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Altered awareness of voluntary action after damage to the parietal cortex

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A central question in the study of human behavior is the origin of willed action. EEG recordings of surface brain activity from human subjects performing a self-initiated movement show that the subjective experience of wanting to move follows, rather than precedes, the 'readiness potential'—an electrophysiological mark of motor preparation. This raises the issue of how conscious experience of willed action is generated. Here we show that patients with parietal lesions can report when they started moving, but not when they first became aware of their intention to move. This stands in contrast with the performance of cerebellar patients who behaved as normal subjects. We thus propose that when a movement is planned, activity in the parietal cortex, as part of a cortico-cortical sensorimotor processing loop, generates a predictive internal model of the upcoming movement. This model might form the neural correlate of motor awareness.

Voluntary action implies a subjective experience of the decision and intention to act, as well as neural control of motor execution. For willed action to be a functional behavior, the brain must have a mechanism for matching the consequences of the motor act against the prior intention. It is widely thought that the brain uses internal anticipatory models for this purpose[1,2], but it is still debated to what extent these models would be available to awareness[3]. Estimating the time of a conscious intention presumably requires access to an internal representation of the desired movement. Internal motor representations—or internal models—predict the future outcome of a given action[4]. Several studies suggest that the parietal cortex is important in activating and maintaining such internal models[5,6]. For instance, when the parietal cortex is damaged, patients lose the ability to predict through mental simulation the time necessary to perform various hand movements[5], indicating that this region is involved in generating conscious motor images. According to some reports[1,2,7], another brain region, the cerebellum, is also involved in predicting the future state of a motor act. For example, when lifting an object, subjects anticipate the increase in load force and accordingly adapt their grip force to hold the object[8]. These fine motor adjustments are clearly predictive and, as suggested by neuropsychological studies, are severely disrupted by cerebellar lesions[9]. However, these processes may not be available to conscious awareness. To investigate the role of the cerebellum and the parietal cortex in the subjective experience of voluntary action, we examined overt reports on the awareness of the intention to move in normal subjects and patients with focal brain lesions. We found that cerebellar patients, similar to normal controls subjects, were able to report when they first intended to move, whereas patients with parietal damage could not. This result suggests that the parietal cortex is involved in monitoring awareness of one's own movements.

We recruited three groups of five subjects each: healthy volunteers, patients with selective lesion in the parietal cortex, and patients with selective lesion in the cerebellum. The experimental design was based on that of Libet *et al.*[10,11]. Subjects were asked to perform a simple voluntary movement, namely pushing a button with their index finger at a time of their own choosing, following a trial start cue. While performing this simple task, subjects were instructed, in separate blocks of trials, to focus their attention on either the actual onset of their finger movement or their internal decision to execute it. Judgments about the time of each event was accomplished in the following way: subjects looked at the single hand of a clock that started to move at the beginning of each trial and stopped at a random time following the button press (**Fig. 1a**). Subjects reported the position of the clock's hand either at the time they pushed the button (M-judgment) or at the time they first became aware of their intention to move (W-judgment). To make explicit to the subjects what they had to focus on in the latter condition, the instruction was phrased as follows: "Note the position of the clock's hand at the time when you felt the urge to move but had not started moving yet." Subjects were told to feel free to execute the movement whenever they wanted, but not before the clock's hand had completed its first turn. During the experiment, onset of muscular activity was measured by electromyography (EMG) from flexor digitorum superficialis of the responding hand. In all controls and in all patients, the electroencephalogram (EEG) was also recorded on the scalp to measure readiness potential[12] (RP) over motor areas (**Fig. 1b**). To assess each subject's ability to correctly estimate time, we included one control condition (S-judgment) in which subjects reported the location of the clock's hand when a beep was delivered by the computer.

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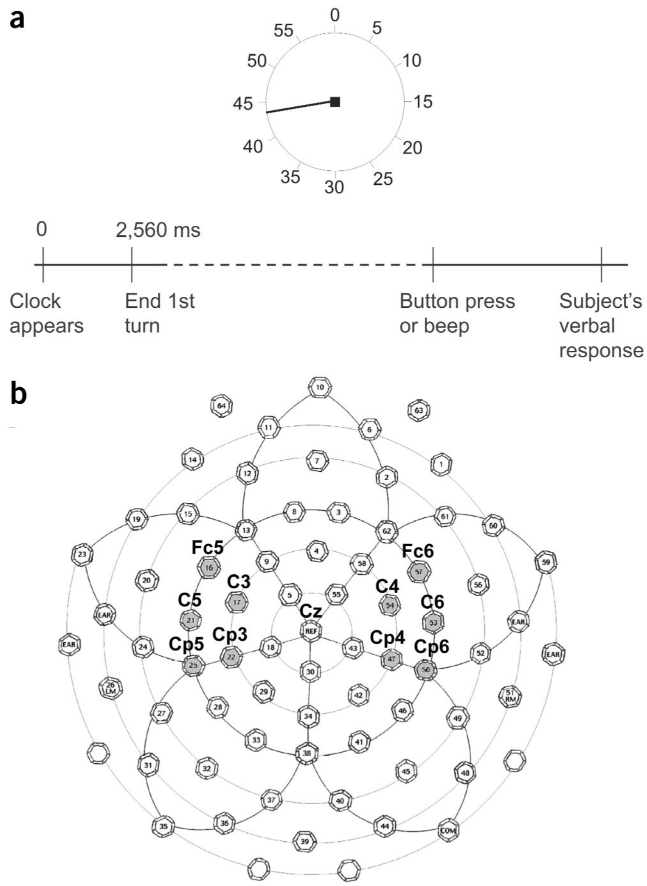

Figure 1 Task procedure and EEG recording sites. (**a**) Time course of the task. At time 0 the clock appears and the hand begins to rotate at a rate of 2,560 ms per complete revolution. Subjects were asked to push the button with their index finger at a time of their own choosing and then to report the position of the clock's hand when they executed the movement (M–judgment) or when they first made their internal decision to move (W–judgment, 'wanting to move'). (**b**) EEG electrode distribution on the scalp. Vertex electrode (Cz) served as reference[23]. For analysis, signals from Fc5, C3, Cp3, C5 and Cp5 electrodes over the left hemisphere (according to the 10-20 system) and Fc6, C4, Cp4, C6, Cp6 over the right hemisphere were averaged.

RESULTS

Behavioral data

Normal subjects were accurate when estimating movement onset (M-judgment): they judged the time of movement execution to be almost at the exact time as when they actually pressed the button (estimated – real time difference, 19.8 ± 39.0 ms; **Fig. 2**). In agreement with previous reports[10,11], subjects estimated the time they first intended to move (W-judgment) in advance of the actual movement onset (mean difference, –239.2 ± 92.9 ms). Cerebellar patients showed a similar behavior: M-judgments coincided with movement onset (mean difference, 10.9 ± 68.1 ms) and W-judgments largely anticipated onset of button press (mean difference, –314.1 ± 193.2 ms). Patients with parietal lesions also made accurate M-judgments (mean difference, –16.4 ± 94.5 ms), but in striking contrast with both normal subjects and cerebellar patients, they reported to have first intended to move at a time very close to that of movement onset (mean difference, –55.0 ± 132.6 ms). An ANOVA run on differences between estimated and actual button press revealed a significant main effect of judgment type ($F_{1,12}$ = 47.925, $P < 0.00001$) and, more interestingly, a significant interaction between group and judgment type ($F_{2,12}$ = 8.343, $P < 0.005$). Thus, whereas the three subject groups performed similarly on M-judgments, the W-judgments of parietal patients were significantly later than those of control subjects and cerebellar patients ($P < 0.004$ and $P < 0.001$, respectively, *post hoc* comparison). No difference was found between the latter two groups. A separate ANOVA compared the three groups on the control task (S-judgment). Results showed a similar pattern across subjects, in agreement with previous studies[13]: estimated time preceded beep occurrence in all subjects (control, mean difference, –85.8 ± 31.0 ms; cerebellar, –38.6 ± 46.6 ms; parietal, –60.2 ± 15.9). Indeed, no significant differences emerged across groups, confirming the selectivity of the impairment of parietal patients for the W-judgment.

Electrophysiological data

EEG patterns differed according to group. As previously shown[10–12], self-initiated movements are characterized by a progressive, negative rise in the potential recorded on the motor areas of the hemisphere contralateral to the responding hand, beginning about 1.5 s before the motor response. Here, detection of the initial rise in this potential varied between subjects and judgment conditions, but it was present in both control subjects and cerebellar patients, and for both M- and W-judgments. In controls, RP onset was detected prior to button press (897.0 ± 517.8 ms, mean ± standard deviation, s.d.) when estimating movement time and at –1331.0 ± 514.3 ms when estimating intention to move (**Fig. 3a**). A similar pattern was found in four cerebellar patients (one patient's recording was discarded because of artifacts), where RP onset was recorded in advance of movement onset in the hemisphere contralateral to the responding hand in both conditions (M-judgment:

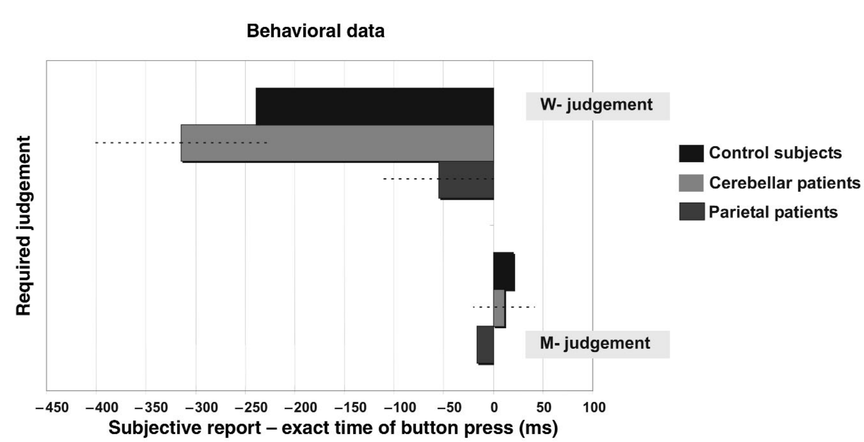

Figure 2 Behavioral data. Results for W-judgments (upper bars) and M-judgments (lower bars) in control subjects (white), cerebellar (gray) and parietal (black) patients. Dashed lines indicate standard deviation. Each bar represents the difference (in ms) between subjective report and exact time of button press. Additional data on subject response distribution across conditions can be found in **Supplementary Figure 3** online.

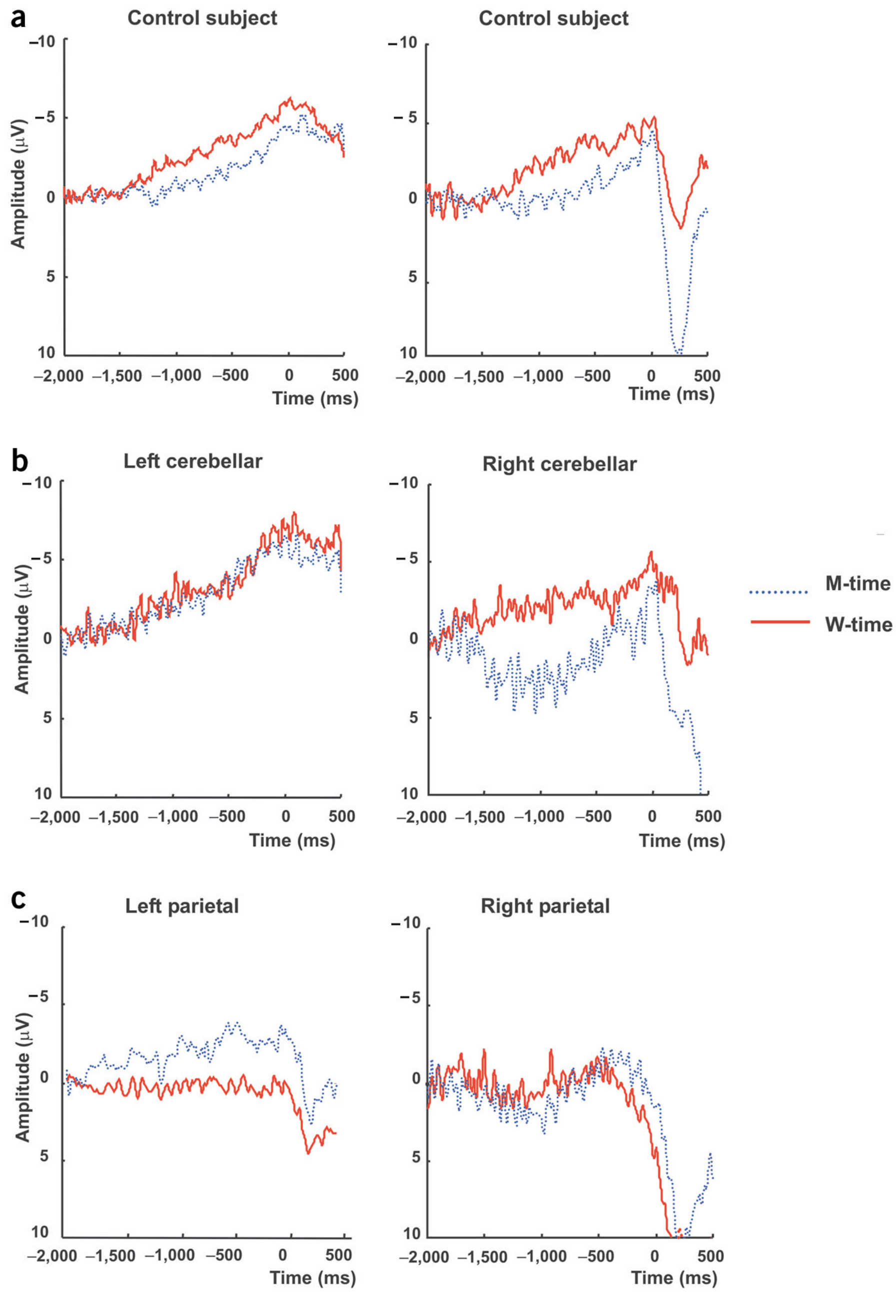

Figure 3 Samples of EEG recording. Readiness potential recorded from (**a**) two control subjects (right-hand movements, left-hemisphere recording), (**b**) a left cerebellar patient (C1, left-hand movements, right-hemisphere recording) and a right cerebellar patient (C3, right-hand movements, left-hemisphere recording) and (**c**) a left parietal patient (P5, right-hand movements, left- hemisphere recording) and a right parietal patient (P3, left-hand movements, right-hemisphere recording). Dotted blue traces indicate M-judgment trials, red lines indicate W-judgment trials. RP data for all parietal patients can be found in **Supplementary Figure 4** online. Interestingly, in normal subjects and in three cerebellar patients, RP onset in the W-condition appeared earlier than it did in the M-condition. It is well known that RPs are modulated by motor preparation and expectancy[24]. Asking subjects to focus attention on their decision to move probably involved more cognitive effort and deliberate action, thus producing the increase in RP.

–974.0 ± 411.9 ms, W-judgment: –1214.0 ± 398.1 ms; **Fig. 3b**). In the parietal patients, a different pattern was found: when W-judgments were required, RP in the motor areas of the hemisphere contralateral to the moving hand was poorly detectable. An EEG negativity with a low amplitude was found prior to button press in the case of M-judgments (M-judgment: –1551.3 ± 515.3 ms; **Fig. 3c**). A potential concern regarding the absence of a RP during W-judgment in parietal patients may be a poor EEG signal quality due to individual differences, noise, and so on. We can rule out this possibility by inspecting other components of the electrophysiological signal. First, movement-related EEG responses were present in these patients in the M-judgement condition. Comparison of amplitudes of EEG activity at the time of finger press across groups (Kruskall-Wallis test) did not show any statistical differences ($P = 0.118$, n.s.), although amplitude of maximal negativity was reduced in both patients' group compared to controls (median value: cerebellar patients –1.4; parietal patients –1.6; controls –3.1). Second, signal-related activity in response to the control stimulus (beep) showed comparable stimulus-related potentials (namely P100, N200 and P300) in parietal patients and normal controls (**Supplementary Fig. 1** online).

DISCUSSION

The results of the present experiment are highly suggestive of the different contributions of parietal cortex and the cerebellum to the production and maintenance of internal models of willed actions. By asking subjects to report the moment when they first felt the urge to move, we forced them to directly access an early stage of motor preparation, namely to access an internal model of the desired movement. As postulated above, we expected that damage to the cerebellum and/or to the parietal cortex would impair this judgment. Our results show that cerebellar patients have normal awareness of both intention and action, suggesting that this structure is not involved in this aspect of motor awareness. We can speculate that, although the cerebellum is involved in the predictive control of action[4,7] its predictions may not reach awareness[14]. On the other hand, our results show that parietal patients have lost the ability to correctly estimate the instant in time when their intention to move was defined. This deficit does not result from a nonspecific impairment in making correct temporal estimations, as shown by the fact that the patients' ability to estimate movement time was unimpaired, as was the temporal detection of the onset of a sound used in the control task (see Methods). Might the delayed judgement in the W-condition result from sensory impairment of the contralesional hand? Because of this impairment, could these patients have relied more on vision of their hand moving rather than on an internal estimate? This interpretation seems unlikely. Subjects were forced to watch the clock rather than their hand during each trial. In addition, only one subject (P4) presented a mild sensory

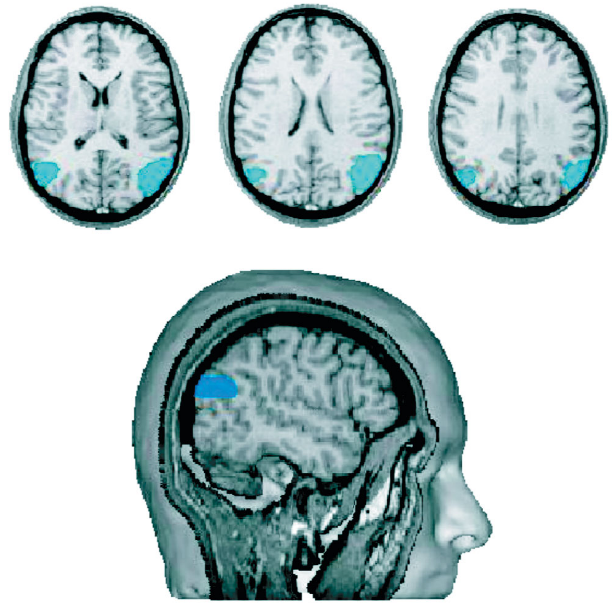

Figure 4 Lesioned cortical region (blue area) common to all five parietal patients. The ischemic lesions involved mainly the angular gyrus (Brodmann area 39) of the parietal cortex. Top, transverse slices. From left to right, Talairach coordinates (*z*-plane) of each slice: +17, +23, +28. Bottom, lateral view.

impairment for the contralesional hand, whereas the others performed normally on clinical sensory testing.

We can speculate that lesions of the parietal cortex affected either the neural processes involved in generating motor mental representations of a voluntary action or those involved in gaining subjective access to them. These hypotheses are consistent with the view that the parietal cortex contains an internal model used for conscious monitoring of voluntary actions[5,6].

Although our EEG data should be taken cautiously because of the small sample studied and to limitations intrinsic to the technique, a further suggestion could be drawn from the present study. The reduced RP observed in parietal patients is in line with their behavioral responses. It could reflect a more general deficit in EEG motor responses, but an alternative possibility is that the reduced RP in parietal patients may be a consequence of an impaired feedback loop with the frontal motor areas for elaborating and developing plans for voluntary action[15]. Interestingly, the apparent absence of volition and longer-range planning that follows extensive frontal damage suggests that prefrontal areas may be involved in generating prior intention[16,17]. Given that the parietal patients otherwise had no difficulty in initiating willed actions, our results imply that one of the parietal lobe's principal functions might be to self-monitor motor intentions, rather than being directly involved in forming intentions. This would be consistent with the idea that this brain region is necessary for anticipatory control of action[6]. Whereas the frontal cortex may thus participate in the formation of intentions, the parietal cortex might be responsible for constructing the way we experience them as linked to our actions. Further studies should directly address this hypothesis.

In all parietal patients examined, cortical damage overlapped in the inferior parietal lobule, more precisely in the angular gyrus (Brodmann area 39; **Fig. 4**). Lesions of the inferior left or the right parietal lobule produce severe and selective impairments in motor imagery[5]. When the lesions are located in the left parietal areas, a gesture disorder known as apraxia is observed. Apraxic patients are usually aware that their gestural production is inadequate, but they lack insight about what exactly they are doing wrong[18]. When placed in a ambiguous situation requiring discrimination of their own movements from that performed simultaneously by another agent, parietal patients often attribute to themselves the movement made by the other agent[19]. Finally, when a lesion of the right inferior parietal lobule occurs, patients are frequently unaware of and even deny coexisting motor disturbance[20]. Common to all of these impairments is a failure of introspection specific to the domain of action, consistent with our hypothesis that the parietal lobe plays a critical role in the conscious monitoring of motor intentions.

We suggest that the brain may contain several internal models used for predictive control of voluntary action. An implicit module in the cerebellum would provide fast processing for execution of actions and predicting their sensory consequences[7,21]. A second system, in the parietal cortex, would monitor intentions and motor plans at a higher level, detecting when actions match their desired goals. These processes typically involve conscious experience.

METHODS

Subjects. Participants were: (i) five healthy volunteers (S; all women; mean age 54.2 years, range 41–66; mean educational level 15.2 years, range 12–20) (ii) five cerebellar patients (C; three women, two men; mean age 46.0, range 24–55; mean educational level 11.6, range 5–19; mean time since lesion 11.6 months, range 7–24) (iii) five patients with selective lesion in the parietal cortex (P; all men; mean age 50.2, range 36–64; mean educational level 12.2, range 8–17; mean time since lesion 47.4 months, range 5–134). All patients were in the chronic phase. All participants were strongly right-handed according to the Edinburgh Inventory[22], except patients C4 and P4 (ambidextrous). Patients signed an informed consent to participate in the study.

Patient details. Within the cerebellar group, three patients suffered lesion to the left cerebellar hemisphere (C1, C4, C5) and two to the right (C2, C3). Except for one case (C2) in which the lesion was secondary to tumor removal, the lesion was due to either spontaneous hematoma (C1, C3) or stroke (C4, C5). Lesions of parietal patients followed stroke and involved selectively the right (P1, P2, P3) or the left parietal cortex (P4, P5). In all parietal patients, the lesion involved the angular gyrus (BA 39); in patient P4, this region alone was affected. In patients P1, P2 and P3, it extended into the supramarginal gyrus (BA 40) and in P5 into the middle temporal cortex. Lesions were reconstructed using patients' MRI (1.5-T clinical whole-body scanner, Siemens) and projected into Bancaud and Talairach MRI template (**Fig. 4**).

For each patient, elementary sensorimotor functions, gestural, visuospatial and perceptual abilities were evaluated (**Supplementary Table 1** online). A general neuropsychological screening assessed non-verbal intellectual abilities, memory functions, language comprehension and naming. No severe cognitive impairments, language deficits or visuospatial deficits were found. All patients could make voluntary hand actions with normal muscular force. Two cerebellar patients (C1, C4) showed mild optic ataxia for the ipsilesional hand. Two parietal subjects (P1, P4) showed apraxia. P1 presented mild sensory disturbance for the contralesional hand.

Procedure. Subjects sat in front of a computer (40 cm from screen), their hand on a button box. A clock (diameter 2.2 cm; marked in steps of 5 units from 0 to 60 like a traditional clock) appeared in the center of the screen (**Fig. 1a**). At the beginning of each trial, the clock's hand started to move clockwise from a random location and completed a full sweep in 2,560 ms. Subjects were asked to push the button with their index finger at a time of their own choosing: they were told to feel free to execute the movement whenever they wanted, but not before the clock's hand had completed its first full sweep. In one block of trials, subjects were instructed to attend to the actual onset of their finger movement and report the location of the clock's hand when they executed the movement

(M-judgment). In a separate block of trials, they were required to report the location of the clock's hand when they first made their internal decision to move (W-judgment, for 'wanting to move'). The clock's hand stopped its rotation at a random interval (400–800 ms) after the button press. Control subjects executed the button presses with their right index finger, cerebellar patients used the index finger of their ipsilesional hand, and parietal patients used the index finger of their contralesional hand. To assess each subject's ability to correctly estimate time, we used a control condition (S-judgment) in which the subject reported the location of the clock's hand when a beep was delivered by the computer. For M-, W- and S-judgment, two blocks of 40 trials were run. Order of block presentation was balanced.

Behavioral data recording and analysis. For each trial, the time the button press actually occurred was subtracted from the time that subjects reported that they executed (M-judgment) or first intended to execute the movement (W-judgment). For the control task (S-judgment), the time when the sound actually occurred (as recorded by the computer) was subtracted from the time at which subjects reported hearing the sound. A negative value indicates that subject's estimate preceded the real event; a positive value indicates that it followed the real event.

EEG recordings. We recorded on the scalp with a 64-channels net (**Fig. 1b**; Geodesic System, EGI) equipped with carbon-silver electrodes (sampling frequency 500 Hz). Signals were amplified, filtered (high pass 0.01, low-pass 200 Hz), collected into movements-locked epochs ranging from 2,000 ms before button press (–2,000) to 500 ms afterwards (+500), and then they were averaged. The first 200 ms of each epoch were used for baseline correction. Eye-movement artifacts were automatically filtered before averaging. EEG data analysis was performed separately for each subject.

Electrophysiological data analysis. Onset of the readiness potential (RP) was analyzed by two electrophysiologists who were naive with regard to the purpose of the experiment and the identity of the subjects (for details on computation of RP onset, see **Supplementary Fig. 2** online). Onset of muscular activity was collected by electromyography (EMG) from flexor digitorum superficialis of the responding hand (sampling frequency 1,000 Hz). EMG signals were amplified and filtered (low-pass filter 50 Hz). The first burst of muscular activity preceding a button press was considered as muscular onset. On average, this measure preceded a button press by 40.6 ms (± 12.0 ms, s.d.) in controls and by 43.8 ± 19.8 ms and 60.08 ± 19.4 ms in cerebellar and parietal patients, respectively.

Note: Supplementary information is available on the Nature Neuroscience website.

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COMPETING INTERESTS STATEMENT
The authors declare that they have no competing financial interests.

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