An accumulator model for spontaneous neural activity prior to self-initiated movement

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A gradual buildup of neuronal activity known as the "readiness potential" reliably precedes voluntary self-initiated movements, in the average time locked to movement onset. This buildup is presumed to reflect the final stages of planning and preparation for movement. Here we present a different interpretation of the premovement buildup. We used a leaky stochastic accumulator to model the neural decision of "when" to move in a task where there is no specific temporal cue, but only a general imperative to produce a movement after an unspecified delay on the order of several seconds. According to our model, when the imperative to produce a movement is weak, the precise moment at which the decision threshold is crossed leading to movement is largely determined by spontaneous subthreshold fluctuations in neuronal activity. Time locking to movement onset ensures that these fluctuations appear in the average as a gradual exponential-looking increase in neuronal activity. Our model accounts for the behavioral and electroencephalography data recorded from human subjects performing the task and also makes a specific prediction that we confirmed in a second electroencephalography experiment: Fast responses to temporally unpredictable interruptions should be preceded by a slow negative-going voltage deflection beginning well before the interruption itself, even when the subject was not preparing to move at that particular moment.

resting state | autocorrelation | volition | power-law

The role of ongoing spontaneous fluctuations in neural activity has been widely studied in the domain of perceptual decision making (1–5), but their potential role in self-initiated movement has been largely overlooked. This oversight probably arises because changes in neural activity that reliably precede the onset of self-initiated movements are attributed de facto to specific movement preparation, and thus the possibility that these might reflect random fluctuations simply never arises. The initiation of spontaneous, uncued movements raises some unique questions: If there is no external signal to trigger the movement, then what in the brain is responsible for triggering the movement, and how is the precise time of onset determined? These questions have been raised in the past (6, 7), but the possible role of ongoing spontaneous neural activity has not been considered.

The term *bereitschaftspotential* or "readiness potential" (RP) refers to a slow buildup of electrical potential, measured using electroencephalography (EEG), that reliably precedes self-initiated movements (8). Discovered in 1965 by Kornhuber and Deecke (8), the RP appears in the average over many data epochs time locked to movement onset and may begin its negative deflection one full second or more before movement onset (depending upon the subject, task, and methods) (8–11). The RP is taken to be "the electro-physiological sign of planning, preparation, and initiation of volitional acts" (ref. 12, p. 14), echoing the widely held assumption that the gradual increase in firing rate and electrical potential that precedes spontaneous movements does in fact reflect the goal-directed operations that cause those movements. Surprisingly, more than 40 y after the discovery of the RP, this assumption has only recently been questioned (13, 14).

The premovement buildup of neuronal activity apparent in the RP and the assumption of causality invested in it have become a cornerstone in the study of volition. Notably, Benjamin Libet (9, 15) tried to measure the temporal relationship between the onset of the RP and the feeling of an "urge" to move. The results of Libet et al.'s experiments (9, 15) suggested that the objective neural events in the brain that cause movement precede the urge to move by 300 ms or more. A recent experiment, using Libet's paradigm, confirms the same preurge buildup at the single-neuron level (16). Such demonstrations have had an unrivaled influence on the prevailing view that movement is initiated preconsciously and the feeling of intending to move is grafted on after the fact.

In fact a gradual increase in neural activity preceding spontaneous movements appears to be a very general phenomenon, common to both vertebrates (8, 16, 17) and invertebrates (18) alike. Why do both humans and crayfish (18) exhibit the same 1- to 2-s buildup of neural activity in advance of self-initiated movements? Kornhuber and Deecke's (12) interpretation of the RP as a sign of planning and preparation for movement fails to explain what specific neural operations underlie the spontaneous self-initiation of movement and why these operations are reflected in the specific exponential shape of the RP.

Here we present a very different interpretation of mounting neural activity preceding spontaneous movements made in the context of a spontaneous-movement production task. Our model shows that a decision threshold applied to autocorrelated noise—in this case the output of a leaky stochastic accumulator—can account for the specific shape of the RP as well as the distribution of waiting times from subjects performing Libet et al.'s (9, 15) spontaneous-movement task. We replicated Libet et al.'s (9) behavioral and EEG results and validated our model by fitting the shape of the RP, using parameters chosen by fitting the behavioral data. In addition, our model also directed us to a specific prediction that we tested with a second EEG experiment.

Spontaneous Movement Tasks

Two different paradigms are prevalent in the literature on self-initiated movement in humans. One is the paradigm of Kornhuber and Deecke (8), and the other is the paradigm of Libet et al. (9). These two paradigms are different in important ways, although both reveal a readiness potential when the data are time locked to movement onset or onset of EMG activity. In the Kornhuber and Deecke (K&D) paradigm, subjects produce self-paced movements at irregular intervals for periods of a few

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minutes at a time. Subjects are explicitly asked to avoid making rhythmic movements and to vary the intervals between movements. In studies that have used the K&D paradigm, subjects are typically told to keep the intervals within certain limits (cf. ref. 19). For example, Kornhuber and Deecke (ref. 8, pp. 3–4) asked subjects to "pause at least 15 seconds between movements, but not more than about 25 seconds"; Ball et al. (20) asked subjects to vary the interval between 12 and 24 s, and Jahanshahi et al. (21) asked subjects to produce a movement once every 3 s on average. Thus, the K&D paradigm often includes a time-interval approximation task and therefore processes of time estimation may be confounded with those specifically involved in self-initiation of movement. Both motor timing and time-estimation tasks have been associated with activation in some of the very same regions that are associated with self-initiated or self-paced movement, notably the supplementary motor area (SMA) and dorsolateral prefrontal cortex (dlPFC) (22).

In Libet et al.'s (9) task, which we adopted here, subjects do not repeatedly perform a movement at irregular intervals as in the K&D task. Instead, there are discrete "trials," with exactly one movement per trial. Once the trial begins, there is a minimum waiting interval of 3 s (indicated by a rotating clock dial on the screen), and then the subject may make the instructed movement spontaneously at any time. Subjects are specifically instructed to *not* target a particular time interval or preplan the time of their movement in any way. After the movement is made, the subject recalls the approximate position of the clock dial at the moment she or he first was aware of the urge to move. Then the subject waits for the next trial to begin.

Although our study is not concerned with the subjective urge to move, we included the clock monitoring component for completeness. The mean subjective urge to move that we report from our experiment (−150 ms) is consistent with that of prior studies (9, 16). The clock dial also ensures that subjects would not need to rely on internal time-estimation mechanisms even if they were basing their movement decisions on time elapsed.

We refer to the interval between the start of the trial and the issuance of a movement as the "waiting time" (WT). Taken literally, Libet's instructions allow the subject to wait an indefinite amount of time to produce a single movement. However, it is implicit in the demand characteristics of the task that the subject should not wait too long: The task is to produce a movement on each trial, and the subject knows this. Thus, subjects rarely wait longer than 20 s (ref. 16 and our data; *Results*).

The Stochastic-Decision Model and the Neural Decision to Move

Human subjects are able to comply with the instruction to produce spontaneous movements, at seemingly random times, when asked to do so (9, 16). We propose that the brain uses the same machinery for decision making in this sort of task as it would in any decision-making task: a threshold applied to the output of a neural accumulator (23–25). This possibility is supported by a recent study pointing to a common neural mechanism for voluntary and stimulus-driven actions (26). Decision-making tasks are typically modeled in terms of the accumulation of evidence. What is unique to the spontaneous-movement task is that subjects are specifically instructed to *not* base their movement decisions on any specific evidence, sensory or otherwise. One simple solution, given these instructions, is to apply the same accumulator-plus-threshold decision mechanism, but fed solely with internal physiological noise. In our model this solution amounts to simply shifting premotor activation up closer to the threshold for initiation of the instructed movement and waiting for a random threshold-crossing event. We refer to this as the stochastic-decision model (Fig. 1*A*, *Inset*) and implement it using a leaky stochastic accumulator process (27) with three parameters (threshold, drift, and leak; *Materials and Methods*). Accumulator models have been used extensively to characterize neural decision making (23–25, 27). These processes produce autocorrelated time series with a $1/f$ spectral profile ($1/f^{\beta}$, with $\beta \sim 2$) similar to that observed in human electrophysiology data (28).

The interpretation of premovement neural activity and its relation to other phenomena depends critically on what we mean when we refer to "the initiation of movement" in the brain—a phrase that is often used and yet poorly defined. In work on perceptual decision making, the neural decision has been likened to a *commitment* to a particular response (24) that corresponds to the crossing of a sensory-motor threshold. We apply the same logic to the spontaneous initiation of a specific movement (in the absence of any immediate sensory cue) except that in this case the decision is about *when* to move. Thus, in the context of our model, the initiation of movement corresponds to a commitment to perform a given movement *now*—a threshold-crossing event that we refer to as the "neural decision to move now." (This event is conceptually distinct from the conscious decision to move, which refers to the feeling of an urge or intention to move that may or may not play a causal role.) Note that the neural decision to inhibit (29) or veto (9) movement may intervene *after* the "neural decision to move now." Thus, we liken the "neural decision to move now" to tipping over the first in a row of dominoes—it sets into motion a cascade that is ballistic, but not deterministic (one could quickly remove the penultimate domino before the cascade reaches it).

Our model is intended to account for the activity leading up to the "neural decision to move now," but not its immediate consequences in motor cortex. We take the former to correspond to the early phase of premovement activity, until ∼150 ms premovement when the activity becomes lateralized (ref. 11 and our data; *Materials and Methods*). Activity after that time is most likely attributable to motor execution (30) rather than motor preparation. This time window also coincides with an abrupt increase in cortico-spinal excitability in primary motor cortex (31) and with subjective estimates of the time of a conscious urge to move (9, 11).

Prediction Made by the Stochastic-Decision Model

One of the most important outstanding questions surrounding the nature of the RP is, What is happening when there is no movement (32)? Our model makes a specific prediction in this regard. According to our view, the motor system constantly undergoes covert fluctuations that bring it closer to or farther from threshold. These fluctuations are ongoing throughout the epoch, far before any actual specific motor response, thus sharply distinguishing our view from the hypothesis of a fixed set of goal-directed operations occurring solely 1–2 s before an actual movement. We reasoned that we should be able to capture these ongoing fluctuations by interrupting subjects with a compulsory response cue and sorting trials by their reaction times. Assuming that the interrupted responses arise from the same decision accumulator as the self-initiated ones (26, 33), short response times should come primarily from trials in which the spontaneous fluctuations happened to be already close to threshold at the time of the interruption. Indeed, simulations show that when the model is interrupted at random times and forced to produce a speeded response (*Materials and Methods*), the fastest responses are preceded by a slow amplitude deflection (in the direction of the threshold) that long precedes the interruption itself, whereas the slower responses are not. Hence, even sensory-cued responses can be preceded by a readiness potential.

Thus, we predicted that the subject's fastest responses to unpredictable interruptions would be preceded by a significantly higher-amplitude negative-going voltage trend compared with the subject's slow responses—at the same sensors that exhibit the readiness potential. If the difference were to reflect a mounting preparation to move that was building over the course of the entire trial [i.e., the "contingent negative variation" (CNV)] (34),

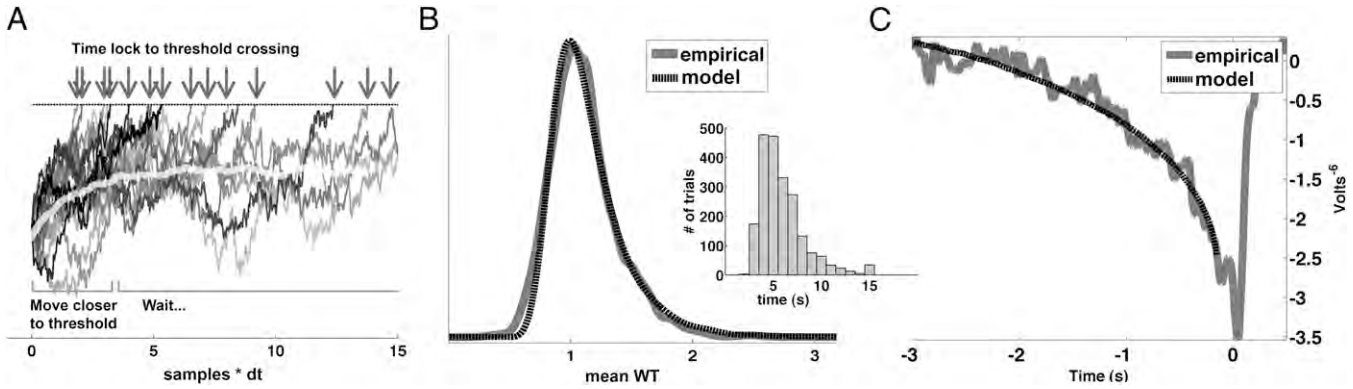

Fig. 1. The stochastic-decision model reproduces the distribution of waiting times as well as the characteristic shape and time course of the readiness potential. (*A*) Visual depiction of the model: After a stochastic exponential transition period, determined by the ratio of urgency and leak parameters, the leaky accumulator generates noisy trajectories whose threshold crossings determine movement times. When the threshold is crossed (t_0), we extract an "epoch" centered on t_0 and then reset the accumulator to zero and start the next trial. The "waiting time" is the time from trial onset to threshold crossing, and the "RP" is the average over all of the simulated epochs (sign reversed) time locked to threshold crossing. The shaded thick line in the foreground shows the mean trajectory over 1,000 simulated trials. (*B*) Mean waiting-time distribution (normalized to the mean for each subject) from the empirical data (shaded line) and the best fit of the output of the simulation (dashed solid line). *Inset* shows the distribution when the data from all subjects are pooled together (for comparison with ref. 16). (*C*) Mean empirical RP from the classic Libet task (minus the mean from −3.0 to −2.5 s; shaded line; $n = 14$) and the mean sign-reversed output of the simulation fit to the time range −3.0 to −0.15 s ($r^2 = 0.96$, $P < 10^{-9}$). To avoid overfitting, the parameters of the model (threshold, drift, and leak) were chosen on the basis of the best fit to the empirical waiting-time distribution, and then those same parameters were used to fit the RP (*C*) and for all other analyses.

then one would predict that fast responses would tend to happen relatively late in the trial compared with slow responses. However, if the difference were to reflect ongoing spontaneous fluctuations, then one would expect slow and fast reactions to be distributed equally across time within trials.

To test this empirically we devised a variant of Libet et al.'s (9, 15) task that we refer to as *Libetus interruptus*. Recall that in Libet et al.'s (9) task (henceforth the *classic* task), the subject monitors a quickly rotating clock dial and on each trial makes a single specific movement, spontaneously, at an arbitrary moment, without preplanning. The Libetus interruptus task is identical to the classic Libet task except for the addition of random interruptions: an audible "click" that cues the subject to make the movement immediately, as quickly as possible (in our experiment the movement was a button press made with the thumb of the dominant hand; *Materials and Methods*). Each trial ends when the subject either makes the movement spontaneously or is interrupted. Subjects were encouraged not to make any effort to avoid the interruptions, but to simply do as they had done previously in the classic task. By interrupting subjects at unpredictable times we set out to reveal the spontaneous brain activity that might also play a role in the onset of self-initiated movements in this task.

Results

Subjects completed 50 trials of the classic Libet task and then three blocks (150 trials in total) of the Libetus interruptus task. The mean subjective estimate of the time of the conscious urge to move (classic task) was 152 ms premovement (±33 ms SEM), consistent with previous reports (9, 11). The majority of subjects exhibited a readiness potential in the classic Libet task. In two subjects, the readiness potential (a negative-going voltage deflection before movement onset) could not be identified from the available EEG sensors, and these subjects were excluded from further EEG analyses.

We first tested the ability of the proposed drift-diffusion model to account for the distribution of behavioral WTs in the classic Libet task. When the data are pooled across subjects, the Poisson-like shape of the WT distribution is consistent with a prior replication of Libet's task (16) (Fig. 1*B*, *Inset*). Pooling the data, however, confounds variance within and variance between subjects. When each subject's distribution was normalized to its mean, the average distribution across subjects (Fig. 1*B*) showed the broad, rightward skewed shape typical of response-time distributions. We searched for parameters (threshold, leak, and drift) that best fit the empirical WT distribution from the classic Libet task and obtained an excellent fit (Fig. 1*B*). Also, the SD of reaction time is known to scale linearly with the mean in a wide range of response-time tasks, and this relationship is also true of the first crossing times in a drift-diffusion process (35). We verified that this relationship also held for the specific model and parameters that we used (Fig. 2*A*). Our empirical waiting-time data from the classic task also exhibited a clear linear relationship between the mean and SD across subjects ($r = 0.9$, $P < 0.00001$; Fig. 2*B*). This result counts as an additional validation of the model and further reinforces our claim that the same mechanisms involved in generating motor responses are at work in reaction-time tasks and the Libet task.

Using the very same model parameters derived from fitting the behavioral data, we then attempted to fit the shape of the early part of the empirical RP (−3 to −0.15 s), with the average over all of the fluctuating time series produced by the model, time-locked to threshold crossing. Again we obtained an excellent fit ($r^2 = 0.96$, $P < 10^{-9}$; Fig. 1*C*). This result is a nontrivial validation of the model, because nearby parameters yielded a poorer fit to the RP than the ones chosen by fitting to the WT distribution (Fig. S1).

We then analyzed the behavioral and EEG data from the interruptus experiment. First, we verified that the insertion of interruptions did not dramatically distort the self-initiated movement task. The mean RPs and waiting-time distributions for self-initiated responses in the classic Libet and interruptus experiments are compared in Fig. 3. Introducing random interruptions did not have any measurable effect on the shape of the mean RP on noninterrupted trials for either the model-generated or the empirical RPs (Fig. 3). Second, to test the main prediction described earlier, we focused on the trials in which the subject was interrupted by a click, grouping these trials according to whether the response time to the click was slow or fast (upper and lower third of reaction times, respectively, for each subject). Recall that the model predicted that fast responses to clicks would tend to be preceded by a slow negative-going voltage

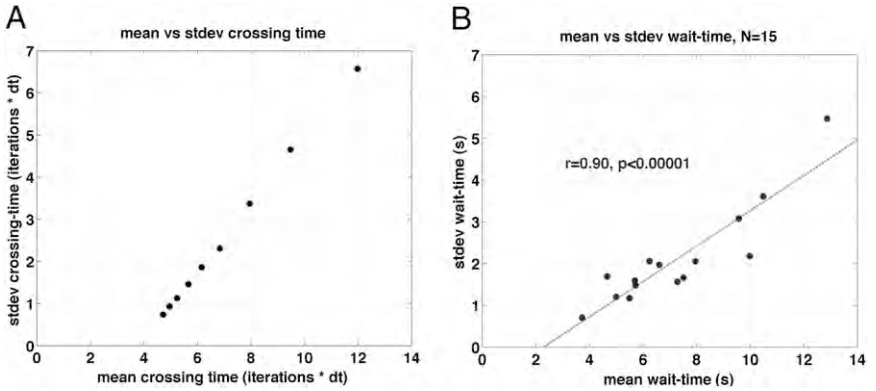

Fig. 2. (*A* and *B*) Linear relationship between mean and SD of (*A*) threshold crossing times in the simulation and (*B*) empirical waiting times in the classic Libet task. This relationship is predicted by the drift-diffusion model and by data from reaction-time tasks (35). The values in *A* were obtained by varying the urgency parameter from 0.06 to 0.22 in steps of 0.02, while keeping the other parameters (leak and threshold) fixed at the values selected by fitting to the WT distribution (Fig. 1*B*). The presence of this relationship is evidence that the same mechanism (bounded integration) thought to be involved in perceptual decision-making tasks is also at work in a spontaneous movement task.

deflection beginning well before the click itself (Fig. 4 *E* and *F*). This prediction was confirmed by the data (Fig. 4 *A*–*D*). When the data were time locked to the onset of movement, the mean difference in signal amplitude (fast minus slow) over the last 500 ms before the approximate time of the click (−0.8 to −0.3 s premovement) was significantly less than zero ($P < 0.005$, two-sided signed rank test; Fig. 4 *A* and *C*). When the data were time locked to the click, the difference was significantly less than zero ($P < 0.005$, two-sided signed rank test) over the last 500 ms before the click (−0.5 to −0.0 s preclick; Fig. 4 *B* and *D*).

Presumably the increased (negative) electrical potential preceding faster responses cannot reflect specific preparatory neural activity, because the clicks were unpredictable. However, to rule out coincidental movement preparation as an explanation, we instructed subjects to say the word "coincidence" if the click should ever happen just as they were about to move, or were actually performing the movement, and these trials, although rare, were excluded (4% of trials on average). Preconscious preparation can also be ruled out as an explanation because such coincidences would also be quite rare (similar to the frequency of conscious coincidences) and thus would have to be extreme outliers to account for the effect. We excluded trials where the mean EEG amplitude from −500 to −200 ms before movement onset (in response to a click) was different from the median by more than two times the interquartile range, individually for each subject/response speed. Therefore, it is highly unlikely that the fast responses were fast because of specific movement preparation (conscious or unconscious) coincident with the click. [One could argue that preconscious motor preparation is happening more often than once in a given trial, thus invalidating our argument. Apart from the fact that this essentially *is* our argument (with "motor preparation" replaced by "spontaneous fluctuations"), according to Libet et al. (9), these would have to be consciously aborted by the subject for them to not produce movements. Subjects were interviewed after the experiment and none reported using a strategy of repeatedly aborting movements about to occur.] Another alternative explanation for the effect is that fast responses to clicks might tend to happen later in the trial when the subject is behaviorally more primed for movement and that the preclick negativity reflects a general readiness to move that was building over the course of the trial (i.e., the CNV) (34). This buildup in readiness would predict a tendency for fast responses to happen later in the trial. Although there does appear to be a general negative trend preceding both fast and slow responses (Fig. 4 *A* and *B*), this trend cannot account for the *difference* between the signals preceding fast- and slow-click RTs: An analysis

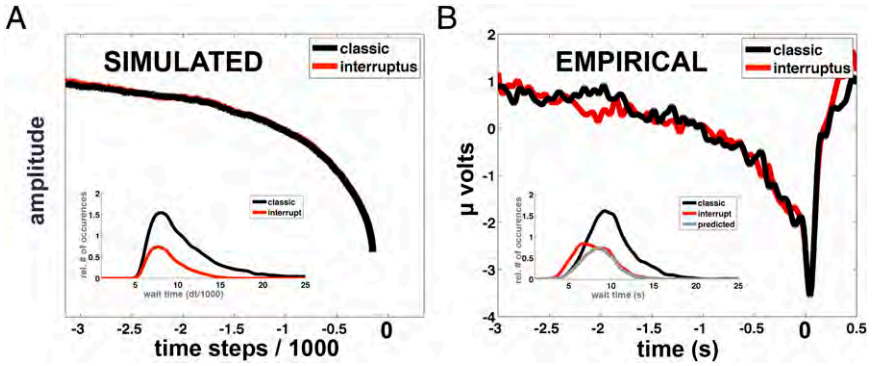

Fig. 3. Readiness potential and waiting-time distribution from the classic Libet and interruptus paradigms. (*A* and *B*) The black traces show the mean RP from the classic Libet paradigm and the red traces show the RP from noninterrupted trials of the interruptus paradigm, for the simulated (*A*) and empirical (*B*) data, respectively. *Insets* show the distribution of waiting times for the classic (black) and interruptus (red) paradigms. The truncated distribution from the classic experiment is shown in *B* (gray) for comparison with that obtained from the interruptus experiment. There were no significant differences between the RPs from the two paradigms, in either the simulated or the empirical data. The empirical waiting-time distribution from the interruptus task (*B*, *Inset*, red line) differs from that predicted (*B*, *Inset*, gray line) for shorter waiting times (<8 s), because some subjects changed their behavior during this task, tending to make their movements earlier on average. No baseline correction was applied in *B*.

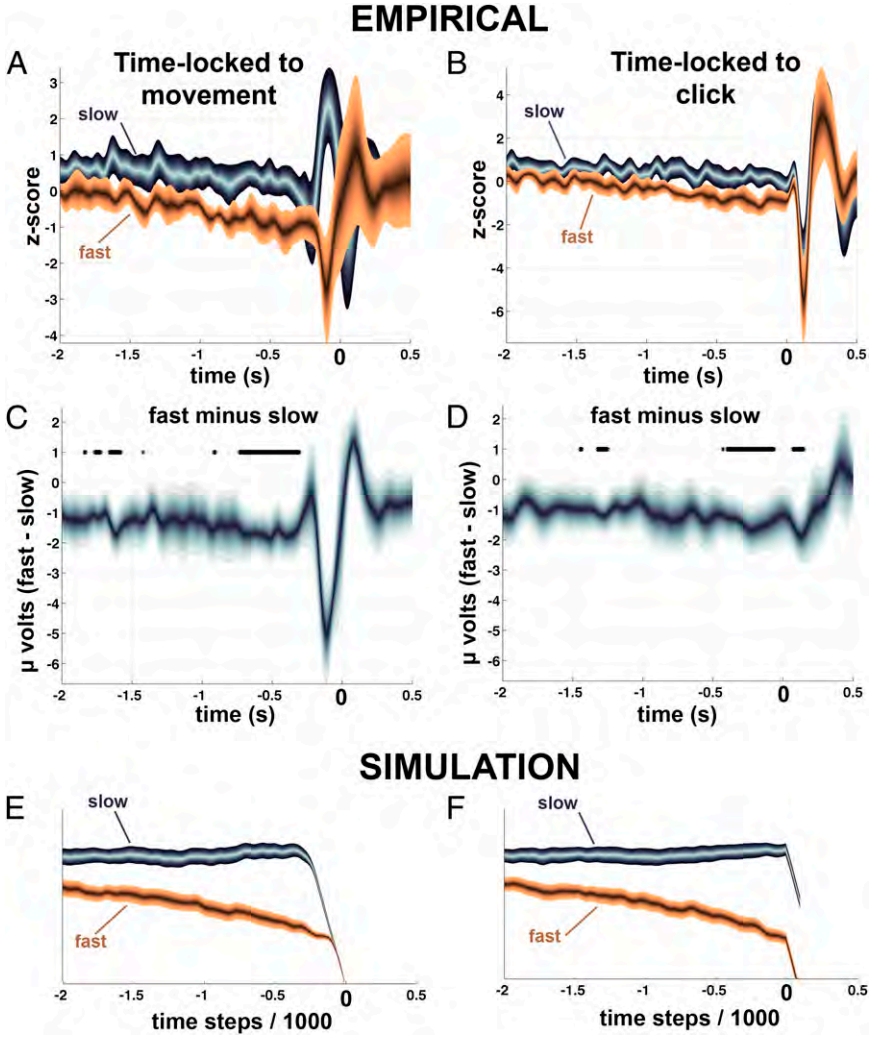

Fig. 4. Libetus Interruptus experiment. (*A*) Premovement potential (from the same electrode, near the vertex, as the RP) for fast (orange) and slow (gray) responses to clicks (intermediate responses were similar to fast responses, being only slightly lower in amplitude during the preclick interval). All graded error boundaries extend out to 95% confidence. (*C*) Difference between fast and slow responses. The black asterisks at the top mark time points where the difference is significant ($P < 0.01$, two-sided signed-rank test). (*B* and *D*) Same as *A* and *C*, except that the data are time locked to the click rather than to the movement. We propose that the faster responses (top 33rd percentile) were faster because ongoing spontaneous activity was closer to threshold at the time of the interruption. When time locked to the click, an auditory evoked potential is evident (*B*), but this potential is canceled out in the difference (*D*). Because the variance in reaction times to the click was relatively small (subjects were asked to respond as quickly as possible), a diluted auditory evoked potential is also visible when the data are time locked to the movement (*A*). The weaker and inverted evoked potential in the difference between fast and slow responses time locked to the movement (*C*) is due to the difference in reaction time (i.e., delay between click and movement) for slow vs. fast responses (the auditory evoked potentials fail to completely cancel out as they do in *D*, where the data were time locked to the click). (*E* and *F*) Results of the simulation, time locked to threshold crossing (*E*) and time locked to the interruption (*F*). A speeded response was simulated by introducing a steep linear ramp at the time of the random interruption, which is visible at the end of each trace. Interruption times were chosen randomly from a uniform distribution extending from the minimum to the maximum of the WT distribution, just as was done in the experiment. In roughly half of simulated trials the output crossed the threshold before the interruption occurred, and these were treated as "spontaneous movement" trials. For details of the model, see *Materials and Methods*. For *A* and *B* the data for each subject were normalized to the overall mean and SD in the time range −2.5 to −0.3 s (*A*) or −2.5–0 s (*B*) to remove between-subject variance.

of the distribution of preclick waiting times for slow and fast responses to clicks shows that these times were distributed equally throughout the time span of the trial ($P = 0.64$, paired-samples two-sided signed rank test, $n = 13$; Fig. S2).

We also examined the distribution of waiting times for spontaneous movements in each condition (Fig. 3, *Insets*). If subjects were able to comply with the experimenter's instruction to avoid trying to "beat the clock" (i.e., trying to always make a spontaneous movement before a click happens), then the waiting-time distribution should simply be a truncated version of the distribution in the classic Libet task. For each subject we computed the estimated waiting-time distribution for the interruptus task as the product of the distribution in the classic Libet task and the cumulative distribution of interruption times. The estimated truncated distribution closely matched part of the empirical distribution obtained for the interruptus task (Fig. 3*B*, *Inset*), but the empirical distribution showed a higher incidence of relatively short waiting times than predicted, meaning that some subjects altered their behavior by initiating movements earlier on average in the presence of interruptions.

As with any model, there are likely to be factors that are relevant to the empirical observations, but are not accounted for (explicitly or implicitly) in the model. For example, the model treats each trial as completely independent of the one before it—

there is no memory between trials. However, empirically we observed a clear relationship (positive correlation) between the waiting times in trials t and $t-1$ (Fig. S3). This relationship could arise in the model if the threshold showed slow autocorrelated fluctuations. We also found that subjects showed a small but systematic preference for making movements at the "bottom" of the clock, i.e., roughly between "15" and "45" on the clock, independent of the number of cycles (Fig. S4). These two observations are likely to reflect automatisms, although strategic factors, such as an intentional effort on the part of subjects to produce a "random" distribution of movement times with respect to the clock dial, cannot be excluded. These factors could be incorporated into a future model, but it is important to note that the model was able to account for the data quite well with only three free parameters.

Discussion

The origin of self-initiated movement is a multifaceted question, and there are numerous different contexts in which spontaneous self-initiated movements may arise: the initiation of foraging or grooming behaviors, adjusting one's position after having been seated for awhile, and even musical improvisation. The various factors involved and possible remote causes of movement initiation in these different contexts could be as varied as the contexts themselves, and the brain mechanisms involved might be equally diverse. Our study concerns events in the brain near the end of the causal chain leading to self-initiated movement, in the last 1 or 2 s before movement onset, in a context where a single specific movement is to be made "spontaneously" at an arbitrary unspecified time. Our model is intended to account for (*i*) the shape of the premovement buildup in neural activity that is known to precede spontaneous self-initiated movements made in this context and (*ii*) the distribution of waiting times observed in this context. A plethora of phenomena surround self-initiation of movement and our model is not intended to account for all of them. However, our model is conceptually sufficient to account for the two phenomena listed above, and it is empirically sufficient to account for our behavioral and EEG data.

A large body of work, spanning more than four decades, has examined the properties of the readiness potential: its temporal profile, topography at different latencies, variability in different task contexts and disease states, potential cortical "generators," and even its relevance to "free will" (36, 37). However, we still lack a precise mechanistic account of what the RP reflects, beyond descriptive phrases such as "planning and preparation for movement." Here we have offered such an account—in terms of ongoing spontaneous fluctuations in neural activity, a neural accumulator, and a threshold—that is both plausible and parsimonious. Our account departs from the prevailing assumptions about the nature of the RP and thus suggests that some very basic questions be revisited from a different perspective.

For example, there is a lack of consensus in the field on how best to divide the RP into separate partially overlapping quasi-linear phases (37), each associated with a distinct cortical generator. By contrast, according to our model, the RP can be described in terms of two nonlinear components: an early precommitment phase dominated by stochastic fluctuations (with an evolving spatial distribution) and a late postcommitment motor-execution phase (the last 150 ms). Also, the notion of an unconscious slow buildup of activity biasing supposedly "voluntary" decisions has been demonstrated in prior studies (38, 39). Our model is consistent with such predecision biases, but suggests that they may reflect stochastic fluctuations rather than an intentional (preconscious) decision process.

It is widely assumed that the neural decision to move coincides with the onset of the RP (which, given its slow nonlinear character, is difficult to pinpoint) (11). Our model challenges that assumption by suggesting that the "neural decision to move now" might come very late in the time course of the RP. Prior research shows an involvement of motor areas, including primary motor cortex, in motor imagery, in the absence of overt movement (40). Thus, movement-specific activity in motor cortex, even primary motor cortex, although it might vary with the *probability* that a movement will occur, does not necessarily signal the final commitment to produce a movement *now*. In addition, a recent study shows that the dynamics of an evolving decision process can be "read out" from activity in the motor system even before the decision threshold has been crossed, further supporting our claim that the early phase of the RP might reflect a predecision rather than a postdecision buildup (33).

We propose that the neural decision to move corresponds to a commitment to produce a movement *now* and that this commitment is associated with a threshold crossing of the accumulator underlying the response decision (33), a lateralization of the premovement potential (11), and an abrupt increase in excitability in primary motor cortex ~100 ms before the onset of muscle flexion (31) (or ~150 ms before the button press, for the hardware that we used). We propose that the precise time of the "neural decision to move now" is partly determined by spontaneous fluctuations that are temporally autocorrelated.

Temporal autocorrelation is a well-known characteristic of spontaneous neural activity at both macroscopic (41–44) and microscopic (45–49) scales and can explain why evidence-based neural decisions are partially predictable even before the evidence is provided (50). A backward selection bias (only epochs ending with an actual movement are subject to analysis) ensures that the spontaneous fluctuations that contributed to the threshold crossing are recovered in the average (8, 9) or in the probability of classifying a small segment of data as coming from early or late in the epoch (ref. 16 and Fig. S5). It also guarantees that the sequence of neural events necessary for producing a movement, no matter how complex it may be, will be reflected in the data (because a movement did in fact occur at the end of each epoch). Thus, according to our model, uncued movements in a task like Libet's tend to be preceded by a gradual increase in neural activity [measured at the scalp (8, 9) or the single-neuron level (16)] whose causal role is incidental—not directed (consciously or otherwise) at producing a movement.

The goal in each trial in Libet's task is to produce a movement at an unspecified moment sometime in the near future. We propose that this goal is effected by setting up circumstances (moving baseline premotor activation up closer to threshold) that favor the spontaneous initiation of a movement at some moment in the near future. However, the *precise* moment is not directly decided by a goal-directed operation—it is determined stochastically by ongoing spontaneous fluctuations in neural activity.

In an attempt to capture the contribution of ongoing spontaneous brain activity to unplanned movements, we introduced random interruptions with speeded responses into Libet et al.'s (9) classic paradigm. Our primary prediction was that fast responses to interruptions (an auditory click) would tend to be preceded by a gradual negative-going voltage deflection: If the motor cortex is already somewhat closer to the threshold for movement at the time that the interruption occurs, then the movement will be initiated more quickly in response. By contrast, the widely held view of the RP as a sequence of specific computations preceding a self-initiated movement does not predict a similar buildup before an unexpected response cue.

Prestimulus activity has previously been shown to influence reaction time in a choice reaction-time task (30). Our data show that the same is also true for unpredictable movement cues in a temporally unconstrained task, thus exposing ongoing spontaneous neural activity as a possible factor in the initiation of spontaneous movement. [A similar idea was once proposed (ref. 51, cited in ref. 52), but was ignored because it was dualist.]

Spontaneous subthreshold membrane potential fluctuations have been shown to influence spike times (53) and spontaneous neural activity has been shown to influence the time of perceptual transitions (54). Our study shows that there may also be a specific interaction with the onset time of spontaneous movement. However, although our study demonstrates that the readiness potential *could* reflect non–goal-directed (spontaneous) neural activity, it does not prove that this possibility is in fact the case. Further research will be required to confirm this.

Hughes et al. (26) also interrupted subjects while they prepared to make a movement. However, their subjects were trained to produce a movement no sooner than 1200 ms and no later than 2000 ms after trial onset. Thus, although the choice of which movement to make (left hand or right hand) was left to the subject, the choice of *when* to move was highly constrained—and, importantly, it was constrained to within the characteristic timescale of the RP (roughly 0.5–2.5 s). In similar work on monkeys (6, 7), also involving interruptions, waiting times were also well within the characteristic timescale of the RP and trials were short (mean waiting time of ∼2.5 s) and always ended in a movement. Thus, effects of premovement neural activity on stimulus reaction time in these studies can be attributed to specific goal-directed motor preparation.

Although the implicit demand characteristics of Libet's task (the paradigm to which we added random interruptions) ensure that subjects typically will not wait more than ∼20 s before producing a movement, the typical waiting times in our experiment (roughly 5–20 s) were considerably longer than the characteristic timescale of the RP. This span of waiting times allows us to attribute pre-interruption variability in the EEG signal to spontaneous fluctuations that are ongoing during such a task, having accounted for other factors such as urgency and coincidental motor preparation. Given that such spontaneous fluctuations are always present (55), even when we are not even thinking about moving, is it reasonable to conclude that the brain "decided" to move 2 s before the threshold crossing? We suggest reserving the term "decision" to the commitment to move achieved once neural activity (spontaneous or goal directed) crosses a specific threshold. Libet et al.'s (9) findings were surprising because they suggested that the neural decision to move happens well before we are aware of the urge to move, by 1/2 s or more. According to our model, this conclusion is unfounded. The reason we do not experience the urge to move as having happened earlier than about 200 ms before movement onset is simply because, at that time, the neural decision to move (crossing the decision threshold) has not yet been made. A very similar fluctuation in neuronal firing could equally well, at some other time, have not preceded a movement.

The connection between spontaneous fluctuations in neural activity and self-initiated movement can be generalized to real-world settings. Consider the simple act of reaching for a cup of coffee while reading the newspaper. If you set the cup of coffee within reach with the idea of drinking it, then sooner or later you will probably reach for it and take the next sip. However, why did you reach for it at the precise moment that you did and not, e.g., 500 ms earlier or later? One can extend this idea to choice behaviors such as choosing between reaching for a coffee cup *or* reaching for a muffin. If you are somewhat hungry and also somewhat thirsty, then spontaneous fluctuations might play a role in tipping the scales in favor of one or the other, as is the case with cued perceptual decisions (56). This notion might also help in understanding behavioral traits such as impulsivity, which can be predicted in individuals on the basis of a measure of long-range dependency (the Hurst exponent) applied to spontaneous fluctuations in brain activity (44).

Our model may also help to resolve certain puzzling questions, like the one posed in the introductory section: Why do both humans and crayfish (18) exhibit the same ∼2-s buildup of neural activity in advance of self-initiated movements? According to our model, all that is necessary is that the temporal autocorrelation present in spontaneous neuronal fluctuations (characterized by the $1/f$ exponent) be highly conserved across the animal kingdom, which appears to be the case (49). Just as in our model, if the precise onset time of a bout of foraging on the part of a crayfish is partly determined by spontaneous fluctuations, then these fluctuations are likely to be recovered in the average time locked to movement onset. Our model might also help to explain why the RP has not proved to be a particularly robust predictor in the development of asynchronous brain–computer interfaces (BCIs) (57–59): We assume that spontaneous fluctuations are ongoing even when the subject is not preparing to move and that these can often approach the threshold without crossing it. Therefore, false alarms will be a limiting factor in the overall sensitivity of an interface that uses slow fluctuations to infer movement intention. [There are two broad classes of brain–computer interface, *synchronous* and *asynchronous*. Synchronous BCI applications use a priori knowledge of the time of the event, e.g., by cueing the subject to form an intention. The BCI then examines the data in a small temporal window beginning with the cue and tries to determine *what* the intention is (e.g., "move the cursor left" or "move the cursor right"). By contrast, an asynchronous, or self-paced, BCI continuously monitors the signal streaming from the sensors and has to detect *when* the intention has emerged (and possibly what as well) and then trigger some external event (60).]

Finally, although our model is silent with respect to the urge to move and its temporal relation to motor decisions, it helps dissolve another puzzling question that seemed to arise from Libet's paradigm. Libet himself found that subjects were able to estimate the time of a tactile sensory decision in relation to a quickly rotating clock dial with only about 50 ms of error on average (9). Why then should there be such a long and variable gap between the time of a motor decision and the subjective estimate of the time of the motor decision, whereas no such gap exists for sensory decisions? In fact, this question arises only when we assume that the motor decision coincides in time with the onset of the RP. We have argued that this need not be the case and that the neural decision to move may come much closer in time to the movement itself (e.g., −150 ms). We propose that the neural decision to move coincides in time with average subjective estimates of the time of awareness of intention to move (9, 11) and that the brain produces a reasonably accurate estimate of the time of its movement-causing decision events.

Materials and Methods

Subjects. A total of 16 subjects participated in the experiment (6 females, mean age 28 y, 1 left handed). All had normal or corrected-to-normal visual acuity. Subjects were recruited from the surrounding community and nearby universities, and all subjects gave written informed consent to participate and were paid for their participation. Two subjects did not exhibit a negative trend in voltage (at Cz or any adjacent electrode) before movement onset and so were excluded from all EEG analyses. One subject completed only the classic Libet task. So for the classic Libet task, $n = 14$, and for the interruptus task, $n = 13$. For behavioral analyses comparing behavior between the two tasks, $n = 15$.

Stimuli and Task. Visual stimuli were back-projected onto a translucent viewing screen positioned ∼60 cm in front of the subject's eyes (Panasonic DLP projector, model PT-D7700E-K, 60 Hz refresh rate). The stimulus was a circular clock dial (white on a black background) with a small fixation cross in the center. The diameter of the clock dial subtended ∼6° of viewing angle. A small white circle (∼0.3° in diameter) moved along the inner edge of the clock dial, making one cycle every 3 s (as in ref. 9). Stimuli were presented using E-Prime (PST Software). A five-button fiber-optic response bar (Cambridge Research Systems) was held in the dominant hand. The subject cradled the bar with the fingers and pressed the topmost button with the thumb. The hand rested comfortably in the subject's lap or on a tabletop in front of the subject (according to the subject's preference). The experi-

menter sat outside of the shielded room and communicated with the subject via an intercom.

Each session began with a 5-min resting-state recording (part of a separate experiment). After this recording the subject performed 50 trials of the classic Libet task and then 150 trials of the interruptus task (three rounds of 50 trials each), in that order. Instructions for the interruptus task were explained to the subject only after the classic Libet task had been completed. The only difference between the two tasks was the possibility of interruptions in the latter task (a nonaversive auditory "pip" played through an EEG-compatible earphone). In all other respects the trial sequence was the same for the two tasks.

Classic Libet Task. Each trial began with the appearance of the fixation cross at the center of the screen. The experimenter would press a key on the stimulus computer keyboard, causing the clock face to appear. The subject would then initiate the trial by pressing the button, at which point the dot would appear and begin (starting at the top of the clock) to circle the clock face. Subjects were instructed to wait for one full cycle on the clock and then, at any time after that, to press the button. Subjects were instructed to maintain the thumb relaxed and in contact with the button throughout the entire trial (i.e., to not lift the thumb just before pressing the button) and to make one single abrupt flexion of the thumb at an unspecified time. Subjects were told to try not to decide or plan in advance when to press the button, but to make the event as spontaneous and capricious as possible. Subjects were reminded that, after the first cycle of the dot around the clock face, the movement could be made at any time. Despite this, no subject ever waited longer than 30 s to produce a movement.

After the subject pressed the button, the dot would continue to circle the clock for 1 s and then the screen would go blank. The subject would then indicate, verbally, the approximate position of the dot at the time that she or he was first aware of the urge to press the button (subjects were reminded that this is not the same as indicating the time of the movement itself, and we made sure that they understood the difference). [Libet's method for measuring the onset of felt urges has been criticized (61), but is irrelevant to this experiment, which concerns only the initiation of movement. We nevertheless report these data, for completeness.] The experimenter would then verbally repeat the number back to the subject for verification and note the time alongside the trial number in a log book (these were later entered manually onto a computer spreadsheet, alongside the trial information exported from E-Prime). The experimenter would then press a key to initiate the next trial.

Libetus Interruptus Task. The instructions for the interruptus task were given only after the subject completed the classic task. Subjects were told that they were to repeat the same task as before and were given the following additional instructions (in French): "At any time during a trial you might hear a brief click. If you hear the click, then you should press the button immediately, as quickly as possible. The trial ends when you either make a spontaneous movement or are interrupted by a click, whichever happens first." Subjects were reminded to make the movement as spontaneous as possible and were also reminded that the task is not a race to press the button before the click—the experimenter has no preference for "click trials" or "spontaneous-movement trials" (cf. ref. 7).

For the interruptus task, random interruptions were scheduled (by the computer software) for every trial. In some trials the subject made a self-initiated movement before the scheduled interruption, and in some trials the subject was interrupted before making a self-initiated movement. The time of interruptions was selected randomly from a uniform distribution with the range being selected to encompass the subject's waiting-time distribution from the preceding session. The low end of the range was never earlier than 100 ms ("10" on the clock) after the first clock cycle, to avoid extremely early interruptions. The precise range over which interruption times were randomly selected was recorded for each round for each subject, and these ranges were used for the fitting of each subject's waiting-time distribution and to derive the predicted waiting-time distribution for the interruptus task (Fig. 3*B*). The use of a Poisson distribution would have ensured that subjects could not use elapsed time to predict the probability of an interruption. However, this method would also have resulted in a preponderance of early interruptions and may have been more likely to incite subjects to rush their responses to beat the clock. Also this method would have resulted in the time of interruptions being biased toward the early part of the trial. Thus, we opted for a uniform distribution.

EEG Recording. EEG signals were recorded inside a shielded chamber at a sampling rate of 1,000 Hz (Elekta NeuroMag EEG/MEG system), while the subject performed the tasks. The subject wore a 60-channel EEG cap (Elekta NeuroMag) and sat in a reclined position. To shorten the EEG preparation time, we used a subset of the 60 electrodes, encompassing the standard 10–20 montage, with the addition of C1, C2, FC1, and FC2. We endeavored to keep impedances below 10 kOhm, while being mindful of any reported discomfort during the preparation. Electrooculograms (EOG) (horizontal and vertical) and electromyograms (EMG) (flexor pollicis longus muscle) were also recorded, using pairs of electrodes connected to bipolar recording channels. Time locking to the rectified, high-pass–filtered EMG signal did not noticeably change the results, but only shifted them ∼50 ms forward in time. Because EMG data were unavailable for three subjects (due to excess hair on the arm or an electrode coming loose) and were unreliable for a fourth, we chose to time lock to the button press.

EEG Data Analysis. Data analysis was performed using MatLab (MathWorks) with the help of the FieldTrip toolbox for MatLab (http://fieldtrip.fcdonders.nl/). A dedicated trigger channel was used to insert temporal markers in the data, corresponding to trial onset, button press, and auditory interruptions. Data epochs were time locked to the first button press after trial onset (whether spontaneous or in response to an interruption) and epochs covered the time window from −3.5 s to +1.0 s relative to that event. For time locking to interruptions, the trigger pulse corresponding to the auditory pip was located within the epoch, and the whole epoch was realigned to this sample. Independent component analysis (ICA) was used to remove ocular artifacts from the data (62). Ocular ICA components were identified by visual inspection and comparison with the EOG signals. Trials with artifacts remaining after this procedure were excluded by visual inspection. Because we were interested in slow fluctuations, no detrending, baseline correction, or hi-pass filtering was performed. Data were downsampled to 250 Hz during preprocessing, before data analysis.

Due to anatomical differences between subjects, variation in the positioning of the electrode cap, and the fact that our EEG caps came in three discrete sizes, it is unlikely that any given electrode will be optimally placed to record the RP in all subjects. Most subjects exhibited an RP at electrode Cz and one or more adjacent electrodes, especially contralateral to the dominant hand (used to perform the task), but the center of the spatial distribution varied from subject to subject. Therefore, for each subject we selected an electrode from Cz, C1, or FC1 (Cz, C2, or FC2 if left handed) on the basis of data from the classic task, showing the highest-amplitude RP. This same electrode was then used for analysis of the data from the interruptus task (so the choice of electrode used in Fig. 3 was independent of the data presented in Fig. 3). Limiting the choice to C1 (C2) or FC1 (FC2) did not change the outcome.

Model and Simulations. All simulations were performed using MatLab (MathWorks). The model includes two components: a leaky stochastic accumulator (with a threshold on its output) and a time-locking/epoching procedure. We used a well-known accumulator model (DDM) (27), which is an extension of an earlier model developed by Ratcliff (23). Simulation of the model amounts to iterative numerical integration of the differential equation

$$\delta x_i = (I - kx_i)\Delta t + c\xi_i\sqrt{\Delta t}, \quad [1]$$

where I is drift rate, k is leak (exponential decay in x), ξ is Gaussian noise, and c is a noise-scaling factor (we used $c = 0.1$). Δt is the discrete time step used in the simulation (we used $\Delta t = 0.001$). In the context of our model, I corresponds to a general (and we assume constant) urgency to respond that is inherent in the demand characteristics of the task. A small amount of urgency is necessary in the model to account for the fact that subjects rarely if ever wait longer than ∼20 s to produce a movement in any given trial. Because of the leak term, the urgency does not set up a linear trajectory toward the threshold (i.e., if we were to increase the threshold that we used by a factor of 2, the output of the accumulator would essentially never reach it), but simply moves the baseline level of activity closer to the threshold so that a crossing is very likely to happen soon (Fig. 1, *Inset*).

Thus, the model has three free parameters, urgency (I), leak (k), and threshold (β). The threshold was expressed as a percentile of the output amplitude over a set of 1,000 simulated trials (50,000 time steps each). These three parameters were chosen on the basis of the best fit of the first crossing-time distribution to the empirical waiting-time distribution from the classic Libet task (we use the term "waiting time" instead of "reaction time"). The parameters were then fixed at these values for all other simulations and analyses, including the fitting of the RP. The three parameter values assigned were $k = 0.5$, $I = 0.11$, and $\beta = 0.298$ (corresponding to the 80th percentile). We modeled the classic task by simply identifying the time point of the first threshold crossing in each simulated trial and then extracting the time series (the output of the accumulator) from 5,000 time steps before the threshold

crossing to 500 time steps after. If the first crossing was earlier than sample no. 5,000 by $n > 0$ samples, then we padded the beginning of the epoch with n null values (*nan*s or "not-a-number" in MatLab). These values do not contribute to the average across simulated trials, so the simulated average RP becomes noisier at very early time points in the epoch. Thus, one limitation of our model is that history cannot extend back earlier than the beginning of the trial.

We modeled the interruptus task by selecting random interruption times from a uniform distribution (just as we had done in the real experiment). For each simulated trial, if the output exceeded the threshold before the scheduled interruption, then a spontaneous-movement epoch was recorded, as explained above. If not, then we added a steep linear ramp to the output at the time of the simulated interruption. The difference between the crossing time of the ramp and the interruption time was recorded as the simulated reaction time.

Choice of Time Range over Which to Fit the Model Output to the RP. The difference between EEG signals contralateral and ipsilateral to the responding limb, known as the lateralized readiness potential (LRP), has previously been linked to awareness of movement initiation (11) and might mark the time of a threshold-crossing event: Its amplitude does not vary with reaction time (for cued movements) (30) and reaches a critical threshold level only when a movement is actually made (but not when a movement is prepared and then inhibited) (29). Thus, we apply our model to account for the signal up until 150 ms before button press—the time of maximum (negative) slope of the LRP in our data. This point in time also coincides with an abrupt increase in cortico-spinal excitability at ~100 ms before EMG onset (31) (equivalent to ~150 ms before the button press in our experiment). We computed the LRP as the difference between sensors C1 and C2, for right-handed subjects, or C2 and C1, for left-handed subjects. Activity after that time is most likely attributable to motor execution (30)—i.e., to activity that follows rather than precedes the threshold crossing. The goodness of fit did not depend heavily on the precise time range chosen: Good fits could be obtained by placing the leading end of the model output at −200, −150, or −100 ms (with the best fit being at −100 ms). We made an a priori choice of −150 ms.

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