Veto and Vacillation: A Neural Precursor of the Decision to Withhold Action

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Abstract

■ The capacity to inhibit a planned action gives human behavior its characteristic flexibility. How this mechanism operates and what factors influence a decision to act or not act remain relatively unexplored. We used EEG readiness potentials (RPs) to examine preparatory activity before each action of an ongoing sequence, in which one action was occasionally omitted. We compared RPs between sequences in which omissions were instructed by a rule (e.g., "omit every fourth action") and sequences in which the participant themselves freely decided which action to omit. RP amplitude was reduced for actions that immediately preceded a voluntary omission but not a rule-based omission. We also used the regular temporal pattern of the action sequences to explore brain processes linked to omitting an action by time-locking EEG averages to the inferred time when an action would have occurred had it not been omitted. When omissions were instructed by a rule, there was a negative-going trend in the EEG, recalling the rising ramp of an RP. No such component was found for voluntary omissions. The results are consistent with a model in which spontaneously fluctuating activity in motor areas of the brain could bias "free" decisions to act or not. ■

INTRODUCTION

In everyday life, our initial impulses do not always produce optimal actions. Most people recognize the experience of deciding against saying what one really feels to avoid offending a friend. In such cases, the decision to inhibit the action is intentional, self-generated, and often very wise. However, most previous studies of action inhibition have focused on external "stop" signals (Smith, Johnstone, & Barry, 2008; Verbruggen & Logan, 2008; Falkenstein, Hoormann, & Hohnsbein, 1999). These tasks capture only a part of self-control and cannot capture the familiar case of an endogenous decision to cancel an action, referred to as "intentional inhibition" (Filevich, Kühn, & Haggard, 2012). Recent studies have explored intentional inhibition by asking people to prepare an action and then decide for themselves whether to execute or inhibit it. Intentional inhibition produced distinct fMRI activations in medial pFC (Kühn, Haggard, & Brass, 2009; Brass & Haggard, 2007) and changes in EEG power around the time of the decision (Walsh, Kühn, Brass, Wenke, & Haggard, 2010).

Although intentional inhibition may seem closer to human self-control than external stop signals, the brain mechanisms involved remain unclear. Most neurocomputational models of voluntary action have focused on action generation rather than inhibition. For example, several models of frontal cortex are based on hierarchies (e.g., Kouneiher, Charron, & Koechlin, 2009; Koechlin, Ody, & Kouneiher, 2003; Brass & Von Cramon, 2002) with anterior areas generating abstract aspects of a plan and posterior motor areas executing them or generating stimulus-driven responses. However, the mechanisms that initiate plans at the highest level areas remain unexplained.

One could instead think of the voluntary motor system as a loop, in which each action depends on a preceding action, rather than as a linear process with an unexplained initiation. Frontal cortico- BG loops (Alexander & Crutcher, 1990; Alexander, DeLong, & Strick, 1986) could produce internally generated action sequences (Boecker et al., 1998; Tanji & Shima, 1994; Brotchie, Iansek, & Horne, 1991) by chaining each action to the one before. On this view, there need not be any obvious hierarchical starting point for voluntary behaviors. Thinking of voluntary action as an iterating loop with a characteristic activation level may also explain the strong relation between cognitive resources and action inhibition. Inhibition of action becomes difficult and self-control may break down when a drive to act is sustainedly present (Baumeister, Vohs, & Tice, 2007; Mischel & Ebbesen, 1970). Here we examine the opposite possibility, whether action inhibition emerges at points where the level of activation in a repeated behavior is momentarily reduced.

We have considered how voluntary decisions to act or not to act arise within a continuous action sequence. Participants were asked to omit one particular action within a repetitive manual motor sequence, based either on an endogenous voluntary choice or an external instruction. Incorporating intentional inhibition into a regular action sequence provides a background of prepotent action. As a result, it may be necessary to truly inhibit an

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action, as opposed to merely failing to initiate it (Filevich et al., 2012; Kühn et al., 2009). Furthermore, studying a regular sequence of actions helps to fix action timing, allowing us to infer when inhibition of action should occur, if it is present.

We investigated the relation between preparation of the next element in a continuous motor sequence and the voluntary decision to omit an action by examining the late, lateralized component of the readiness potential (RP; Shibasaki & Hallett, 2006). Because this component immediately precedes voluntary actions (Matsuhashi & Hallett, 2008; Sirigu et al., 2004; Libet, Gleason, Wright, & Pearl, 1983), its magnitude offers a valuable neural signature of the generation versus inhibition of voluntary action. We described above a nonhierarchical loop model for voluntary chaining of sequences of motor actions. Such models predict that activation states are passed around successive iterations of the loop. On this view, the generation or inhibition of a current action may depend on the level of system activity associated with a previous action. For example, a falling level of activation over successive loop iterations may eventually lead to an inhibition or failure to generate the next action.

METHODS

Participants

Twenty-six right-handed participants (15 men, 11 women) were tested. Eight participants were excluded (three had excessive blink/ EOG artifacts, one could not produce a regular action sequence, one could not avoid tapping their foot in addition to their finger, one made excessive finger movements between actions, and two made too few voluntary omissions for ERP analysis to be possible), leaving 18 participants with usable data. All had normal or corrected-to-normal vision, and none had a history of neurological or psychiatric disorders.

Design

In all tasks, participants pressed the space button on a keyboard with their right index finger once every 2 sec in a self-paced manner. In the rule-based omission task, participants used a rule given by the experimenter to omit every fourth or sixth keypress in the sequence. In the voluntary omission task, participants were instructed to omit a keypress when they themselves chose. Participants were asked to be as spontaneous as possible in voluntary omissions and to decide at the very last moment prior to action. They were asked to avoid preplanning omissions or following a rule. Rule-based and voluntary tasks had 20 trials each. The order of these two tasks was alternated across participants. Individual trials ended once 30 keypresses were made, resulting in trial durations of approximately 1 min.

For the first nine participants, the instruction for the rule-based condition was to omit every fourth keypress. However, preliminary inspection of the data showed that voluntary omissions tended to occur more rarely than this, producing a confound between condition and motor activity. Therefore, the remaining nine participants were instructed to omit every sixth keypress. This successfully balanced overall action and omission frequency across conditions.

Procedure

Participants first practiced synchronizing keypresses to a 0.5-Hz auditory metronome, allowing them to learn the required rhythm. In the subsequent tasks, no external pacing stimulus was given. Participants were asked to avoid counting seconds in their timing and simply to follow the rhythm they had learned in the synchronization phase. In all trials, participants were first presented with an instruction to "Press space to begin the trial." Following the keypress, a white fixation cross on a black background appeared centrally on the monitor, which participants were asked to remain fixated on while continuing keypresses at an internally paced rate of approximately 0.5 Hz.

In the practice task, participants produced a sequence of 30 keypresses at 0.5 Hz in each trial. Then the experimental tasks began. In the rule-based omission condition, participants were instructed to omit every fourth or every sixth keypress (see Design). In the voluntary omission condition, participants freely chose when to omit keypresses. Precise timing between keypresses was incentivized in the experimental session. Participants received feedback about their performance at the end of each trial. The mean interval between their actions had to be within 1700–2300 msec, and the standard deviation of these intervals had to be below 200. Omitted actions required an extended average interval of 3500–4500 msec between consecutive actions and standard deviation below 500. Fifteen pence per trial was gained for passing all criteria. Optimal performance could potentially increase participant income by £6.

EEG

Twenty-seven EEG channels (FT8, FC6, FC4, FC2, FCz, FC1, FC3, FC5, FT7, T8, C6, C4, C2, Cz, C1, C3, C5, T7, TP8, CP6, CP4, CP2, CPz, CP1, CP3, CP5, TP7) were recorded from sensorimotor areas. The ground electrode was at scalp position AFz, and the reference electrode was attached to the right earlobe. EOG electrodes were attached to the external canthi of each eye and the supra and suborbital areas of the right eye. A bandpass filter between 0.1 and 30 Hz and a notch filter of 50 Hz were applied, and the sampling rate was 256 Hz. Data were preprocessed and analyzed in EEGLAB v10.2.5.6b running in Matlab 7.10.

Epochs were defined from 1000 msec before to 500 msec after each keypress and baseline-corrected at −1000 to −800 msec. The baseline correction served to remove effects of very slow EEG drifts and isolate the component of the EEG related specifically to each action. Omission events were inferred using the temporal interval between immediately preceding actions. If the omitted action is labeled n and the preceding actions $n − 1$ and $n − 2$, then whenever an extended interkeypress interval indicated an omission, the temporal interval between $n − 1$ and $n − 2$ was repeated to insert an omission event in the data. Although this was only an estimate of the omitted event timing, its accuracy was assumed to be similar for rule-based and voluntary omissions.

Epochs were discarded if the potential from any EOG electrode fell outside +80 to −80 μV or any other electrode fell outside +100 to −100 μV. Improbable epochs that contained EEG signal amplitudes exceeding five standard deviations of the mean probability distribution or the mean kurtosis value were removed (Delorme, Sejnowski, & Makeig, 2007). Linear detrending was applied over the recording period to identify and remove drift (Matsuhashi & Hallett, 2008). Participants were discarded if the number of events for any condition fell below 50 after artifact rejection (see Participants).

To investigate action preparation, the EEG signal for the last 500 msec before action onset was averaged from the C3 electrode (the late bereitschaftspotential (or late RP) over the contralateral motor area; Shibasaki & Hallett, 2006). Given the short intervals of approximately 2 sec between each action event, earlier components risked contamination from previous action related activity. Therefore, only the late RP found at C3 was analyzed. The same procedure was used for inferred omission onsets.

RESULTS

Inspection of EEG traces and statistical comparisons showed no differences between the groups that omitted every fourth and every sixth action in the rule-based condition. Therefore, the data were pooled across groups. We defined "omission − 1" actions as those that immediately precede omissions and "omission + 1" actions as those that follow omissions. All other actions were classified as "standard actions."

Behavioral Data

Behavioral data are shown in Table 1.

There was no difference between the rule-based and voluntary conditions in the number of rewarded, that is, accurately timed trials, $t(17) = 0.41, p > .05$. The temporal intervals between successive actions tended to be shorter in the rule-based than the voluntary condition, although this effect did not reach significance $t(17) = −1.93, p = .07$. There was no difference in the duration of omission intervals, $t(17) = −1.18, p > .05$. This sug-

Table 1. Rewards (i.e., Appropriately Timed Actions, See Text) and Mean Temporal Intervals in Rule-based and Voluntary Conditions

	Rule-based	Voluntary
Rewards (%)	70 (23.3)	68.3 (24.4)
Action intervals (msec)	1977.2 (109.0)	2045.5 (110.7)
Inhibition intervals (msec)	3870.5 (198.5)	3935.9 (206.8)

gests that the conditions did not differ substantially in difficulty and participants maintained broadly similar timing across both. In the voluntary condition, participants made 5.54 actions on average between omissions with a standard deviation of 1.1. In the rule-based condition, by contrast, the number of actions between omissions was instructed to be 3 or 5 (for "omit every fourth action" and "omit every sixth action," respectively; see Design).

EEG Data

Figure 1 shows ERPs for the different types of action at electrode C3.

RP amplitudes were calculated prior to actions in the late RP period (mean of the signal during the period −500 to 0 msec). We separately averaged actions immediately before and after the omission and all other "standard" actions. A 2 × 3 ANOVA with factors of Omission Type (rule-based/voluntary) and Action Position (standard actions/omission − 1 actions/omission + 1 actions) showed no main effects of either Omission Type, $F(1, 17) = 1.34$, $p > .05$, or Action Position, $F(2, 34) = 1.15, p > .05$. However, a significant interaction was found between these factors, $F(2, 34) = 6.68, p < .01$.

To explore this interaction, simple effects tests were used to compare voluntary and rule-based RPs for each action. There were no differences in RP amplitudes between rule-based and voluntary conditions for standard actions across the conditions, $t(17) = 0.45, p > .05$, or omission + 1 actions, $t(17) = 1.61, p > .05$, but a significant difference was found for omission − 1 actions, $t(17) = −4.01, p = .001$ (scalp map plots directly showing the difference between conditions can also be seen in the supplementary data). The crucial difference between conditions therefore lies in preparatory activity for actions that immediately precede an omission. Simple effects were also tested by comparing each RP within the rule-based and voluntary conditions. RP amplitude for omission − 1 actions was significantly reduced compared with standard actions in the voluntary condition, $t(17) = 2.56$, $p < .05$, but no difference was found in the rule-based condition, $t(17) = −1.36, p > .05$. Omission − 1 RPs were reduced relative to omission + 1 RPs in the voluntary condition, $t(17) = 2.89, p = .01$, but not in the rule-based condition, $t(17) = −0.32, p > .05$. Omission + 1 potentials did not differ from standard actions in either
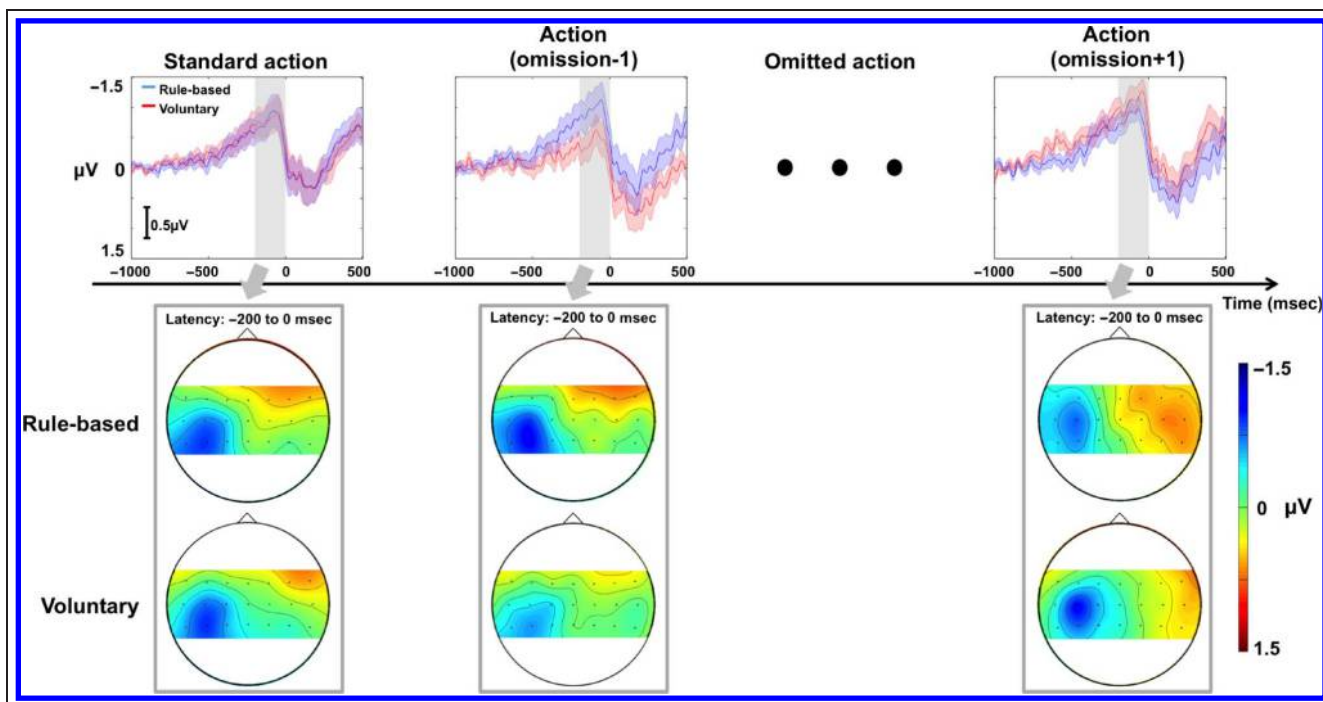
Figure 1. ERP data ($n = 18$) for standard, omission -1, and omission $+1$ actions at electrode C3—the position of the omitted action in the sequence is indicated by the dots. Shaded colors around ERPs show standard error. Data are time-locked to action onset (keypress). Note difference between conditions in RPs for actions immediately prior to omission.

the voluntary condition, $t(17) = 1.58$, $p > .05$, or the rule-based condition, $t(17) = 0.37$, $p > .05$.

We also explored the EEG activity related to action omission by time-locking to the expected time of action. We had no strong prior hypothesis about the scalp location or form of omission potentials. However, we note that response inhibition has been frequently localized to medial frontal areas (Simmonds, Pekar, & Mostofsky, 2008; Picton et al., 2007; Mostofsky et al., 2003) and that departures and omissions from regular sequences of events are typically measured by vertex potentials (e.g., Nordby, Hammerborg, Roth, & Hugdahl, 1994). We therefore compared the omission potential at Cz using the same time window as for RPs preceding action. The data are shown in Figure 2. In the period before rule-based omissions, the trace showed a negative-going deflection. This deflection was maximal over the contralateral sensorimotor cortex and had a similar form to an RP, though a somewhat smaller amplitude. Furthermore, the abrupt shift to positivity just before movement onset that marks the end of the classical RP was not present for rule-based omission trials. Because the classical RP is characterized by a negative-going ramp-like form, we used linear fits to the averaged EEG in the -500 to 0 msec time window corresponding to the late RP to investigate whether a component similar to RP might be present on omission trials. We found a trend toward a negative slope for rule-based omissions, $t(17) = -1.89$, $p = .08$. In contrast, we found a positive-going slope before voluntary omissions. This slope was significantly greater than zero: $t(17) = 3.4$, $p < .01$. Furthermore, the

slopes significantly differed between the two conditions: $t(17) = -5.02$, $p < .001$.

Finally, we compared mean amplitudes during the time window of the late RP for omissions in the same way as we previously did for actions. This showed a significantly greater amplitude for voluntary than for rule-based omission potentials, $t(17) = 2.99$, $p < .01$.

DISCUSSION

We measured event-related EEG associated with actions and with decisions to omit actions in a regular sequence.
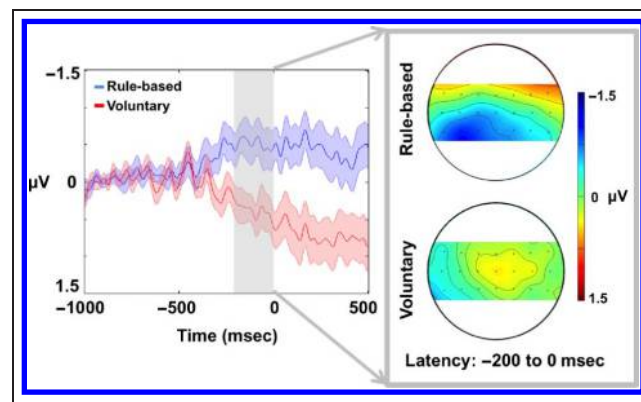

Figure 2. ERP data ($n = 18$) for omissions at electrode Cz (left) and across the scalp (right). Shaded colors around ERPs show standard error. Zero milliseconds indicates the inferred time of action omission.

Our results indicated that the "voluntary" decision to omit a particular action was prefigured by a reduced RP for the immediately preceding action in the sequence. The motor system seems primed in advance to omit an action voluntarily. This was not the case in a rule-based condition, where the particular action to be omitted was specified beforehand by a rule. Therefore, the decrease in action-related processing prior to voluntary action is unlikely to reflect simple advance planning for the forthcoming omission, because such advance planning should be even more evident when using a rule than when choosing "freely." Any difference in task difficulty across the rule-based and voluntary tasks also seems unable to account for the findings. Although a difference in difficulty could explain a main effect of task, it cannot readily explain the interaction between task and action type (i.e., standard/preomission/postomission actions) found in our RPs. One might suggest that the effect of task difficulty could be temporally focused on the period just prior to omission, but this seems implausible, because scalp topographies show the main modulation during these periods to be over motor areas, rather than the distributed network associated with task difficulty (e.g., Sunaert, Van Hecke, Marchal, & Orban, 2000). Instead, these results are consistent with a loop model for action generation, in which the level of activation in an iterating motor loop influences decisions to act or not. In particular, background fluctuations in the activation level of such a loop could affect a high-level choice process. A purely hierarchical, feedforward model, in which decisions originate at high levels and cascade unidirectionally to lower levels for execution (e.g., Kouneiher et al., 2009), cannot easily explain the association between the activation associated with execution for one action and the decision to omit the next. Our result does not rule out hierarchical models per se, but it does imply that the higher levels in the hierarchy are influenced by feedback from lower-level execution processes.

Because our sequential action task had regular timing, we were also able to calculate ERPs associated with actions that are inhibited by time-locking to the moment when the action would have been expected to occur. The latencies of ERP components for these averages should be interpreted with caution, because the time-locking point is only inferred, rather than measured. Any inaccuracy in this inference will produce a temporal smearing of ERP components and a reduction in ERP amplitude. Therefore, comparing amplitudes between omission-related potentials and action-related potentials may be problematic. However, we can compare omission-related potentials between rule-based and voluntary conditions. Both conditions should be equally affected by smearing, and indeed temporal intervals for actions and omissions did not differ between the conditions (see Results). We found a trend toward a negative-going, ramp-like component, similar in some ways to the form of an RP, prior to instructed, rule-based omissions. Voluntary omissions, however, were preceded by a positive-going potential. We cannot exclude the possibility that this prolonged positive shift may include other components. For example, studies of stimulus-locked no-go potentials found a no-go-P3 component (Bokura, Yamaguchi, & Kobayashi, 2001; Falkenstein et al., 1999), directly related to response inhibition. A temporally smeared version of these components could contribute to our omission-related potentials, but the difference between conditions nevertheless remains. Alternatively, the negative-going omission-related potential in the rule-based condition could conceivably represent a "simulated" but not executed action. For example, participants might represent the rule-based action sequence as a rhythmic pattern. They might then simulate the "missed beat" of this rhythm to follow the omission rule.[1] In any case, this component was not present prior to voluntary omissions, suggesting an important difference between voluntary and rule-based omissions.

Previous studies of intentional inhibition have been hampered by the difficulty of assessing whether a failure to act was because of a predecision to not initiate any action processing or because of a specific last moment process of inhibition (Filevich et al., 2012). Because there is no clear behavioral marker to indicate the time of inhibition, it is difficult to distinguish whether inhibition occurs early or late relative to action preparation. This distinction is important, because an early inhibition effectively reduces the decision to inhibit to action selection (Mostofsky & Simmonds, 2008), whereas late inhibition implies a specialized cognitive process reminiscent of self-control. The design of our task controls this aspect. In particular, rule-based omission implies predecision about inhibition. In contrast, our voluntary condition invited participants to decide spontaneously to omit an action, as a result of their own real-time choice. If participants had in fact predecided which action to omit in the voluntary condition, then no difference would be expected between voluntary and rule-based conditions. The results showed that voluntary omission was associated with a reduced RP for preceding actions, whereas rule-based omission was not. Reduction of preceding RPs may reflect a mechanism underlying voluntary decisions to inhibit which is independent of conscious prior decision and which could potentially explain the spontaneous nature of some action choices (Libet et al., 1983). In essence, free decisions may capitalize on the momentary state of activation in motor circuits.

Competition between Action and Omission

Recent models of action selection have proposed that plans for multiple response alternatives compete simultaneously in the motor system (Klaes, Westendorff, Chakrabarti, & Gail, 2011; Cisek & Kalaska, 2010; Cisek, 2007). Accumulating information and biasing influences from the BG and pFC contribute to resolving the competition and to selecting a particular response.

Ongoing fluctuations in the level of activity of the cortico-BG-thalamocortical circuit (Alexander & Crutcher, 1990; Alexander et al., 1986) might provide the basis for binary decisions about action and inhibition behavior. Low activity would make omission more likely, whereas higher activity would favor action. Progressively reducing motor activity would lead to the "voluntary" decision to omit, as shown by our RPs for actions immediately preceding omission.

The lack of preparatory motor activity or excitability during voluntary omissions is consistent with the idea that low spontaneous motor activity biases the choice to omit an action. At electrode Cz, voluntary omissions showed an increasing positivity replacing the ramp-like negativity of the normal RP. EEG provides only a weak indication about the location of underlying generators, which may not correspond to the maximal location of the component on the scalp. However, the central distribution of this positive-going potential could reflect activity in pre-SMA or other medial frontal areas involved in inhibition (Simmonds et al., 2008; Brass & Haggard, 2007; Picton et al., 2007). In any case, our results suggest a specific inhibitory process associated with voluntary inhibition and marked by a positive-going potential at the scalp.

Although both voluntary and rule-based action selections employ a prefrontal control component in the planning of the temporal structures of events and the control of goal-directed action behaviors (Tanji & Hoshi, 2008), a clear external rule appears to override the biasing effects of spontaneous activity in the motor systems. Thus, we found no reduction in RP for actions prior to omission in the rule-based condition. In fact, we found a trend toward a negative-going shift even before rule-based omissions themselves. We speculate that this may correspond to an internal preparation or simulation process, which occurs even when action execution is omitted (Osman, Albert, Ridderinkhof, Band, & van der Molen, 2006) —indeed several fMRI studies confirm that primary motor cortex is often activated during simulated or imagined action (Lacourse, Orr, Cramer, & Cohen, 2005; Gerardin et al., 2000; Lotze et al., 1999). Interestingly, this component was not present for voluntary decisions to omit. This finding is consistent with our hypothesis that voluntary omissions are associated with a reducing level of motor activation.

Another possible account for the present findings is based on changing levels of uncertainty about action in the voluntary condition. Greater probability (certainty) of an impending action has been associated with larger preparatory motor potentials (Scheibe, Schubert, Sommer, & Heekeren, 2009; Low & Miller, 1999). In the voluntary task of this study, there is ongoing uncertainty about whether one should act or omit action in each moment. Given that actions should be omitted at some point in the sequence, voluntary decisions to omit action may involve a hazard function. Each successive action in the sequence up until the omission involves greater uncertainty than the one before, because it is increasingly likely that the omission will shortly occur. This growing uncertainty might progressively reduce RP amplitudes and could therefore account for the reduced RP we found for omission − 1 actions. In contrast, there is never uncertainty about action in the rule-based task. An account based on uncertainty therefore makes two clear predictions. First, the voluntary task should have globally smaller RPs compared with the rule-based task. The near-identical RPs found for standard actions across the voluntary and rule-based conditions goes against this prediction. Second, in the voluntary task only, RPs should progressively decrease in amplitude as the omission approaches, following a hazard function. In principle, this second prediction could be tested by comparing RPs for omission − 1, omission − 2, …, omission − n actions. However, our design gave too few trials at omission − 2 and earlier actions to calculate reliable ERPs for testing this prediction. A study with more trials and longer sequences of actions prior to omission would be required to test the uncertainty hypothesis in detail.

The Influential Role of Spontaneous Motor Activity in Voluntary Decisions

There is strong evidence indicating that ongoing spontaneous activity in neural systems influences motor behaviors (Mazaheri, Nieuwenhuis, van Dijk, & Jensen, 2009; Fox, Snyder, Vincent, & Raichle, 2007; Churchland, Afshar, & Shenoy, 2006; Connolly, Goodale, Goltz, & Munoz, 2005). In fact, the RP itself may reflect spontaneously fluctuating neural activity. If the fluctuation is sufficient to cross a threshold, a movement may be triggered, whereas subthreshold fluctuations spontaneously decay without causing a movement (Schurger, Sitt, & Dehaene, 2012). According to this model, the ramp-like shape of the RP may simply reflect averaging those fluctuations, which eventually succeed in crossing the threshold level for action. Several researchers emphasize the functional relevance of spontaneous brain activity and the risk of dismissing such activity as irrelevant noise (Sadaghiani, Hesselmann, Friston, & Kleinschmidt, 2010; Fox & Raichle, 2007). Such fluctuating activity is typically shown to affect behavior when it is examined immediately prestimulus (Sadaghiani et al., 2010). Our results extend this view to the case of action inhibition.

The relation between the EEG signal and these hypothesized fluctuating activation levels is an important issue. The EEG time series contains low-frequency components, including "slow drifts," whose physiological significance is unclear. As a result, there will be trivial dependence between EEG amplitudes at successive time points. Baseline correction removes these low-frequency components. Our analysis is based on ERPs during brief, nonoverlapping epochs, baseline-corrected at the start of each epoch. This approach reduces the probability of detecting a spurious association between the activity levels for successive actions/omissions because of both events riding upon

the same slow drift. Thus, our findings imply fluctuation in signals related to processing successive action events rather than long-lasting shifts in global brain state. For example, Figure 1 shows a greater postmovement positivity for the action just prior to omission in the voluntary condition relative to the rule-based condition. However, this cannot be assumed to continue into the positive-going shift seen during subsequent voluntary omissions, because a baseline correction intervenes between the two components. That is, our results demonstrate a relation between event-related processing for successive events rather than a trivial continuity of the EEG time series. The focus on event-related processing rather than EEG level across interevent intervals is methodologically appropriate for removing artifactual correlations because of global slow drifts. It is also scientifically appropriate, given that our task was constructed around action and omission events, with no instruction regarding the relatively long 2-sec interval in between.

Inhibition, Cognitive Control, and Consciousness

Many theories of inhibition accord it special status, as a specific cognitive control function with a privileged link to consciousness (Hughes, Velmans, & De Fockert, 2009; Dehaene et al., 2003). Our data suggest a rather different view. Instead of intervention by a high-level process, intentional inhibition may also reflect fluctuating activity in low-level motor circuits. In the real world, when the external motivations for acting or withholding an action are clear-cut and an easy decision between competing options can be made—as is the case in rule-based action selection—spontaneous fluctuations in the motor system may have little influence on voluntary decisions. However, in situations where there are competing motivations to act or not to act, the action selection system must resolve the conflict by choosing between equally attractive alternatives. Our results suggest that such "decisions" could simply capitalize on the preceding state of the motor system. Many scientists have suggested that inhibition is a necessarily conscious top–down override (Dehaene & Naccache, 2001; Jack & Shallice, 2001; Merikle, Joordens, & Stolz, 1995) or "free won't" veto mechanism (Libet et al., 1983). Indeed, legal systems assume that the capacity to refrain from inappropriate action is the basis of human moral responsibility. Our results suggest a less homuncular view, namely that "decisions" to inhibit may be consequences of the ongoing state of the cortical and subcortical motor systems. Some theories of volition have involved the very strong contention that "free will" simply reduces to random fluctuations in neural processes (Carpenter, 1999; Eccles, 1985). However, these theories could not convincingly identify the locus of randomness. Our findings suggest that intentional inhibition, like other cognitive processes, indeed interacts with background fluctuations of neural activity. However, we add two important caveats: Our study cannot provide direct evidence that these fluctuations are random, and our study does not preclude other processes contributing to intentional inhibition. However, the design of our task does offer some hints about the mechanism where this fluctuating influence acts. Specifically, intentional inhibition may be determined by the interaction between cognitive, prefrontal decision processes and levels of activation in an iterative motor execution loop that links each action to the next (Marsden, 1984).

In conclusion, endogenous decisions to spontaneously inhibit an action are influenced by lower-level motor activity. Neural activity related to actions preceding and leading up to intentional inhibition can be predictive of its upcoming occurrence. In situations where we are making a difficult decision about whether to act or not, spontaneous levels of activity in our motor system may feed into our decision, biasing us to go one way or the other.

Note

1. We are grateful to an anonymous reviewer for suggesting this interpretation.

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