Tracking Keystroke Sequences at the Cortical Level Reveals the Dynamics of Serial Order Production

Svetlana Pinet[1,2], Gary S. Dell[3], and F.-Xavier Alario[1]

Abstract

■ Response selection is often studied by examining single responses, although most actions are performed within an overarching sequence. Understanding processes that order and execute items in a sequence is thus essential to give a complete picture of response selection. In this study, we investigate response selection by comparing single responses and response sequences as well as unimanual and bimanual sequences. We recorded EEG while participants were typing one- or two-keystroke sequences. Irrespective of stimulus modality (visual or auditory), response-locked analysis revealed distinct contralateral and ipsilateral components previously associated with activation and inhibition of alternative responses. Unimanual sequences exhibited a similar activation/inhibition pattern as single responses, but with the activation component of the pattern expressed more strongly, reflecting the fact that the hand will be used for two strokes. In contrast, bimanual sequences were associated with successive activation of each of the corresponding motor cortices controlling each keystroke and no traceable inhibitory component. In short, the activation component of the two-keystroke sequence EEG pattern can be understood from the addition of activation components of single-stroke sequences; the inhibition of the hand not being used is only evidenced when that hand is not planned for the next stroke. ■

INTRODUCTION

Producing a behavioral sequence involves retrieving and activating each sequence unit in an ordered and timely fashion, a requirement often referred to as the problem of serial order (Lashley, 1951). An important theory of serial order is expressed by competitive queuing (CQ) models. These models have been successfully applied in several cognitive domains, such as memory (e.g., serial recall; Houghton, 1990) and language (e.g., typing; Rumelhart & Norman, 1982). CQ models propose that all elements of a sequence are activated, such that there is a gradient of activation consistent with the order of items in the sequence. For example, the gradient may be set up by each item inhibiting all subsequent items, and the sequence may be executed by selecting the currently most activated item, and then inhibiting it, thus leading to the next item in the queue possessing the most activation. Then, a balance of activation and inhibition of items leads to the correct production of the planned sequence.

The CQ model's activation and inhibition processes constitute an algorithmic (Marr, 1982) account, one that makes no claims about physiological implementation. A significant step toward such an implementation was taken by Averbeck, Chafee, Crowe, and Georgopoulos (2002), who showed that pFC of behaving monkeys displayed a gradient of activation of future items, with their degree of activation following their order in the sequence. These data show that at least some assumptions from cognitive models of sequence planning can be linked to physiological activities and to their neural implementation.

In the case of humans, when they give manual responses with either hand, it is possible to follow the activation of a response and the inhibition of its alternative with EEG recordings (e.g., Servant, White, Montagnini, & Burle, 2016). Readiness potentials and their lateralized computation (lateralized readiness potential [LRP]) have been widely used to describe such dynamics (Coles, 1989; de Jong, Wierda, Mulder, & Mulder, 1988; Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988). However, a more detailed approach consists of using a spatial filter (Laplacian transform) that allows a more direct assessment of the activity of each motor cortex (Vidal et al., 2015; Perrin, Pernier, Bertrand, & Echallier, 1989). Using this approach, the component recorded over the contralateral motor cortex of a response effector has been directly linked to the activation of that cortical area, and the analogous ipsilateral component has been linked to the inhibition of the corresponding ipsilateral area (Selen, Shadlen, & Wolpert, 2012; Donner, Siegel, Fries, & Engel, 2009; Burle, Vidal, Tandonnet, & Hasbroucq, 2004; Vidal, Grapperon, & Bonnet, 2003).

What this research on single responses does not address is whether and how these components and

[1]Aix-Marseille University, CNRS, LPC, [2]Johns Hopkins University, [3]University of Illinois, Urbana-Champaign

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processes would be involved in sequence production, minimally a sequence of two strokes on a keyboard. The simplest additive hypothesis would state that the production of two responses can be understood from the addition of each single response. Figure 1 presents the predictions of such a hypothesis on the associated motor components, separately for unimanual (both responses use the same hand) and bimanual (each response uses a different hand) sequences, based on the components known to be associated with single responses. The additive hypothesis was schematized by considering that a two-stroke sequence consists of the simple addition of each component from the single stroke, adjusted for the side of each keystroke, and with a 170-msec delay between keystrokes (estimated from the recorded average interkeystroke interval). For unimanual sequences, the activation and inhibition components associated with each keystroke are added, and each hemisphere would then exhibit something like double the amplitude compared with the components associated with single responses. Bimanual sequences require the inversion of the role of each hemisphere in terms of activation and inhibition from the first to second keystroke. The addition of the resulting components yields specific patterns for each hemisphere, each of which is quite different from the expectation for unimanual sequences. Any deviation from the expected patterns displayed in Figure 1 would indicate the existence of specific sequence mechanisms.

Previous studies about bimanual sequence production are not incompatible with the above predictions. Focusing on the preparation period before an execution cue, the LRP can index the amount of preparation of the following sequence. The LRP displays a higher amplitude when two movements are being prepared rather than one (Gladwin, 't Hart, & de Jong, 2008; de Jong, Gladwin, & 't Hart, 2006). However, results also show that bimanual movements cannot be easily understood as the sum of two unimanual movements as evidenced in particular on the motor potentials, suggesting that specific processes might be in place during sequence preparation (Cui & Deecke, 1999). In particular, the effectors involved in a movement sequence influence how the sequence is being prepared, initiated, and executed. However, without separating activity coming from each hemisphere, it is not possible to formulate precise predictions, especially those regarding the inhibition (ipsilateral) component, and thus linking neurophysiological results with the hypothesis of cognitive models.

In contrast with evoked potentials, time–frequency estimates reveal the selection of motor goals or the foreknowledge of a sequence (Park, Kim, & Chung, 2013; Gladwin et al., 2008). Both alpha and beta bands show desynchronization at the start of a movement sequence, sustained for the whole duration of the movement (Alegre et al., 2004). Because of the slower time frame of processes indexed by time–frequency, however, potentials seem more appropriate to test the predictions laid out by the additive model, as they reflect processes closer to response initiation, which is of particular interest here (Gladwin et al., 2008).

The activation and inhibition components described above for single responses have been shown to be present in the context of word typing (Scaltritti, Pinet, Longcamp, & Alario, 2017; Pinet, Dubarry, & Alario, 2016; Pinet, Hamamé, Longcamp, Vidal, & Alario, 2015;

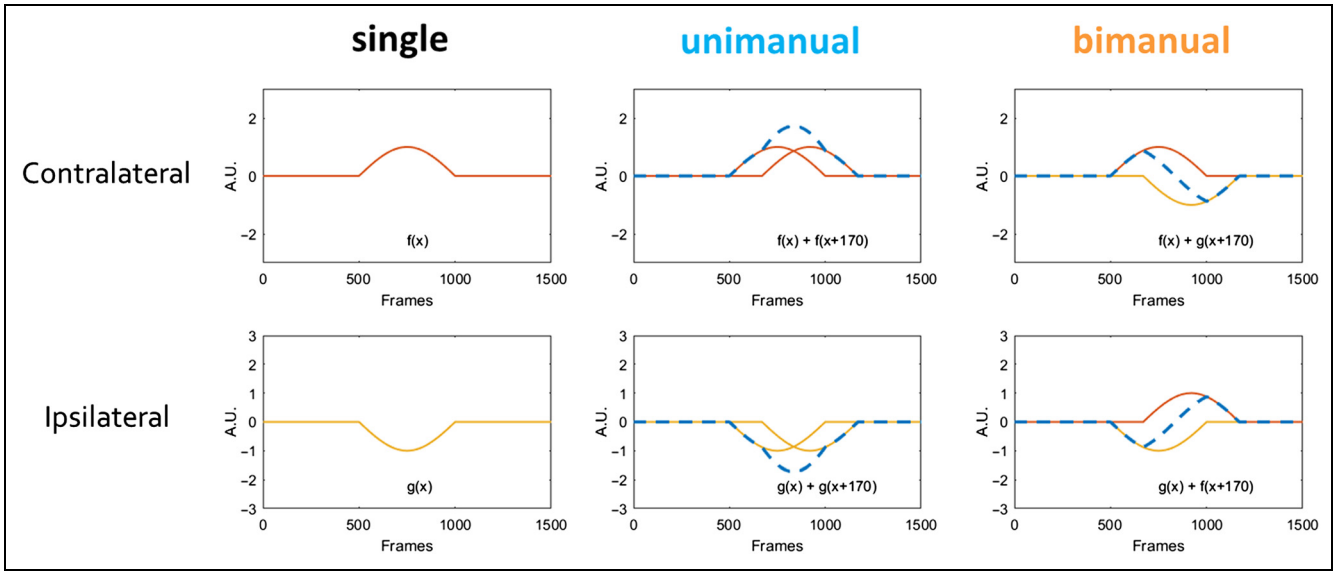

Figure 1. Schematic illustration of the additive hypothesis. Electrodes contralateral and ipsilateral to the first keystroke are plotted separately. An orange line represents the contralateral component f(x), and a yellow line represents the ipsilateral component g(x). A dashed blue line corresponds to the addition of the components for each electrode and represents the components predicted by the additive hypothesis (see main text for details). Equations on each graph specify the addition of components that were computed. The second keystroke is modeled to be delayed 170 msec relative to the first keystroke.

see also Logan, Miller, & Strayer, 2011), a quintessential serial order task that could provide a simple and natural domain for addressing sequence production. Most recently, Scaltritti, Alario, and Longcamp (2018) explored the scope of planning in typing. They showed that the neurophysiological signature associated with response selection is modulated by item position within the upcoming sequence (close vs. distant). Consistently, Behmer et al. (2018) used TMS to show a gradient of activation of motor cortex that corresponded to the graded position of future keystrokes.

The goal of our work was to identify the physiological implementation of some assumptions made by cognitive models, such as the CQ model, and particularly the assumptions regarding the successive activation of each item and the inhibition of upcoming items. In this study, we tracked the cortical dynamics driving response programming in single keystrokes and two-keystroke sequences that were either unimanual or bimanual. Because previous studies allowed us to formulate precise predictions on activation/inhibition components (Figure 1), we restricted our analysis to the time domain. Comparing single keystrokes with two-keystroke sequences informs us about whether and when activation and inhibition processes identified for single responses are modified by the requirement to type an additional keystroke in a sequence context. Each contrast of sequence type (unimanual or bimanual) versus single strokes informs us further about the interplay between the hemispheres. Specifically, the unimanual versus single contrast keeps the recruited effectors constant but increases the number of strokes in the unimanual case, perhaps requiring more processing from the contralateral hemisphere. The bimanual versus single contrast tests the role of both effectors, particularly the possible influence of inhibition of the hemisphere not involved in the immediate keystroke.

METHODS

Participants

Eighteen right-handed participants were selected for their ability to touch-type, that is, typing with all (or almost all) 10 fingers without the need to look at their hands. Four participants were excluded because of problematic eye movements around the moment of response or poor signal-to-noise ratio. The final sample (five men, nine women) was 24.9 years old on average (range: 20–33 years old). Participants' typing ability was assessed via a typing test (e.g., Pinet et al., 2016). Participants had a mean accuracy of 84% (range: 78–91%) and a mean typing speed of 48 words per minute (wpm; five-character wpm; range: 34.6–57.5 wpm).

Stimuli and Design

Eight single letters and six two-letter words were used as stimuli. Half of the single letters were typed with the left hand ("Z," "E," "S," "D"); and the other half, with the right hand ("I," "O," "K," "L") in the AZERTY keyboard. The words selected were the French names of musical notes, to ensure homogeneity of meaning and because they present interesting sequence properties. Four musical note names started with the left hand ("DO," "RE," "FA," and "SI"), and two started with the right hand ("MI" and "LA"); half were typed with one hand (unimanual: "RE," "FA," "MI"), and the other half were typed with both hands (bimanual: "DO," "SI," "LA"). Hence, stimuli were divided into three conditions: single (one letter), unimanual (two letters, one hand), and bimanual (two letters, two hands). The only three-letter musical note ("SOL") was also included for completeness, but data from SOL trials were not analyzed. Stimulus presentation was visual (printed letters) and auditory (spoken letter or music note names). Stimulus modality (visual vs. auditory) and stimulus type (letters vs. musical notes) were presented in four independent blocks. Each participant saw all conditions in a randomized order.

Procedure

Visual stimuli were displayed on a 17-in. CRT computer screen placed at about 70 cm from the participant. Auditory stimuli were presented binaurally through earphones. Responses were collected from a DirectIN High Speed Keyboard PCB v2010 (Empirisoft) to obtain keystroke timing data with at least 1-msec accuracy. Stimuli presentation and response acquisition were controlled using the Presentation software (NeuroBehavioral Systems).

Participants sat in a dimly lighted, electrically shielded room. Their sitting position was adjusted so that they were comfortable typing. The task was to type the letter or musical note name on the keyboard as fast and accurately as possible after presentation. Letter blocks comprised 200 trials (25 repetitions of each of the eight stimuli). Music blocks comprised 350 trials (50 repetitions of each of the seven note names). Each block included a short break.

A trial consisted of a fixation cross presented during a random duration from 400 to 600 msec, followed by presentation of the stimulus (maximal duration = 2000 msec). After the response, the stimulus stayed on for 500 msec, and then feedback (correct or incorrect, indicated by a green check mark or a red cross or by high- and low-pitch beeps) was displayed for 500 msec in the same modality as the stimulus (visual or auditory). The screen then remained black for 500 msec. Every two to three trials, there was a 2-sec interval to allow participants to blink and avoid contamination of the signal.

Behavioral Data Analysis

RTs (time of the first keystroke) and accuracy rates were analyzed with linear mixed-effect models, as is commonly

done in cognitive studies of language (Baayen, Davidson, & Bates, 2008; Jaeger, 2008). RTs were log-transformed, following the result of a Box Cox test. RTs below 300 msec or incorrect responses were removed from the RT analysis. RTs and accuracy rates were analyzed according to the following predictors: modality (auditory or visual), first keystroke hand (left or right), and second keystroke (single, unimanual, bimanual). To account for the three levels of the second keystroke predictor, the predictors were Helmert-coded to contrast sequence length (one key vs. two keys) and second keystroke side (same/different). By-participant random slopes were added for all predictors of interest. Random intercepts by participant and by item were also added to the model. Trial number was added as a control variable. Accuracy rate analysis included a random slope for modality only, as the model would not converge otherwise.

EEG Recordings and Preprocessing

EEG was acquired from 128 scalp locations using Ag/AgCl active electrodes (BioSemi Active Two system), referenced to the CMS-DRL ground. The sampling rate was 512 Hz (filters: DC to 104 Hz, 3-dB/octave slope). Vertical and horizontal EOGs were recorded with three surface electrodes (Ag/AgCl) placed below the left eye and next to the two outer canthi.

Offline analyses were performed using the MATLAB toolboxes Brainstorm (Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011) and Fieldtrip (Oostenveld, Fries, Maris, & Schoffelen, 2011), as well as custom routines. Data were rereferenced to the average of both mastoids. Continuous data were filtered (Butterworth Filter Order 4: 0.1–100 Hz). Bad electrodes were removed and interpolated. A first mild artifact rejection was performed before computing independent component analysis (algorithm: Infomax from EEGLAB toolbox; Delorme & Makeig, 2004). Component(s) corresponding to eye movements was (were) removed. A second stricter artifact rejection was then performed to reject remaining noisy segments. A −200- to 0-msec prestimulus baseline was applied by subtraction. Response-locked epochs were then extracted (−1500 to +800 msec around the first or second keystroke).

Current source density transformation was applied (number of spherical splines: 4, maximal degree of Legendre polynomial: 20, smoothing parameter: 10-5) to enhance spatial resolution of the EEG signal (Perrin et al., 1989).

EEG Statistical Analysis

Unless stated otherwise, activities on the contralateral hemisphere from left- and right-hand responses were averaged together. Similarly, activities on the ipsilateral hemisphere from left- and right-hand responses were averaged together. The signal is presented relative to left-hand responses (i.e., ipsilateral hemisphere corresponds to the left hemisphere).

Two main contrasts (unimanual vs. single and bimanual vs. single) were tested from −500 to 0 msec including all 128 electrodes, using cluster-based nonparametric statistics (Maris & Oostenveld, 2007). This procedure allows us to deal with the multiple-comparison problem by clustering significant neighboring channels and time points and building the statistical distribution directly from the observed data by successive permutations. More specifically, two conditions are compared with a paired t test at each time point. Clusters are composed of the time points presenting t values above a specific threshold ($p < .05$) based on spatial and temporal adjacency. The sum of t values within each cluster gives the cluster-level statistic, and the significance of each cluster is computed using permutations. However, one should refrain from overinterpreting the spatial or temporal extension of any cluster. Because the significance is only tested between conditions, one should not conclude strongly about the boundaries of any cluster (any point is not tested against another). Nevertheless, we depict the significant clusters as Channel × Time matrices for illustrative purposes. Although all electrodes within a cluster show a significant effect, each electrode can display a slightly different pattern from other electrodes of the same cluster. For that reason, we present an array of electrodes rather than the averaged signal over cluster electrodes. To compare our results with previous literature, we also display specific electrodes over the motor cortex, close to C3/C4 (i.e., D18 and B21 in our 128-electrode system), based on Pinet et al. (2016).

The two main contrasts were run for data collapsed over modality and hand (main analysis reported). They were also run for each modality and hand separately (eight additional contrasts).

RESULTS

Behavioral Results

The RT analysis (see Table 1) revealed a main effect of Modality, with auditory stimuli eliciting slower responses than visual stimuli (ß = 0.14, t = 4.5, 95% CI [0.076, 0.20], M_{visual} = 697.7 ± 231.4 msec, $M_{auditory}$ = 792.4 ± 255.3 msec). RTs also exhibited a practice effect, strongly decreasing with trial number (ß = −8.43E-5, t = −13.2, 95% CI [−9.7E-5, −7.2E-5]). None of the other effects was significant.

Mean accuracy was 93.5%. Accuracy rate analysis (see Table 2) revealed that unimanual sequences were produced more accurately than bimanual sequences (ß = 1.1, z = 3.4, 95% CI [0.45, 1.7], $M_{unimanual}$ = 94.1 ± 2.8%, $M_{bimanual}$ = 93.1 ± 5.0%). None of the other effects was significant.

Table 1. Mixed Model Regression Results for RT

Fixed Effects	*Coefficient*	*SE*	*t*	*95% CI*		*p*
Intercept	6.568	0.046	143.115	6.478	6.658	<2e-16
Modality (visual/auditory)	0.136	0.031	4.46	0.076	0.196	6.49E-04
First key (left/right)	−0.051	0.029	−1.78	−0.108	0.005	.090
Second key (one/two keys)	0.036	0.035	1.04	−0.032	0.104	.312
Second key (same/different hand)	−0.012	0.043	−0.28	−0.097	0.073	.782
Trial	−8.43E-05	0.000	−13.22	−9.68E-05	−7.18E-05	<2e-16

Random Effects	*Variance*
Participant intercept	0.027
Modality | participant	0.013
First key | participant	0.006
Second key (one/two keys) | participant	0.011
Second key (same/different hand) | participant	0.015
Item intercept	0.001
Residual	0.046

The Signature of Sequence Programming Depends on Its Constituents

EEG analyses were performed on correct trials only. Trials presenting EEG artifacts (19.4%) were rejected. Response-locked averages are depicted in Figure 2. All topographies are presented relative to left-hand responses (i.e., right hemisphere corresponds to contralateral hemisphere). We depict one representative electrode on each side (contralateral [B21] and ipsilateral [D18] to the response, near C3 and C4 in the standard 10–10 system), to provide comparison with previous studies (e.g., Pinet et al., 2016; Vidal et al., 2003).

Prior to the execution of a single keystroke (single condition; Figure 2A, left), we observed a clear negativity/positivity pattern over contralateral/ipsilateral hemispheres, replicating the pattern repeatedly observed in 2AFC tasks (Meynier, Burle, Possamaï, & Vidal, 2009; Vidal et al., 2003) and more recently in word typing (Scaltritti et al., 2017, 2018; Pinet et al., 2015, 2016). The same general pattern is observed for unimanual sequences (Figure 2B). In contrast, both the topographies and the

Table 2. Mixed Model Logistic Regression Results for Accuracy Rates

Fixed Effects	*Coefficient*	*SE*	*t*	*95% CI*		*p*
Intercept	2.937	0.229	12.813	2.488	3.386	<2e-16
First key (left/right)	−0.044	0.212	−0.209	−0.459	0.371	.834
Second key (absent/present)	0.037	0.210	0.177	−0.375	0.450	.859
Second key (same/different hand)	1.057	0.308	3.432	0.453	1.661	6.00E-04
Modality (visual/auditory)	0.078	0.117	0.667	−0.152	0.308	.505

Random Effects	*Variance*
Participant intercept	0.433
Modality | participant	0.100
Item intercept	0.127

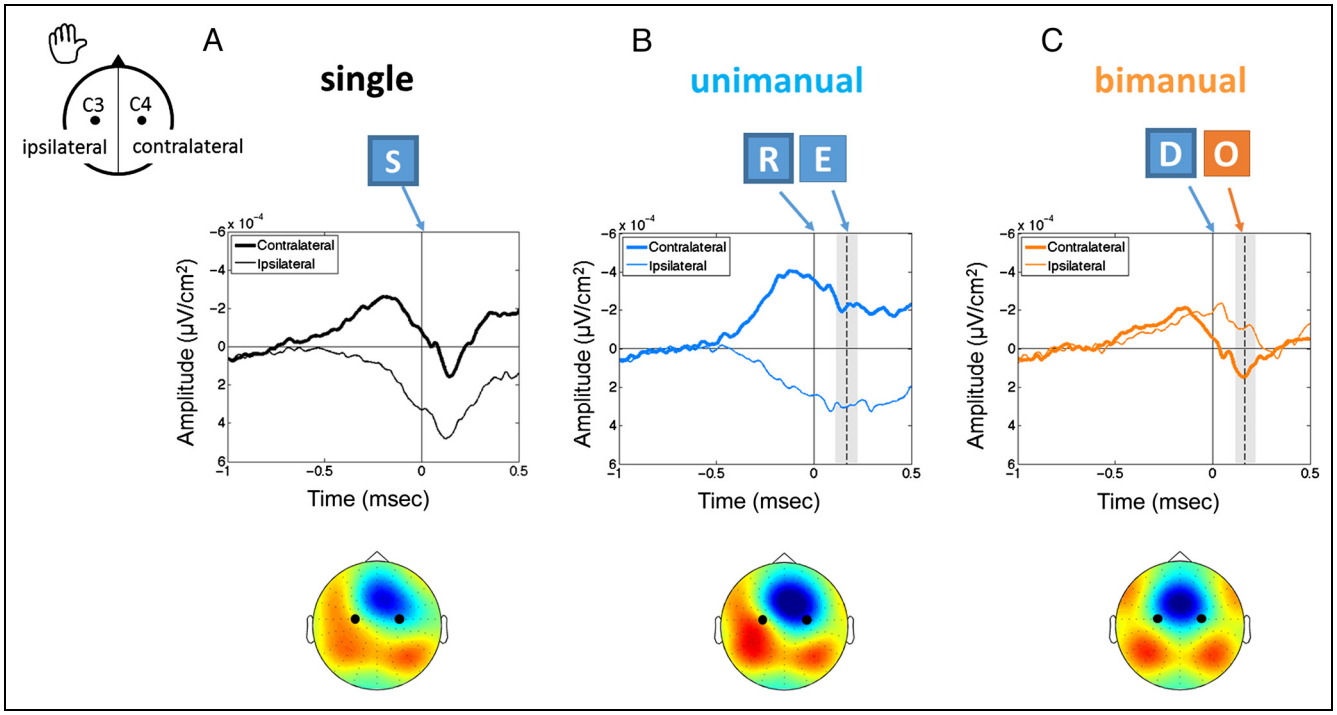

Figure 2. Activities recorded over contralateral and ipsilateral hemispheres for single, unimanual, and bimanual conditions. Zero represents the first keystroke. The dotted line represents the mean time interval between keystrokes in two-keystroke conditions (shaded area: standard deviation). Topographies are plotted in the −200 to −150 msec time window, corresponding to latency of the contralateral peak, and displayed contralateral and ipsilateral electrodes are indicated by black dots on the topographies.

ERP time courses indicate a different pattern for bimanual sequences, with a negative central component present on both ipsilateral and contralateral hemispheres, and a symmetric topography.

Direct comparisons between conditions over a range of electrodes are presented in Figure 3A. Unimanual sequences (vs. single; see Figure 3A) yielded an amplitude increase of the negative component mainly over contralateral hemisphere (cluster-based nonparametric test: $p = .016$; Figure 3B), but virtually no modulation of the ipsilateral positivity. The topography of the statistic confirmed an effect focused over central and contralateral electrodes.

Bimanual sequences contrasted with single responses in a different way. Focusing first on central electrodes, bimanual sequences (vs. single; see Figure 3A) presented a difference over ipsilateral hemisphere (cluster-based nonparametric test: $p = .002$; Figure 3C). The ipsilateral component in bimanual sequences was of opposite polarity than in single responses, clearly suggesting different processes in the contralateral and ipsilateral hemispheres. The topography of the statistic confirmed that this positive effect was focused on midline and ipsilateral electrodes. Second, peripheral contralateral electrodes also presented a negative difference in amplitude (cluster-based nonparametric test: $p = .02$). This stems from the fact that central components were more spatially focused in the bimanual condition (see topography in Figures 2C and 3) compared with the single condition, which could indicate a mixture of processes in the production of bimanual sequences (see Discussion below).

These two contrasts reveal that the contralateral and ipsilateral components are modulated by different factors, hence stem from distinct processes.

Over midline frontal electrodes (see Figure 3A), higher amplitude was observed for both unimanual and bimanual sequences relative to single (confirmed by cluster-based nonparametric tests reported above, with midline electrodes being part of the positive clusters). Thus, midline electrodes presented a very different pattern from their neighboring lateralized electrodes.

The patterns described were observed in each stimulus modality (visual or auditory) and were obtained regardless of the hand of the first (or only) keystroke (i.e., without mirror averaging). Only some of eight contrasts tested, however, reached significance when the data were broken down by hand or modality, presumably because of lack of power.

Preparation of a Bimanual Sequence

A closer look at bimanual sequences is informative about timing. The data from these sequences differed considerably from the pattern obtained in the single and unimanual conditions. Instead of the expected positive component, the ipsilateral hemisphere presented a negative component whose time course was similar to the contralateral component, albeit shifted in time (Figure 2C). We

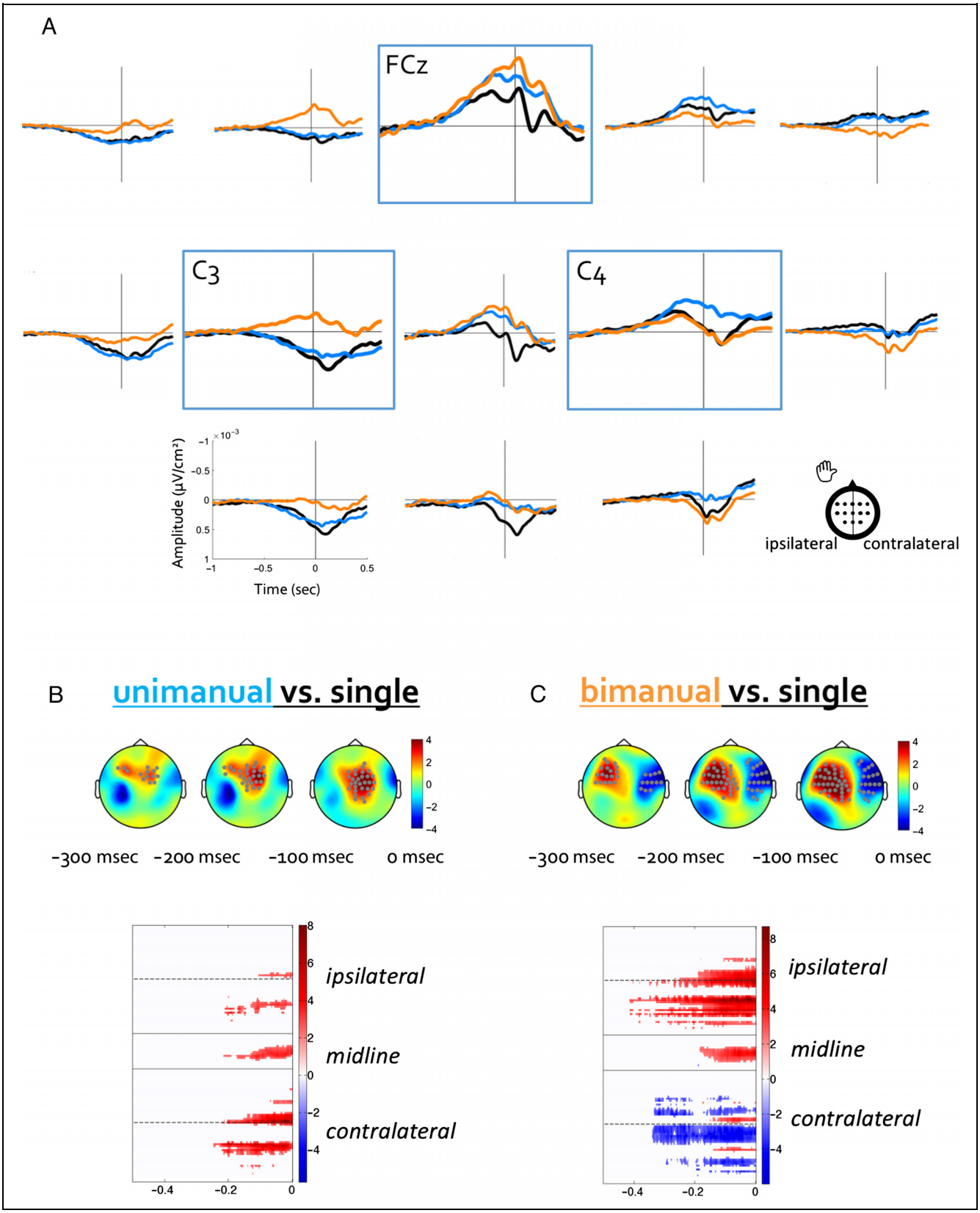

Figure 3. Evoked potential results. (A) Response-locked potentials comparing unimanual (blue) and bimanual (orange) conditions against single (black). The position of the 13 electrodes displayed is indicated on the scalp. C3, C4, and FCz electrodes are displayed larger. (B, C) Results of the cluster-based permutation tests for unimanual versus single (B) and bimanual versus single (C) contrasts. Results are presented as topographies from −300 to 0 msec in 100-msec time windows, with significant electrodes in each time window outlined as gray dots. A matrix of Channels × Time Frames, grouped by ipsilateral hemisphere, midline, and contralateral hemisphere, ordered from posterior to anterior, and masked for statistical significance, indicates the full extent of the cluster in space and time. Zero represents the first keystroke.

extracted the peak latency for each component on the grand-averaged ERPs on contralateral (B21) and ipsilateral (D18) electrodes in the −500 to +200 msec time window around the first keystroke. This temporal shift measured on average ERPs between ipsilateral and contralateral peaks (184 msec) was in the range of the average interkeystroke interval (M = 167 ± 50 msec). Extracting timing from averaged ERP waves is not that straightforward ("The average of the mean is not the mean of the average"; Meyer, Osman, Irwin, & Yantis, 1988; Fabiani, Gratton, Karis, & Donchin, 1987). Still, the timing difference observed between the two peaks is compatible with the interpretation of the second peak as being linked to the second stroke. In contrast, in the unimanual condition, only one peak was visible, over the contralateral hemisphere (Figure 2B), although the mean interkeystroke interval was in the same range (M = 171 ± 51 msec).

We also examined each bimanual sequence separately (left–right or right–left keystroke sequences; Figure 4A). Peak latencies were extracted for each participant on

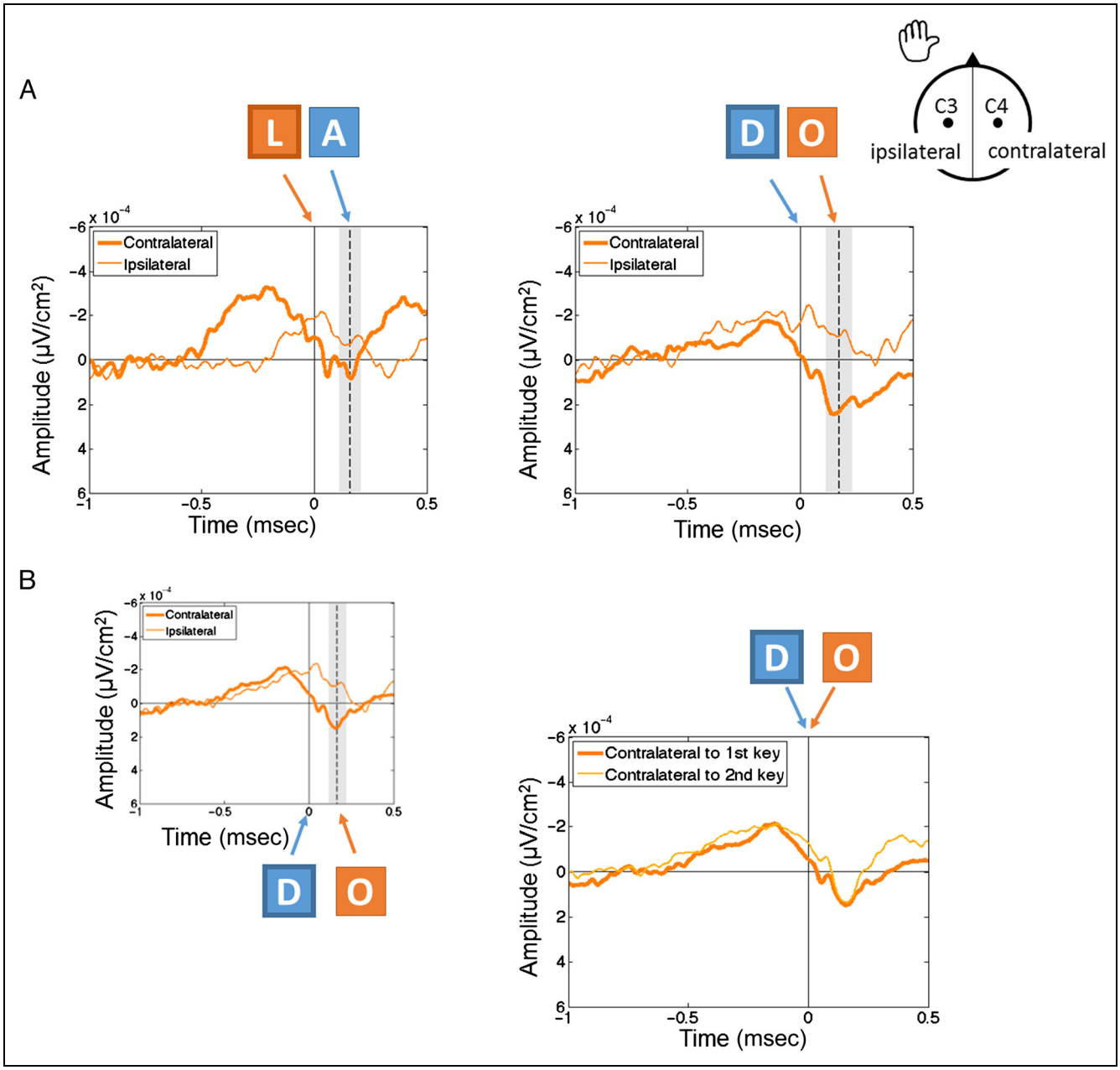

Figure 4. Response-locked averages in the bimanual condition. (A) Bimanual sequences that start with a left keystroke (left–right; e.g., "DO") or a right keystroke (right–left; e.g., "LA") are presented separately. Contralateral and ipsilateral hemispheres are defined relative to the first keystroke of each sequence. Zero represents the first keystroke. (B) To track preparation of each keystroke, signal is plotted over the hemisphere contralateral to the forthcoming keystroke. Zero represents the first or second keystroke accordingly. The small figure on the left is similar to Figure 2C and is provided to indicate time stamps relative to each keystroke along execution of the sequence.

contralateral (B21) and ipsilateral (D18) electrodes in the −500 to +200 msec time window around the first keystroke. In both sequence types, the component recorded over the hemisphere contralateral to the first keystroke always peaked before the component over the ipsilateral hemisphere, as confirmed by a Wilcoxon signed-rank test (Left Right sequences: $z = -2.48$, $p = .013$; Right Left sequences: $z = -2.61$, $p = .009$), despite the signal being noisier than in the main analysis. That is, the order of peak activity across hemispheres followed the order of the keystrokes performed.

In addition, the contralateral components considered relative to the first or second keystroke were quite similar, irrespective of the upcoming keystroke (Figure 4B). Notably, the timing or relative position of each component relative to the corresponding keystroke was similar.

Together, the above observations consistently converge to indicate that the ipsilateral peak is indeed associated with the preparation of the second keystroke.

DISCUSSION

In this study, we tested hypotheses derived from CQ models of sequence production using neurophysiological indices. In particular, we sought to understand how activation and inhibition processes are employed during the production of a sequence. Our starting point was the programming of a single keystroke (single condition). This condition yielded the expected preresponse pattern of a negative component and a positive component (e.g., Vidal et al., 2003) that has been consistently interpreted in the cognitive control literature as, respectively, contralateral activation and ipsilateral inhibition (Servant et al., 2016; Diedrichsen, Wiestler, & Krakauer, 2013; Meckler et al., 2011; Burle et al., 2004). Our single-key results go further than previous single-response studies, however, in that our results were obtained with eight alternative responses (the eight letters). Previous studies contrasted fewer responses (up to four: Meynier et al., 2009).

We then manipulated the number of keystrokes to be produced (up to two) and the effectors used to produce them (one or both hands). Thereafter, any deviation from the single pattern will necessarily be explained by the presence of a second keystroke. To ease the interpretation of our results, we schematically illustrate the observed patterns in Figure 5 and compare them to the predictions made in the Introduction (Figure 1, reproduced in Figure 5A). This schematized description was inspired by Figure 4 in Greenhouse, Sias, Labruna, and Ivry (2015), among others. A decomposition of the observed pattern as the "single" patterns that would be associated with each keystroke in the sequence is presented in Figure 5C and will guide our interpretation of the results.

Activity over the contralateral hemisphere is informative about the dynamics of keystroke activation. In the single and bimanual conditions, a component of similar amplitude is observed over the contralateral hemisphere associated with the production of a single keystroke. This suggests that similar processes are associated with the activation of each single keystroke, regardless of whether this keystroke is part of a sequence or isolated. In line with this idea, in a bimanual sequence, each keystroke is associated with such a component over the hemisphere contralateral to each respective keystroke; in a unimanual sequence, the hemisphere contralateral to both keystrokes presents a component of around twice the amplitude than in single, in line with the additive hypothesis (see Figure 5B). Both these results confirm the idea that activation of a keystroke is an additive process: Preparing one right-handed response leads to a left-side brain response, and preparing two such responses leads to a doubly strong left-side response (Gladwin et al., 2008; Cui & Deecke, 1999).

Beyond the electrodes of primary interest, the spatial extent of the components was less distributed in bimanual sequences than in single and unimanual conditions, thus yielding a significant contrast over peripheral electrodes. This result may be indicative of a mixture of processes in the bimanual condition, although our data cannot provide definitive evidence in that respect (Diedrichsen et al., 2013; Cui & Deecke, 1999).

In addition, activation closely follows the sequence of keystrokes. This is especially visible in the bimanual condition, where sequential activation can be traced over opposite hemispheres following the order of keystrokes (Figure 5C). There, the time between activation peaks corresponds to the average interkeystroke interval. This is evidence for an electrophysiological pattern that mirrors the sequential launching of each item in the sequence.

Overall, then, contralateral neurophysiological activity associated with response activation follows what was expected from single response data, namely, additive response activations (Gladwin et al., 2008).

Neurophysiological activity recorded from ipsilateral electrodes is typically linked, in choice RT tasks, with inhibition processes (Servant et al., 2016; Diedrichsen et al., 2013; Meckler et al., 2011; Burle et al., 2004). Both single keystrokes and unimanual sequences revealed an ipsilateral positive component, which, in accord with the literature, we interpret as inhibition (Vidal et al., 2015; Burle et al., 2004). Moreover, the ipsilateral components in both conditions were similar in terms of amplitude and timing. This similarity is incompatible with an additive hypothesis for the ipsilateral component (see Figure 5B). Specifically, there is no "doubling" of the ipsilateral component when there are two keystrokes using the same hand. Hence, we conclude that ipsilateral inhibition is independent of the number of keystrokes to be produced (one or two) in our experimental setting. This is in sharp contrast with the activation component that followed closely the number of keystrokes (Figure 5C). The differences in whether activation and inhibition components associated with the

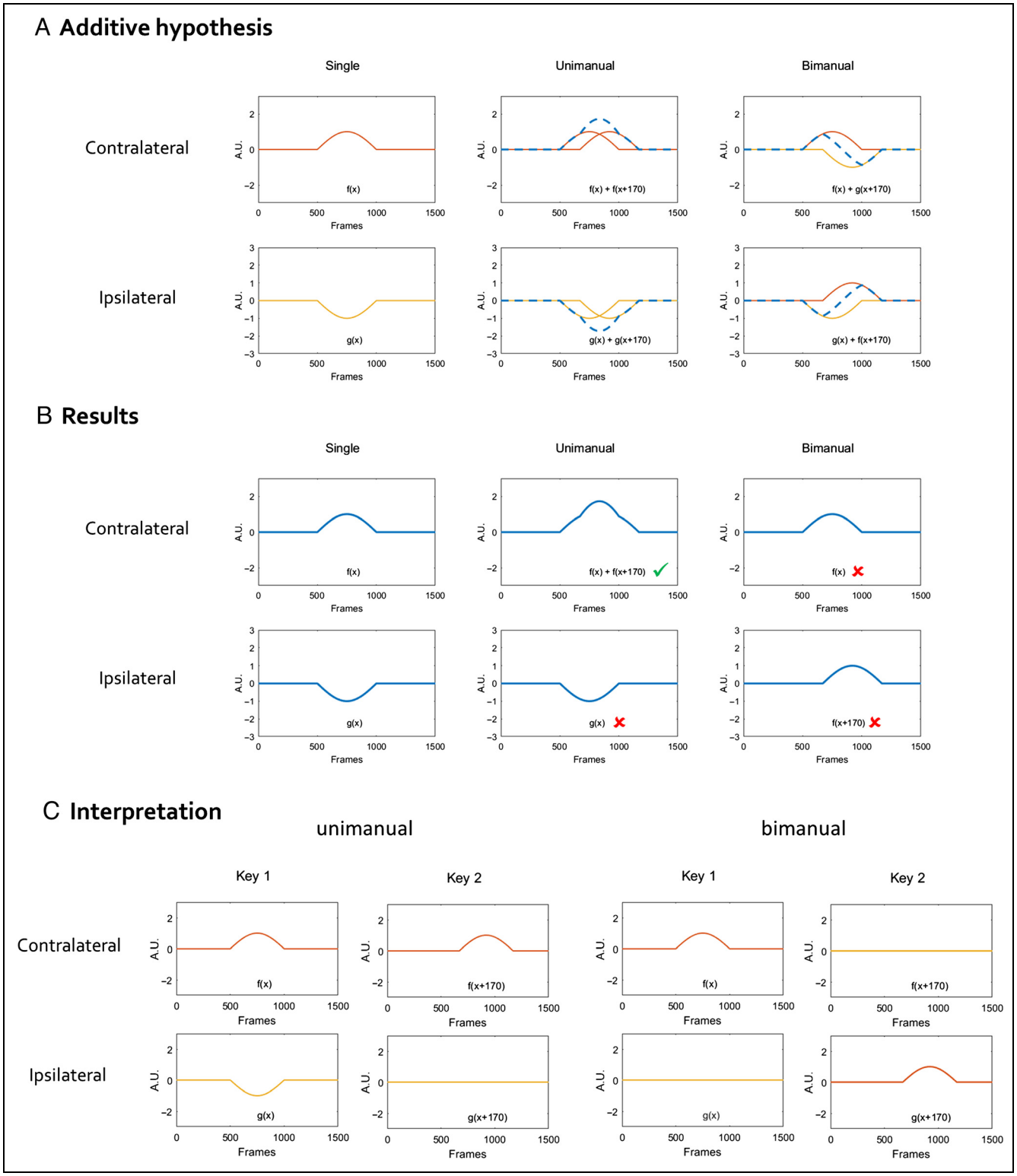

Figure 5. Illustration of (A) the additive hypothesis, (B) the observed patterns, and (C) their interpretation. A is similar to Figure 1. (B) Results are put in the form of equations, based on the computation from simple component time courses (f[t] and g[t]) that lead to the appropriate amplitude and polarity. Only the contralateral electrode of unimanual sequences is in line with the additive hypothesis. (C) The "single" pattern that would be associated with each stroke (Key 1 and Key 2) is plotted separately for unimanual and bimanual sequences. Activity over the contralateral hemisphere to each keystroke is plotted in orange lines; and that over the ipsilateral hemisphere, in yellow lines. Contralateral and ipsilateral hemispheres are swapped for bimanual sequences between Key 1 and Key 2.

two keystrokes summed or not support the commonly held view that that activation and inhibition arise from independent processes (Meckler et al., 2011; Tandonnet, Burle, Vidal, & Hasbroucq, 2003).

Turning to the bimanual sequences, we did not see any ipsilateral activity that could be linked to inhibition. We show that it could not have been hindered by activation components either, like the additive hypothesis would suggest (Figure 5A); otherwise, we would have observed lower amplitude for the activation component. Moreover, the exact pattern predicted by the additive model has been found in the case of corrective actions, when one erroneous strike is followed by a ballistic correction (Roger, Núñez Castellar, Pourtois, & Fias, 2014; Rodriguez-Fornells, Schmitt, Kutas, & Münte, 2002), which demonstrates the validity of the additive hypothesis in a different context.

Figure 5C summarizes our findings. We depict the lack of an inhibitory component in the bimanual condition and the presence of an inhibition component in unimanual sequences associated with the first keystroke of the sequence only. This interpretation matches the timing of the inhibitory component relative to the first keystroke for unimanual sequences.

By definition, bimanual sequences require both effectors. Conversely, a single keystroke and a unimanual sequence are similar in that they both require the use of a unique effector. The present findings suggest that ipsilateral inhibition depends on the effectors recruited in a particular action (Cui & Deecke, 1999): If an effector is not required for a particular trial, for example, as is the case for unimanual sequences, it gets "excluded" through inhibition. Crucially, we demonstrate here that inhibition does not depend on the number of keystrokes performed. This contradicts the idea that ipsilateral inhibition corresponds to inhibition of following items and suggests a different process at play than that postulated by CQ models (Pinet et al., 2015; Houghton, 1990).

The interpretation of ipsilateral positivity as the inhibition of an effector makes sense in the context of various models. First, it can be linked to evidence accumulation models in decision-making, such as the drift diffusion model (Ratcliff, Smith, Brown, & McKoon, 2016), where evidence for an alternative is equally evident against the other alternative (Servant et al., 2016; Wolpert & Landy, 2012). Recent experimental evidence suggested that decision-making arises from a continuous flow of information from the perceptual system to the motor system, leading to the build-up of evidence for one alternative along the system (e.g., Donner et al., 2009), which makes it plausible to find response competition up to the motor system (Calderon, Gevers, & Verguts, 2018). Previous studies have described inhibition at the level of an effector, using TMS (Greenhouse, Saks, Hoang, & Ivry, 2015; Duque, Lew, Mazzocchio, Olivier, & Ivry, 2010; Burle, Bonnet, Vidal, Possamaï, & Hasbroucq, 2002; for typing, see Behmer et al., 2018). Interestingly, inhibition seemed restricted to relevant effectors, that is, those involved in the block/task (Labruna et al., 2014). Our findings are compatible with this idea and go further by showing that inhibition could be applied dynamically at the level of single trials within a block, alternating between trials where an effector had to be excluded or not.

Second, and specifically relative to typing, our results are compatible with the features of keystroke representations postulated by cognitive models of this skill (Grudin, 1983; Rumelhart & Norman, 1982). Keystroke representations or "schemata" assume a crucial role of the effector; they are thought to hold information about the hand and finger responsible for typing each keystroke as well as the spatial position of the key on the keyboard. The validity of such features had been confirmed behaviorally (Logan, 2003). Our results provide the first neurophysiological evidence for such keystroke schemata, by showing that the effector (hand) is a relevant feature at the physiological level. Moreover, we go one step further by arguing that "hand" should be viewed as a specific decision selection level, a hypothesis that is still absent from current models of typing (Logan, 2018), although it is present in other models of action selection (Calderon et al., 2018; Herbort & Rosenbaum, 2014). Indeed, for an effector to be excluded during response programming, there needs to be a processing step dealing with selecting the appropriate effector(s) for the current trial. We speculate that this step comes right after keystroke selection when keystroke features have been activated and unnecessary features (e.g., an irrelevant effector) can be excluded.

In a larger context, we set up this study to test assumptions of cognitive models of sequence production, namely, successive activation and inhibition between items, by searching for their physiological implementation. Our results confirmed the additive activation over contralateral hemisphere(s) associated with each keystroke. However, the physiological evidence we report contradicts one prediction from CQ models, namely, that each item inhibits the following ones. Although we could not find traceable evidence for such inhibition between items, we report inhibition at the effector level. By demonstrating the existence of inhibition of irrelevant effectors, our results can then further constrain cognitive models. For a simple computation that could be "pressing two keys in the right order," we were able to describe some crucial properties of the neurophysiological implementation, based on previous assumptions, and to further clarify the algorithm that needs to be performed (Krakauer, Ghazanfar, Gomez-Marin, MacIver, & Poeppel, 2017; Marr, 1982).

Contrasting sequences to single keystrokes leads to a final question regarding response complexity. Typing two keystrokes in a row is necessarily more complex than typing one, in terms of both planning and execution (Greenhouse, Saks, et al., 2015). It is true that we observed higher amplitude for sequences compared with single keystrokes over midline electrodes, which would suggest stronger processing associated with the complexity of the

response. This observation is spatially compatible with the activity of premotor areas (dorsal premotor area and SMA) associated with response planning (recall that we report current source density estimates derived from spatial sharpening by Laplacian: Verstynen & Ivry, 2011; Vidal et al., 2003; Verwey, Lammens, & van Honk, 2002; Tanji, 2001; Shima & Tanji, 1998). However, RTs were not different between single keystrokes and sequences. Although this result can seem surprising in light of previous findings on sequence production (Sternberg, Monsell, Knoll, & Wright, 1978; Henry & Rogers, 1960), specifics about our paradigm such as the high number of repetitions of each item and the short length of sequences (two strokes maximum), as well as the fact that one- and two-keystroke conditions were presented in different blocks, could all explain a performance near ceiling and no effect of response complexity. Moreover, the activation components of single keystrokes and bimanual sequences were similar; likewise, the inhibition components of single keystrokes and unimanual sequences were similar too. The fact that we can observe similar activity for single keystrokes and sequences shows that the activity we are observing over motor cortices is not because of response complexity but rather specific to mechanisms of sequence production. Thus, we provided a refined description along the motor hierarchy, from planning to execution (Grafton & Hamilton, 2007). Future studies should further characterize the specific role of each area along the motor pathway and their interactions particularly during sequence production, where typing provides a fruitful model, including upstream areas such as pFC or the posterior parietal cortex (Le, Vesia, Yan, Niemeier, & Crawford, 2014; Nakajima, Hosaka, Tsuda, Tanji, & Mushiake, 2013; Cui & Andersen, 2007; Bohland & Guenther, 2006; Koechlin & Jubault, 2006; Averbeck, Chafee, Crowe, & Georgopoulos, 2003).

We also note that our analysis of the lateralization pattern was driven by previous descriptions of positive and negative potentials that have been observed around the RT at relatively specific electrode locations. This approach is justified by previous founding work in motor control and typing (Scaltritti et al., 2018; Pinet et al., 2015; Vidal et al., 2003). Nonetheless, future broader explorations will have to reveal and explore other EEG components that may reflect response preparation in this task. This might be, in particular, relevant to characterize whether there is a mixture of processes in the programming of bimanual sequences (Cui & Deecke, 1999). In addition, we did not present analyses in the frequency domain. This approach has been useful in the past to characterize response preparation in complement to the analysis of potentials (Park et al., 2013; Gladwin et al., 2008; de Jong et al., 2006). Although it did not fit with our detailed hypotheses regarding the link with CQ models, we believe further exploration should take advantage of frequency analyses to characterize sequence preparation (Pinet et al., 2015, 2016).

Typing is a complex sequential activity that requires precise hand and finger coordination. Using metrics that have proven to be effective in studying response selection in motor control, we demonstrated that contralateral activation was directly linked to response execution, in an additive fashion. The activity over ipsilateral cortex shed light on the intricacies of response programming. These results led us to argue for the existence of an effector processing level that is compatible with models of both decision-making and typing. In that sense, our data help to bridge the gap between cognitive models of sequence production and their physiological implementation.

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Reprint requests should be sent to Svetlana Pinet, Department of Neurology, School of Medicine, Johns Hopkins University, 1629 Thames Street, Suite 350, Baltimore, MD 21231, or via e-mail: svetlana.pinet@gmail.com.

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