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Neural correlates of online movement preparation

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Abstract

The ability to prepare future action while controlling the ongoing execution is a fundamental characteristic of complex sequential behavior. Recent evidence suggests that when movement preparation and execution are separated in time, brain activity patterns for preparation are highly correlated with those underlying execution. But what happens when the brain needs to prepare and execute movements at the same time, as in the context of rapid movement sequences? We designed a 7T functional magnetic resonance imaging experiment with conditions where the next response preparation either overlapped with the current response execution or did not. Although overlap and non-overlap conditions were matched in all basic perceptual and motor processes, we observed significantly higher activation in the parietal and occipital regions during the overlap condition. The difference between these two conditions was the same, whether the required movement was a simple finger press or a more complex three-finger chord. This suggests that the extra activity was due to the overlap between concurrent execution with action selection but not motor planning, which we found to be more time-consuming for the chord than for the simple finger press. We also did not find significant differences between overlap and non-overlap conditions in the dorsal premotor cortex (PMd), a region traditionally associated with motor planning, even though control analysis showed that it was heavily engaged during motor planning. Our results, therefore, support the hypothesis that motor planning, but not action selection, can run in parallel to ongoing execution with very little need for extra brain activity.

Keywords: Motor planning, Action selection, Online movement preparation, fMRI

Summary for Lay Audience

Before we start any motor action, our brain needs to go through a preparation phase aiming to bring our motor system into a state of readiness from which our action can unfold. Most of our daily behavior consists of movement sequences. In this context, our brain needs to prepare the future movements while it is busy controlling the ongoing execution. This ability to multi-task appears to be essential for skillful performance of movement sequences such as playing piano. Nonetheless, it is currently unknown how the brain achieves the simultaneous preparation of future actions during the execution of current ones. In our study, we show that the posterior parietal cortex becomes increasingly engaged when preparation and execution need to be done at the same time. The anatomical location of this activity, and its independence of motor complexity suggest that the extra cost arises at the level of action selection, but not at the level of motor planning.

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Introduction

In the lab, the neural bases of action have almost always been studied using a discrete set of trials, each starting with the presentation of a stimulus followed by a motor response with a short pause before the next trial begins. Yet, most real-world behaviors, such as typing and playing basketball, involve a continuous stream of actions. These complex behaviors require simultaneously preparing the next action goal as well as monitoring and executing the ongoing movement. Consider the example of brewing coffee. While adding the coffee powder to the pot, the brain is preparing to pour hot water into the pot. To understand how the brain deals with this dual-task requirement, it is necessary to depart from traditional task design and adopt novel tasks that involve overlap between movement preparation and execution. One example of such tasks is finger press sequences. A recent finding suggests that even short, over-practiced finger sequences are not fully prepared in advance. Instead, the preparation of the remaining elements must continue online and throughout the sequence production (Ariani & Diedrichsen, 2019). While online preparation appears to be a key element in the skillful execution of sequences, it is unknown whether and how the brain deals with its dual task requirement.

We use movement preparation here as a collective term encompassing all processes between the perception of the stimulus and the onset of muscle activity. Movement preparation, therefore, encompasses two main processes: Action selection and motor planning.

Background

Action selection. As the first process of movement preparation, we need to select the next action among a set of alternatives. In experiments, the correct action is often signaled by a visual stimulus

via an arbitrary cue-response association (Diedrichsen & Kornysheva, 2015). The difficulty of action selection increases as the number of alternatives grows (Hick, 1952). In a choice-reaction time task, in which participants were instructed to select the correct response among multiple alternatives (e.g., which stimulus had a different color) as fast as they could, Hick showed that required reaction time is a monotonically increasing function of the number of the options. The dissimilarity of the response alternatives also affects the reaction time (Heuer, 1987; Rosenbaum et al., 1988). Heuer and others presented participants with a visual stimulus on either the right or left side of the screen. If the stimulus was on the left side, participants produced a response with their left hand, otherwise with their right hand. The responses were either tapping or alternating finger responses. The left-hand and the right-hand responses were either the same (e.g., both alternating) or different (e.g., one tapping and the other alternating). In the case where the responses were different, participants showed longer reaction times. The discriminability of the visual stimuli has been reported as one important factor affecting the selection difficulty (Haith et al., 2015). Haith and others designed a task in which participants were instructed to perform a center-out arm reach in each trial. At a random time prior to the go signal, the location of the target changed, and participants had to prepare for the new movement in the short remaining time. In trials where the targets were spatially separated using virtual barriers that constrained trajectories, the new movement goal could be selected more efficiently.

Motor planning. Once the correct action goal is selected, it needs to be planned, a process that is thought to specify the details of the movement and to get the motor system ready for execution (Shenoy et al., 2013). Such movement details include specification of the effector, direction,

amplitude, and force. Ghez and others (Ghez et al., 1997) trained human subjects to produce an isometric wrist muscle pulse toward either of two 90-degree separated directions. The response in each direction was either a 5 or a 10 N wrist pulse. The data suggested when the preparation period was short, generated force was not accurate. Another experiment, (Rosenbaum, 1980), investigated the required time for the specification of different movement details. Rosenbaum and others presented participants with a reach target during the instructed delay. By withholding some information about the target, they inhibited the completion of the planning process before the go signal. In some trials, the effector or reach direction or extent was not specified. The data suggested that reaction time (from the go cue until movement onset) increased by this manipulation. Therefore, planning during the instructed delay enables faster reaction times.

Selection and motor planning can overlap. Evidence supports the idea that selection and motor planning are not strictly serial processes (Cisek & Kalaska, 2005). The suggestion is that the brain is able to plan multiple potential actions in parallel while collecting evidence for the selection of the right one. To test this, Cisek and Kalaska trained monkeys to make an arm-reach movement. At the beginning of each trial, two potential reach targets were presented; after a short period, the actual target of reach was specified. During the first phase, when monkeys were uncertain about the target of reach, recordings from the dorsal premotor cortex (PMd) revealed that both targets were represented in the neural activity of this area. This evidence suggests while the brain is still collecting evidence to select to correct action goal, it can plan potential actions in parallel. This ability might help in the rapid execution of the motor command once the time-consuming selection process is completed (Cisek & Kalaska, 2010).

Despite this overlap, there are a number of studies that have successfully dissociated selection from planning by changing the assignment between the stimuli and the motor responses (Kiani & Shadlen, 2009; Leoné et al., 2014; Shushruth et al., 2022). In our study, we distinguish between selection and planning processes by varying the motoric complexity of the required movement, assuming that motor planning requires more time for complex actions.

Interaction between movement preparation and execution. In most real-life behaviors, preparation (i.e., action selection and motor planning) for the next movement occurs concurrently with the execution of the ongoing movement. How do movement preparation patterns for the next movement not interfere with the neural patterns underlying the execution of the ongoing movement? While there is very little research relating to this question, researchers have addressed this issue in the context of a single movement, asking how the motor output is prevented during preparation.

Through anatomical separation. One simple way to avoid overt movement during preparation would be to anatomically separate the two processes. Indeed, textbooks often suggest that while the primary motor cortex executes the ongoing movement, premotor and parietal areas prepare for the upcoming action. Neurophysiological studies, however, have shown that it is not that simple. While the primary motor cortex shows more execution-related activity and the premotor cortex more planning-related activity, both types of signals are often mixed within areas and even within single neurons (Crammond & Kalaska, 2000). The primary motor (M1) and dorsal premotor

cortices (PMd) have long been shown to play an essential role in driving muscle activity (Dum & Strick, 2002; Leyton & Sherrington, 1917; Weinrich & Wise, 1982; Wise et al., 1986). More recently, Churchland and others (Churchland et al., 2012) have shown that during an arm-reaching movement, neural state space in these areas evolves with a rotational pattern. These rotations then directly drive the neurons in the motor pool to execute the proper muscle activity. Both M1 and PMd are also active before execution even starts with patterns encoding features of the upcoming movement, such as the direction (Crammond & Kalaska, 2000; Tanji & Evarts, 1976), speed, and reaction time (Bastian et al., 2003; Churchland et al., 2006). Churchland and others (Churchland et al., 2006) investigated the relationship between preparatory activity and reaction time. They trained monkeys to produce a center-out arm reach toward a visual target immediately after the go signal. The neural recording from M1 and PMd suggest that with presenting the target, neural state space evolved and converged to a fixed point. In the trials where the neural state fell within the proximity of the fixed point, reaction times were fast. Interestingly, in a separate study (Churchland et al., 2010), Churchland et al. showed that each target had a distinct fixed point, and these fixed points are highly reliable predictors of the execution rotational dynamics. Therefore, this finding suggests that movement preparation is simply the process that initializes a dynamical system whose dynamic governs movement production.

Through orthogonality of preparation- and execution-related activity. So how does the brain avoid overt movement during preparation if not via simple anatomical separation? Recent investigations propose a computational model that explains this phenomenon (Elsayed et al., 2016; Kaufman et al., 2014; Lara et al., 2018). Consider a simple example of a system that receives two inputs and is

only sensitive to the changes in the summation of inputs. Therefore, as long as the summation is constant, the system is blind to any changes. This example illustrates that the variability of the input signals is not sufficient for driving the output. Now, let's generalize this example to a system where muscle activity is the output and neural activity in PMd and M1 is the input. It is likely that the output changes only if some linear combination of input neurons changes. If the preparatory activity does not change the corresponding linear combination, it will not drive muscle activity. To test this hypothesis, Kaufman and others trained monkeys on a center-out reach task. By regressing muscle activity on neural activity in M1 and PMd during the execution, they could find the linear combinations that drive muscle activity. These linear combinations formed bases of a subspace where preparatory neural activity did not have any projection on it. Simply said, this finding suggests that neural patterns underlying preparation are orthogonal to execution patterns.

How does the brain deal with online movement preparation? More recently, Zimnik and Churchland (Zimnik & Churchland, 2021) reported the orthogonality also between the preparation of the next movement and the execution of the ongoing movement. The monkeys were instructed to either produce a reach toward a single target or a compound reach toward two targets. Similar to (Kaufman et al., 2014), they used single-reach trials to find preparation and execution subspaces. Projection of neural activity of compound reach trials on these subspaces showed that preparation for reach toward the second target occurred in parallel with the execution toward the first target. Moreover, this online preparation occupied a subspace orthogonal to the ongoing execution patterns. This observation suggests that the brain can prepare for an upcoming movement without interfering with the control of the ongoing movement.

Study-specific introduction

Most neuroscientific studies, be they on perceptual processes, decision-making, or motor planning, consist of distinct trials: A sequence of stimulus, response, and feedback is followed by a short pause before the next trial begins. In contrast, most real-world activities, such as typing or playing basketball, involve a continuous stream of actions. This requires the brain to prepare the next action while controlling the currently ongoing movement (Ariani & Diedrichsen, 2019). How the brain deals with the dual-task requirement of this online action preparation remains largely unknown.

Action preparation consists of two processes: First, we need to select the next action among a set of alternatives. In experiments, the correct action is often signaled by a visual stimulus via an arbitrary cue-responses association (Diedrichsen & Kornysheva, 2015). Second, the corresponding motor action needs to be planned, a process that is thought to specify the details of the movement and to get the motor system ready for execution (Shenoy et al., 2013).

Does the brain need to work harder for online preparation? The coordination of simultaneous preparation and execution may require an extra process. A recent study by (Ariani et al., 2022) showed that action preparation involves the primary motor (M1) and sensory (S1) cortex and that brain activity patterns during preparation and execution are highly correlated. To avoid interference during online preparation, the brain may need to recruit extra processes, either by activating other regions or by activating different neuronal subpopulations in the same regions. Alternatively, the brain may have a mechanism to coordinate simultaneous preparation with execution effortlessly.

To test these hypotheses, we designed an ultra-high field (7T) fMRI experiment with two main conditions: In one condition, preparation for the impending movement overlaps with the execution of the ongoing movement (overlap). In the other condition, movement preparations and execution happen sequentially (non-overlap). Since overlap and non-overlap conditions were matched in basic perceptual and motor planning processes, their contrast will indicate brain regions that are more engaged during online preparation.

In our study, we distinguish between selection and planning processes by varying the motoric complexity of the required movement, assuming that motor planning requires more time for complex actions. Participants were either required to produce a single-finger press or a chord of three simultaneous finger presses. In Experiment 1, we showed that chords require longer planning time than single-finger movement, even if we control for the complexity of action selection. In Experiment 2, we then scanned participants in overlapping and non-overlapping conditions, both for single finger presses and chords.

The overlap/non-overlap contrast for single-finger and chord indicated the areas that showed higher activation during online preparation. If the size of the overlap/non-overlap contrast changes with the complexity of the motor response, the extra engagement can be attributed to the motor planning.

Materials and Methods

Participants

A total of 11 individuals participated in Experiment 1 (4 females, mean age = 26 ± 4), and 22 took part in Experiment 2 (12 females, mean age = 24 ± 4). Four individuals participated in both experiments. Criteria for study inclusion were right-handedness and no prior history of psychiatric or neurologic disorders. Participants provided written informed consent to all procedures and data usage before the study started. The experimental procedures were approved by the Human Research Ethics Board at Western University.

Apparatus

Finger configurations were produced on a right-hand MRI-compatible keyboard with five 10.5 x 2 cm keys (FIG 1C). Each key had an indentation so the fingertip could securely be placed. The keys could not be depressed, so the finger presses were isometric. Forces were measured by the transducers (FSG-15N1A; Sensing and Control Honeywell; dynamic range of 0–25 N; update rate 5 ms) located below the fingertip indentation of each key. For the key to be recognized as pressed, the applied force had to exceed 0.8 N. Five white lines—hereafter referred to as “force cursors”—were displayed on a computer screen such that the vertical position of each line was proportional to the force exerted by each finger on the respective key (FIG 1A).

Continuous Paced Response Task

In both experiments, the task required participants to produce a sequence of responses at a continuous pace. The responses were either single-finger or simultaneous three-finger presses (chord). We used symbols for stimulus-response mapping (FIG 1B). To help participants keep a regular pace, we presented a sequence of background tones and, similar to the “forced-response” paradigm (Haith et al., 2016), instructed them to respond synchronously with these predictable tones. We defined response time as the moment when the amount of force produced by all fingers reaches its peak.

As feedback on the temporal accuracy of the response, we displayed a bar in the lower part of the screen (FIG 1A). If the response was too early, the bar pointed to the right, if the response was too late, it pointed to the left. The length of the bar indicated the deviation size. The acceptable deviation size was 200 ms, specified by the box boundaries. If the selected response was correct, the bar was displayed in green, if not, in red.

Points were awarded online and based on the press and time accuracy according to the following scheme: -2 points in case of timing error independent of response accuracy (deviation size > 200 ms); 0 points for pressing any wrong key and no timing error; 1 point in case of a correct response and no timing error.

Experiment 1

At the beginning of the session, participants were trained in symbol-response mapping. In separate blocks for single-finger and chord, we presented a symbol on the screen and asked them to produce the corresponding response. We encouraged them to delay their response until they felt confident that the response was correct. Each block consisted of 60 responses with symbols presented in random order, except for the fact that symbols were never repeated. We continued training until participants achieved an accuracy above 95% for both single-finger and chord blocks.

After training, in separate test blocks, participants produced a sequence of chords or single-finger presses at a continuous pace of 1 response per 2 seconds. A tone was presented each second, alternating between high-pitch and low-pitch sounds (gray and black notes in FIG 1A, respectively). Participants were instructed to respond simultaneously with the high-pitch tone. At a random time before each high-pitch tone, a symbol appeared on the screen that instructed the required response. The preparation time for each response ranged randomly between 240 and 1750 ms. We included low-pitch tones to make response times more temporally predictable.

Five single-finger blocks were interleaved with five chord blocks. Each block consisted of 60 responses. Symbols could occur with equal probability, but no repetitions were allowed. Additionally, we switched symbol-response mapping across participants (FIG 1B).

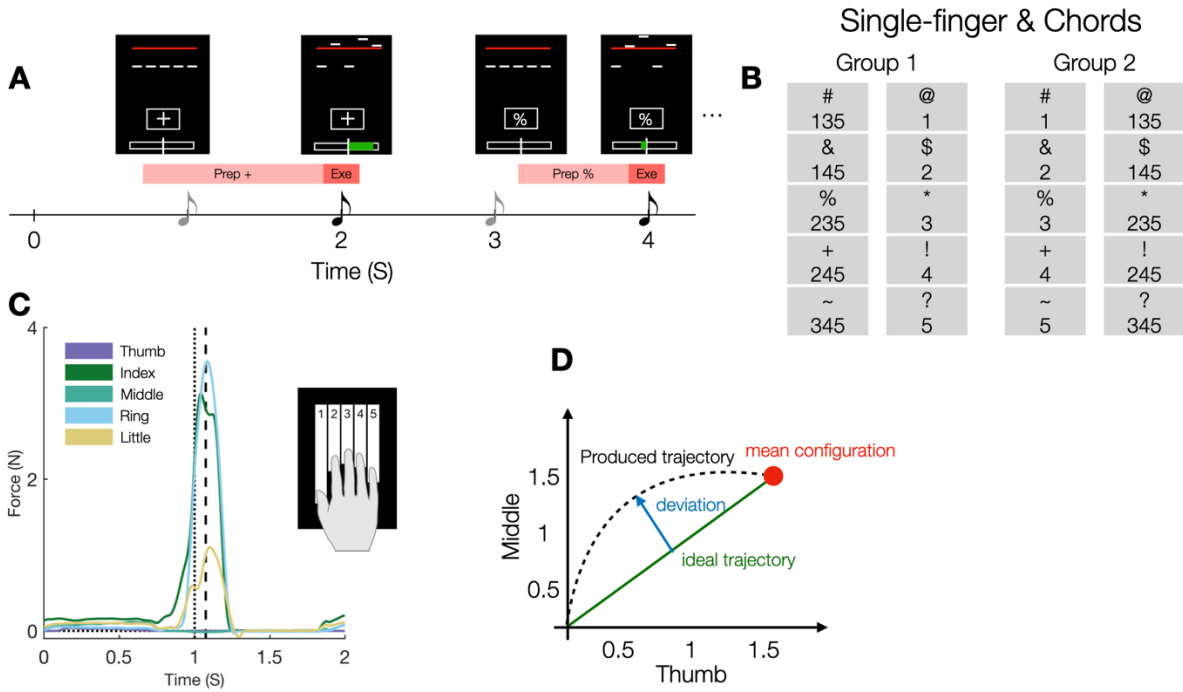


Figure 1. Task design for Experiment 1.

(A) Example block slice. Before each high-pitch tone (black notes), a symbol appeared on the screen, and participants produced the corresponding response synchronous with the high-pitch tone. Synchrony with the tone was announced through the length and direction of the bar at the lower screen part. The bar's color represented response selection accuracy. Five small lines on the top of the screen indicated the applied force on each key, with the red line indicating 0.8 N. (B) Single-finger presses and chords. The participants were divided into two groups, which practiced the same single-finger presses and chords, but the symbol-response mappings were switched across press types. (C) An example of a chord production. The dotted line to a moment when a high-pitch tone was heard. The dashed line indicates the time when the overall force peaks. The difference between these two times formed the deviation. (D) Toy example force trajectory (black line) in a two-dimensional finger space consisting of thumb and middle. The ideal force trajectory is the green line and the average deviation (blue arrow) from it over time forms the "mean deviation." Although only two finger dimensions are shown here, the mean deviation was calculated over all five dimensions.

Experiment 2

At the beginning of the behavioral training session, participants were familiarized with the symbol-response mapping similar to Experiment 1.

In the task for experiment 2, participants again produced a sequence of responses synchronized to a sequence of pace tones. Tones came in triplets with a frequency of 1 tone per 750 ms. The first tone was low-pitch, and the next two were high-pitch, and participants needed to produce their responses at high-pitch tones.

On the screen, symbols were presented in two boxes (FIG 2A). The lower box contained the cue about the upcoming response. The upper box informed participants about future responses. 550 ms before each high-pitch tone, the symbol from the upper box shifted to the lower box (small red arrows in Fig 2A).

We first trained participants on a simpler version of the task (FIG 2A). 1300 ms prior to each high-pitch tone, a symbol appeared in the upper box. After 750 ms, the symbol shifted to the lower box, and a new symbol appeared in the upper box. This way, participants could produce their immediate response while preparing the next movement. Each training block contained three sequences of single-finger presses and three sequences of chords. Each sequence started with a 5-second instruction screen (“Single” or “Chord”), followed by 16 responses. Participants completed four blocks for this phase of training.

We then trained participants on the main task, in which the preparation of the second response either overlapped with the execution of the first response (overlap condition; FIG 2C) or not (non-overlap and non-overlap-control; FIG 2B and 2D). The overlap or non-overlap conditions each had a response with 1300 ms preparation time and a response with 750 ms preparation time.

In the control condition, both responses had 750 ms preparation time. Each block contained two sequences of each condition for each press type. Participants practiced six blocks of the main task. (FIG 1B).

The day after, participants underwent one fMRI session consisting of 10 functional runs and 1 anatomical scan. Similar to training, each condition type (overlap, non-overlap, non-overlap-control) x (single-finger, chord) was repeated two times per functional run. The order of conditions was randomly interleaved. Two periods of 15 s rest, each preceded by a 5 s fixate screen, randomly interspersed between conditions. In addition, two periods of 10 s rest were added at the beginning and the end of each functional run. The rest periods allowed better estimation of the baseline activation. Each of the 10 functional runs took about 6 min, and the entire scanning session (including setup and anatomical scan) lasted for about 100 min.

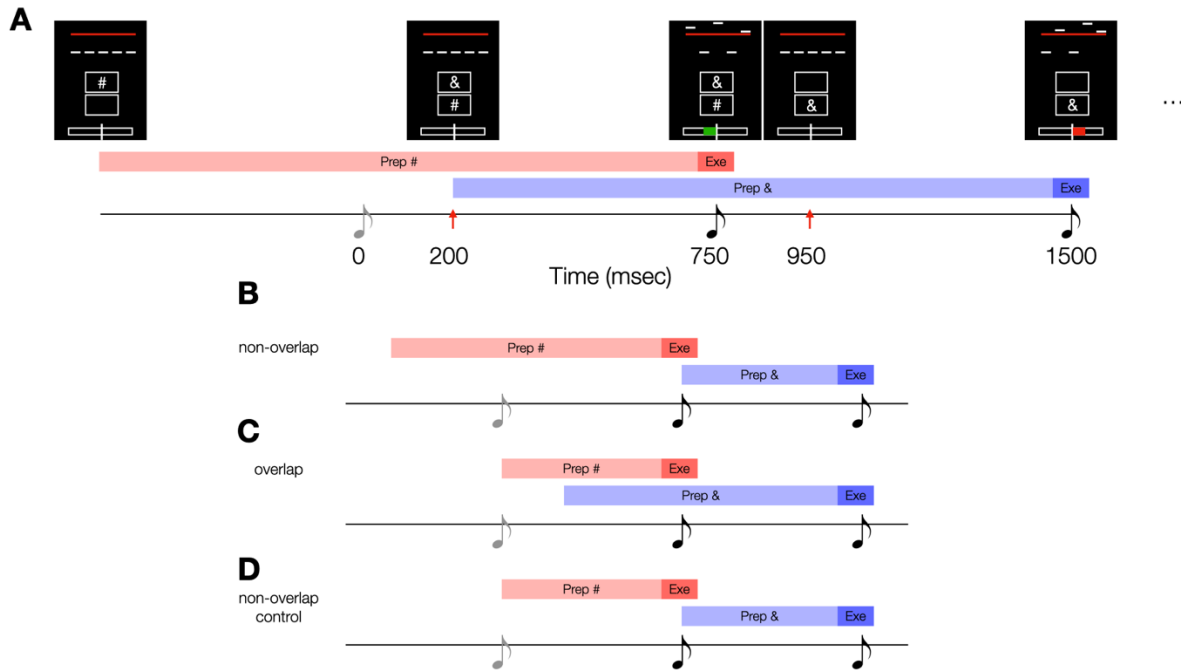


Figure 2. Task design for Experiment 2.

(A) The participants were first trained in a simple version of the task. A sequence of tones (1.25 Hz), alternating between 1 low and 2 high-pitch sounds, was presented. 1300 ms prior to each high-pitch sound, a symbol appeared on the upper box and was shifted to the lower box 750 ms later. The participants were instructed to produce the corresponding response to the symbol in the lower box synchronously with each high-pitch sound. (B) Non-overlap condition. The first response had a 1300 ms preparation time and 750 ms for the second one. (C) Overlap condition. The first response had 750 ms preparation time and the second one had 1300 ms. In this condition, the preparation time for the second response overlapped with the execution of the first response. (D) Non-overlap-control condition in which both responses had 750 ms preparation time.

Behavioral data analysis

We calculated press accuracy by evaluating the force trajectory in five-dimensional finger space from response initiation time until the amount of force reached its peak. The initiation time for each response was when the overall force (summation of all finger forces) growth rate exceeded 5% of the maximum rate. If the three fingers were pressed simultaneously, the force trajectory corresponded to a straight line (green line in FIG 1D). Sequential presses, involuntary coactivation of passive fingers, or pressing the wrong fingers caused deviation from this straight-line trajectory. We, therefore, quantified accuracy as the Euclidean norm between the produced force and the projection of the produced force onto the straight-line trajectory (blue line in FIG 1D). This distance was averaged over all time points from the initiation of the response till the peak time to produce the “mean deviation.”

We assessed the effect of preparation time on execution quality by calculating the mean deviation as a function of preparation time separately for each participant and for single-finger and chord. We then fitted the data to the following Gaussian kernel separately for each subject and each press type:

$$\hat{y}_n = ae^{-\frac{(x_n-b)^2}{c}} + d,$$

where \hat{y}_n is the predicated mean deviation when the preparation time is x_n ; a, b, c, and d are free parameters determining, respectively, the scale, the shift, steepness, and offset of the function. Parameters were then fitted to the data of press type separately using MATLAB’s `fminsearch` routine to minimize the mean squared error loss function.

Statistical analyses to assess the required preparation time for single-finger presses and chords or to evaluate changes in the execution quality across conditions with different preparation

times included two-tailed paired-sample t-tests and a within-subject repeated-measures ANOVA with factors conditions and press types.

Imaging data acquisition

High-field fMRI data were acquired on a 7T Siemens Magnetom MRI scanner with a 32-channel head coil at Western University (London, Ontario, Canada). The anatomical T1-weighted scan of each participant was acquired halfway through the scanning session (after the first five functional runs) using a Magnetization-Prepared Rapid Gradient Echo sequence (MPRAGE) with an isotropic voxel size of 0.75 mm (field of view = 208 × 157 × 110 mm [A–P, R–L, F–H], encoding direction coronal). To measure the blood-oxygen-level-dependent (BOLD) responses in human participants, each functional scan (352 volumes) used the following sequence parameters: GRAPPA 3, multiband acceleration factor 2, repetition time (TR) = 1.0 s, echo time (TE) = 20 ms, flip angle (FA) = 30°, slice number: 46, voxel size: 2.3 mm isotropic resolution. To estimate and correct for magnetic field inhomogeneities, we also acquired a gradient-echo field map (transversal orientation, the field of view: 210 × 210 × 160 mm, 64 slices, 2.5 mm thickness, TR = 475 ms, TE = 4.08 ms, FA = 35°.)

Preprocessing and first-level analysis

Data analysis was performed using SPM12 (<http://www.fil.ion.ucl.ac.uk/spm/>) and custom-written MATLAB (MathWorks) routines. Images were corrected for field inhomogeneities and head motion (Hutton et al., 2002). Due to the short TR, we did not adjust images for the sequence of slice acquisition. The data were high-pass filtered to remove slowly varying trends with a cutoff frequency of 1/128 Hz and coregistered to the individual anatomical scan. No smoothing or normalization to a group template was implemented during preprocessing. The

preprocessed images were analyzed with a general linear model (GLM) to estimate how much each task of the 6 conditions (overlap, non-overlap, non-overlap-control) x (single-finger, chord) activated each voxel in each of the 10 functional runs. In the design matrix, the regressor for each condition consisted of two boxcar functions (1 for each repetition; length 18.75 s). We also added a regressor for the instruction periods (2 s length boxcar functions). The estimate of this regressor was not used in further analysis.

The boxcar functions were convolved with an individual-specific hemodynamic response function. For each participant, we tested which of 20 HRF functions drawn from the GLMsingle library (<https://github.com/cvnlab/GLMsingle/>) maximized the proportion of the variance that the model could explain of the time series of voxels in the left primary motor and dorsal premotor cortex. The selected HRF was then applied to the whole brain. For HRF selection, we treated all conditions as one condition; therefore, this procedure did not bias any subsequent analysis that concerned differences between conditions. Ultimately, the first-level analysis resulted in one activation image per condition per run. We then calculated the percent signal change for each condition relative to the baseline activation for each voxel for each functional run and averaged it across runs.

Surface-based analysis

Individual subjects' cortical surfaces were reconstructed using FreeSurfer (Dale et al., 1999). Individual white-gray matter and pial surfaces were extracted and spherically morphed to match a group template atlas based on the sulcal depth and local surface curvature information (Fischl et al., 1999). Subsequently, surfaces were resampled to a left-right symmetric template

(fs_LR.32k.spec) included in the connectome workbench distribution. Individual data were then projected onto the group map via the individual surface.

Regions of interest (ROIs)

We defined ten regions of interest to cover the main anatomical areas that showed task-related activations in general (Fig 5A). Based on probabilistic cytoarchitectonic maps (Fischl et al., 2008), we selected surface nodes that belonged to Brodmann area (BA) 4 with maximal probability for the primary motor cortex (M1) ROI, 2 cm above and below the hand knob (Yousry et al., 1997). The primary somatosensory cortex (S1) was defined similarly as the hand-related aspect of BA 1, 2, and 3. The supplementary motor area (SMA/pre-SMA) was defined as the medial aspect of the BA 6. The dorsal premotor (PMd) ROI is located at the junction between the superior frontal sulcus and the precentral sulcus in the lateral aspect of the BA 6. The posterior parietal cortex was divided into an anterior region, including anterior, medial, and ventral IPS, and a posterior region, including the medial and lateral OPJ (Culham & Valyear, 2006). We defined three ROIs for the occipital cortex. The transverse occipital sulcus (TOS) is defined as the dorsolateral aspect of the occipital lobe covering V3A, V3B, V6A, V7, IPS1, and IPO specified in (Glasser et al., 2016). The lateral aspect of the occipitotemporal cortex (LOT) covers LO1, LO2, LO3, V3CD, V4t, FST, MT, MST, and PH. Finally, the ventral occipitotemporal cortex (vOT) covers areas FFC, VVC, V8, VMV1, VMV2, VMV3, and PIT.

We averaged all voxels within each ROI. Statistical analyses to assess differences in cortical engagement during chords compared with single-finger presses included two-tailed paired-sample t-tests. To evaluate the effect of the online preparation and its interaction with response

complexity within each ROI, we used two-tailed paired-sample t-tests and within-subject repeated-measures ANOVA with factors conditions and press types.

Results

Complex actions require longer motor planning time

In Experiment 1, we aimed to determine how long it takes to prepare a simple (single finger) or complex (chord) hand action. In each block, 5 different symbols indicated one of five single-finger presses or one of five chords (FIG 1B). We counterbalanced the symbols across participants, which allowed us to control for the effect of specific cues on preparation time. Differences in the preparation time, therefore, could be attributed to the process of motor planning.

When there was not enough time to prepare an action, participants tended to produce low-quality responses, quantified with a large mean deviation. The mean deviation for single-finger presses and chords clearly decreased with increasing preparation time (FIG 3). We fitted a Gaussian kernel with a constant offset (see methods) to these data to estimate when the mean deviation was within 5% of the steady state. This criterion was reached for a single-finger presses in 1005 ± 51 ms and for chords in 1204 ± 75 ms, with a significant difference ($t_{10}=4.21$, $p=0.0018$).

This result clearly shows that preparation time impacts the quality of execution. Also, the required preparation time was larger for a more complex action, with preparing for a chord taking 200 ± 47 ms longer than for a single finger press.

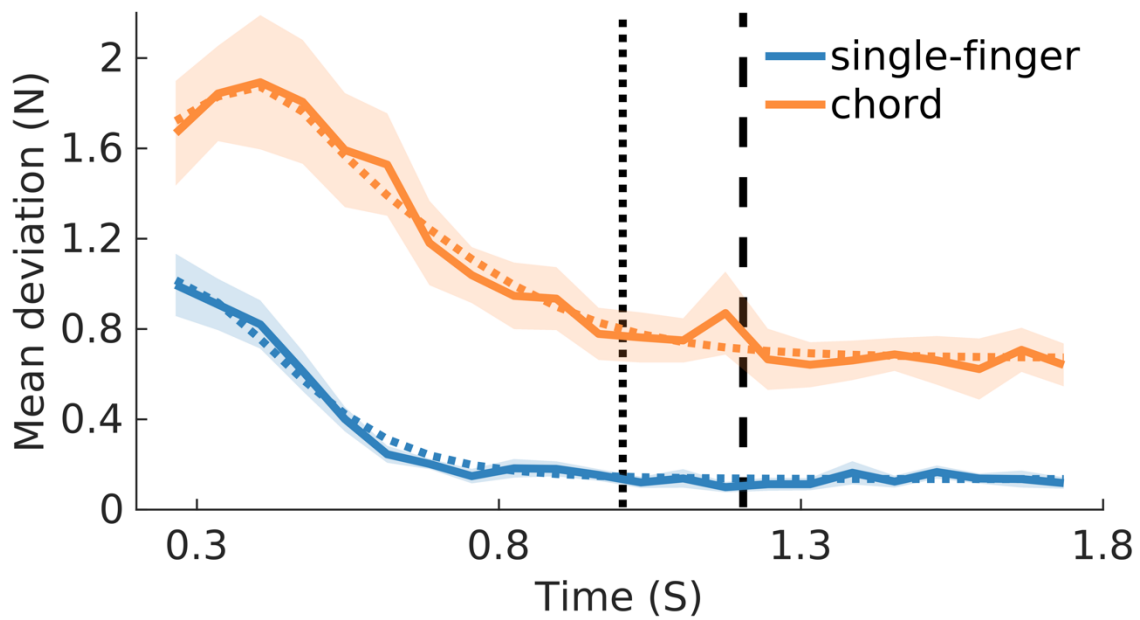


Figure 3. Preparation time affects the quality of execution.

The solid lines represent the group-averaged deviation (see methods) as a function of preparation time for single-finger presses (blue) and chords (orange). The dotted line indicates the fit of a Gaussian kernel with an offset. The fit was used to determine when the performance for single finger press (dotted line) and chord (dashed line) came within 5% of the steady-state mean deviations. Shaded areas indicate SEM across participants.

Online preparation improves execution quality

In Experiment 2, we aimed to include a condition that taps into the neural circuitry that makes online preparation feasible. We were aiming to use a time between two responses which would not be enough to fully prepare a chord and barely enough to prepare a single finger press. Based on the estimates of Experiment 1, 750 ms could satisfy these two requirements. In the overlap condition, the second response information (blue bar in FIG 2C) was presented 550 ms before the first response execution. Whereas the second response in the non-overlap and control conditions (blue bars in FIG 2B & 2D) did not have the extra 550 ms preparation time. Therefore, with online preparation, the second response execution quality will be higher in the overlap condition than the other two. The comparison between overlap and control gives a more direct measure of online preparation since their first response preparation times are also matched.

We first analyzed the mean deviation of the first response. Here the results replicated Experiment 1: longer preparation time resulted in lower mean deviation for chords in the non-overlap condition, as compared to control ($t_{21}=4.842$, $p=9e-5$) and overlap ($t_{21}=3.677$, $p=0.0014$). We also observed a similar pattern of results in the single-finger conditions. Still, as expected, the benefit of a longer preparation time was smaller, as shown by a significant condition x press type interaction ($F_{1,21}=8.091$, $p=0.0011$).

Did participants plan the second response during the execution of the first response? For chords, the second response showed a lower mean deviation in the overlap condition, as compared to the control ($t_{21}=2.888$, $p=0.0088$) and non-overlap ($t_{21}=1.664$, $p=0.1109$) conditions. A similar pattern was visible for the single-finger presses, but here the advantage of online

preparation was smaller, as shown by a significant condition x press type interaction ($F_{1,21} = 4.387$, $p = 0.0186$).

Our results suggest that preparation during the ongoing movement improves the execution quality of the upcoming response. Moreover, this benefit was larger for complex actions.

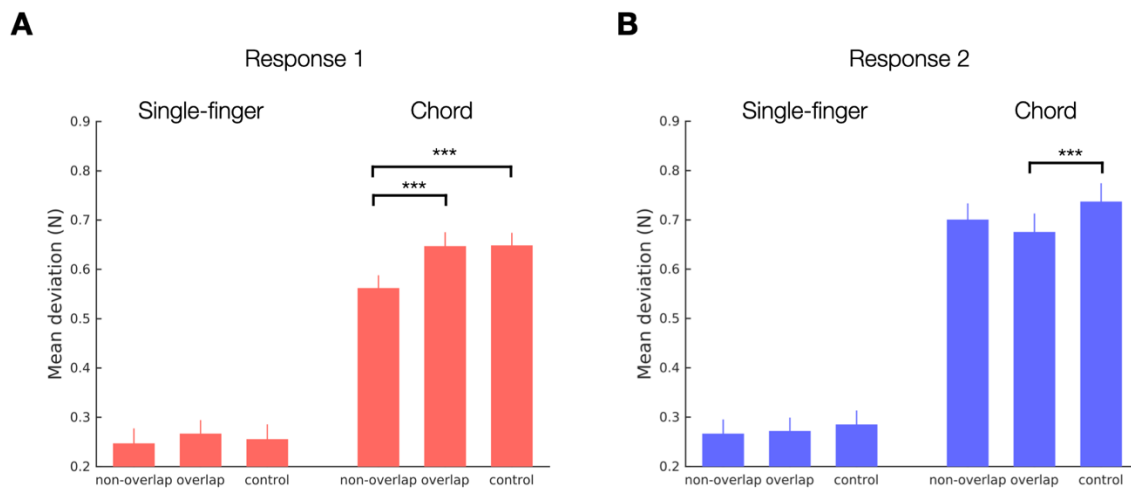


Figure 4. **Online preparation leads to improvement in motor planning.**

(A) Replication of Experiment 1 results. The non-overlap condition has the lowest mean deviation for the first response in chords. A similar pattern is also observable for single-finger presses. (B) The overlap condition has the lowest mean deviation for the second response in chords with a similar pattern for single-finger presses. Error bars indicate the SEM across participants. *** $P < 0.001$, two-tailed paired-samples t -test.

Chords induce higher activation than single-finger presses across the cortex

Before testing which regions are engaged in the coordination between simultaneous movement execution and preparation, we identified the task-relevant regions. Both single-finger and chord conditions activated a broad network consisting of sensorimotor, parietal, and occipital cortical regions (FIG 5A & 5B).

Consistent with previous results (Arbuckle et al., 2022), the entire sensorimotor network (S1, M1, PMd, PMv, SMA, all $t_{21} > 6.002$, $p < 1e-5$) was more activated in the chord conditions. Since chords have more complex execution and motor planning processes than single-finger presses, this finding is in line with the well-established literature suggesting the essential role of these areas in these two processes (Crammond & Kalaska, 2000; Nakayama et al., 2008; Tanji & Shima, 1994).

We also observed higher activity in chord conditions in the parietal (IPS, OPJ, both $t_{21} > 7.477$, $p < 1e-6$) and occipital (TOS, LOT, vOT, all $t_{21} > 4.912$, $p < 7e-4$) regions. This is despite the fact that both chord and single-finger conditions were matched in terms of the visual information, thus the attentional requirements were matched. Therefore, the extra activity may indicate that these regions were involved in the motor planning (Gallivan et al., 2011; Lingnau & Downing, 2015). Alternatively, some of these regions may only be involved in the identification of the visual stimuli and action selection but stayed on task longer during the planning of a chord (see discussion).

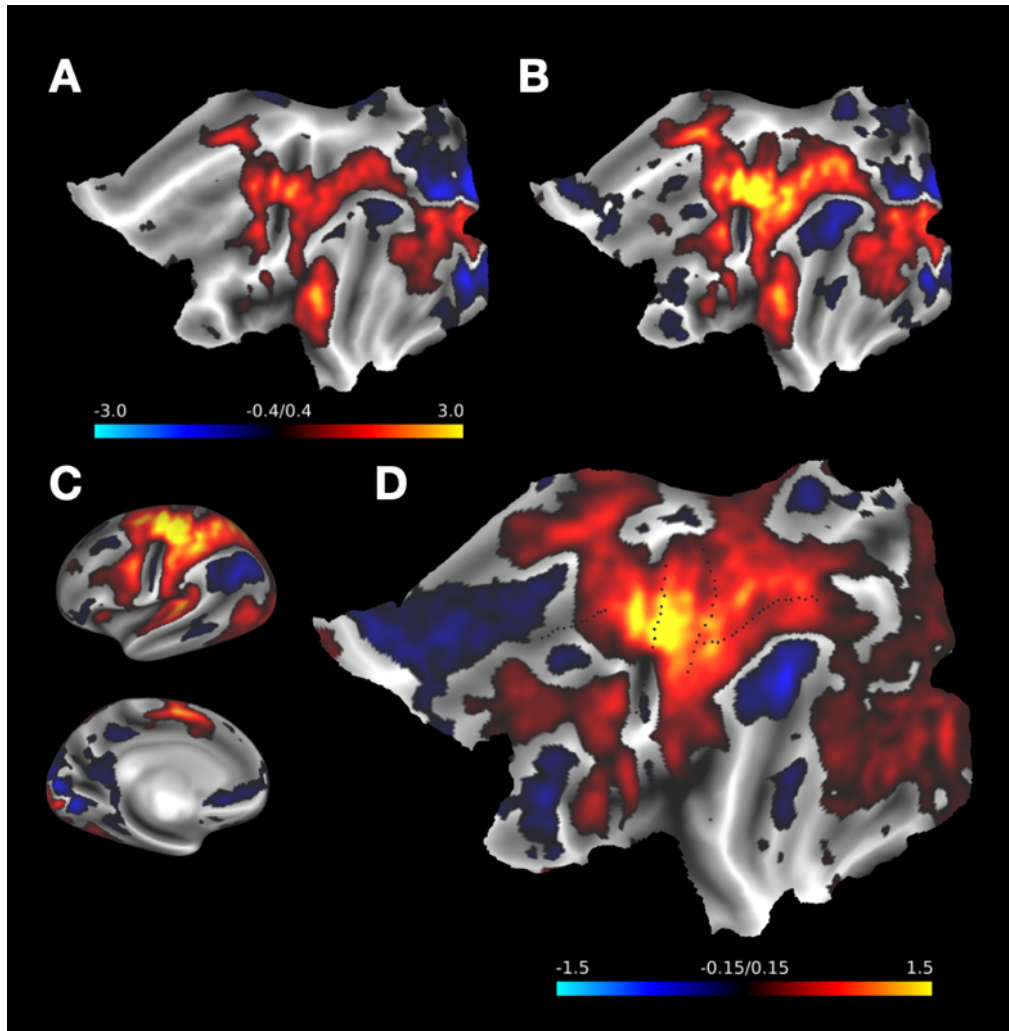


Figure 5: Activation during chord and single-finger press conditions.

Group-averaged evoked activation, measured as percent signal change over resting baseline, averaged across all conditions (overlap, non-overlap, non-overlap-control) separately for single-finger (A) and chord (B). Data are projected to a flattened representation of the left hemisphere, i.e., the hemisphere contralateral to the performing hand. (C) same as (B) but in an inflated representation of the left hemisphere. (D) The difference in evoked activation between chord and single-finger conditions. Yellow represents the relative activation of the chord relative to single-finger conditions.

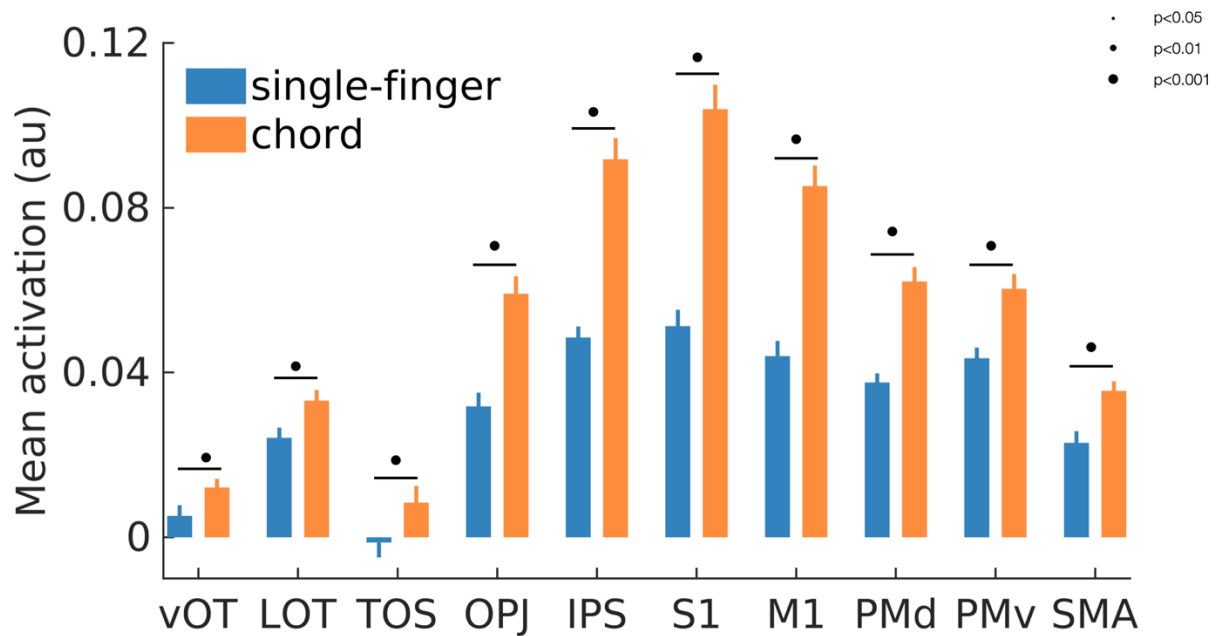


Figure 6. Activation estimates in the predefined ROIs for single-finger (blue) and chord (orange) conditions. ROIs are sorted posterior to anterior from left to right. Activation is plotted in arbitrary units (beta-weights from the regression). Error bars indicate SEM across participants. Regions of interest (ROIs): ventral occipitotemporal cortex (vOT), lateral occipitotemporal cortex (LOT), transverse occipital sulcus (TOS), occipitoparietal junction (OPJ), intraparietal sulcus (IPS), primary somatosensory cortex (S1), primary motor cortex (M1), dorsal premotor cortex (PMd), ventral premotor cortex (PMv), secondary motor area (SMA). Significant pairwise differences are indicated using bars.

Online preparation engages the parietal and occipital areas

To investigate which of those brain regions that showed higher activity during chord conditions need to work harder during online preparation, we compared the activity in the overlap (FIG 2C) and non-overlap (FIG 2B) conditions. These two conditions are matched in terms of overall preparation time available across the two actions, such that any differences can be attributed to the fact that preparation and execution overlap in one condition but not in the other.

For single finger, the overlap condition showed higher activation in a large region (see FIG 7A), including occipital (LOT, vOT, TOS; all $t_{21} > 3.519$, $p < 0.0020$) and parietal (IPS, OPJ; both $t_{21} > 2.343$, $p < 0.0290$) regions. In the chord condition (FIG 7B), we observed a similar pattern for chords in visual areas (all $t_{21} > 3.769$, $p < 0.0011$). Parietal regions failed to reach significance in chords. This was likely due to a lack of statistical power, as we found no significant interaction between condition and press type (both regions $F_{1,21} < 1.166$, $p > 0.2926$).

To see if this extra engagement was due to motor planning, we tested if it changes with motoric complexity. For all parietal and occipital regions, we found no evidence for such change as indicated by non-significant condition x press type interaction (Parietal: $F_{1,21} < 1.166$, $p > 0.2926$; Occipital: $F_{1,21} < 0.106$, $p > 0.7475$). Thus, the complexity of the motor response did not change the size of the overlap/non-overlap contrast, suggesting that the extra activity was due to the overlap between concurrent execution with action selection but not motor planning.

Consistent with this conclusion, we also did not find a significant difference between overlap and non-overlap conditions in PMd, a region that has been traditionally associated with the motor planning (Shenoy et al., 2013). This is despite the fact that PMd was substantially more activated during the chord as compared to the single finger condition (FIG 5D), which suggests

that it was heavily engaged during motor planning. Our results, therefore, argue that these planning processes can run in parallel to ongoing execution with very little need for extra activity.

An interesting detail is that in M1 and S1, we observed a slight decrease in activation in the overlap condition compared with the non-overlap condition when pressing chords (M1: $t_{21}=2.847$, $p=0.0096$; S1: $t_{21}=2.643$, $p=0.0152$). This lower activation was specific to chords, as indicated by a significant condition x press type interaction effect (M1: $F_{1,21}=5.510$, $p=0.0288$; S1: $F_{1,21}=4.283$, $p=0.0510$).

Overall, our data suggest that during online preparation, the parietal and visual regions of the brain need to work much harder. Also, the planning component of the online preparation does not add extra load to the motor system.

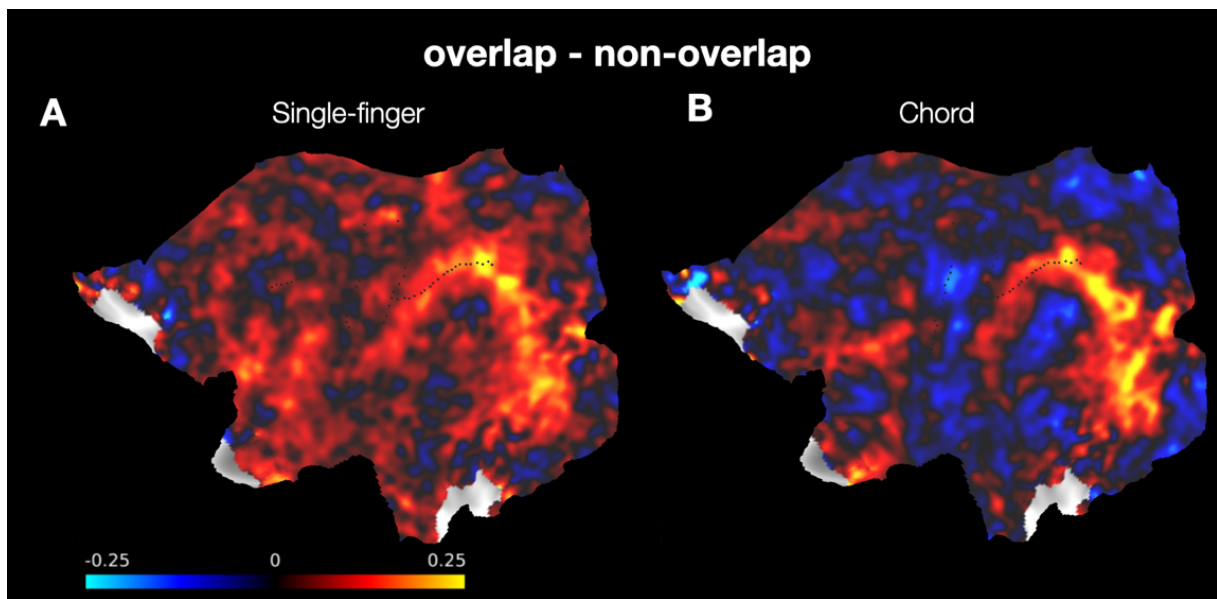


Figure 7. Online preparation engages parietal and occipital brain regions.

The difference in evoked activation between overlap and non-overlap conditions for single finger (A) and chord (B).

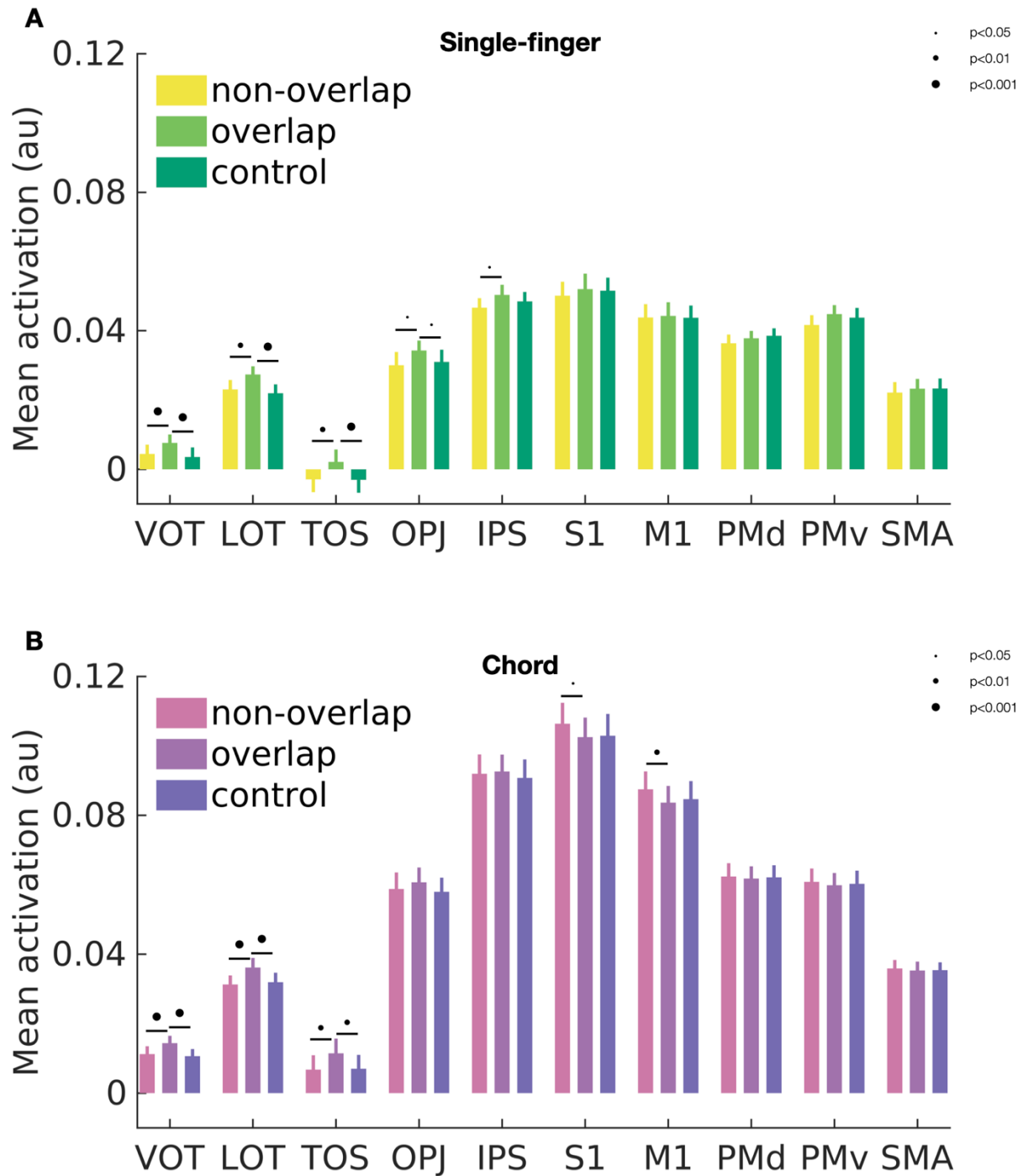


Figure 8. Group-averaged Activation estimates for single finger (A) and chord (B) conditions for non-overlap, overlap, and control conditions.

Activation is plotted in arbitrary units (beta-weights from regression). Error bars indicate standard error of the mean across participants. – significant pairwise differences are indicated using bars.

Discussion

In the present study, we asked participants to produce single-finger presses or chords while undergoing 7T fMRI. In one condition, the preparation for the upcoming movement occurred simultaneously with the execution of the ongoing movement (overlap), while in the other two (non-overlap, control), it did not. We found that the overlap condition engaged the parietal and occipital regions more than the non-overlap condition, even though we tightly controlled for equal overall preparation times and motoric requirements across the two conditions. While this extra cortical recruitment during online preparation was highly significant for both single-finger presses and chords, it did not increase with the motoric complexity of the response, even though chords benefitted more from online preparation than single-finger presses. Interestingly, online preparation did not increase the activity of PMd compared with the non-overlap condition, even though control analyses showed that PMd was heavily engaged in motor planning.

Our finding that the overlap condition activated PMd as much as the non-overlap condition suggests that movement preparation and execution can run in parallel without causing extra metabolic activity. It has been reported that for a single upper limb movement, patterns of movement preparation are orthogonal to the patterns underlying the movement execution (Elsayed et al., 2016; Kaufman et al., 2014). This arrangement allows movement preparation without causing unwanted execution. Most recently, Zimnik and Churchland (Zimnik & Churchland, 2021) showed that such orthogonality also holds between the preparation of the next movement and the execution of the ongoing one. In this way, the brain can achieve online preparation without causing interference with the ongoing execution process. If movement

preparation and execution occupy orthogonal subspaces, it is likely that the overall metabolic activity when two processes overlap or not (non-overlap) be the same.

The other important finding in our study was that cortical activation was higher in parietal and occipital regions during online preparation. This was the case for both single-finger presses and chords without differences between the two. This suggests that the extra activity was related to stimulus identification or action selection. The fact that this extra cortical recruitment was not modulated by motoric complexity is indeed in line with previous literature showing that sensory information, when unyoked from the motor response, is maintained in parietal or occipital regions (Henderson et al., 2022; Shushruth et al., 2022).

On the other hand, the same regions were also more highly activated during chords than single-finger presses overall. This could suggest that these regions were involved in motor planning. The parietal regions have been shown to encode features of the upcoming movement (Leoné et al., 2014) and maintain finger sequence representation in the muscle coordinate frames (Wiestler et al., 2014). Thus, it is possible that the brain shifts the motor planning activity of the next movement to the parietal and occipital regions while the motor system controls the execution of the current movement. In our experiment, since we only manipulated the difficulty of motor planning and not the action selection, the possibility that this extra engagement might partially relate to motor-related processes cannot be fully excluded.

Interestingly, when pressing chords, M1 and S1 are less activated during the overlap and control conditions compared with the non-overlap condition (FIG 8B). In a recent study, Ariani and others (Ariani et al., 2022) observed that preparation for a single finger press activated M1 and S1 microcircuits that will later be used during the execution, suggesting the active role of these areas

in movement preparation. In both non-overlap and control conditions, preparation and execution occurred sequentially, with the only difference of the first response had a shorter preparation time in the control condition (FIG 2B & 2D). The fact that we observed lower activity in the control condition compared with the non-overlap condition may suggest that the preparatory processes of the first response could not be fully completed in the control condition due to the short preparation time. What happens when there is enough preparation time, but it overlaps with another execution? Comparing the activity of these areas between non-overlap and overlap conditions showed relative suppression of the overlap condition. This could suggest that when these areas were busy executing the current movement, they were less involved in the preparation of the next movement. This appears to be at odds with the orthogonality of preparation and execution (Kaufman et al., 2014). If orthogonality holds, we should have observed equal activity during overlap and non-overlap conditions and lower activity in the control condition. The orthogonality of preparation and execution was reported in the spiking outputs of the neurons in area PMd and rostral M1. However, the areas where we observed relative suppression are located deep into the central sulcus close to the caudal M1 and BA 3a. Thus, in the close surrounding of the central sulcus, the orthogonality might not hold, and to inhibit the interference between preparation and execution brain might simply shift the preparatory processes to another area (e.g., parietal regions) while the system is busy with execution. Another interesting detail about this suppression was that it was only observed in chords, not single-finger presses. This is indeed in line with our finding that the motor planning process for chords takes a longer time. During single-finger presses, since motor planning processes could be completed even within the short interval, no pattern of suppression was expected.

The other possibility for such suppression could lie in the non-linearity of the BOLD signal when the events are not equally distributed in time. In the block design fMRI experiments, such as ours, activation maps reflect the average BOLD activity of all the responses within a block. It has been shown that the BOLD signals for responses within a block are summated linearly as long as inter-response intervals are long enough (Dale & Buckner, 1997). Dale and Buckner reported that when presenting two flickering checkerboards, the second one evoked lower activity in the visual areas when the delay between two stimuli was shorter than 6 seconds. The nature of this nonlinearity is mostly attributed to the transformation of the neural activity into a hemodynamic response as opposed to the nonlinearity in the neural firing rates. The nonlinearity of the BOLD dynamics is also reported in a finger-tapping task in motor areas (Birn et al., 2001). To control for this important detail, all of our conditions were matched in terms of execution time for the motor responses. However, one thing that could not be easily controlled was the delay between the preparation processes of two responses within each condition. For instance, in the non-overlap condition (FIG 2), the first response preparation could be initiated 1300 ms prior to the second response preparation even starting, whereas this delay for the control and overlap conditions was 750 ms. Hence it is likely that since the two preparation events are closer in time during the overlap and control conditions, the elicited activation was smaller. However, such nonlinearity should have also existed during single-finger conditions, and the fact that we did not observe it may rule out this possibility.

Overall, our results suggest the following model of online movement preparation. The model asserts that the main bottleneck for online preparation is limited attentional resources. During online preparation maintaining the stimulus of the upcoming action while analyzing the

next action stimulus requires extra resources. Such extra engagement to allocate attentional resources to multiple tasks is consistent with classical models of the psychological refractory period (Welford, 1952; Smith, 1967; McLeod, 1977). Additionally, consistent with the theory of orthogonal subspaces for motor planning and execution (Kaufman et al., 2014), the motor planning process for the next action can run in parallel with the execution of the upcoming action without extra resources required.

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