Prospective rewards enhance motor skill performance and skill coding in LPFC

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Abstract

People are capable of rapid improvements in skill performance when they are presented with large prospective incentive cues. We investigated this phenomenon by offering prospective offers of monetary reward to human participants, contingent on their successful production of discrete motor sequences. We found that people executed cued motor sequences more quickly and accurately when they were offered large rewards. Reward offers were associated with elevated activity throughout the brain and fine-grained patterns in these regions encoded information about sequence identity. Follow-up analyses provided evidence that sequence-coding in LPFC was enhanced by reward and related to subsequence performance. This work sheds light on the neurocognitive mechanisms underlying incentive-motivated skill performance, suggesting that it may depend critically on executive-control related processes in the LPFC.

Introduction

People perform better when they are highly motivated. In experimental settings, motivation has been shown to enhance motor skills (Mosberger et al., 2016; Wächter et al., 2009), working memory (Kennerley and Wallis, 2009; Krawczyk et al., 2007), attention (Engelmann and Pessoa, 2007), cognitive control (Etzel et al., 2016), model-based decision-making (Patzelt et al., 2018), and perception (Serences, 2008). Motivation is often manipulated using prospective cues that involve offers of future monetary gains or threats of future losses. People are capable of rapid improvements in skill performance when they are presented with large prospective incentive cues. This capacity suggests that people update their expectations of future reward prospectively, leading to more attention and effort being invested in the task, and ultimately increasing the probability of success (Kool and Botvinick, 2018).

Motor skill learning is often studied in the context of motor sequencing tasks such as the serial reaction time task (SRTT) or the Discrete Sequence Production (DSP) task (Krakauer et al., 2019). In these tasks, participants train to quickly and accurately perform specific sequences of finger movements. Early on in skill learning, performance is slow, effortful, and unstructured and appears to rely heavily on cognitive processes such as attention and working memory. This is evidenced by the susceptibility of novice skills to distraction effects (Nissen and Bullemer, 1987), the dependency of skill acquisition on working memory capacity (Anguera et al., 2011; Seidler et al., 2012), and the increased activity in brain regions important for cognitive control such as lateral prefrontal cortex (LPFC) during the performance of novice skills (Grafton et al., 1995; Schendan et al., 2003; Willingham et al., 2002). After extensive training, however,

previously independent movements that comprise the skill become concatenated and organized into chunks (Sakai et al., 2003), a process which is accompanied by measurable changes in skill representation in the primary motor cortex (Diedrichsen and Kornysheva, 2015; Wiestler and Diedrichsen, 2013) (M1). With sufficient practice, skill performance becomes automatized, less reliant on cognitive control circuits, and more reliant on cortical motor regions and the sensorimotor striatum (Dayan and Cohen, 2011). Since novice and well-trained motor skills depend on distinct psychological and neuronal mechanisms, motivational effects on their performance will also likely depend on distinct mechanisms. However, no study to date has tested whether the mechanisms of motivational enhancement are different for novice and well-trained skills.

One specific mechanism by which motivation might enhance skill performance is by enhancing the fidelity of neuronal representations of skill. Several studies show that motor skills can be decoded from patterns of brain activity using multivariate techniques such as pattern classification and representational similarity analysis. For example, discrete motor sequences can be decoded from brain activity before and during movement (Nambu et al., 2015; Wiestler and Diedrichsen, 2013) and representational similarity analysis has recently been used to model the structure of motor-skill representations in a motor planning hierarchy spanning from pre-SMA to M1 (Yokoi and Diedrichsen, 2019). In the context of a cognitive control task, one recent study showed that motivation enhances temporary goal representations in the prefrontal cortex and that this enhancement mediated the effect of motivation on performance (Etzel et al., 2016). This work suggests that increased motivation may also enhance motor skill representations, especially if they are still reliant on mechanisms of cognitive control. However, no study to date has examined this possibility.

We administered a discrete sequence production task during functional magnetic resonance imaging (fMRI) to 30 healthy human participants. Participants trained for 40 trials on one sequence and 200 trials on another and returned 48 hours later to perform these sequences for prospective rewards ($5, $10, or $30). We found that skill performance was enhanced for $30 trials compared to $5 trials. Our data revealed a widespread network of brain areas whose activity scaled linearly with reward magnitude. From this reward-responsive network, we decoded novice and well-trained skill identity from patterns of activity preceding movement. This distributed representation included clusters in M1, SMA, and LPFC. We then examined whether skill decoding in these ROIs was influenced by reward magnitude. We found that novice skill decoding in LPFC was enhanced for $30 trials compared to $5 trials and that this decoding was associated with improved behavior in the upcoming trial. These results did not hold for the well-trained skill or the other ROIs. These results suggest that the

motivated performance of novice skills depends on enhanced skill coding in LPFC, but the motivated performance of well-trained skills does not.

Results

30 human participants performed a discrete sequence production (DSP) task (Figure 1) with concurrent fMRI. This task required participants to quickly produce 8-item sequences of button presses following a cue indicating sequence identity. Participants trained extensively on one sequence (200 trials) and minimally on another (40 trials). Two days after training, they returned to perform the practiced sequences with trial-wise offers of performance-contingent monetary rewards ($5, $10, or $30). To perform the sequence "successfully", participants had to produce all 8 button presses without error under an assigned time-limit. Time-limits were calibrated separately for each person and each sequence based on performance during a warm-up phase in the scanner on day 2. Our behavioral analyses focused on trial-wise behavioral success and our neuroimaging analyses focused on trial-wise cue-related activity.

Figure 1. Discrete sequence production task. To study the effects of motivation on skilled action, participants performed two 8-item motor sequences for monetary incentives. The diagram above depicts an example trial from the reward session. Reward and sequence (color) were cued at the start of each trial. Our fMRI analyses focused on hemodynamic responses to this cue. After a brief delay, the sequence was performed. If it was completed under a specific time limit, the trial was successful.

Motivation enhanced skilled performance

We fit a multilevel logistic regression model to participants' accuracies to test whether they were more likely to succeed on trials with large rewards ($30) compared to trials with small rewards ($5). To estimate the effect of reward magnitude on accuracy, we used Bayesian parameter estimation with weakly informative priors ($\mathcal{N}(0,1)$). Since our predictors were binary, these priors assigned low prior probabilities to large effects and high prior probabilities to small effects (especially null effects). We performed Bayesian null hypothesis testing by examining whether the 90% credible interval (CI) for a parameter excluded zero. If it did, then there was less than a 5% posterior probability that the effect was null (or in the opposite direction), which we take as evidence against the null hypothesis. We use 90% CIs rather than 95% because the former is more stable than the latter (Kruschke, 2014) and because the 90% CI lets enables easy 1-tailed null hypothesis testing at the conventional $p < 0.05$.

We found evidence that our participants were more likely to succeed in the DSP task on trials with large rewards compared to trials with small rewards ($\beta = 0.30$, CI = [0.14, 0.45], $p < 0.05$; Figure 2). However, we did not find evidence that accuracy improved on

trials with medium rewards compared to trials with small rewards ($\beta = 0.04$, CI = [-0.12, 0.19], $p > 0.05$). To our surprise, we found evidence that accuracy was higher for the novice sequence compared to the well-trained sequence ($\beta = 0.23$, CI = [0.01, 0.44], $p < 0.05$). Although the time limits were chosen in part to match accuracy across the two sequences (see Methods), the time limits of the well-trained sequences were likely too strict, as evidenced by the disproportionate number of 'too slow' trials for well-trained sequences (36%) compared to novice sequences (28%). However, we found no evidence of an interaction between reward and sequence on performance ($p > 0.05$). These results suggest that offering large performance-contingent rewards motivated people to perform skilled actions more efficiently.

Figure 2. Reward enhanced skill performance. We tested for effects of prospective reward on skill performance using a Bayesian multilevel logistic regression model. The line plot shows mean skill performance (i.e., DSP success rate) for each reward condition with standard error bars. The density plot shows the posterior probability density over the $5 vs $30 reward effect in our model. The bold blue line is the median parameter estimate, the shaded region indicates the 90% credible interval, and the red dashed lines indicate the point null hypotheses. More than 95% of the posterior estimates were greater than zero, which provides evidence that skill performance was higher on $30 trials compared to $5 trials.

Reward modulated activity in motor planning regions

We first asked which regions of the brain were linearly responsive to motivation (i.e., prospective reward value) just prior to movement. We used generalized linear models (GLM) to estimate the neuronal responses to the sequence/reward cue. To determine which brain areas were responsive to prospective rewards, we fit GLMs with reward-magnitude regressors, which predict that the amplitude of the hemodynamic response in a voxel will increase linearly with reward magnitude. We used a standard 2nd level analysis to identify brain areas whose activity increased in response to reward at the group-level. Our group-level inferences assume a cluster-corrected alpha threshold of $p < 0.05$.

This analysis revealed clusters of reward-related activity in most of the brain regions that we expected to be engaged during the DSP task, including LPFC, supplementary motor area (SMA), premotor cortex (PMC), and primary motor cortex (M1). Unsurprisingly, we also observed clusters of reward-related activity in reward regions such as the striatum and the pallidum. This analysis provided a reliable map of the brain regions whose activity was modulated by prospective rewards. Of particular interest to this study is the finding that many regions involved in motor-skill performance were responsive to reward, including the primary motor cortex, premotor cortex and prefrontal cortex.

Figure 3. Reward-responsive brain areas. We used GLMs to test for effects of reward on hemodynamic responses to the pre-movement cue. The images above show the results of a group-level analysis of subject-level coefficient maps. For visualization, we used threshold-free cluster correction and projected the results to surface space. The ellipses indicate the approximate locations of our ROIs.

Skill decoding in reward-responsive brain areas

We performed whole-brain MVPA to localize a network of areas whose patterns of activity contained information about motor skill. Whole-brain MVPA is often performed using an iterative searchlight approach, however this technique only performs decoding in small neighborhoods of voxels but does not consider representations distributed across the cortex. For this reason, we used SpaceNet, a whole-brain multivariate decoding method that employs spatial priors to produce sparse and clustered coefficient maps. SpaceNet has been shown to yield higher classification scores and more interpretable maps than alternative whole brain decoding techniques for classic brain decoding problems (Baldassarre et al., 2012; Dohmatob et al., 2014; Grosenick et al., 2013; Michel et al., 2012). In order to uncover regions that contain a dual code for both motor skill and reward information, we restricted our whole-brain MVPA to voxels that were reward-responsive at the group level (uncorrected $p < 0.001$) (Figure 3). We created individualized reward-related masks using a leave-one-subject-out (LOSO) approach to ensure that feature selection was independent from the MVPA. The SpaceNet classifiers were trained on coefficient maps from a GLM with trial-wise regressors predicting a canonical hemodynamic response to cue-onset. We used a standard 2nd level analysis to identify brain areas that contained information about motor sequence at the group-level. Our inferences assume a cluster-corrected alpha threshold of $p < 0.05$.

Our first set of SpaceNet classifiers were trained to predict the identity of the intended motor sequence from patterns of brain activity preceding movement. At the group level, these classifiers predicted the intended motor sequence (on a held-out 20% of data) with a mean accuracy of 0.61 and a standard deviation of 0.12 across subjects (Figure 4a). We found skill representations distributed across the cortex including LPFC, SMA, and M1 (Figure 4b). Importantly, this analysis considered only voxels that were responsive to reward magnitude. The regions in Figure 4b therefore simultaneously respond to changes in motivation and contribute to a representation of the motor skill being prepared. These findings are consistent with prior work showing converging reward and action signals in prefrontal areas and motor areas.

Figure 4. Skill coding in reward-responsive brain areas. We trained multivariate classifiers to decode motor sequence identity from patterns of hemodynamic responses to the pre-movement cue. This analysis only considered voxels that were responsive to reward (see Figure 3). (a) Box plot of mean SpaceNet decoding accuracies for each subject. (b)

Results of a group-level analysis of subject-level SpaceNet coefficient maps. visualization, we used threshold-free cluster correction, spatial smoothing with a 2mm kernel, and projected the results to surface space. The ellipses indicate the approximate locations of our ROIs.

Performance-relevant patterns in reward-responsive brain areas

While information about reward and skill appear to converge in the LPFC, SMA, and M1, it remains a possibility that these areas have no practical relevance to future behavior. To test this, we ran a second set of whole-brain classifiers that used patterns of activity prior to movement to predict whether a participant would be successful in the forthcoming DSP trial. At the group level, the classifiers predicted future behavioral performance (on a held-out 20% of data) with a mean accuracy of 0.79 and standard deviation of 0.09 across subjects. This decoding analysis revealed a more restricted information map than the analysis of skill decoding, but the map still included informative clusters in LPFC, SMA, and M1 (Figure 5). These results suggest that the reward-related regions identified previously are not only responsive to changes in motivation, but also relevant to future behavior. Furthermore, the information maps from our two MVPAs (Figures 4 and 5) were found to overlap in LPFC, SMA, and M1. This conjunction map delineates voxels that (1) respond to changes in motivation, (2) carry information about motor sequence, and (2) carry information about future behavioral success. Therefore, we used this conjunctive information map as a mask for our subsequent ROI analyses.

Figure 5. Performance-prediction with patterns in reward-responsive brain areas. We trained multivariate classifiers to predict future behavioral success from patterns of hemodynamic responses to the pre-movement cue. This analysis only considered voxels that were responsive to reward (see Figure 3). (a) Box plot of mean classification accuracies for each subject. (b) Results of a group-level analysis of subject-level SpaceNet coefficient maps. For visualization, we used threshold-free cluster correction, spatial smoothing with a 2mm kernel, and projected the results to surface space. The ellipses indicate the approximate locations of our ROIs.

Skill decoding in LPFC predicts improved novice performance

We hypothesized that motivation preferentially enhances skill representations based on their relevance to future performance. While our whole-brain analysis above revealed a widely distributed cortical representation of motor skills, we were interested in effects of motivation on local skill representations in specific ROIs. We therefore performed follow-up ROI analyses, focusing on skill decoding in lateral prefrontal cortex (LPFC), supplementary motor area (SMA), and primary motor cortex (M1). We expected that skill decoding in LPFC would be predictive of behavioral success for the novice skill but not the well-trained skill. We initialized our ROIs using the multi-modal Glasser atlas

which provided a priori masks (see Methods). Next, we excluded voxels that were *not* contained in the overlap of our two group-level information maps (Figure 6). This functional masking was performed using a LOSO approach to ensure that feature selection was independent from the MVPA.

Figure 6. Conjunction of group-level sequence and performance information maps. This map only includes voxels that were significant in the earlier group analyses of the information maps. We intersect this conjunction map with a priori ROIs to obtain our ROIs for the follow-up decoding analysis.

Next, we used linear support vector machines (SVM) to decode motor sequence identity from patterns of cue-related activity in our ROIs. To ensure that our classifiers had enough samples to estimate a reliable classification boundary, we used a leave-one-trial out (LOTO) cross-validation procedure, which provided trial-wise binary decoding accuracies. Finally, we used multilevel logistic regression models to test whether skill decoding in our ROIs was predictive of future performance for the novice or well-trained skills. As with our Bayesian analysis of DSP performance, we estimated posteriors over parameters and performed null-hypothesis testing using 90% credible intervals.

This analysis showed that skill decoding in LPFC was more strongly associated with successful performance of novice but not well-trained skills ($\beta = 0.23$, CI = [0.07, 0.40], $p < 0.05$). However, we found no evidence of a relationship between behavior and sequence decoding in SMA or M1 ($p > 0.05$). These results show that skill decoding in LPFC had high utility for novice skills but not well-trained skills.

Figure 7. Novice skill decoding in LPFC enhanced novice skill performance. We tested for effects of skill decoding in LPFC on future skill performance using a Bayesian multilevel logistic regression model. This was the same model whose results were reported in Figure 2. The line plot shows observed group mean skill performance (i.e., DSP success rate) for each skill-decoding outcome and each skill (i.e., novice vs well-trained sequences); error bars show standard errors of subject means. The density plot shows posterior probability density over the decoding by skill-level interaction effect in the model. The bold blue line is the median estimate, the shaded region is the 90% credible interval, and the red dashed line indicates the point null hypotheses.

Motivation enhanced novice skill decoding in LPFC

The above analysis provided evidence that skill decoding in LPFC was linked to improved behavior for novice skills only, which suggests that skill representations in LPFC have high utility for novice skills only. We hypothesized that rewards would preferentially enhance skill representations that are useful for performance, so we predicted that motivation (a la reward magnitude) would enhance skill decoding in LPFC for novice skills but not well-trained skills. To test this, we used the same ROI decoding

data from the previous analysis, but this time we fit multilevel logistic regression models to trial-wise decoding accuracies (with separate models for each ROI) to test for effects of reward on skill decoding.

We observed a positive effect of motivation on novice skill decoding in LPFC, which was much stronger than the motivation effect on well-trained skill decoding ($\beta = 0.34$, CI = [0.15, 0.52], $p < 0.05$). Our analyses of decoding from SMA and M1 returned null results, suggesting that the skill coding locally in these regions was not affected by reward. Overall, these results suggest that motivation enhanced novice but not well trained skill coding in LPFC. This is significant because skill decoding in LPFC is only behaviorally relevant for the novice skill, suggesting that motivation preferentially modulated skill representations according to their utility for future performance.

Figure 8. Reward enhanced novice skill decoding in LPFC. We tested for effects of reward on skill decoding in LPFC using a Bayesian multilevel logistic regression model. The line plot shows observed group mean skill decoding (i.e., correct classification rate) with standard errors for reward condition and each skill-level (i.e., novice vs well-trained sequences). The density plot shows posterior probability density over the reward by skill-level interaction effect in the model. The bold green line is the median estimate, the shaded region is the 90% credible interval, and the red dashed line indicates the point null hypotheses. 95+% of the posterior was greater than zero, which provides evidence that the reward ($30 - $5) effect on skill decoding in LPFC was greater for the novice skill compared to the well-trained skill.

Discussion

We sought to examine the neural mechanisms that contribute to the motivation-based enhancement of motor skills. We found that performance on a motor sequencing task improved as prospective reward values grew larger. When examining cue-related whole-brain activity just before movement onset, we uncovered distributed patterns of activity across a relatively large network of regions important for visuo-motor skill that simultaneously coded for reward value, motor skill identity, and the quality of skill execution. Importantly, we found a dissociation between the neuronal mechanisms of incentive-motivated performance of novice and well-trained motor skills. While both novice and well-trained skills were performed more quickly and accurately on high-value trials (Figure 2), the underlying changes in brain activity preceding performance was different for the two skills (Figure 6). Our results suggest that the incentive-motivated performance of novice motor skills depends on enhanced representations of skill in the LPFC.

Reward modulates a widespread task-relevant network

Our results show that motivation (i.e, prospective reward value) modulated a widespread task network prior to movement (Figure 3). In these regions, the amplitude

of the hemodynamic response to the cue was larger for high-value trials compared to low-value trials. This motivation-modulated network included canonical reward regions such as the striatum (Apicella et al., 1991; Balleine et al., 2007; Delgado, 2007; Samejima et al., 2005) and ventromedial frontal cortex. However, we also found that prospective reward magnitude parametrically increased activity in many regions thought to be involved in motor planning including lateral frontal cortex, premotor cortex, primary motor cortex, and parietal cortex. This finding is consistent with prior work showing anticipatory reward modulation in task-relevant brain areas across a variety of both cognitive and motor tasks (Galaro et al., 2018; Kennerley and Wallis, 2009; Knutson et al., 2003; Leon and Shadlen, 1999; Marsh et al., 2015; Peterson and Seger, 2013; Ramakrishnan et al., 2017; Ramkumar et al., 2016; Roesch and Olson, 2004, 2003; Wallis and Kennerley, 2010; Wallis and Miller, 2003)(Peterson and Seger, 2013; Ramkumar et al., 2016; Roesch and Olson, 2003)(Galaro et al., 2018; Marsh et al., 2015; Ramakrishnan et al., 2017; Ramkumar et al., 2016).

Multiplexed code for reward, skill identity, and the quality of performance

To investigate how prospective reward enhances the neural coding of motor skills, we sought to determine which of these reward-responsive areas specifically carried information about both the identity and the quality of the upcoming action. Using a whole-brain decoding technique, we found that distributed patterns of activity across fronto-parietal cortices, visual cortex, and the striatum simultaneously carried information about prospective reward value, motor skill identity and the quality of future performance. Previous studies have shown that reward signals and action signals converge in including the prefrontal cortex (Cai and Padoa-Schioppa, 2014; FitzGerald et al., 2012; Hunt et al., 2015; Kargo et al., 2007; McNamee et al., 2015), the striatum (Cai and Padoa-Schioppa, 2014; FitzGerald et al., 2012; Hunt et al., 2015; Kargo et al., 2007; McNamee et al., 2015), anterior cingulate cortex (Hayden and Platt, 2010), and primary motor cortex (Galaro et al., 2018; Ramakrishnan et al., 2017). Our work adds to these findings by showing that information about reward, skill, and future performance converge across a more widespread task network, spanning areas specialized for sensory, cognitive, motor, and affective processing.

Prospective rewards enhance motor skill decoding in LPFC

Our whole-brain analyses showed that motivational signals and preparatory action representations converge in several brain areas. While such convergence is likely necessary for motivation to enhance behavior, it is unclear exactly what happens when these signals converge. One possibility is that motivation enhances cortical skill representations on which performance depends. We addressed this possibility in follow-

up ROI analyses and found evidence for such enhancement in LPFC, but not in more downstream regions in the hierarchy of action control (SMA and M1). We quantified the utility of skill representations in LPFC by estimating the effect of skill decoding on future behavioral success. Our results show that anticipatory skill decoding in LPFC was more strongly linked to future performance of novice skills compared to well-trained skills (Figure 7), indicating that skill representations in LPFC had greater utility for the novice skill compared to the well-trained skill. This is consistent with the research showing that novice skill performance depends more on skill-focused attention, working memory, and planning (Anguera et al., 2011; Doyon et al., 2003; Galaro et al., 2018; Marsh et al., 2015; Ramakrishnan et al., 2017; Ramkumar et al., 2016; Seidler et al., 2012; Yokoi et al., 2018).

LPFC is perhaps ideally suited to modulate skilled motor behavior due to increases in motivation. Explicit cueing of sequence a motor sequence as employed in this study enables advanced motor planning (Diedrichsen and Kornysheva, 2015). Especially early on in training, cognitive control processes have been shown to aid in the performance of motor sequencing skills. For example, working memory capacity relates to the rate of skill learning (Anguera et al., 2011) and novice motor sequencing performance coincides with increased activity in LPFC (Grafton et al., 1995; Schendan et al., 2003; Willingham et al., 2002). Performance-contingent rewards can enhance these control processes. In particular, rewards have been associated with improvements in the advanced maintenance of goal information (Botvinick and Braver, 2014; Etzel et al., 2016; Jimura et al., 2010). Additionally, prior work has shown that information about reward and simple action choices converge in LPFC (McNamee et al., 2015) and that information about prospective rewards is introduced to goal-directed action networks through LPFC (Ballard et al., 2011) We propose that motivation facilitates the preferential enhancement of task-relevant representations—that is, representations that have high utility for future performance (Botvinick and Braver, 2014; Westbrook and Braver, 2015; Yee and Braver, 2018).

Crucially, motivation increased the novice skill decoding in LPFC, but not well-trained skill decoding (Figure 6). This suggests that skill representations in LPFC were enhanced preferentially in contexts where doing so would be useful for achieving greater success (i.e., for novice skills). As noted above, prior research has demonstrated motivational enhancements of representations in PFC (Etzel et al., 2016; Kargo et al., 2007; Kobayashi et al., 2002; Leon and Shadlen, 1999; Parro et al., 2018; Watanabe et al., 2002). Our results go beyond this work by showing that this motivational effect on task coding in PFC generalizes to motor skills. Our findings support the hypothesis that motivation enhances skill coding in a goal-directed manner,

preferentially amplifying representations that are poised to positively impact future behavior.

However, it must be noted that we did not find any analogous increased skill decoding for the more highly trained skill despite the fact that behavioral performance showed similar motivation-based enhancements. We also did not observe any increase in skill decoding in downstream motor areas (i.e. M1 and SMA) although clearly any skill enhancement must ultimately involve altered activity in these areas. This study was focused on skill coding in the neocortex prior to movement because we believed that processing at this stage would best dissociate novice and well-trained skill performance. It is possible that enhanced performance for more well-trained skills is supported by altered processing during the execution period itself. Unfortunately, there were several factors that made reliably measuring brain activity during movement a challenge. Aside from simple movement artifacts, the duration of the movement period varied considerably across time, skill, and participant. Additionally, relatively strict time limits were necessary to prevent the strategic slowing of execution speed on high reward trials. This design choice led to a relatively high number of errors during execution, limiting the number of successfully completed trials that could be used for analysis of the movement period itself. Nonetheless, it is important to consider the effects of motivation on brain activity during execution, especially because this may be the locus of enhancement for skills that depend less on anticipatory cognitive processing (e.g., well-trained motor sequences).

Further limitations

Our results show that the neuronal mechanisms by which motivation enhances skill performance differ as a function of skill-level. However, we cannot rule out the possibility that our decoding analyses merely distinguished neuronal patterns based on skill-level rather than skill-identity per se. However, we believe that our key theoretical inferences do not critically depend on this distinction. As discussed above, prior work has implicated the lateral PFC in the performance and acquisition of relatively novice motor skills. We show that we can more readily decode the pattern of activity during the preparation of a novice skill when prospective reward value is higher. Although it is possible that our classifier was able to distinguish the two motor sequences based on the differential recruitment of a given region due to differences in expertise, our results suggest that this distinction was sharpest at higher levels of motivation.

Our analyses also focused heavily on decoding skill information from patterns of cortical activity. We focused on this aspect of our dataset because prior work validated the approach of measuring cortical skill representations using MVPA (Nambu et al., 2015;

Wiestler and Diedrichsen, 2013; Yokoi et al., 2018; Yokoi and Diedrichsen, 2019) and because recent work has shown that multivariate decoding from cortex can be affected by motivation (Etzel et al., 2016; Parro et al., 2018). However, incentive-motivated performance depends on dynamic coordination between cortical and sub-cortical systems, as evidenced by the well-documented function of cortico-striatal loops in skill learning and performance (Dayan and Cohen, 2011; Doyon et al., 2003; Dudman and Krakauer, 2016; Frank, 2011; Hikosaka et al., 2018; Turner and Desmurget, 2010) and the convergence of action, reward, and performance information in the striatum in the present work. Future analyses should examine whether changes in functional connectivity between the striatum and the cortex drive motivational enhancements of cortical representations of skill.

Closing remarks

In sum, we provide evidence that both novice and well-trained motor skills are enhanced by motivation and that a widespread network of visuomotor regions jointly contain information about motor skill and reward value. We also showed that the underlying neuronal mechanisms of motivational enhancement differs between novice and well-trained skills. The motivated performance of novice skills was preceded by enhanced skill coding in LPFC, but we observed no such relationship for well-trained skills. This asymmetry likely results from the differential cognitive demands imposed by novice and well-trained skills, with novice skill performance depending more on prospective goal representations in WM. We propose that motivation increases the expected value of deploying sustained attention to skill relevant representations, thereby increasing their signal to noise ratio and consequently improving behavioral performance.

Methods

Participants

30 undergraduate students from the University of Michigan participated in this study. All participants gave written informed consent to participate and were compensated at a rate of $15 per hour plus cash bonuses for successful performance. All materials and methods were approved by the University of Michigan Institutional Review Board.

Behavioral task

Participants learned to perform two sequences of eight keypresses. Before each trial, participants were instructed by a color cue (1.5 s) to perform one of the two sequences. After a brief delay (2-6 s), participants could perform the instructed

sequence using the A-S-D-F keys. During movement, an array of 4 grey rectangles (representing the keys) 'lit up' in sequence to remind the participant of which key to press next. We expected that our participants would rely less on these on-line visual cues, and more on advanced planning, as learning progressed. In the reward session, sequence cues were presented concurrently with incentive. We imposed movement time limits on performance during the reward session, defined as the 70th percentile of movement times in a warm-up session. Separate time limits were assigned for each sequence and each participant with a maximum of 3 s, and the time limit was reset to be stricter each block if participants' accuracy was above 70% on the previous block. Stimulus orderings for sequence identity and the duration of cue-to-execution intervals (2-6 s) and inter-trial intervals (2-6s) were optimized to estimate effects of interest using AFNI's make_random_timing tool by running 5000 iterations of different random orderings/timings and selecting those explained the most variance in simulated GLM analyses.

Experimental Protocol

The experiment included two sessions on separate days 48 hours apart. In session one, participants performed eight blocks of 35 trials each. During this training session, participants performed 200 trials of one sequence ("heavily trained"), 40 trials of a second sequence ("lightly trained"), and 40 trials of un-cued pseudorandom sequences ("random"). The identity of each of the two sequences was counterbalanced across participants. In session two, participants performed 8 blocks of 30 trials, 120 heavily trained trials and 120 lightly trained trials. Session two also introduced monetary incentives of varying magnitude. Each trial was associated with one of three incentive magnitudes: $5, $10, or $30. The order of reward values was set to be an m-sequence to mitigate carryover effects (Buracas and Boynton, 2002). Participants were informed that a trial would be selected at random at the end of the experiment, and that they would earn the associated reward provided they performed the target sequence without error under the time limit. Our metric of task performance therefore incorporated both speed and accuracy per se.

Incentive-behavior analysis

We used a multilevel Logistic regression model with Bayesian parameter estimation to examine the effects of incentive magnitude (r) and skill-level (k) on the probability of behavioral success. This formula can be expressed as follows, where s is a subject ID:

$$p(success) \sim 1 + r + k + r * k + (1 + r + k \mid s)$$

The reward variable *r* was coded using a treatment contrast, such that it decomposed into to two binary comparisons: $5 vs $10 and $5 vs $30. The final parenthetical term in the model is the random effects term, which forces the model to estimate the variation in intercepts and main effects across subjects.

fMRI acquisition and pre-processing

MR data were acquired with a 3T GE scanner (MR 750) with a 32-channel head coil. Functional data were obtained using a 1-shot multi-band T_2^*-weighted echo-planar imaging (EPI) sequence sensitive to blood oxygenation level-dependent (BOLD) contrast (TR = 1200 msec, TE = 30 msec, flip angle = 70º, 21 cm field of view, in-plane resolution = 2.4 mm × 2.4 mm, MB acceleration = 3). Each functional volume contained 51 contiguous 2.5 mm-thick axial slices separated by a 0 mm inter- slice gap acquired in an interleaved manner. Whole-brain T_1-weighted scans were acquired for anatomical localization. Functional data were realigned to the third volume acquired, slice-time corrected, and registered to the MNI-152 template using a non-linear warp. Functional data were smoothed with a 6mm FWHM kernel for the whole-brain univariate analysis but left unsmoothed for all multivariate analyses (see below).

Whole-brain Univariate Analysis

We modeled BOLD responses to the preparatory cue using generalized linear models (GLM). The preparatory cue conveyed information about the reward that could be obtained (e.g., “$30”) and the sequence that should be performed (e.g., a blue square for sequence A). One GLM was used to capture the spatially distributed patterns of brain responses to the cue on each trial. This GLM modeled each trial’s response to the cue as a separate regressor, enabling us to obtain separate coefficient maps for each trial. The resulting coefficient maps were used as samples in a multivariate decoding analysis. Motor execution regressors were created by convolving a gamma function with a square wave starting at movement onset with duration equal to the movement time. Another GLM was used to measure the extent to which BOLD responses were larger for larger monetary incentives. This GLM used the same motor execution regressors, but contained 2 separate regressors for the cue period. One regressor captured the mean response to the cue, while the other captured parametric modulation due to reward magnitude. This latter regressor was coded to predict linear changes in activity with reward magnitude while accounting for the mean response to the cue. The resulting coefficient maps (one per participant) were fed into a second-level group analysis which helped us identify the voxels whose activity reliably scaled with reward magnitude across participants.

Whole-brain Multivariate Analysis

We used multivariate pattern analysis (MVPA) localize the areas in the brain that contained information about the identity of an upcoming action and whether the action will be performed successfully. Multivariate techniques—such as machine learning classifiers—are powerful tools for measuring information in the brain, because they are capable of discovering complex, high-dimensional mappings between spatially distributed patterns of brain activity and stimuli (or behaviors, or many other things the brain might contain information about). We performed an initial round of MVPAs using a SpaceNet classifier, which uses spatial priors and TV-L1 regularization to construct sparse but blobby coefficient maps. These maps can then be used to perform classification of whole-brain patterns of activity. When the classifier achieves high out-of-sample classification accuracy, it's coefficient maps can be interpreted as information maps specifying which voxels contain information about the class. We ran one round of SpaceNets to classify patterns according to the motor sequence that was cued (A vs B) and another set of SpaceNet classifiers which predicted whether the forthcoming trial would be performed successfully.

The classifiers were run separately on each subject and were given the trial-wise cue-related activity maps as input. Importantly, these maps were filtered using a binary mask encoding which voxels were reward responsive. The group map from the univariate GLM was thresholded at an alpha level of 0.05 and converted to a mask. This mask was then applied), to exclude from our multivariate decoding analysis the voxels that were not reliably reward-responsive at the group level. We used a leave-one-participant-out approach to ensure that the reward-related group maps and masks were independent from each participant's trial-wise cue-related activity maps. This masking greatly reduced the dimensionality of the decoding problem and ensured that the decoders only used voxels that were modulated by incentives. One round of classifiers constructed maps of voxels that were informative about which motor sequence participants were preparing to perform (Sequence A vs Sequence B), and another round of classifiers constructed maps of voxels that were informative of the future behavioral performance (success vs failure). We fed the resulting maps into a second-level conjunction analysis, with an alpha cutoff of 0.05, to produce a mask of voxels that were informative about both action and performance at the group level (Fgure 6).

Post-hoc Multivariate Analysis

Next, we took a closer look at the anatomical sub-components of the action and performance information maps. After conjoining the action and performance information maps, we intersected the conjunction map with specific anatomical regions of interest, defined using the multi-modal Glasser atlas (Glasser et al., 2016). We focused here on the lateral prefrontal cortex (parcel indices: 67, 70, 71, 73, 79, 80, 81, 83, 84, 86), supplementary motor area (43, 44), and primary motor cortex (8). Next, for each subject, we performed a leave-one-trial-out cross-validated MVPA using a linear support

vector classifier with default parameters (Pedregosa et al., 2012). The classification target here was motor sequence (A vs B) and the analysis yielded binary accuracy scores for each trial, representing whether the motor sequence cued on a trial could be successfully decoded. Since we obtained decoding performance for each trial, we were able to test whether sequence decoding was enhanced for trials with large incentives ($30) compared to small incentives ($5). We used multilevel logistic regression models with Bayesian parameter estimation to test for effects of incentive magnitude on sequence decoding accuracy in our LPFC, SMA, and M1 ROIs. These models had the same structure as the model used to test for effects of incentives on behavior.

Brain-behavior Analysis

Lastly, we examined the link between brain activity and behavior. We used a multilevel logistic regression model with Bayesian parameter estimation to model our participants' behavioral accuracy, defined as performing the correct motor sequence under the time limit. The model included skill and skill-decoding predictors. This model was designed to test whether higher sequence decoding accuracy in these regions was associated with higher behavioral accuracy.

Bayesian Hyperparameters

We used Bayesian parameter estimation to quantify the size and uncertainty of various effects in included in various regression models of behavior and brain activity. We used weakly informative priors (Gelman et al., 2008) on all effects, specified as normal distributions around zero with standard deviations of one. These priors assign high probabilities to small effects and low probabilities to large effects. All continuous predictors were mean-centered and scaled to have standard-deviation of 0.5, putting them on the same scale as binary predictors and allowing us to responsibly apply the same N(0,1) priors to all effects (Gelman, 2008). We estimated posteriors on effects using a No-U-Turn MCMC sampler provided via Stan (Carpenter et al., 2017). All Bayesian models were specified using the R package brms (Bürkner, 2018, 2017). In the results section, we report 90% credible intervals (a.k.a. highest density intervals, uncertainty intervals), as well as well as whether these credible intervals exclude zero. When a 90% credible interval excludes zero, 95% of the corresponding posterior probability mass is beyond (greater than or less than) zero. For example, if the 90% credible interval for a parameter β excludes zero and the median estimate of β is positive, then $p(\beta > 0 \mid \text{data}) > 0.95$ and $p(\beta < 0 \mid \text{data}) < 0.05$. For brevity, we report such cases as simply having $p < 0.05$.

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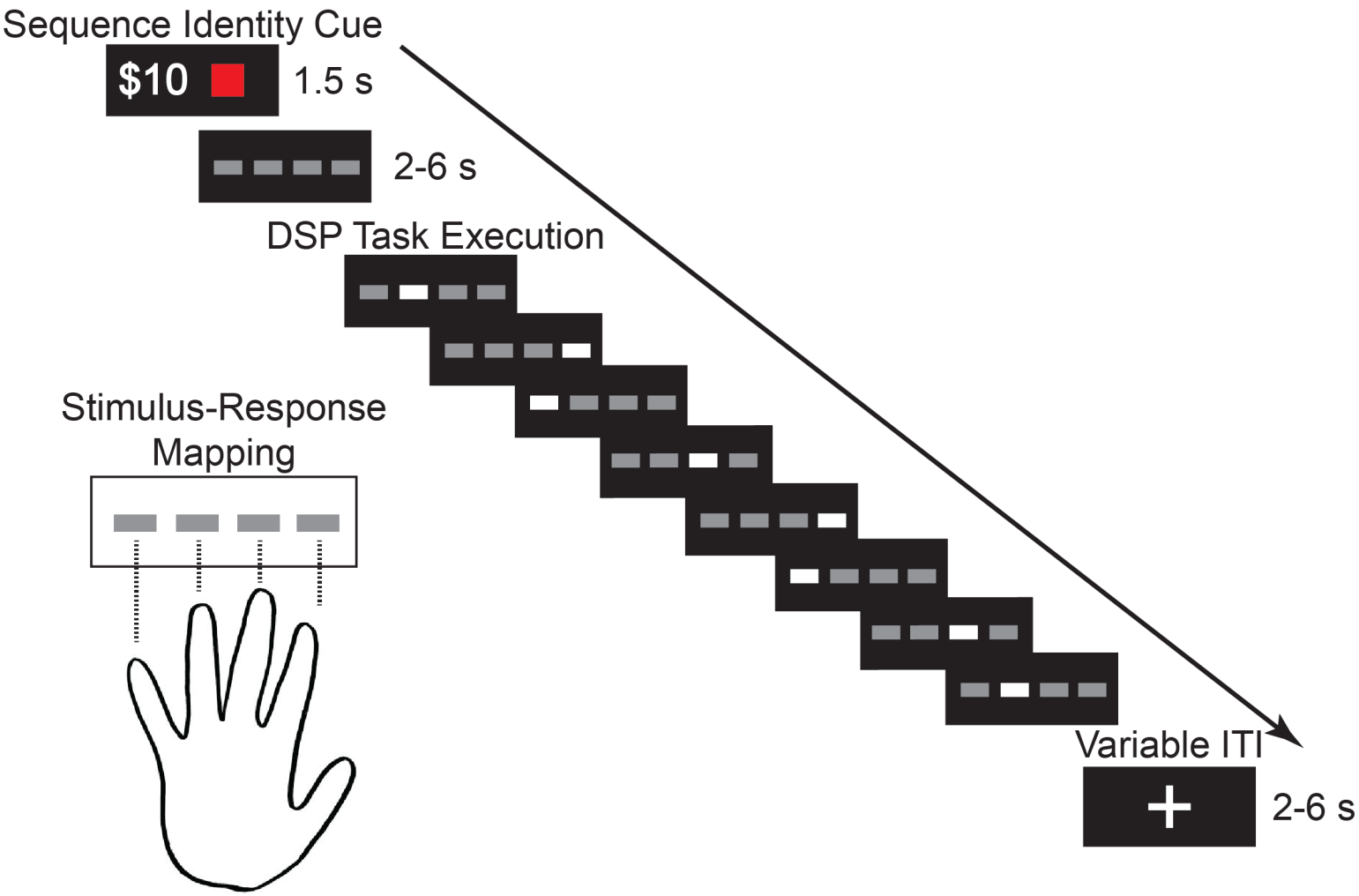
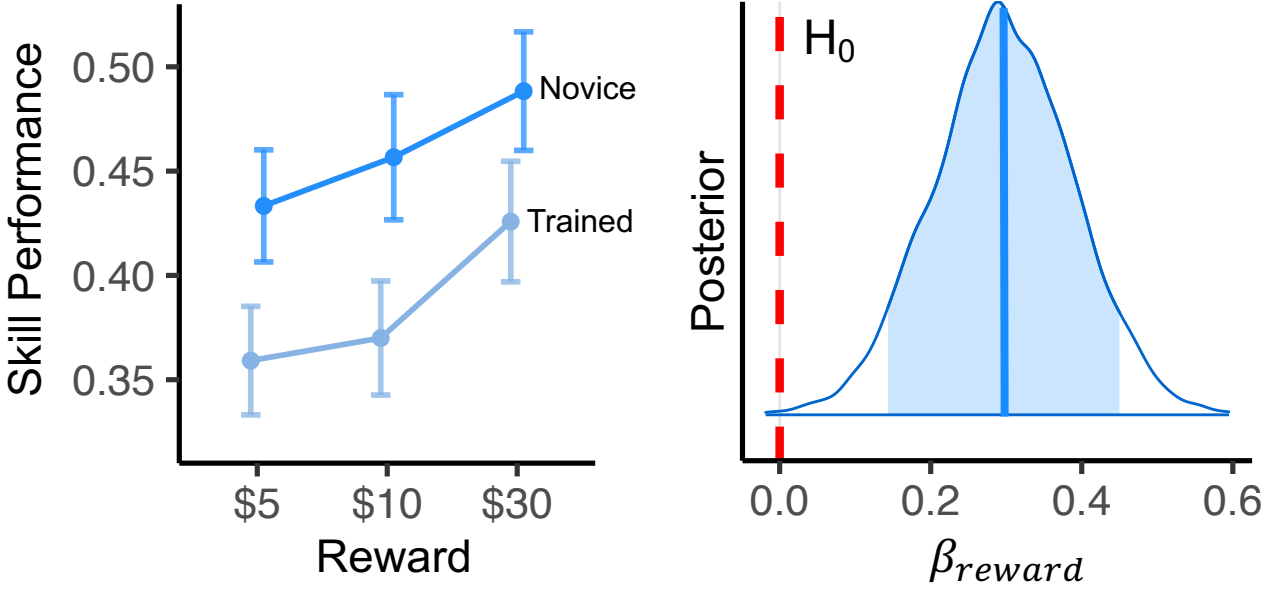
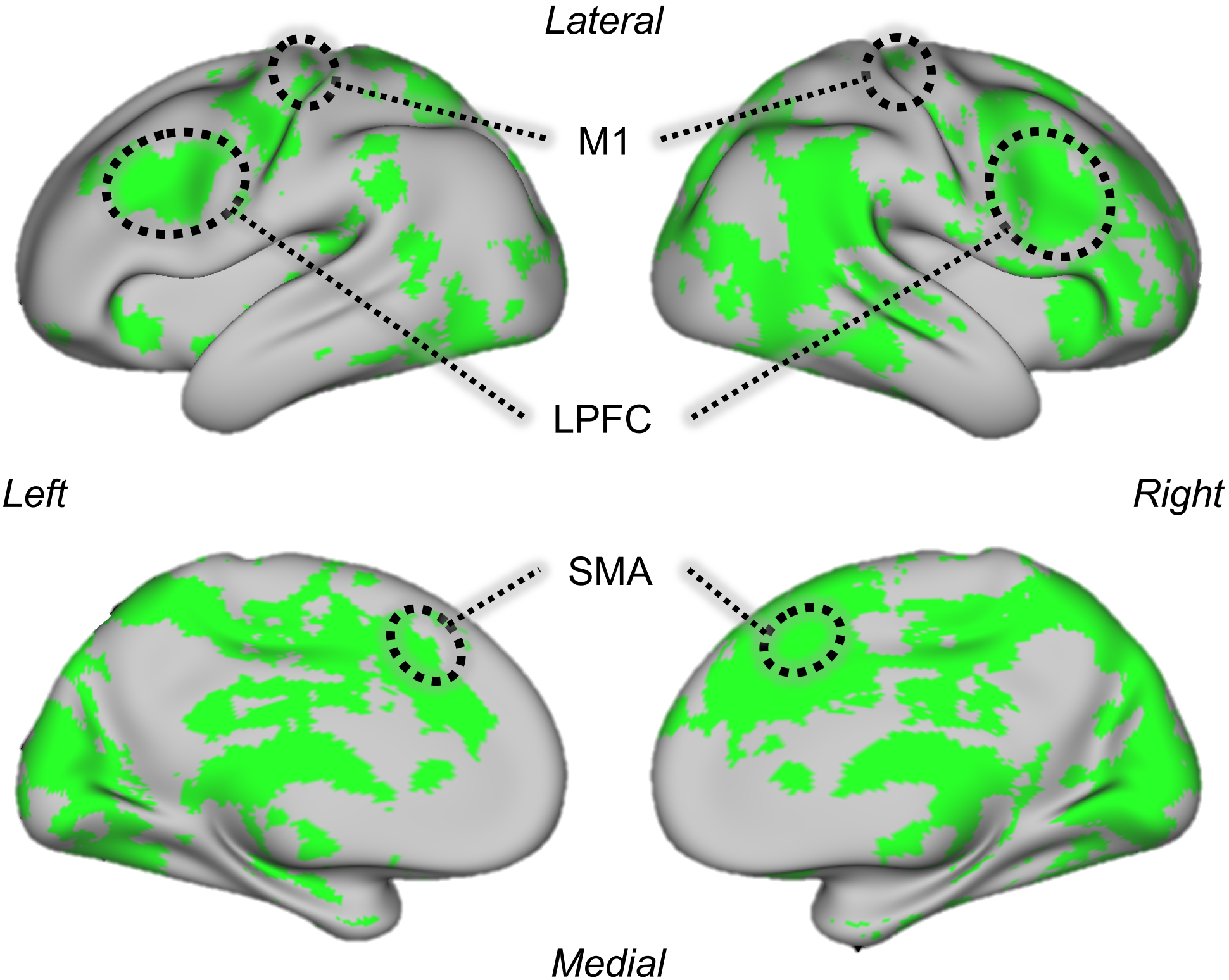
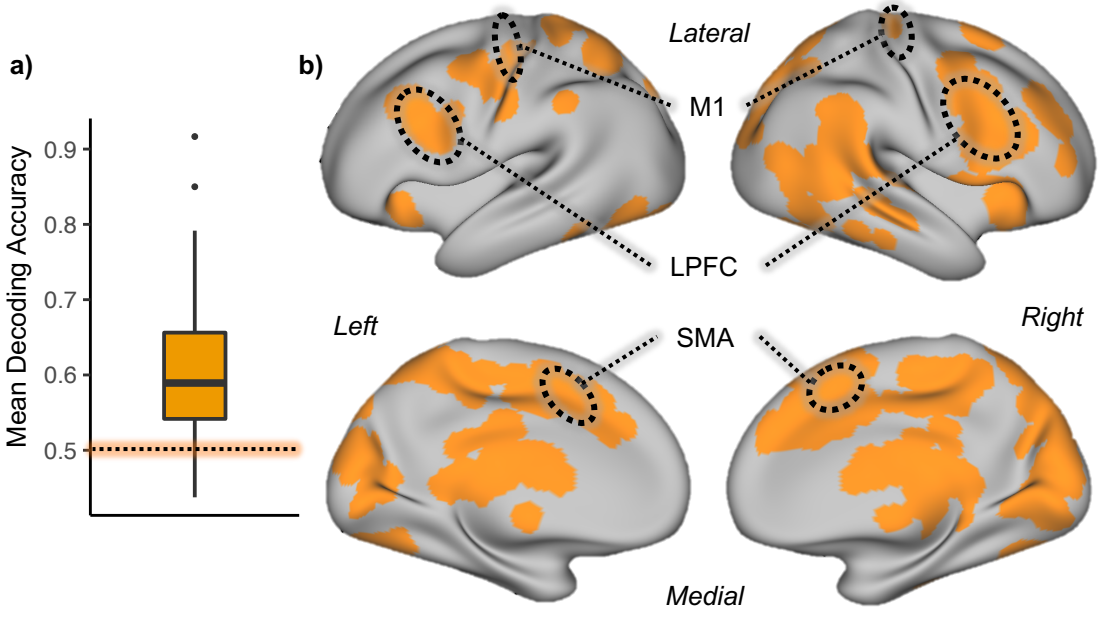
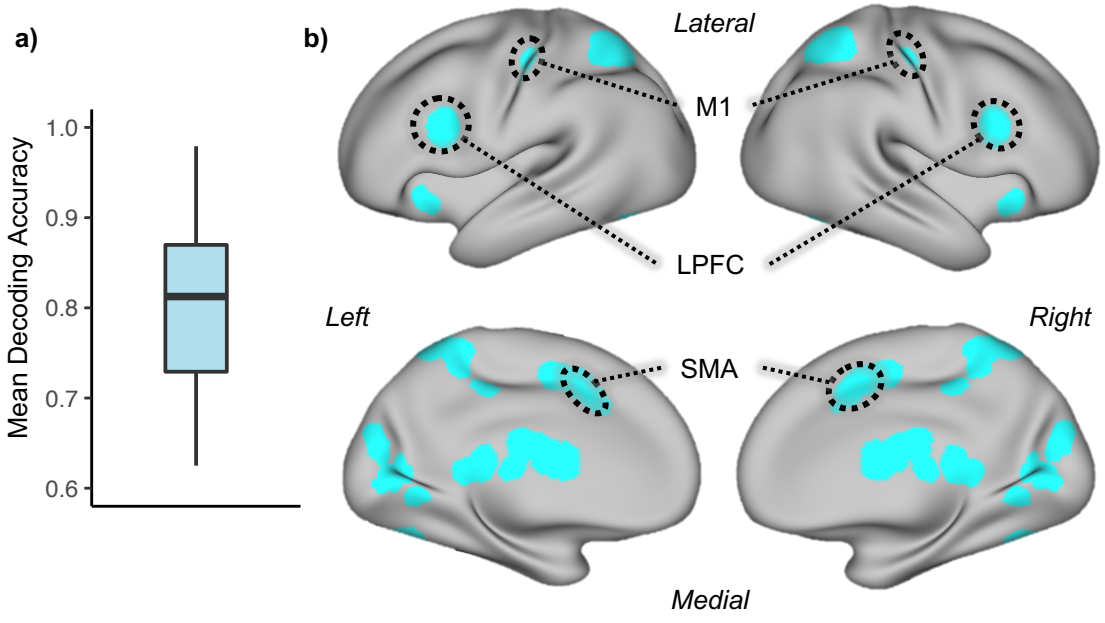
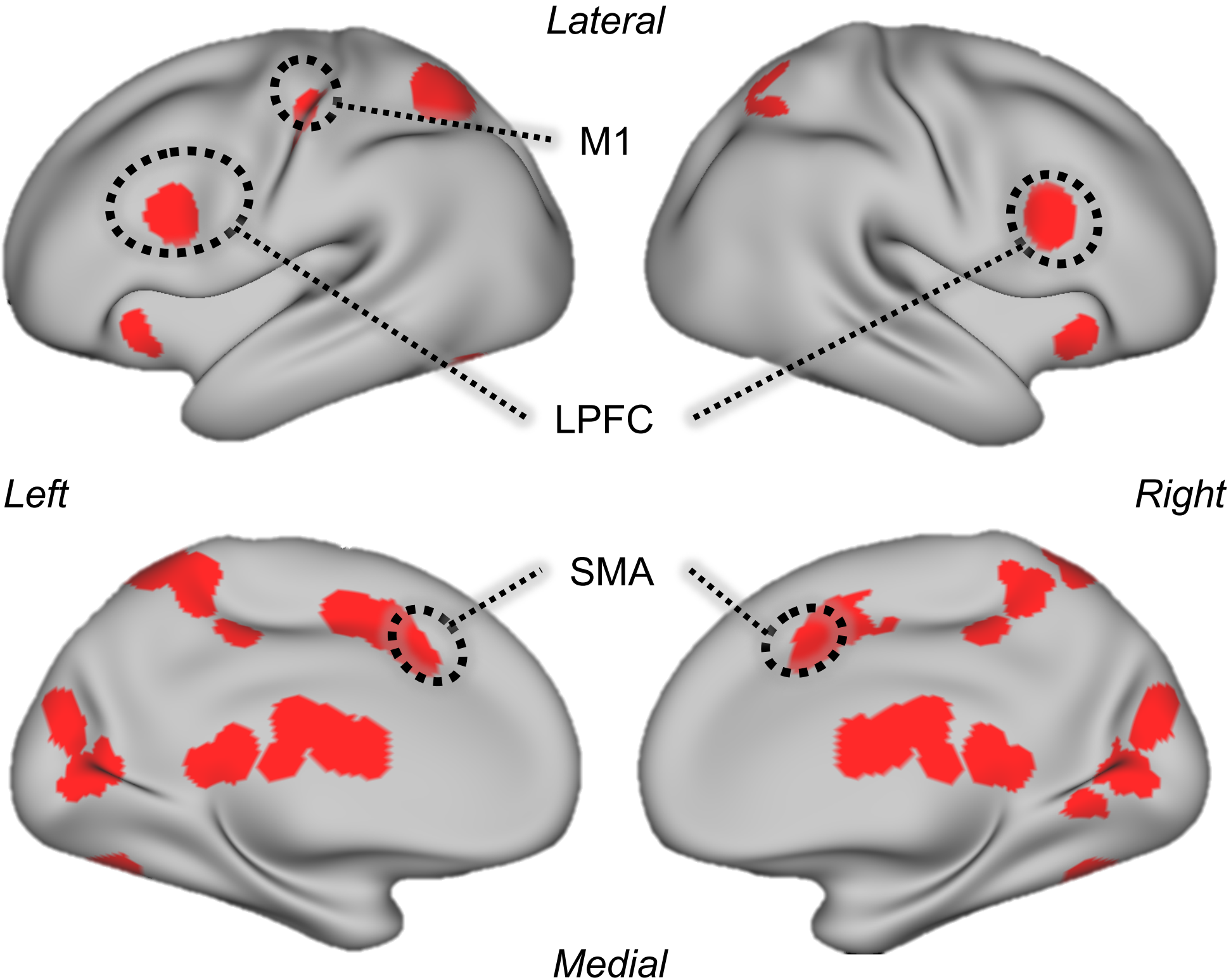

Sequence Identity Cue
$10
1.5 s
2-6 s
DSP Task Execution
Stimulus-Response
Mapping
Variable ITI
2-6 s

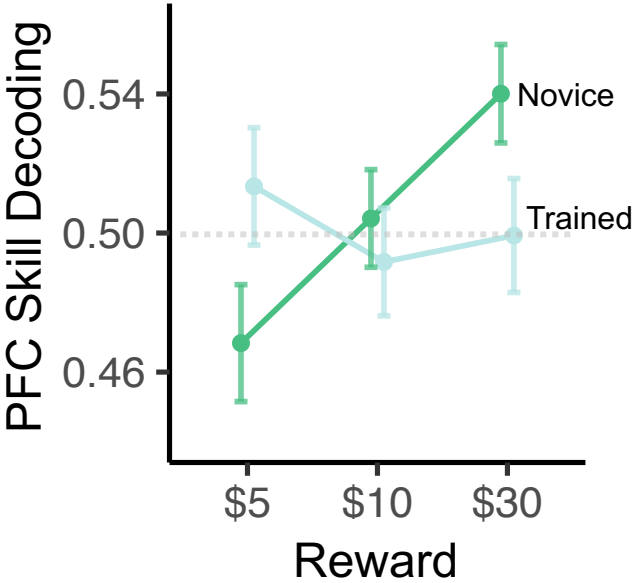

Skill Performance
0.50
0.45
0.40
0.35
Novice
Trained
$5
$10
$30
Reward
Posterior
H0
0.0
0.2
0.4
0.6
β_{reward}

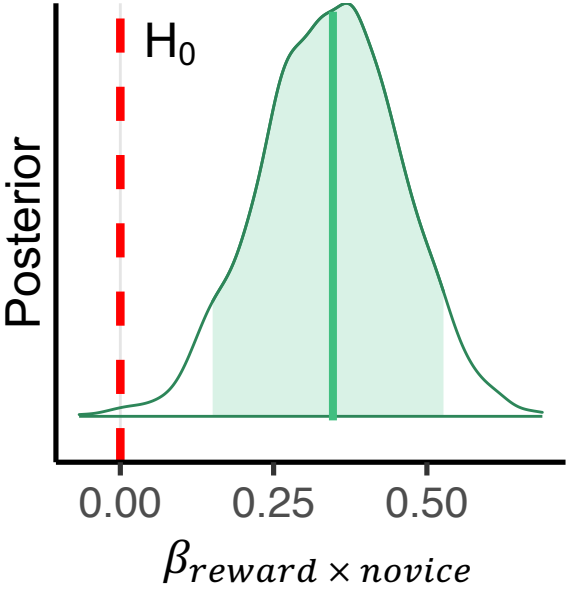

Lateral
M1
LPFC
Left
Right
SMA
Medial

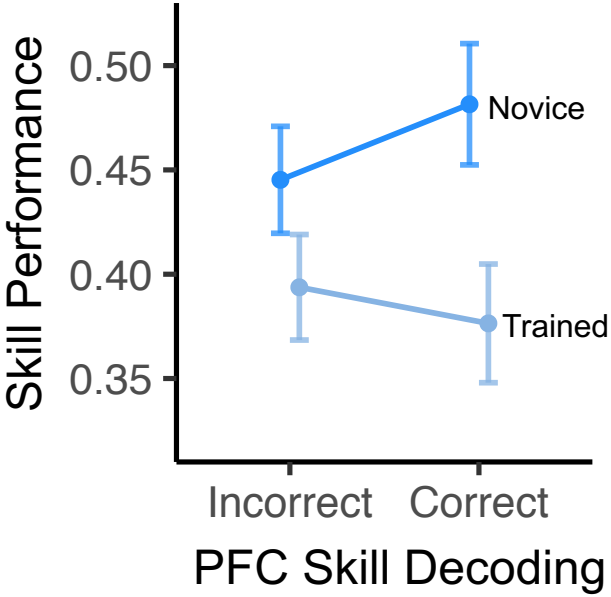

a)
Mean Decoding Accuracy
0.9
0.8
0.7
0.6
0.5
b)
Lateral
M1
LPFC
Left
Right
SMA
Medial

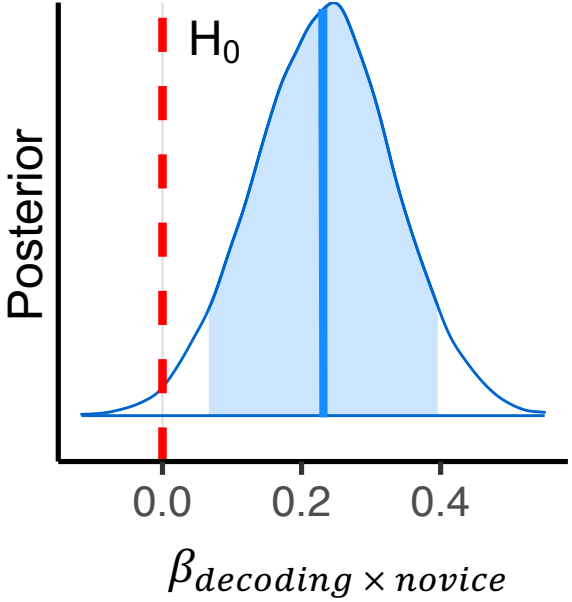

a)
Mean Decoding Accuracy
1.0
0.9
0.8
0.7
0.6
b)
Lateral
M1
LPFC
Left
Right
SMA
Medial


Lateral
M1
LPFC
Left
Right
SMA
Medial


PFC Skill Decoding
0.54
0.50
0.46
Novice
Trained
$5
$10
$30
Reward


H0
Posterior
0.00
0.25
0.50
$\beta_{reward \times novice}$


Skill Performance
0.50
0.45
0.40
0.35
Novice
Trained
Incorrect
Correct
PFC Skill Decoding


Posterior
H_0
0.0
0.2
0.4
$\beta_{decoding \times novice}$