. Andersson, G. & Armstrong, D. M. Complex spikes in Purkinje cells in the lateral vermis of the cat cerebellum during locomotion. *J. Physiol. (Lond.)* 385, 107–134 (1987).
22. Simpson, J. L., Wylie, D. R. & De Zeeuw, C. I. On climbing fiber signals and their consequence(s) *Brain Behav. Sci.* 19, 368–383 (1995).
23. Morrissette, J. & Bower, J. M. Contribution of somatosensory cortex to responses in the rat cerebellar granule cell layer following peripheral tactile stimulation. *Exp. Brain Res.* 109, 240–250 (1996).
24. Leiner, H. C., Leiner, A. L. & Dow, R. S. The underestimated cerebellum. *Hum. Brain Mapp.* 2, 244–254 (1995).
25. Gao, J-H *et al.* Cerebellum implicated in sensory acquisition and discrimination rather than motor control. *Science* 272, 545–546 (1996).
26. Bower, J. M. Is the cerebellum sensory for motor's sake, or motor for sensory's sake: the view from the whiskers of a rat? *Prog. Brain Res.* 114, 463–496 (1997).
27. Bower, J. M. Control of sensory data acquisition. *Int. Rev. Neurobiol.* 41, 489–513 (1997).
28. Deiber, M.-P. *et al.* Cortical areas and the selection of movement: a study with positron emission tomography. *Exp. Brain Res.* 84, 393–402 (1991).
29. Frith, C. D., Friston, K. J., Liddle, P. F. & Frackowiak, R. S. J. Willed action and the prefrontal cortex in man: a study with PET. *Proc. R. Soc. Lond. B Biol. Sci.* 244, 241–246 (1991).
30. Paulsen, E., Frackowiak, R. S. J. & Bottini, G. in *Human Brain Function* (eds Frackowiak, R. S. J., Friston, K. J., Frith, C. D., Dolan, R. J. & Mazziotta, J. C.) 183–242 (Academic, San Diego, California 1997).
31. Krubitzer, L., Clarrey, J., Tweedale, R., Elston, G. & Calford, M. A redefinition of somatosensory areas in the lateral sulcus of macaque monkeys. *J. Neurosci.* 15, 3821–3839 (1995).
32. Jansma, J. M., Ramsey, N. F. & Kahn, R. S. Tactile stimulation during finger opposition does not contribute to 3D fMRI brain activity pattern. *Neuroreport* 9, 501–505 (1998).
33. Vogt, B. A., Finch, D. M. & Olson, C. R. Functional heterogeneity in cingulate cortex: the anterior executive and posterior evaluative regions. *Cereb. Cortex* 2, 435–443 (1992).
34. Vogt, B. A. & Gabriel, M. eds *Neurobiology of Cingulate Cortex and Limbic Thalamus* (Birkhauser, Boston, 1993).
35. Coghill, R. C. *et al.* Distributed processing of pain and vibration by the human brain. *J. Neurosci.* 14, 4095–4108 (1994).
36. Porrino, L. J. Functional consequences of acute cocaine treatment depend on route of administration. *Psychopharmacol. Berl.* 112, 343–351 (1993).
37. Friston, K. J. *et al.* Spatial registration and normalization of images. *Hum. Brain Mapp.* 3, 165–189 (1995).
38. Talairach, J. & Tournoux, P. *Co-Planar Stereotaxic Atlas of the Human Brain* (Thieme, New York, 1988).
39. Friston, K. J. *et al.* The relationship between global and local changes in PET scans. *J. Cereb. Blood Flow Metab.* 10, 458–466 (1990).
40. Friston, K. J. *et al.* Statistical parametric maps in functional imaging: a general linear approach. *Hum. Brain Mapp.* 2, 189–210 (1995).
41. Friston, K. J. in *Human Brain Function* (eds Frackowiak, R. S. J., Friston, K. J., Frith, C. D., Dolan, R. J. & Mazziotta, J. C.) 107–126 (Academic, San Diego, California, 1997).

