



Freely chosen and instructed actions are terminated by different neural mechanisms revealed by kinematics-informed EEG

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ABSTRACT

Neurophysiological accounts of human volition are dominated by debates on the origin of voluntary choices but the neural consequences that follow such choices remain poorly understood. For instance, could one predict whether or not an action was chosen voluntarily based only on how that action is motorically executed? We investigated this possibility by integrating scalp electroencephalograms and index-finger accelerometer recordings acquired while people chose between pressing a left or right button either freely or as instructed by a visual cue. Even though freely selected and instructed actions were executed with equal vigor, the timing of the movement to release the button was comparatively delayed for freely selected actions. This chromometric difference was six-times larger for the β -oscillations over the sensorimotor cortex that characteristically accompany an action's termination. This surprising modulation of an action's termination by volition was traceable to volition-modulated differences in how the competing yet non-selected action was represented and regulated.

1. Introduction

A person's ability to autonomously and endogenously choose between alternative courses of action in daily life is a key presumption of many social, political, legal and economic arrangements. The current understanding of how the brain implements this important cognitive capability for voluntary action is, however, complicated by volition's multiple connotations (Libet et al., 1983; Wegner, 2002; Roskies, 2010). Due to the dominant focus on resolving ambiguities surrounding the neural origin of a voluntary choice (Haggard, 2008; Soon et al., 2008; Desmurget et al., 2009; Bode et al., 2014; Schurger and Uithol, 2015), the neurophysiological consequences of choosing an action voluntarily remain poorly understood. The unknown scope of volition's consequences raises a basic question (Becchio et al., 2014): is it possible to reliably predict whether or not an action was voluntarily selected based only on how that action was motorically executed? Here, we sought an answer to this question by investigating the execution of index-finger actions that were either selected freely or selected to comply with external instructions.

An influential experimental approach to investigate volition's neural substrate, both in healthy and clinical populations, has been to modulate the volitional content of a choice using external instructions (Kutas and Donchin, 1980; Libet et al., 1982; Frith et al., 1991). This strategy's central rationale is that an action selected to comply with an instruction (such as a sign to "Turn right" at a crossroad) is less free than an action selected based on a whimsical subjective preference ("I want to turn right"). Based on this rationale, numerous studies have compared neural systems engaged by instructed and uninstructed (i.e., self-selected) actions using experimental paradigms that modulate how external instructions inform choices between simple discrete actions (e.g., pressing a button with either the left or right index finger) (Frith et al., 1991; Jahanshahi et al., 1995; Jenkins et al., 2000; Cunnington et al., 2002; Waszak et al., 2005; Van Eimeren et al., 2006; Mueller et al., 2007; Hoffstaedter et al., 2014; Ariani et al., 2015; Michely et al., 2015; Wisniewski et al., 2016). In these comparisons, volition has been associated with brain structures, especially in the medial prefrontal cortex, that exhibit elevated activity when an action is self-selected relative to when that action is instructed (Kriehoff et al., 2011; Brass et al., 2013;

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Zapparoli et al., 2017). However, these findings have been controversial and the topic of an extensive debate due to the difficulty in specifying and interpreting how actions were “self-selected” in these experiments and the numerous confounding differences (Lau et al., 2004; Botvinick et al., 2004; Nachev et al., 2005; Nachev and Husain, 2010; Passingham et al., 2010; Schüür and Haggard, 2011; Bode et al., 2013; Brass et al., 2013). An example of such a confounding difference is the sensory and perceptual demand to identify a stimulus-defined instruction that has no equivalent for freely selected actions. Furthermore, the decision about *what* action to choose and the timing of *when* to act are independent for a freely selected action unlike a stimulus-defined instruction that can ambiguously define both decisions (Schouten and Bekker, 1967; Brass and Haggard, 2008; Hoffstaedter et al., 2013). Nevertheless, despite these theoretical challenges, the experimental strategy of comparing instructed and uninstructed actions provided a pragmatic framework to assess volition's consequences, if any, for the motor execution of a selected action.

In a typical volition modulation paradigm, each trial requires a binary choice between pressing either a left or a right button with the index finger of the corresponding hand. The physical pressing of a button is presumed to follow the cognitive selection of one action over the other. Therefore, a successfully measured button-press event is a post-hoc behavioral indicator that a choice was in fact made on that trial. Furthermore, this event is also a marker of the choice's identity (left or right) and timing relative to a reference event, such as the previous action or the onset of the instruction stimulus. However, a button-press event is not the same as the index finger flexion/extension movements required to actually push the button down and then release it (Oulasvirta et al., 2018). A key assumption in prior studies has been that these index-finger movements to press a button would be unaffected by whether the decision to press that button was self-selected or instructed. Indeed, a violation of this assumed brain/behavior relationship would pose the challenge of explaining the neural logic of how volition's role in expressing a preference between alternative actions (i.e., choose A-or-B?) could possibly influence the physical execution of the selected action (i.e., execute A-not-B) (Obhi and Haggard, 2004; Becchio et al., 2014).

Here, we investigated volition's predicted absence of movement consequences using data from a previously conducted electroencephalography (EEG) study (Popovych et al., 2016; Wang et al., 2017) (see Section 2). In brief, EEG and index finger accelerations were concurrently recorded while participants made binary action choices in two contexts (Fig. 1A). In the *Instructed* context, a visual stimulus depicted either a left- or right-pointing arrow on each trial to indicate the required action. In the *Free* context, actions were self-selected without any prompting stimuli. So, is it possible to distinguish between actions executed in the *Free* or *Instructed* context based on the brain/behavior dynamics that accompany the index finger movements to push and then release a button?

2. Materials and methods

2.1. Participants

Twenty-one healthy individuals (10 females, 11 males; age range: 22–35 years) participated in our experiment and received financial compensation. Participants had normal color vision, were right-handed (mean handedness score = 0.9, according to the Edinburgh Handedness Inventory (Oldfield, 1971)), and had no prior history of psychiatric or neurological disease. All participants provided written informed consent prior to the experiment. The local ethics committee of the Faculty of Medicine, University of Cologne, approved the study protocol. Data from 3 participants were excluded from the analysis based on the poor quality of EEG data (see Section 2.6.3). All results reported here were based on data from the remaining 18 participants.

2.2. Apparatus and data acquisition

Stimuli were generated and displayed using the software Presentation® (version 11.0, Neurobehavioral Systems, Berkeley, CA) on a 47 cm x 29 cm LCD monitor with a screen resolution of 1280 × 1024 pixels, and a refresh rate of 60 Hz. Index-finger button-presses were registered by two LUMITouch™ keypads (Photon Control Inc., Burnaby, BC, Canada), one for each hand.

Scalp EEG was recorded using a 64-channel active electrode system (actiCAP, Brain Products GmbH, Munich, Germany) mounted in a spherical array according to the extended 10–20 international system (Fig. 1B). Three of the 64 electrodes (FT9, FT10 and TP10 in the 10–20 system) were not placed on the scalp but at the bilateral outer canthi and under the left eye to record bilateral horizontal and left vertical electro-oculograms (EOG). All electrodes were referenced online to the left mastoid. All electrode impedances were brought below 15 kΩ prior to the start of the experimental recording. The instantaneous acceleration of the left and right index finger was continuously recorded with an accelerometer (size: 22 × 14 × 8 mm³, weight: 8 gms) (Brain Products GmbH, Munich, Germany) attached to the dorsal-tip of each index finger (Fig. 1C). The X, Y and Z components of the measured acceleration (in a Cartesian coordinate system centered at the fingertip) were converted into voltage signals (sensitivity: 420 mV/g, gain: 3.5) and integrated into the EEG recording as additional channels.

Voltages from the scalp-EEG and accelerometer channels were amplified, band-pass filtered from 0.1 Hz to 250 Hz, and digitized at a sampling rate of 2500 Hz.

2.3. Paradigm

The experiment had two movement related contexts (namely, the *Free* and *Instructed* contexts) and one non-movement control condition (namely, the *Vision-only* context). Although the current study focused exclusively on movement-related phenomena in the *Free* and *Instructed* context, details of the *Vision-only* context are reported here for completeness. Trials in each context were organized into blocks and structured as shown in Fig. 1A. A white fixation dot was displayed on the screen at all times and was augmented with a concentric blue disc during the *Free* context and a blue square during the *Instructed* context as a reminder of the context currently underway.

On each trial of the *Instructed* context, the visual stimulus was a red arrow (width: 2° visual angle, height: 1.2° visual angle), which pointed either to the right or to the left and was displayed at the center of the screen for 200 ms. Participants had to respond to this stimulus by pressing a button with the index finger corresponding to the arrow's direction, i.e., left or right. To ensure that these stimuli were indeed modulating action choices, task instructions emphasized a minimum required accuracy of 90%. At the end of each block, a feedback screen displayed the numerical percentage accuracy value if the accuracy on that block was below 90% or the message – “Well done” – if the accuracy was greater than 90%.

The *Vision-only* context was identical to the *Instructed* context in stimulus materials and display parameters, but participants were instructed to pay attention to the arrow stimuli without making a corresponding response.

In the *Free* context, there were no visual stimuli displayed apart from the continuously present fixation symbol. Participants were instructed to voluntarily produce single index finger button presses over the entire block.

As actions in the *Free* context were initiated without external stimuli, an important concern was that (i) the total number of responses, (ii) the proportion of right and left hand responses, and (iii) the interval between consecutive responses could vary in an idiosyncratic manner from block to block. This could in turn limit the comparability of the *Free* and *Instructed* contexts. Therefore, to increase inter-context comparability, participants were instructed to initiate a response at intervals of

approximately 4–8 s, and to approximately balance the number of left and right index finger button presses over the block, while avoiding stereotyped response patterns and mental counting of the responses or the time-intervals. The feedback screen at the end of each block provided information on performance relative to the desired response timing and balance. The feedback messages were “Timing: Well done” when the total number of responses on that block $N = 10 \pm 2$ responses (based on the ideal rate of a response every 6s over the 60s block), “Timing: Too fast” for $N > 12$ responses, or “Timing: Too slow” for $N < 8$ responses. The extent of unbalanced responses in a block was estimated as, $100 \times |N_{right} - N_{left}| / (N_{right} + N_{left})$, where N_{right} and N_{left} were the number of right and left index finger button presses, respectively. The corresponding feedback messages were “Balance: Well done” when this imbalance value was $\leq 30\%$ (chosen as a soft threshold to avoid overly constraining

participants behavior), or “Balance: Unbalanced” for imbalance values greater than 30%.

2.4. Adaptive trial design

The total task period of the experiment (approx. 70 min) consisted of 48 blocks of trials divided into 4 runs, each having 12 blocks (3 contexts x 4 blocks). Unknown to the participants, an online adaptive procedure matched the number of left and right responses and the inter-response intervals in the *Free* and *Instructed* contexts to increase inter-context comparability (Michely et al., 2015, 2012). Blocks in each run were organized into triplets where a *Free* context block always occurred first, followed by the *Instructed* and *Vision-only* contexts, in randomized order. In each block of the *Free* context, the number of responses produced with

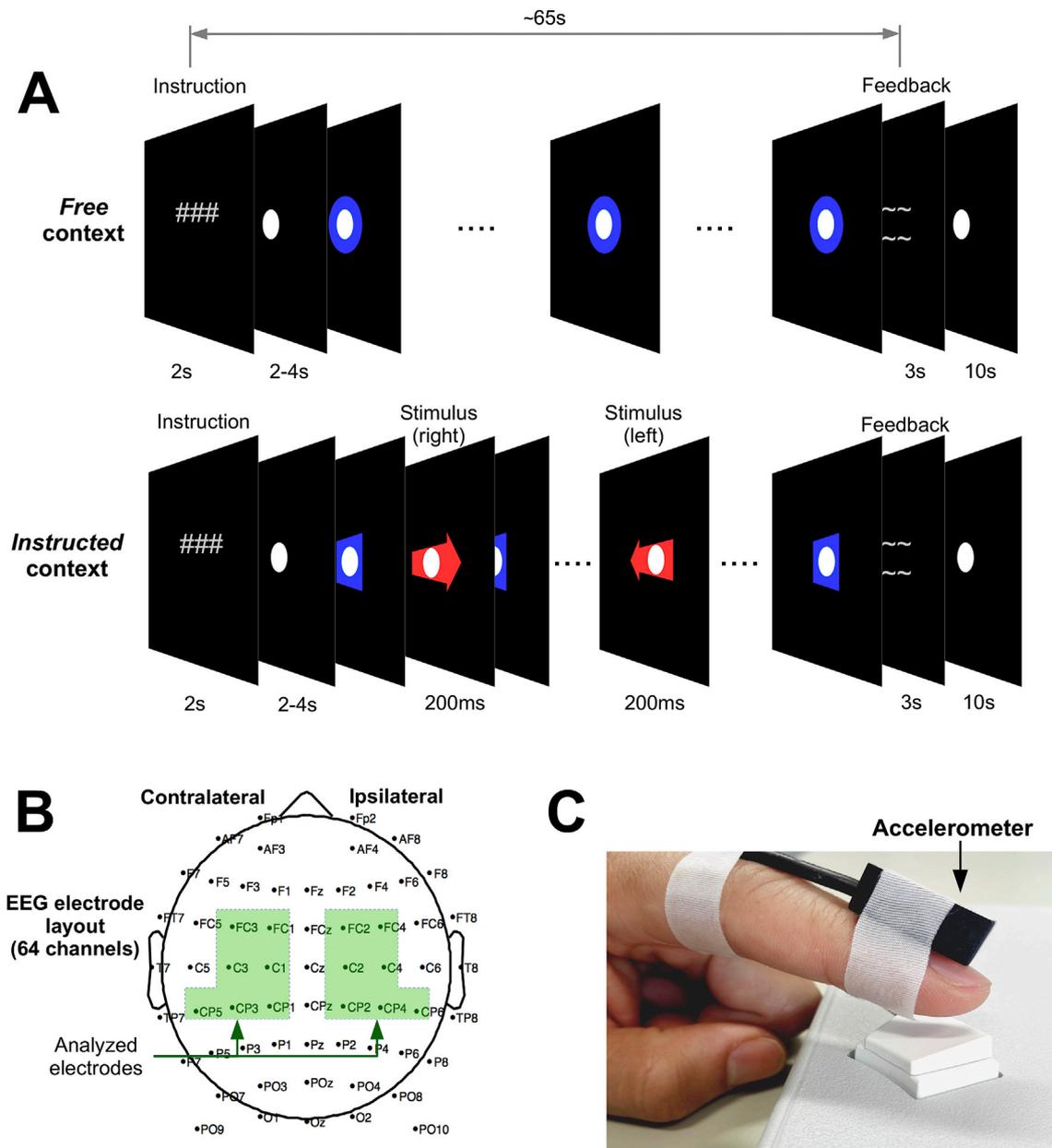


Fig. 1. Experimental paradigm. (A) A schematic of the trial timing for one block of the *Free* and *Instructed* contexts. A white fixation dot was displayed on the screen at all times and was augmented with a concentric blue disc in the *Free* context and a blue square in the *Instructed* context to uniquely identify each context. (B) Green polygons indicate electrodes of interest. EEG from left and right hand trials were collapsed over corresponding electrodes contralateral to the moving finger (similarly for ipsilateral and medial electrodes), with electrodes over the left (right) hemisphere corresponding to contralateral (ipsilateral) electrodes respectively. (C) Accelerometers were firmly taped to the dorsal tip of each index finger.

each hand (i.e., N_{right} and N_{left}) and the inter-response intervals were recorded. The recorded quantities N_{right} and N_{left} were then used to define the number of right-pointing and left-pointing arrows in the *Vision-only* and *Instructed* blocks that followed. The order of the recorded inter-response-intervals was randomized and these intervals were then used as the inter-stimulus intervals in the *Instructed* and *Vision-only* contexts. Intervals shorter than 4s were replaced with randomly chosen intervals in the range 4–8s.

2.5. Procedure

The EEG cap was first secured on the participant's head. Next, during the application of electrode gel to individual electrodes of the EEG cap, participants received verbal instructions and training on the experimental tasks.

All participants were trained in the same sequence of stages. First, the experimenter used a simulation of the actual experiment to familiarize participants with the visual information that they would encounter over the entire experiment (for example, the types of instruction and feedback screens, types of stimuli and fixation points). In the second stage, participants trained at responding to stimulus instructions (namely, left and right-pointing arrows) as required by the *Instructed* context. These stimuli were presented at intervals in the range 4–8s, which was the desired inter-response period for the *Free* context. In the third stage, the objective was to provide participants with a concrete sense for a 4–8s period. Participants were informed that stimuli would be displayed at intervals exactly as in the previous stage but, rather than respond to these stimuli, their task was to predict when each stimulus would be displayed and press a button to coincide with the stimulus onset. Training on the *Free* context followed in the fourth stage. Participants were instructed to freely press a button of their choice, with the guideline to act at intervals that were approximately similar to the “prediction” task that they had just been trained on. Training lasted until participants achieved a suitable response rate and were deemed to have a clear understanding of the instructions. Finally, participants were again shown the unique fixation symbols that they would encounter and had to identify the corresponding context for each fixation symbol correctly.

Following training, participants were instructed to minimize eye-blinks, to maintain fixation at all times during the task blocks, and to minimize unnecessary movements of their index fingers, head and body. The accelerometer measurement was originally intended to precisely record the onset of index finger movements. Therefore, instructions emphasized the need for brief, decisive movements irrespective of context and the avoidance of anticipatory and unnecessary finger movements.

The experimental recordings were conducted in a darkened sound-proof room. Participants were seated in a comfortable chair with their head supported by a chin-rest. Accelerometers were firmly attached to the dorsal tip of both index fingers with adhesive tape. The keypads were placed in a recess under the table where participants placed their hands so that the buttons were pressed without visibility of the index-finger movements. During the experiment, the experimenter continuously monitored the participants via a video camera to ensure that they maintained fixation, minimized eye-blinks, and stayed awake. After the experiment, participants were debriefed to verify their compliance with the instructions.

2.6. EEG and accelerometer data preprocessing

EEG and accelerometer data were preprocessed and analyzed using the EEGLab toolbox (Delorme and Scott, 2004) and custom scripts written in MATLAB (version MatlabR 2015b, MathWorks Inc., Natick, Massachusetts, USA).

2.6.1. Preliminary inspection

Raw data were first bandpass filtered from 0.5 to 48 Hz (to remove

low frequency trends and 50 Hz line noise) and then downsampled to 200 Hz. Next, the continuous EEG data were visually inspected to exclude time-periods contaminated by paroxysmal and muscular artifacts unrelated to eye blinks. The accelerometer recordings were also inspected to exclude trials containing extraneous finger movements prior to the button-press, as well as trials with mirror movements.

2.6.2. Movement onset identification

The movement onset on each trial was identified from the continuous accelerometer recordings. The first derivatives of the acceleration along the X, Y, and Z axes were computed and then combined to obtain the scalar (Euclidean) magnitude of the instantaneous acceleration change at each time point. This time-series was then smoothed and rescaled. Movement onset was defined using a threshold that was set to identify the earliest time point in a 125 ms window prior to each button press that showed a continuous increase in acceleration rate. All trials where the movement onset could not be unambiguously detected within this 125 ms pre-button window were excluded from further analyses. The threshold value was determined by visual inspection and the same threshold was used for all trials and participants. The identified movement onsets were integrated into the continuous EEG and accelerometer data.

2.6.3. Epoching and artifact rejection/correction

The inspected continuous EEG and accelerometer data were segmented into epochs relative to the movement onset on each trial, estimated from the accelerometer recordings. The epoch length for each context was chosen so that the epochs were non-overlapping and were long enough to have a baseline period of 1s. In the *Free* context, due to the ambiguous onset of the readiness potential (or *Bereitschaftspotential*) before the movement onset (Kornhuber and Deecke, 1964; Shibasaki and Hallett, 2006), epochs were defined from -2.5 s to $+1.5$ s relative to the movement onset, with a baseline period from -2.5 s to -1.5 s. As described in section 2.4, the inter-response intervals in the *Free* context were used to define inter-stimulus intervals in the *Instructed* contexts. To accommodate this constraint, epoch lengths in the *Instructed* context were 500 ms shorter than in the *Free* context to ensure that consecutive epochs did not overlap and that no stimuli were displayed during the baseline period. Epochs were defined from -2.0 s to $+1.5$ s relative to movement onset with a baseline period from -2 s to -1 s. Since an action in the *Instructed* context could not be correctly selected before the stimulus display, we assumed that these shorter epochs would not affect comparability to the longer epochs of the *Free* context. To ensure a stimulus-free baseline period, all trials in the *Instructed* context with a response time greater than 1s were excluded from the final analysis.

The epochs obtained after segmentation were again examined for artifacts. Epochs having amplitudes larger than $100 \mu\text{V}$ over the entire epoch or with abnormal drifts greater than $75 \mu\text{V}$ were rejected. Next, a semi-automated procedure based on an independent component analysis (ICA) was used to identify epochs contaminated by blinks, eye movements, muscle activity, and infrequent single-channel noise. The independent components were identified using the Infomax ICA algorithm implemented in EEGLAB. The ADJUST algorithm (Mognon et al., 2011) was then used to identify and reject components containing blink/oculomotor-related and other artifacts distinguishable from the rest of brain activity. Noisy channels were detected automatically by EEGLAB and interpolated using spherical spline interpolation. Subsequently, the artifact-free trials were average-referenced and baseline-corrected relative to the first 1s of the epoch.

At this stage, data from three participants were excluded from further analyses because of an insufficient number of trials satisfying the quality criteria described above. One participant's data had a large number of epochs contaminated by eye movement artifacts; and data from two participants had many epochs contaminated by extraneous movements during the baseline period as detected by the accelerometers. The data of each of the remaining 18 participants had at least 100 artifact-free trials

per context (100–160 *Free* trials, 104–161 correct *Instructed* trials).

2.6.4. Spatial filtering

The final EEG preprocessing stage was spatially filtering of the epoched EEG data using the surface Laplacian procedure. This procedure helps exclude low spatial frequency signals thus reducing the effects of distal generators due to volume conduction and increasing local spatial resolution at the electrodes (Perrin et al., 1989; Nunez et al., 1994; Cohen, 2014). In our study the surface Laplacian was used specifically to (i) enhance topographic localization over the electrodes of interest (clustered bilaterally over the sensorimotor cortex as shown in Fig. 1B) and (ii) limit the influence of volume conducted signals at these electrodes, especially from occipital/parieto-occipital sources involved in sensory processing in the *Instructed* context. Surface Laplacians were estimated from the individual artifact-free EEG epochs using a spherical spline algorithm (Perrin et al., 1989) as implemented by the Current Source Density (CSD) toolbox (Kayser and Tenke, 2006). CSD waveforms were computed for each original surface EEG potential (50 iterations, spline degree = 4).

2.6.5. Push/release identification

The epoched accelerometer data were used to identify the Push and Release movements on each trial. Pressing the button required a rapid flexion of the index finger to push the button down and, after a brief delay, an extension to release the button. The absolute acceleration of these Push and Release movements had distinctive peaks that could be identified from the recorded accelerometer data on each trial.

For each epoch, the scalar magnitude of the (Euclidean) acceleration at each time point was first computed from component accelerations along the X, Y and Z axes. The identification of Push and Release acceleration peaks was restricted to the time range [0 ms, +1000 ms] following movement onset. The mean acceleration over the [-500 ms, 0 ms] period was subtracted from the absolute acceleration time-series to correct for small inter-trial baseline differences. To account for individual differences, the movement identification procedure had two stages that were applied to each participant's movements in each context. The objective of the first stage was to estimate a characteristic time point dividing the Push and Release movements across all trials for each context and participant. In the second stage, the estimated dividing time from the first stage was applied to each trial of that context.

The first estimation stage was implemented as follows. As a starting approximation, the Push and Release acceleration peaks were assumed to occur at least 40 ms apart from each other. Since the maximum acceleration for the Push movement was typically higher than for the Release movement, the 40 ms constraint was necessary to distinguish the representative peak for the Release movement from the multiple peaks associated with the Push movement due to high frequency acceleration changes. For each participant and context, we calculated a *maxAcc* time-series consisting of the maximum acceleration at each time-point across all epochs. This time-series was used to estimate the time-points of two acceleration maxima: (1) the time point of the maximum acceleration value over the entire *maxAcc* time-series (2) the time point of the next highest acceleration value that was at least 40 ms distant from the first time-point. These two maxima were reference time points for the Push and Release movements. The characteristic dividing time-point between the Push and Release movements was defined as the time point of the minimum acceleration *between* the above two maxima. In the second stage of our procedure, the estimated dividing time from the first stage was applied to each trial. For each trial, the time and magnitude of the maximum acceleration before and after the dividing time were treated as the peak acceleration of the Push and Release movements, respectively. We confirmed the successful operation of this identification procedure by visually inspecting the resulting Push and Release estimates for each trial and for each participant.

The Push and Release peak on each trial was described by the respective magnitude and latency relative to movement onset. To obtain

a robust estimate of each participant's mean acceleration and latency of the Push and Release movement per response hand in each context, we used a trimmed mean with a 15% cutoff (i.e., excluding 7.5% of the lowest and highest values) (Ratcliff, 1993). Accelerometer data from left and right index-finger movements were highly similar and were collapsed together for all analyses.

2.7. ERP time-locking

The epoched time-series were averaged to obtain event-related potentials (ERPs). Since the epochs were defined relative to the movement onset, the resulting ERPs are referred to here as movement-related ERPs. The Push-evoked and Release-evoked ERPs were obtained by averaging the epoched time-series relative to the time on each trial's Push acceleration peak and the Release acceleration peak respectively.

2.8. Oscillations

The instantaneous phase of δ -band oscillations (2–4 Hz) and instantaneous amplitude of β -band oscillations (13–30 Hz) was computed as follows. The preprocessed data were band-pass filtered in the required frequency range using a two-pass procedure with a Hamming windowed sinc FIR filter (as implemented by EEGLab). The Hilbert transform (Freeman, 2004; Cohen, 2014) was next applied to these filtered data to obtain the complex analytic representation of each epoch. The angle and absolute magnitude of these complex time-series provided the instantaneous phase and amplitude of the δ -band and β -band at each time point of each epoch. The β -band amplitude epochs were baseline corrected by subtracting the mean amplitude over the baseline period (after excluding the initial 100 ms period which contained edge artifacts) from the amplitude at each time point over the epoch.

The Push-evoked and Release-evoked β -amplitudes were obtained by averaging the epoched β -band time-series relative to the time on each trial of the Push acceleration peak and the Release acceleration peak respectively after subtracting the β -amplitude at this reference point. Phase angle statistics were computed using CircStat (Berens, 2009), a circular statistics toolbox implemented for MATLAB.

2.9. Electrodes of interest

Due to the putative confounds from differences between the contexts (see Section 1), we focused on the motoric demand common to both contexts, namely, to physically press a button on each trial. We, therefore, restricted our primary analysis of both contexts to EEG dynamics over the sensorimotor cortex contralateral and ipsilateral to the executed action (Fig. 1B) (i.e., representing the selected and non-selected action respectively). For all our EEG analyses, data from left and right hand trials were collapsed over corresponding electrodes contralateral to the moving finger (similarly for ipsilateral and medial electrodes), with electrodes over the left (right) hemisphere corresponding to contralateral (ipsilateral) electrodes respectively.

3. Results

3.1. General behavior

The general behavior of participants in both contexts indicated a high compliance with task instructions. In the *Free* context, the mean inter-response interval was 6618 ± 136 ms (mean \pm s.e.m.) and only $1.6 \pm 0.6\%$ of these intervals were shorter than 4s. The mean proportion of left (49.3%) and right index finger button-presses (50.7%) was also closely matched. In the *Instructed* context, the mean response accuracy was $97.7 \pm 0.5\%$ consistent with the simplicity of the task. All subsequent analyses focused on actions in the *Free* context preceded by an inter-response interval greater than 4s and correct trials in the *Instructed* context with responses times shorter than 1s (see section 2.6).

3.2. Inter-hemispheric phase dynamics differ between contexts before the movement

For actions to differ between the *Free* and *Instructed* contexts, a prerequisite is a difference in how those actions were neurally generated. Therefore, we first evaluated the event related potentials (ERPs) in the period immediately prior to and following movement onset.

At movement onset in both contexts, the mean ERPs showed a focal negativity over central electrodes contralateral to the moved finger that was absent at homologous ipsilateral electrodes (Fig. 2A and Fig. S1). This spatial asymmetry in ERP amplitudes was consistent with expected motor activity lateralization before a unilateral index finger action. However, this arithmetic difference in ERP amplitudes at contralateral/ipsilateral locations masks their relative dynamics. When we rescaled the ERPs at representative contralateral and ipsilateral sensorimotor electrodes (C3 and C4) to equalize their minimum and maximum amplitudes, the dynamic rise and fall of these ERPs over time revealed a qualitative difference between contexts (Fig. 2B). At contralateral C3, the mean ERP reached its minimum value (i.e., peak negativity) shortly after movement onset in both contexts (*Free*: +35 ms, *Instructed*: +30 ms). Nonetheless, at ipsilateral C4, the corresponding ERP minimum in the *Instructed* context (−185 ms) was reached 65 ms earlier than in the *Free* context (−120 ms). Although this timing difference was seemingly specific to the ERPs at C4, when they were considered in conjunction with C3, the ERPs at C3/C4 resembled coupled oscillations with a sustained phase difference closer to 0° in the *Free* context but closer to the diametrically opposite value of 180° in the *Instructed*

context (Fig. 2C).

We statistically evaluated this descriptive formulation of ERP dynamics as coupled oscillations using the phase relationship of δ -band oscillations (2–4 Hz) at C3 and C4 (Fig. 2D). Oscillations in the δ -band have been implicated in volitional selection in other tasks (Hamel-Thibault et al., 2016). However, in the current study, these oscillations were of more pragmatic relevance due to their low frequency, which approximated the frequency of the ERP amplitude changes at C3/C4. A simple demonstration of this (approximate) equivalence between δ -band phase and ERP dynamics is the similarity between the ERP dynamics in Fig. 2B and the mean cosine of the δ -band phase angles at C3 and C4 in Fig. 2E. The cosine (rather than sine) is shown as the phase angle at contralateral C3 was close to 180° at movement onset in both contexts.

In the *Instructed* context, the δ -oscillations at C3 and C4 showed a phase difference closer to 180° (rather than 0°) over a sustained 200 ms period before movement onset (Fig. 2F). Over the same 200 ms pre-onset interval, the mean phase difference between C3 and C4 in the *Free* context ($42^\circ \pm 20.90^\circ$; mean \pm 95% CI) remained closer to 0° and was significantly lower than in the *Instructed* context ($125^\circ \pm 52.12^\circ$) [Watson-Williams test, $F(1,34) = 13.94$, $p < 0.001$]. In contrast, over the [+100 ms, +300 ms] period following movement onset, the mean phase difference between C3/C4 was close to 0° in both contexts (*Free*: $-4.59^\circ \pm 22.17^\circ$; *Instructed*: $13.30^\circ \pm 29.94^\circ$) and not significantly different [Watson-Williams test, $F(1,34) = 1.04$, $p > 0.3$].

To control for the potentially spurious origin of these inter-context differences, we additionally evaluated the putative confounding role of the spatially oriented visual stimuli in the *Instructed* context. In this

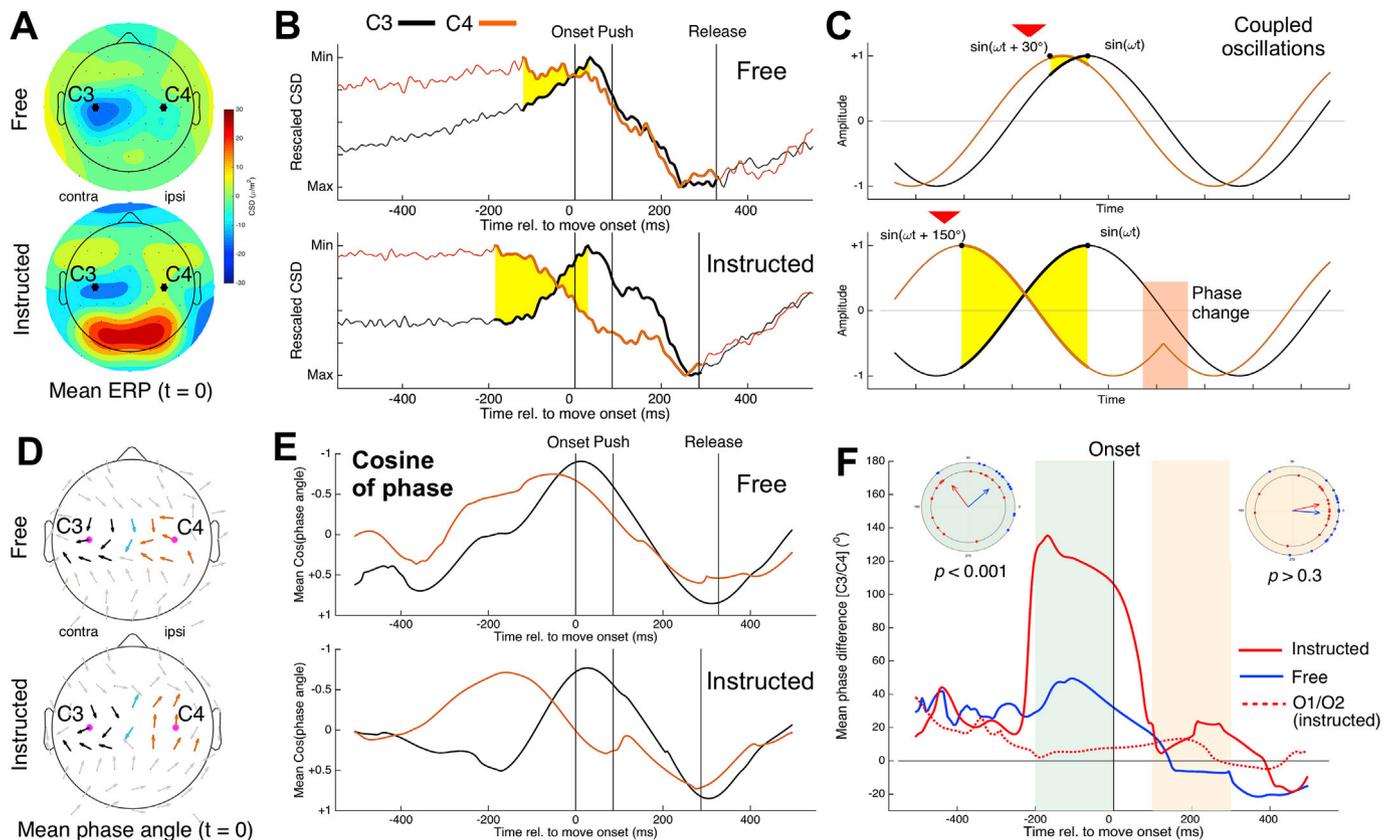


Fig. 2. Interhemispheric ERP dynamics. (A) The topographic distribution of spatially filtered mean ERP amplitudes (Current Source Densities (CSD)) at movement onset. (B) ERPs at C3 and C4 were rescaled to have the same minimum/maximum values. Vertical lines indicate movement events. The duration between minima of C4 and C3 (yellow shading) was longer in *Instructed* context. (C) Hypothetical sine waves with coupled phases. Mismatch duration (yellow shading) is shorter for phase difference of 30° (upper panel) than 150° (lower panel). Phase difference of 150° is shown as changing to 30° via a ‘reset’. (D) Instantaneous δ -band phase angles at movement onset (colors distinguish contra/ipsi/medial electrodes). (E) Mean cosine of instantaneous δ -band phase angles at C3 and C4. (F) Mean phase difference between C3 and C4. The dotted line indicates the mean phase difference between O1 and O2. Light green area indicates [−200 ms, 0 ms], and orange area indicates [+100 ms, +300 ms]. Mean phase angles for each period are shown in colored discs, dots correspond to mean angles for individual participants.

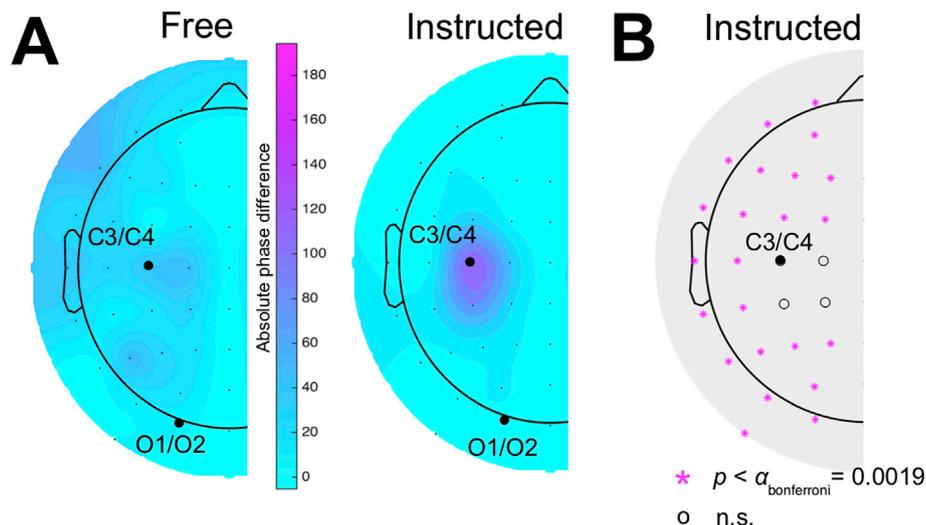


Fig. 3. Phase differences across the scalp. (A) The absolute mean phase differences between each contralateral electrode and its ipsilateral homologue averaged over [-200 ms,0 ms] in the two contexts. (B) The distribution of electrode pairs in the *Instructed* context with a mean phase difference that was significantly different from the mean difference at C3/C4 [corrected for multiple comparisons]. No electrode pair showed a corresponding statistically significant difference in the *Free* context.

context, the arrow stimulus on each trial could plausibly evoke ERPs lateralized relative to the arrow's (left/right) orientation rather than the (left/right) index finger action that it instructed. Even if such stimulus-evoked ERPs were to originate at occipital sources, they might nonetheless drive the phase differences at C3/C4 due to volume conduction. However, incompatible with such spurious effects, the mean phase difference in δ -phase at occipital electrodes (contralateral) O1 and (ipsilateral) O2 remained close to 0° before and after movement onset in the *Instructed* context (dotted line, Fig. 2F). Furthermore, over the [-200 ms, 0 ms] interval, the mean phase difference between O1 and O2 ($5.55^\circ \pm 7.59^\circ$) was significantly lower than the phase difference between C3 and C4 over this period [Watson-Williams test, $F(1,34) = 34.48$, $p < 0.001$]. For completeness, we additionally evaluated the mean δ -phase difference over the [-200 ms, 0 ms] period at contralateral-ipsilateral electrode pairs over the scalp (Fig. 3; please also see the [Movie 1](#) for an animation of instantaneous phase angle changes across the scalp). The inter-hemispheric (absolute) phase differences were uniformly low across the scalp in the *Free* context but phase differences greater than 90° were focally present only over C3/C4 (and its immediate neighbors) in the *Instructed* context. This focally high phase difference at C3/C4 was significantly greater than the corresponding value at all other non-neighboring electrodes (Fig. 3B) and was inconsistent with a spurious origin linked to stimulus orientation.

Supplementary video related to this article can be found at <https://doi.org/10.1016/j.neuroimage.2018.12.005>

In summary, ERP amplitudes over the central electrodes showed a similar pre-movement lateralization in the *Free* and *Instructed* contexts. However, the inter-hemispheric ERP dynamics in the two contexts (expressed in terms of δ -phase differences) were near theoretically opposite extremes of the phase angle scale (i.e., 0° and 180°). At first glance, this striking difference in sensorimotor dynamics was evidence that the binary choice between the same action alternatives in the *Free* and *Instructed* contexts had differing consequences for the motoric representations of these actions. The behavioral relevance of this difference was unclear as the pre-movement ERP amplitude and local dynamics at contralateral C3 were highly similar in the *Free* and *Instructed* contexts. These dynamics could, for instance, be an incidental after-effect of how decision evidence accumulated in the motor system in the two contexts (Selen et al., 2012; Thura and Cisek, 2014), that is, indicating that both actions were equally preferable in the *Free* context (low phase difference) but that one action was preferred over the other in the *Instructed* context

(high phase difference). To assess the behavioral relevance of the inter-context differences in ERP dynamics, we next evaluated the kinematics of the executed actions in the two contexts.

3.3. The timing of the button release movement differs between contexts

To assess the influence of the *Free* and *Instructed* contexts on behaviour, we used the accelerometer recordings to distinguish the two movements involved in pressing the button, namely, the index finger's rapid flexion to push the button down and its subsequent extension to release the button (see Section 2.6.5). On each trial, the Push and the Release movement could each be associated with a separate (absolute) acceleration peak (Fig. 4A, upper panel). The acceleration peak uniquely linked to each Push and each Release movement was described by the peak's magnitude and its latency relative to movement onset.

The mean latency of the Push and Release movements (i.e., acceleration peaks) (Fig. 4B, left panel) were significantly modulated by context [analysis of variance (ANOVA), Context {*Free*, *Instructed*} x Movement {*Push*, *Release*}, Context*Movement: $F(1,17) = 25.57$, $p < 0.001$; Context: $F(1,17) = 27.05$, $p < 0.001$; Movement: $F(1,17) = 277.63$, $p < 0.001$] but the corresponding mean acceleration magnitudes (Fig. 4B, right panel) were not [ANOVA, Context*Movement: $F(1,17) = 0.08$, $p = 0.78$; Context: $F(1,17) = 4.31$, $p = 0.054$; Movement: $F(1,17) = 52.11$, $p < 0.001$]. The mean latency of the Push movement was indistinguishable between contexts [$t(17) = -0.30$, $p > 0.7$] but the mean Release latency in the *Instructed* context (287.14 ± 11.19 ms; mean \pm within-subject s.e.m. (Cousineau, 2005)) was significantly smaller than in the *Free* context (327.26 ± 15.37 ms) [$t(17) = 5.15$, $p < 0.001$]. This inter-context difference in Release latency was present for 17 of our 18 participants and an example of this modulation for one participant is shown in Fig. 4A (lower panels).

To clarify these inter-context kinematic differences, we next assessed the statistical association of the Push and Release kinematics between contexts, i.e., whether the kinematics in one context were informative about corresponding properties in the other context. Even though the mean values of the Push and Release kinematics were similar between contexts, the factors that determined these kinematic properties might be context-specific. This possibility would predict a weak statistical association of the kinematics between contexts. However, inconsistent with this possibility, the Push kinematics in the *Free* and *Instructed* contexts were robustly correlated (i.e., between contexts) [latency: $r(17) = 0.83$,

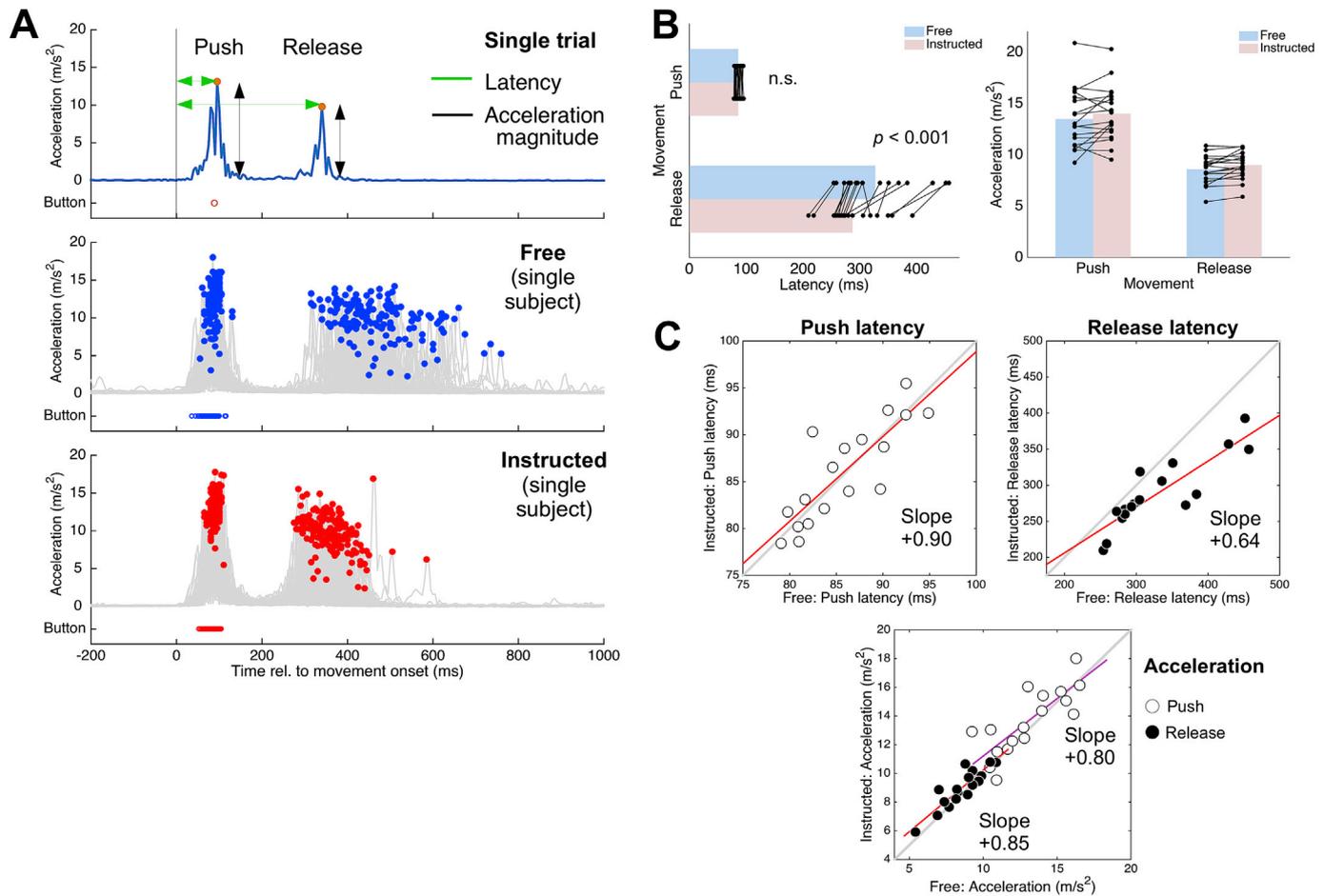


Fig. 4. Movement kinematics. (A) Absolute acceleration of Push and Release movements on a single trial (first panel), and on all trials from one representative subject (lower panels). Colored dots indicate acceleration peaks (Release peaks occurred earlier in the *Instructed* context) (B) Mean latencies (left panel) were significantly modulated by context but mean accelerations (right panel) were not. Each connected pair of black dots represents values for the same participant (C) Between-context correlations in Push latency (upper left), Release latency (upper right), Push (open dots) and Release accelerations (filled dots) (lower). Colored lines indicate the linear relationship (best least-squares fit) between corresponding variables in the *Free* (x-axis) and *Instructed* contexts (y-axis). The unit slope line is shown in gray.

$p < 0.001$; acceleration: $r(17) = 0.86$, $p < 0.001$] and so were the Release kinematics [latency: $r(17) = 0.87$, $p < 0.001$; acceleration: $r(17) = 0.89$, $p < 0.001$](Fig. 4C).

The between-context correlations for the Push and Release latency had similar correlation coefficients ($r = 0.83$ and 0.87 , respectively) but the scaling of their respective linear relationships was different. The slope of the linear relationship of the Push latency in the two contexts was equal to $+0.90$ (i.e., close to 1) but the slope for the Release latency had a lower value of $+0.64$ (Fig. 4C, upper row). This lower value was not a general peculiarity of the Release action as the slope for Release acceleration had a comparatively higher value ($+0.85$) that was closer to the slope for the Push acceleration ($+0.80$) (Fig. 4C, lower row). The lower valued slope for the Release latency highlighted a subtle but critical feature of the ~ 40 ms mean latency difference between contexts. The relationship between Release latency in the two contexts (denoted by L_{Instr} and L_{Free}) could hypothetically have taken the form $L_{Instr} \approx L_{Free}$ (i.e., slope equal to $+1$) rather than $L_{Instr} \approx (0.64)L_{Free}$. This possible alternative would have implied that the mean difference between L_{Instr} and L_{Free} was primarily due to an additive “speedup” (or “slowdown”) in one context relative to the other (see Fig. S3 for one example). By ruling out such a purely additive basis for the Release latency difference, these data constrain the possible origins of this difference to factors tied to both contexts rather than independent factors specific to each context. One such non-independent origin of the Release latency differences that is common to both contexts was the Push action itself.

In the statistical tests above, the Push and Release actions were treated as independent actions even though, by definition, the Release always followed the Push action and the Push and Release involved moving the same index finger in quick succession on each trial. Despite this apparent interdependence of the Push and Release actions, their respective kinematics within the same context were uncorrelated both within the *Free* context [latency: $r(17) = -0.38$, $p = 0.12$; acceleration: $r(17) = 0.08$, $p = 0.74$] and within the *Instructed* context [latency: $r(17) = -0.23$, $p = 0.36$; acceleration: $r(17) = 0.13$, $p = 0.62$]. This behavior-to-behavior relationship was, however, inadequate to account for another important form of Push-Release dependence. On each trial, the Release not only followed the physical execution of the Push action but also the diverse neural processes that the Push action itself evoked, for example, the somatosensory afferents generated by the movement of the “pushing” index finger itself and the finger’s extended physical contact with the button until the Release. We next assessed the dependence of the Release on these Push-evoked neural processes, and if this dependence differs between contexts in a manner that might modulate the latency of the Release action.

3.4. Push-evoked ERPs predict release latency in the instructed, but not free, context

The accelerometer recordings acquired in our experiment did not allow a precise characterization of the contact between the finger and the

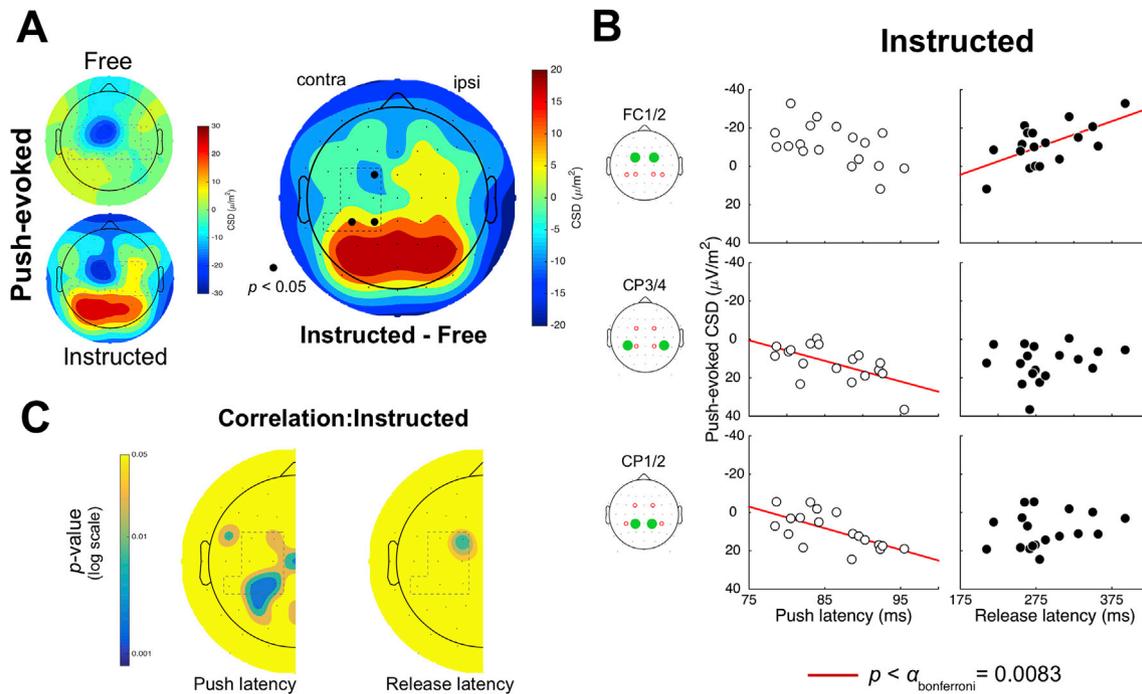


Fig. 5. Movement-evoked ERPs. (A) The topographic distribution of mean Push-evoked ERPs in each context and their difference. (B) Correlations of Push-evoked ERPs to Push latencies (left column) and Release latencies (right column) for *Instructed* context. (C) Topographic distribution of p-values (log scaled) of correlations between Push-evoked ERPs and Push latencies (left) and Release latencies (right) for the *Instructed* context.

button. In its place, the Push and Release latency that were estimated on every trial were used to compute the ERPs evoked by these movements.

We first evaluated whether there was any modulation of the mean Push- and Release-evoked ERP amplitudes (averaged over a 70 ms window following each movement's acceleration peak) by context at each of the 7 contralateral electrodes of interest [ANOVA, Context {*Free*, *Instructed*} \times Movement {*Push*, *Release*}, full statistical details in Table A.1 (upper)](also see Figs. S2A and B). Context significantly modulated the movement-evoked ERPs at three electrodes – frontocentral FC1, centroparietal CP1, CP3 – but notably not at C3. Apart from this general modulation, the mean Push-evoked ERP amplitudes at these three electrodes also differed significantly between contexts (Fig. 5A) [FC1: $t(17) = 2.87$, $p = 0.01$; CP3: $t(17) = -5.14$, $p < 0.001$; CP1: $t(17) = -3.48$, $p = 0.003$]. The polarity of the Push-evoked ERPs at these electrodes (negative at FC1, positive at CP1, CP3) and their lateralization properties (significantly lateralized at FC1/2, but not at CP1/2, CP3/4 (Table A.1 (lower), Fig. S2C)) further suggested that they had distinct neural generators. To incorporate the differing lateralization properties at these electrodes into our analysis, their contralateral and ipsilateral ERP amplitudes were averaged for further tests.

To assess the dependence of Release latency on these Push-evoked neural responses, we evaluated the statistical association between the bilateral Push-evoked ERPs at the three electrode-pairs (FC1/2, CP1/2, CP3/4) to the corresponding Push and Release latencies within the same context (Fig. 5B; full statistical information in Table A.2). In the *Instructed* context, the mean bilateral Push-evoked ERPs at CP1/2 and CP3/4 (but not FC1/2) were significantly correlated with mean Push latency while the ERP at FC1/2 (but not CP1/2, CP3/4) was significantly correlated with mean Release latency. Surprisingly, the corresponding Push-evoked ERPs in the *Free* context were not informative about either the Push or Release latency. For completeness, the topographic distribution of p-values of the ERP-movement correlations in the *Instructed* context for all electrode pairs is shown in Fig. 5C.

The statistical association of the Push-evoked ERP at FC1/2 to the latency of the subsequent Release action, i.e., to be executed at a future

time, confirmed the crucial distinction between the Push-evoked neural processes and the Push action's kinematics (to which the Release was not significantly associated). The divergence in ERP-behavior correlations at FC1/2 and {CP1/2, CP3/4} was consistent with the diverse origins of the Push-evoked neural activity. The multiple brain-to-behavior associations in the *Instructed* context, together with their absence in the *Free* context was surprising since the Push and Release kinematics were robustly associated between contexts (as described in section 3.3).

The categorical absence of these associations both to the Push or Release latency in the *Free* context was prima facie evidence of a difference in sensorimotor organization from the *Instructed* context that might account for their Release latency differences. However, this inference about the *Free* context based on a statistical null effect might instead reflect the role of a confounding process. For example, the *Free*, but not *Instructed*, context required participants to estimate time-intervals of 4–8 s between consecutive button-presses. The neural mechanisms involved in time-estimation involving regions such as the supplementary motor area (SMA) and pre-SMA (Grondin, 2010) might have distorted the Push-evoked ERPs at FC1/2 due to their spatial proximity. To obtain an alternative (non-ERP) perspective to disentangle these alternative possibilities, we evaluated the relationship of the Push and Release movements to a well-established higher frequency oscillatory signature of movement completion.

3.5. Onset of β -power rebound is linked to different movements in the two contexts

Spectral power in the β band (13–30 Hz) has been shown to characteristically increase (or rebound) over the central electrodes following a movement, also known as Event-Related Synchronization (ERS), and has been attributed to an inhibitory reset of the primary motor cortex (Pfurtscheller and Lopes da Silva, 1999; Jurkiewicz et al., 2006; Kilavik et al., 2013). This phenomenon suggested a way to relate the Release-related findings to the mechanisms of how an action was terminated. For this purpose, the “post-movement” dimension of the

β -rebound was of particular relevance. Our decomposition of the actions to press a button into a Push and a Release action presented an ambiguity about which of the two movements would serve as the reference movement for the “post-movement” β -rebound. In prior studies of the execution of self-initiated multi-movement sequences, the β -rebound has been reported to commence after the sequence’s final movement rather than after each individual movement (Cassim et al., 2000; Alegre et al., 2004; Erbil and Urgan, 2007; Cheyne, 2013). A plausible prediction, based on these prior studies, was that the β -rebound would follow the Release movement in both contexts, namely, the final movement of the Push-Release sequence.

In our data, a β -rebound was evident at all seven contralateral electrodes in the *Free* and *Instructed* contexts (Fig. 6A). The baseline-corrected power in the β -band exhibited a decrease prior to movement-onset in both contexts, with this decrease being more rapid and starting closer to movement onset in the *Instructed* context. The rebound occurred at a time

point following movement-onset, where the power changes switched from decreasing continuously over time to increasing monotonically until a plateau value.

The timing of the contralateral β -rebound seemed to be yoked to the Release movement in the *Free* context but, remarkably, this rebound in the *Instructed* context was yoked to the Push movement, i.e., ~ 241 ms earlier than in the *Free* context. We statistically confirmed this observation at all 7 contralateral electrodes by evaluating the context-dependent modulation of the mean Push-evoked and Release-evoked changes in β -amplitude over a 375 ms period (discretized into five 75 ms bins) (ANOVA, Context {*Free*, *Instructed*} \times Time $\{t_1, \dots, t_5\}$, full statistical details in Table A.3) (Fig. 6B). Following the Push movement, the change in β -amplitude over time showed a significant modulation by context (Fig. 6B upper), but this contextual modulation was not statistically significant following the Release movement consistent with the rebound being underway in both contexts (Fig. 6B lower).

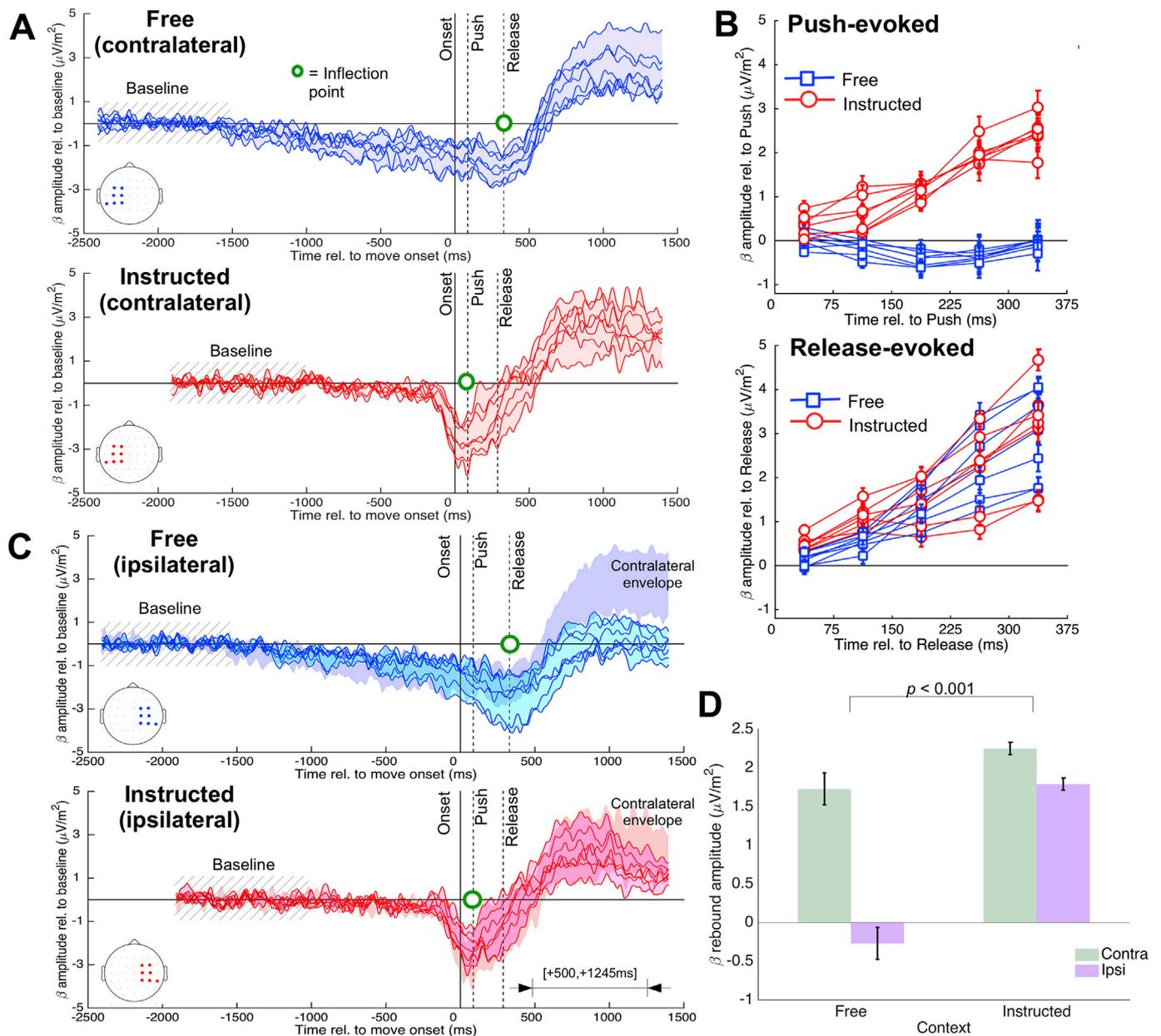


Fig. 6. Context-dependence of β -rebound. (A) Mean β -amplitude at contralateral electrodes relative to baseline (shading indicates amplitude envelope). The green circle marks the movement closest to the β -rebound’s onset time. (B) Push-evoked (upper panel) and Release-evoked (lower panel) changes in β -amplitude over 375 ms post-movement period (5×75 ms bins). Error bars indicate within-subject s.e.m. (Cousineau, 2005). (C) Mean β -amplitude at ipsilateral electrodes. Contralateral amplitude envelopes are shown as a reference. (D) Mean contralateral and ipsilateral β -amplitudes over the period [+500 ms, +1245 ms].

The contralateral and ipsilateral rebound amplitudes were closely matched in the *Instructed* context (Fig. 6C lower panel) but, in the *Free* context, the ipsilateral rebound amplitude did not exceed baseline levels (Fig. 6C upper panel). Over the period [+500 ms, +1245 ms] following movement onset, the relationship of the mean contralateral β amplitude (averaged across electrodes) to the corresponding ipsilateral amplitude was significantly modulated by context [ANOVA, Context {*Free*, *Instructed*} x Laterality {*Contra*, *Ipsi*}, Context*Laterality: $F(1,17) = 17.942$, $p < 0.001$; Context: $F(1,17) = 15.687$, $p < 0.005$; Laterality: $F(1,17) = 23.426$, $p < 0.001$] (Fig. 6D).

These findings provide a converging line of evidence to clarify the ERP-based findings above (section 3.4) hinting at a categorical difference in how actions are terminated in the *Free* and *Instructed* actions. The onset of the β -rebound associated with the Push movement in the *Instructed*, but not *Free*, context was congruent with the presence of Push-evoked ERP-to-Release associations in the *Instructed*, but not *Free*, context. The categorical absence of these Push-related associations in the *Free* context was consistent with a different sensorimotor organization between contexts but not the role of spurious artifacts from time-estimation processes. The onset of the β -rebound specifically linked to the Release movement in the *Free* context, rather than simply being delayed relative to the Push movement, further affirmed the categorical nature of the sensorimotor differences between the *Free* and *Instructed* contexts. The prominent difference in lateralization of the β -rebound between contexts provided an independent validation of the context-dependent difference in inter-hemispheric ERP/ δ -phase dynamics. If the β -rebound is an indicator of the resetting of “active” motor representations then the above findings suggest that the motor representations of both action choices (contra and ipsi) were concurrently active in the *Instructed* context but only the selected action (only contra) was motorically represented in the *Free* context.

4. Discussion

In decision terms, our experiment required participants to develop a preference for one of two alternative courses of action on each trial and report this preference by executing a pre-designated action (i.e., an index finger button press). However, these decisions did not occur in isolation but in the context of multiple experimental features used to constrain the information used to develop the preference, i.e., specified by an explicit instruction (*Instructed* context) or in the explicit absence of an instruction (*Free* context). Here we found multiple lines of evidence that there was a structured difference in how actions were executed in the *Free* and *Instructed* contexts even when reporting the same preference.

It is worth carefully considering how our findings narrowly related to the kinematic minutia of index finger movements and associated motor system dynamics could relate to broader considerations about volition and free choice. A first concern is whether the action differences between contexts could be attributed to the information constraints (i.e., presence/absence of instructions that modulated volition's role) or instead to the factors involved in implementing these constraints (e.g., stimuli, inter-response timing, reward differences, etc.).

4.1. Chronometry of action termination

A novelty of our study was the decomposition of the button-press event into its action elements, namely, a Push and a Release. Unlike the Push action that was required to report the cognitive choice (i.e., either freely selected or instructed), the Release had no direct functional role in the cognitive task and was incidental to the use of index finger button presses in our experiment rather than another action, such as a saccade. Nevertheless, a salient and surprising finding was that the Release movement in the *Instructed* context was executed ~ 40 ms earlier than in the *Free* context, while all other measured aspects of the kinematics were unaffected by context. The two contexts had another chronometric difference closely linked to the Release action. Congruent with

the Release latency difference, the contralateral β -rebound also had an earlier onset in the *Instructed* context than in the *Free* context but with a timing difference (~ 241 ms) that was six times the size of the Release latency difference. This large timing difference was a consequence of the yoking of β -rebound's onset to the Push movement in the *Instructed* context but to the Release movement in the *Free* context.

In an isolated EMG study of right index-finger flexion movements, Obhi and Haggard (2004) found that the electromyogram (EMG) at the first dorsal interosseus muscle of the right hand was slightly larger and sustained for marginally longer when the flexion was self-initiated than when it was instructed. Although suggestive of a similarity to our findings, it is currently unclear whether those EMG duration differences and the Release timing differences in our study are consequences of the same physiological mechanism. In that study, Obhi and Haggard (2004) postulated that the EMG difference that they observed might be a consequence of inter-context differences in motor preparation. Preparation mechanisms might certainly be organized differently in the two contexts (Obhi et al., 2009; Hughes et al., 2011; Schurger et al., 2012; Wang et al., 2017). Yet, a variety of other explanations might also account for the Release latency difference. However, the relationship of the β -rebound to the Release action places a strong constraint on possible explanations of the inter-context chronometric difference.

We now consider some examples of seemingly plausible models of the Release latency differences that are nonetheless incompatible with the timing properties of the β -rebound. One possibility is that the Push-then-Release sequence might be executed as a single action unit having a shorter overall duration in the *Instructed* context than in the *Free* context (Fig. 7A). Another class of possible mechanisms is suggested by analogy to sequential sampling models for Response Times (Ratcliff, 2008; O'Connell et al. 2018). In this framework, the Release action might be initiated when a decision variable linked to the Push action reaches a designated decision criterion. The Release latency differences might therefore arise because this decision criterion was set lower in the *Instructed* context than in the *Free* context (Fig. 7B); or because the decision variable increased more rapidly in the *Instructed* context relative to the *Free* context (Fig. 7C). All the above models assume that actions in both contexts share a common implementation having the same continuously varying parameters (e.g., action duration, decision criteria, accumulation rate, etc.). Accordingly, the Release latency difference is explained as resulting from differences in the parameter settings between contexts. This assumption about shared continuous parameters was, however, incompatible with the categorical difference in β -rebound timing between contexts, i.e., linked to the Push movement in the *Instructed* context but to the Release movement in the *Free* context. This incompatibility would be absent if the β -rebound were similarly structured in both contexts, i.e., linked to the Push or to the Release in both contexts, or if the β -rebound had onset differences between contexts without being linked to either Push or Release action.

Based on physiological considerations, we propose a novel model to reconcile this timing relationship between the Release action and the β -rebound. The central idea is that the Release action might be initiated based on different kinds of information in the two contexts that are generated at different times during action execution.

4.2. Action termination: Dual criterion model

Our accelerometer recordings index the small, rapid movements of the index finger but do not measure the contact forces between the index finger and the surface of the button. In a typical accelerometer trace of movements on a trial, there is a readily noticeable “quiet” period that is free of acceleration changes in between the Push and Release acceleration peaks (Fig. 4A). This period corresponds to the interval when the neural forcing of the finger's movement leads to continued application of pressure by the finger on the button's surface, even when no further downward movement of the button is possible (Oulasvirta et al., 2018). As a result, the contact force and associated compression of the finger's

soft tissue possibly reaches a maximum value at some point during this “quiet” period before reducing with the onset of the Release.

The above mechanical considerations suggest that there might be two relatively independent criteria for the sensorimotor system to determine *when* the button was successfully pressed: (i) the time at which the neural generation of muscular forces no longer produced a corresponding finger movement and (ii) the time at which the contact force reached a suitably high value. Evaluating each criterion requires information that is generated at different periods of time relative to movement onset. Assessing the first, movement-related criterion (henceforth, MOV) would involve integrating efferent motor information with proprioceptive feedback about the moving index finger within a control model (Miall and Wolpert, 1996; Desmurget and Grafton, 2000). However, assessing the second contact-related criterion (henceforth, CON) would depend on tactile percepts generated by the contact between the index finger and button during the “quiet” period.

Based on these simplistic considerations, we propose a model, which we refer to as the *Dual criterion model*. According to this model, neural processes are configured to initiate the Release action primarily based on the MOV criterion in the *Instructed* context and primarily based on the CON criterion in the *Free* context (Fig. 7D). The MOV criterion is assumed

to be successfully satisfied at an earlier time than the CON criterion since the movement-related information is available before the contact-related information reaches its peak intensity. The relative timing of the MOV and CON criteria are predicted to produce the observed difference in Release latency in the two contexts. Specifically, the MOV criterion is assumed to be satisfied at a time point *during* the acceleration changes associated with the Push movement itself, with a short refractory delay before the Release can begin. However, the CON criterion is assumed to be satisfied during the “quiet” period enabling the Release to follow quickly after. The β -rebound's onset is assumed to be related to the neural changes triggered when these criteria are met. The apparent linkage to the Push/Release movements is an indicator of the time period when these criteria are satisfied. The onset of the β -rebound would therefore be closely linked to the Push movement in the *Instructed* context while being more closely linked to the Release movement in the *Free* context.

A crucially relevant body of evidence supporting the existence of two such distinct modes for controlling fine finger movements comes from studies where tactile feedback was blocked by anesthetizing the fingertips. Touch typing (without visual feedback) by expert typists with anesthetized finger tips produced increased spatial errors in finger placement but did not influence movement kinematics or keystroke

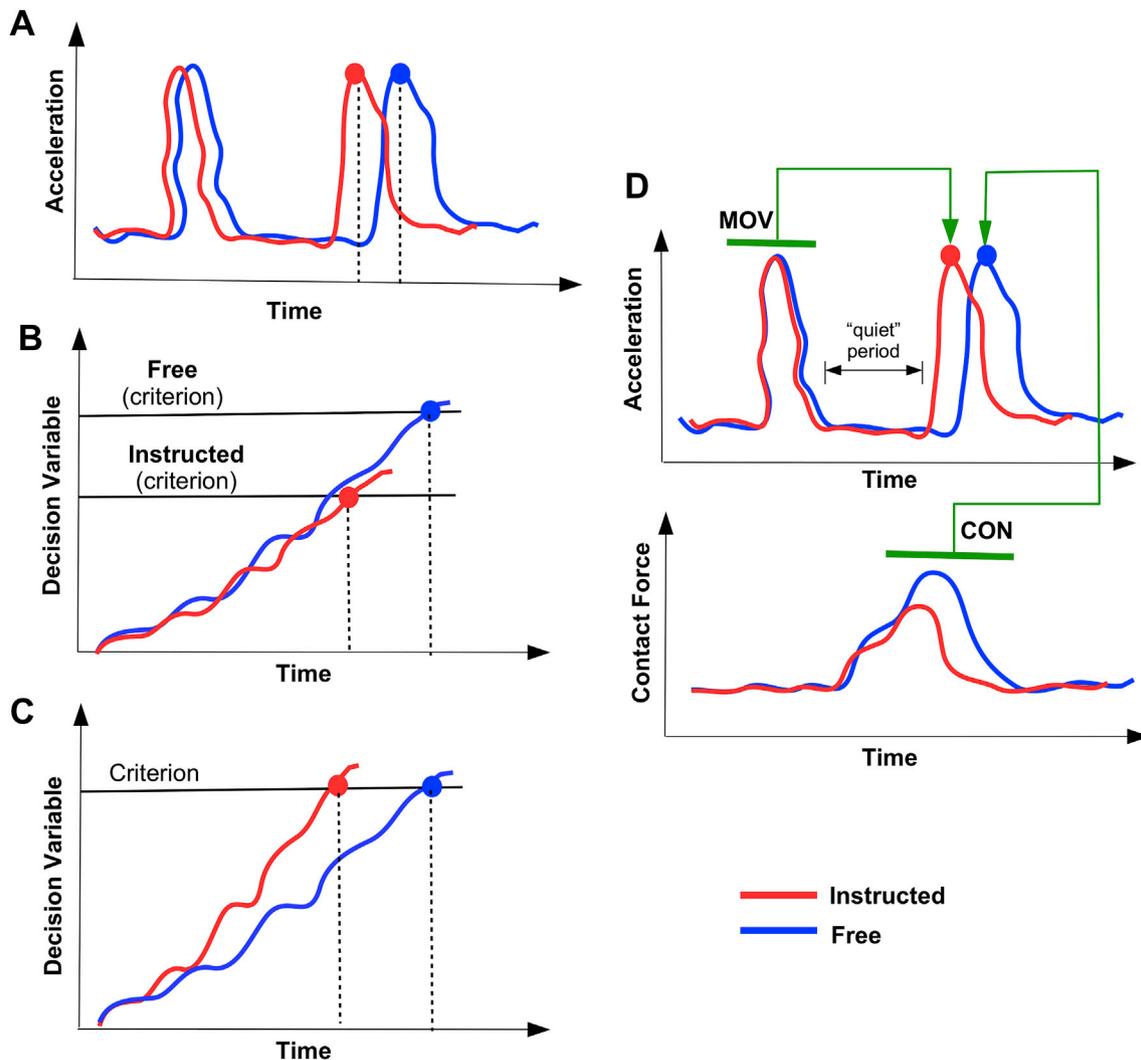


Fig. 7. Release timing models. (A) Differences in overall movement timing in *Free* (blue) and *Instructed* context (red). (B) Difference in post-Push decision criteria between contexts. Colored dots indicate time at which decision criterion is met. (C) Difference in rate of increase in post-Push decision variable. (D) Information driving Release is indicated by thick green lines and arrows: Acceleration changes during Push movement (MOV) (upper panel), and contact forces during post-Push “quiet” period (CON) (lower panel).

timing (Gordon and Soehteing, 1995; Rabin and Gordon, 2004), consistent with a movement-based control of these rapid finger movements. By contrast, in studies of synchronized finger tapping to periodic auditory tones, anesthesia disrupted movement timing (Aschersleben et al., 2001). This timing-related disruption supports the hypothesis that synchronization is achieved by timing finger movements in order to coordinate the timing of the resulting tactile percept with the auditory percept (Aschersleben, 2002; Goebel and Palmer, 2008). This form of touch-governed movement control is consistent with a contact-based criterion.

Another supporting line of evidence has to do with the neural basis for movement awareness. Based on evidence from direct cortical stimulation of neurosurgical patients, Desmurget and Sirigu (2009) emphasize the differential neural basis for movement awareness and the intention/urge to move. They specifically suggest a key role of the posterior parietal cortex in movement awareness and of the premotor cortex in the urge to move. Superficially consistent with this proposal, in our study, Push-evoked ERPs were correlated with movement latency in the *Instructed* context where a key role for the MOV criterion was hypothesized. The Push-evoked ERPs at the centro-parietal electrodes were associated with the Push-latency (consistent with a monitoring of ongoing movements) while the Push-evoked ERPs at FC1/2 were associated with the latency of the upcoming Release movement (consistent with the urge to initiate the Release action). This frontal/parietal distinction in ERP-movement correlations was also evident across the scalp (Fig. 5C). Even though the Push action's kinematics was closely matched between contexts, these ERP-movement-related correlations were absent for the Push-evoked ERPs in the *Free* context where a key role for the CON criterion was hypothesized.

In summary, the *Dual criterion* model accounts for the difference between the contexts in Release latency, the discontinuous timing of the β -rebound, as well as the ERP-behavior correlations. Although based on assumptions about the source of sensory information, this model's central predicted consequence is a difference in the neural organization to terminate actions in the *Free* and *Instructed* contexts. We next consider what might lead to the adoption of such different success criteria in the two contexts.

4.3. Representation for selection

Volition modulation paradigms implicitly assume that alternative actions are *represented* in the same way even if volitional information processing differs for self-selected and instructed choices. However, the target representation for selection is intrinsically ambiguous in binary choices of the kind investigated here (Haggard, 2008). For instance, selection could be object-directed (i.e., which button to press: the left or right button) or instead be action-directed (i.e., which movement to make: a left or right finger flexion) (Allport, 1987; Cisek, 2007; Oliveira et al., 2010). Object-directed selection operates on representations of the possible spatial targets for a subsequent action while action-directed selection instead operates on representations of the possible actions. Our narrow vantage point over the motor system provided a test of whether selection might be action-directed in both the *Instructed* and *Free* contexts.

The nearly anti-phase interhemispheric coupling (δ -band) in the *Instructed* context (Figs. 2 and 3) is consistent with competitive inhibition

targeted at the cortical motor representation of the non-selected action in the ipsilateral hemisphere (Burle et al., 2004; Burle et al., 2016; Grefkes et al., 2008; Duque et al., 2017). However, the nearly in-phase coupling in the *Free* context is an unclear indicator of the motor status of the non-selected action. If the post-movement β -rebound (Fig. 6C and D) is specific to active motor representations then it suggests a resolution. In the *Instructed* context, the symmetric β -rebound over both hemispheres is consistent with the motoric representation of both action options. By contrast, the negligible magnitude of the ipsilateral β -rebound in the *Free* context implies that only *one* action (contralateral) was motorically represented in this context but not the other action option (ipsilateral). Taken together, these findings are consistent with selection being action-directed in the *Instructed* context but not in the *Free* context.

We propose that action-directed selection in the *Instructed*, but not *Free*, context leads to differing control demands for action execution in the two contexts – specifically a verification that the correct movement was executed when selection is movement-directed, and a verification that there was a successful interaction with the target object when selection is object-directed. These differing control demands consequently lead to the use of a movement-related criterion (MOV) in the *Instructed* context and a contact-related criterion (CON) in the *Free* context. The question of what contextual considerations inform this difference in representations between the *Free* and *Instructed* context is an important issue for future studies. The meta-decision about to how to represent the action alternatives in the first place is a major variable in any decision and is informed by broader contextual considerations (Gold and Shadlen, 2007; Haggard, 2008). One contributing factor to this representation difference could be the self-paced structure of the *Free* context. Even though the binary choice on each trial of the *Free* context was free of choice-related performance demands (i.e., accuracy), the timing of the action was subject to performance demands and the risk of errors. The risk of executing an action at an inappropriate time would theoretically be minimal if *neither* action option was motorically prepared in advance. Object-directed selection might therefore be of strategic relevance to the *Free* context as the spatial target for the action (i.e., left or right button) could be selected in advance without motorically representing the action until a suitable time is reached. In this way, at the intended time, the action linked to the selected spatial target could be motorically represented and executed in a controlled manner (cf. Haggard and Eimer, 1999). Representing only one action would make competitive inhibition of the non-selected action unnecessary in the *Free* context.

In conclusion, our findings suggest that, far from being an abstract cognitive activity, volition's effects extend deep into the motor system.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuroimage.2018.12.005>.

Appendix

Table A.1

ANOVA statistics [Context {Free, Instructed} x Movement{Push,Release}] (upper table)(Fig. S2B), and [Context {Push, Release} x Laterality{Contra,Ipsi}](lower table)(Fig. S2C). Shaded cells indicate statistically significant effects corrected for multiple comparisons (Bonferroni $\alpha = 0.0036$) with colors matching those of Figure S2 (B) and (C).

Electrode	Context*Mvmt		Context		Mvmt	
	F(1,17)	p	F(1,17)	p	F(1,17)	p
FC3	0.018	0.8952	0.090	0.7684	42.917	0.0000
FC1	1.230	0.2828	29.216	0.0000	39.623	0.0000
C3	2.813	0.1118	4.690	0.0448	22.777	0.0002
C1	0.512	0.4838	1.197	0.2891	56.927	0.0000
CP5	0.079	0.7824	3.866	0.0658	3.845	0.0665
CP3	4.871	0.0413	37.286	0.0000	0.634	0.4369
CP1	0.321	0.5785	17.145	0.0007	3.337	0.0854

Electrode	Context*Laterality		Context		Laterality	
	F(1,17)	p	F(1,17)	p	F(1,17)	p
FC3	29.060	0.0000	3.518	0.0780	91.407	0.0000
FC1	35.438	0.0000	0.036	0.8524	125.376	0.0000
C3	10.975	0.0041	7.954	0.0118	17.946	0.0006
C1	21.527	0.0002	2.994	0.1017	56.453	0.0000
CP5	3.479	0.0795	0.466	0.5041	40.623	0.0000
CP3	0.066	0.8009	45.653	0.0000	1.278	0.2739
CP1	3.322	0.0860	28.334	0.0001	0.780	0.3894

Table A.2

Correlations of Push-evoked ERPs to Push and Release latencies for the *Instructed* context (Fig. 5B) and *Free* context. Shaded cells indicate statistically significant correlations after correction for multiple comparisons (Bonferroni $\alpha = 0.0083$).

Push-evoked ERPs	<i>Instructed context</i>				<i>Free context</i>			
	Push latency		Release latency		Push latency		Release latency	
	r(17)	p	r(17)	p	r(17)	p	r(17)	p
FC1/2	+0.536	0.022	-0.615	0.0066	+0.379	0.121	-0.389	0.110
CP1/2	+0.654	0.0032	-0.241	0.336	+0.123	0.627	-0.270	0.278
CP3/4	+0.614	0.0067	-0.191	0.447	+0.304	0.2193	-0.198	0.431

Table A.3

Full statistics for ANOVA evaluating β -band amplitude modulation in Fig. 6B with factors Context {Free, Instructed} x Time {t₁,...,t₅}. Shaded cells indicate statistically significant effects corrected for multiple comparisons (Bonferroni $\alpha = 0.0036$).

Modulation of Push-evoked β amplitude

Electrode	Context*Time		Context		Time	
	F(4,68)	p	F(1,17)	p	F(4,68)	p
FC3	2.878	0.0290	11.746	0.0032	4.140	0.0046
FC1	5.657	0.0005	9.965	0.0058	3.367	0.0142
C3	3.820	0.0074	12.427	0.0026	4.056	0.0052
C1	10.275	0.0000	6.924	0.0175	8.477	0.0000
CP5	7.274	0.0001	16.882	0.0007	5.288	0.0009
CP3	9.682	0.0000	21.404	0.0002	12.204	0.0000
CP1	14.103	0.0000	21.359	0.0002	15.566	0.0000

Modulation of Release-evoked β amplitude

Electrode	Context*Time		Context		Time	
	F(4,68)	p	F(1,17)	p	F(4,68)	p
FC3	3.728	0.0084	0.074	0.7888	4.469	0.0029
FC1	0.135	0.9691	0.180	0.6766	7.928	0.0000
C3	2.042	0.0982	1.684	0.2117	12.360	0.0000
C1	0.834	0.5082	0.920	0.3509	13.303	0.0000
CP5	1.927	0.1159	0.080	0.7801	3.888	0.0067
CP3	3.707	0.0087	0.210	0.6528	10.850	0.0000
CP1	0.513	0.7263	4.523	0.0484	13.005	0.0000

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