Rule-based Task Switching in the Anterior Cingulate and Prefrontal Cortex

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Introduction

Cognitive flexibility allows us to change our response to the world given the situation. Selecting the appropriate response to an external stimulus requires prioritizing internal goals and resisting any responses not aligned with the current goal. We call these context-dependent, conditional stimulus-response mappings 'rules.'

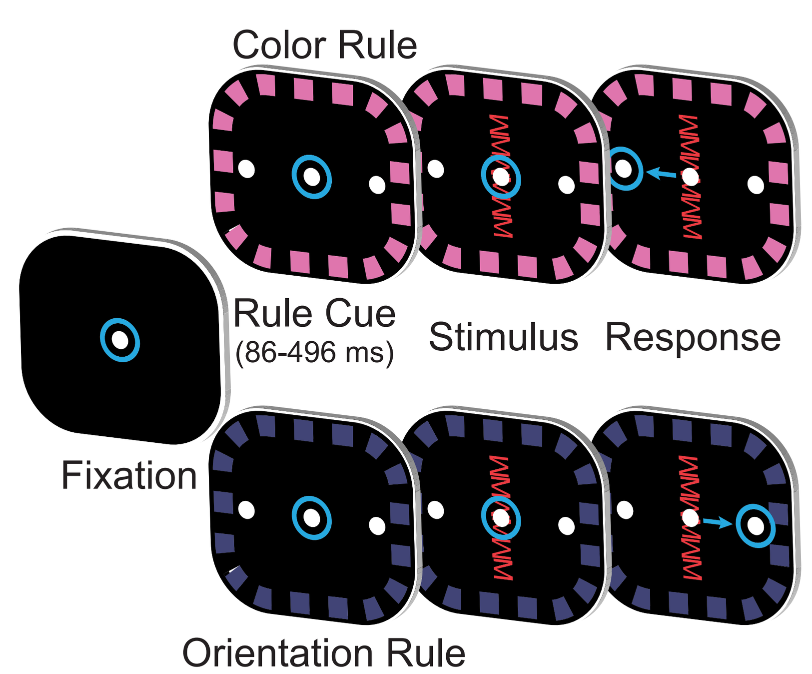
Humans show a remarkable ability to switch flexibly between these rules as situations and internal goals change. Functional imaging and lesion studies have identified the anterior cingulate cortex (ACC) and dorsolateral prefrontal cortex (PFC) as important to rule-based task switching in humans. Electrophysiology studies in non-human primates have also found neural correlates for rules and task switching separately in these regions. Here, we investigate the respective roles of the anterior cingulate and dorsolateral prefrontal cortex in rule-based task switching by simultaneously recording with multiple electrodes in non-human primates.

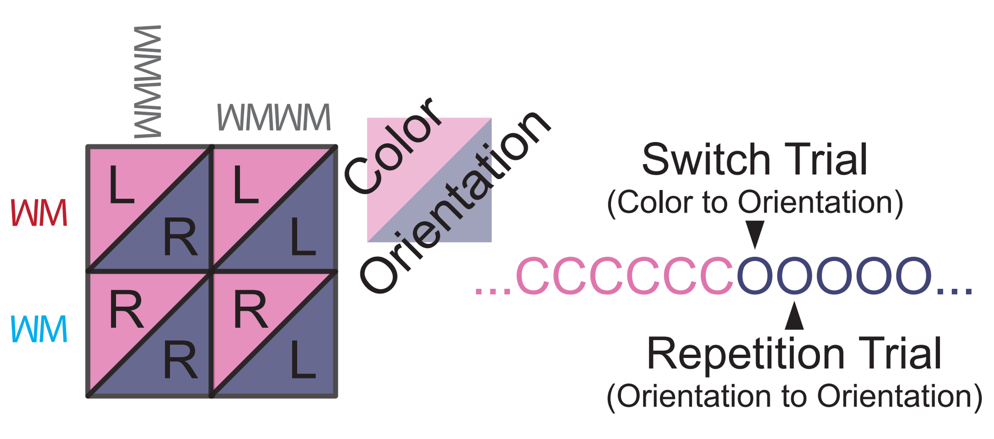
Cued Task Switching in Non-Human Primates

Two monkeys were trained on a cued task switching paradigm. The task began with the presentation of a fixation spot at the center of the screen. After acquiring fixation, a cue bordering the screen indicated one of two rules was in effect – **either discriminate color or orientation**.

The monkeys continued to fixate for a brief, randomized preparatory period until a test stimulus appeared at the center of the screen. Using the cued rule and the relevant feature of the test stimulus, the monkey saccaded to either the left or right response target to receive a juice reward.

For example, if the rule was color and the test stimulus red, the monkey made a leftward saccade. If the rule was orientation and the test stimulus vertical, the monkey made a rightward saccade.

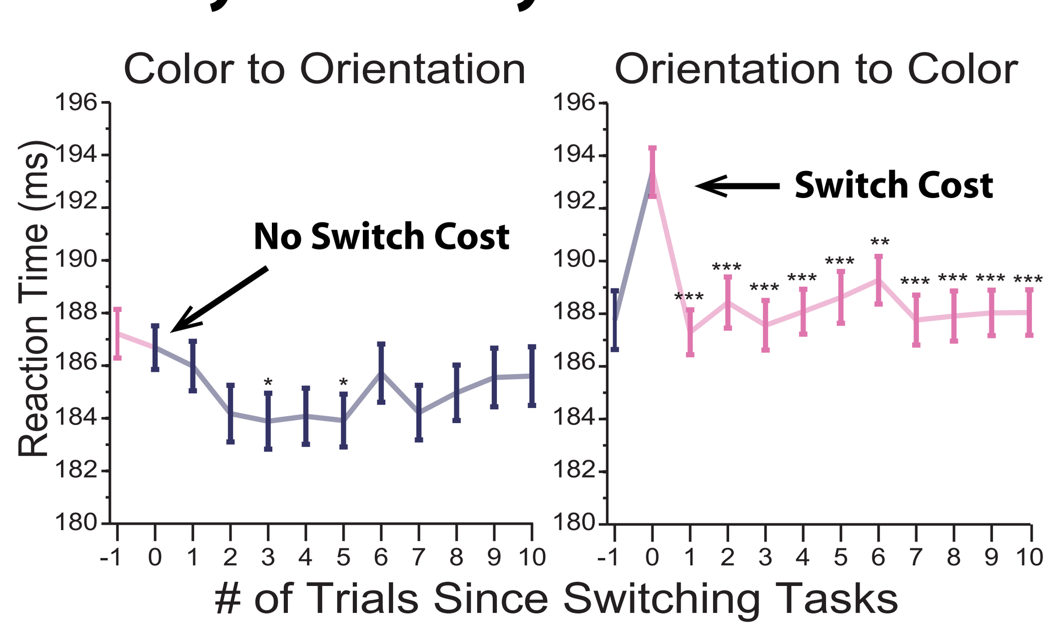




70% of the trials were incongruent – meaning the test stimulus indicated different responses without knowledge of the rule. This made sure the animal consistently applied the rule. The contingency table for all possible combinations of rule and test stimulus is pictured to the left.

Each rule was also repeated for at least 20 trials before a probabilistic switch to the other rule, ensuring the animal could not anticipate the rule switch.

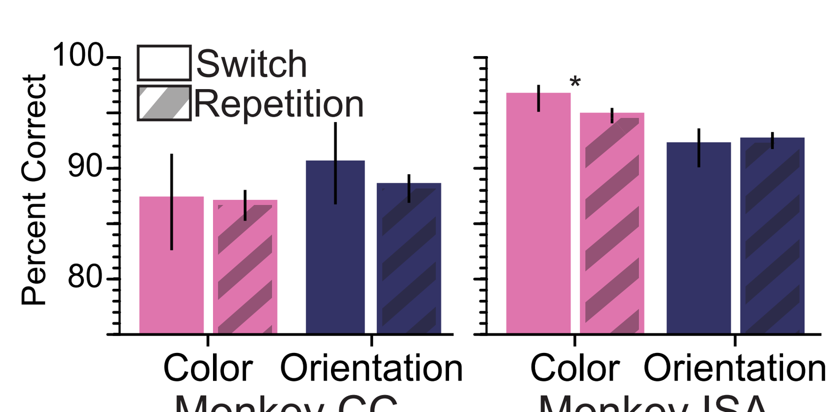
Monkeys show asymmetric switch cost



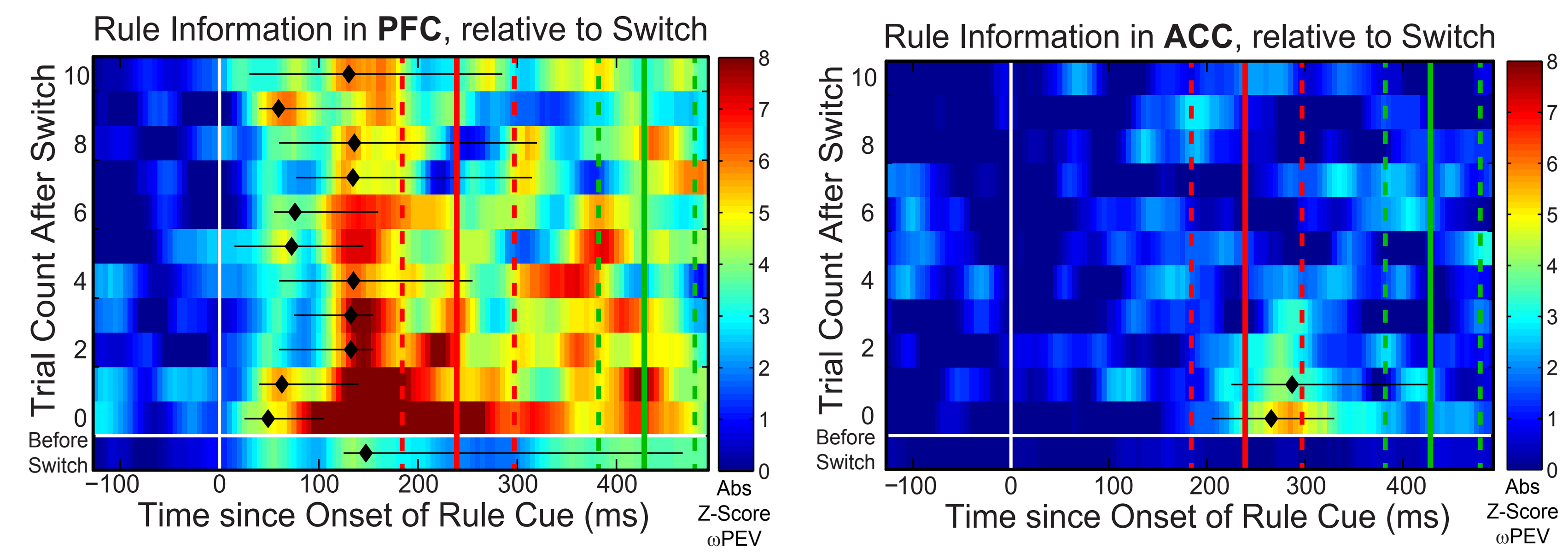
Monkeys were significantly slower when switching away from the orientation rule (into the color rule). In contrast, when switching into the orientation rule, no change in reaction time was observed.

This suggests that orientation was the dominant rule.

No significant difference in percentage of trials correct was observed for either rule. Furthermore, switching rules did not impact the animals' performance, suggesting they were able to effectively switch rules by slowing their response time.



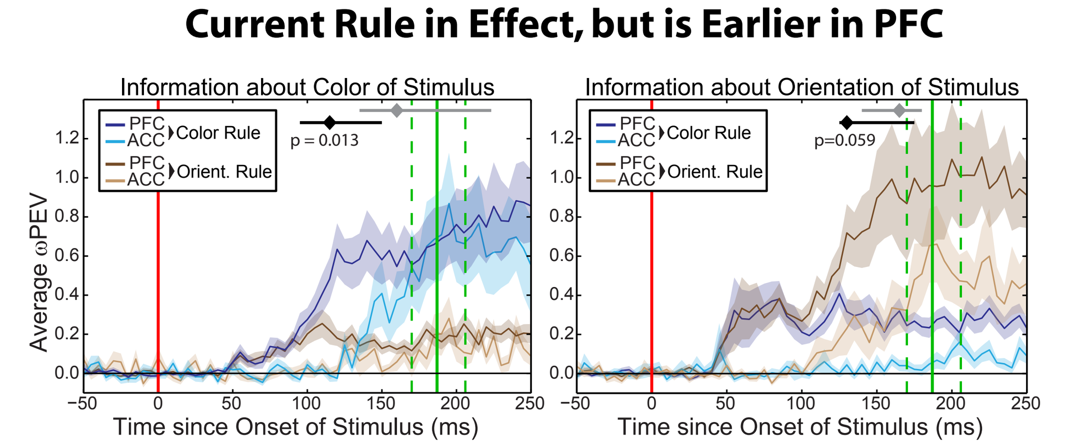
PFC Encodes Information Before ACC



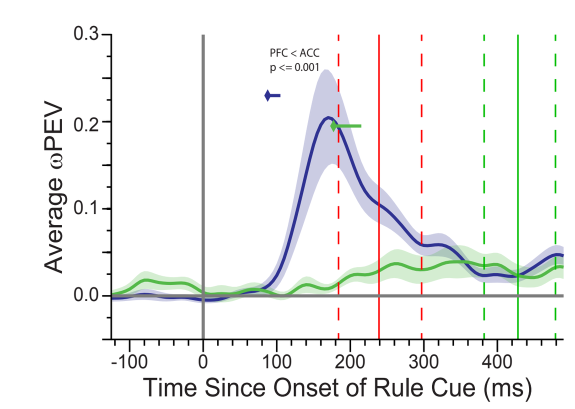
We recorded from 313 neurons in PFC and 262 neurons in ACC over 34 sessions. The task-related "information" was assessed by using a bias-corrected Percent Explained Variance statistic (ωPEV) – a measure of effect size indicating how much of the variance in a neuron's firing rate was explained by a particular task variable.

We found PFC carried rule-related information (average latency: 49 ms from rule cue onset) on **every trial** following the rule switch (pictured top left). However, ACC carried rule-related information **only around the time of stimulus onset** (average latency: 265 ms from rule cue onset) and **only one to two trials after the switch** (pictured top right).

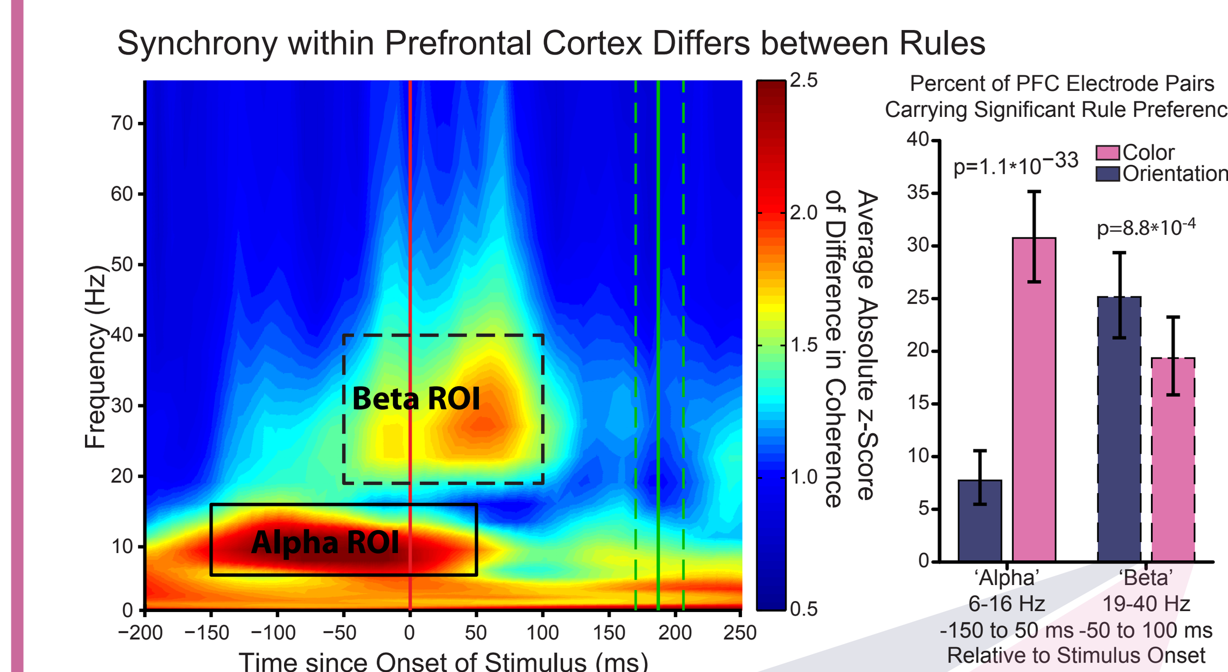
Stimulus-Information is Modulated in Both Regions by Current Rule in Effect, but is Earlier in PFC



PFC Encodes Rule-General Switch Signals before ACC



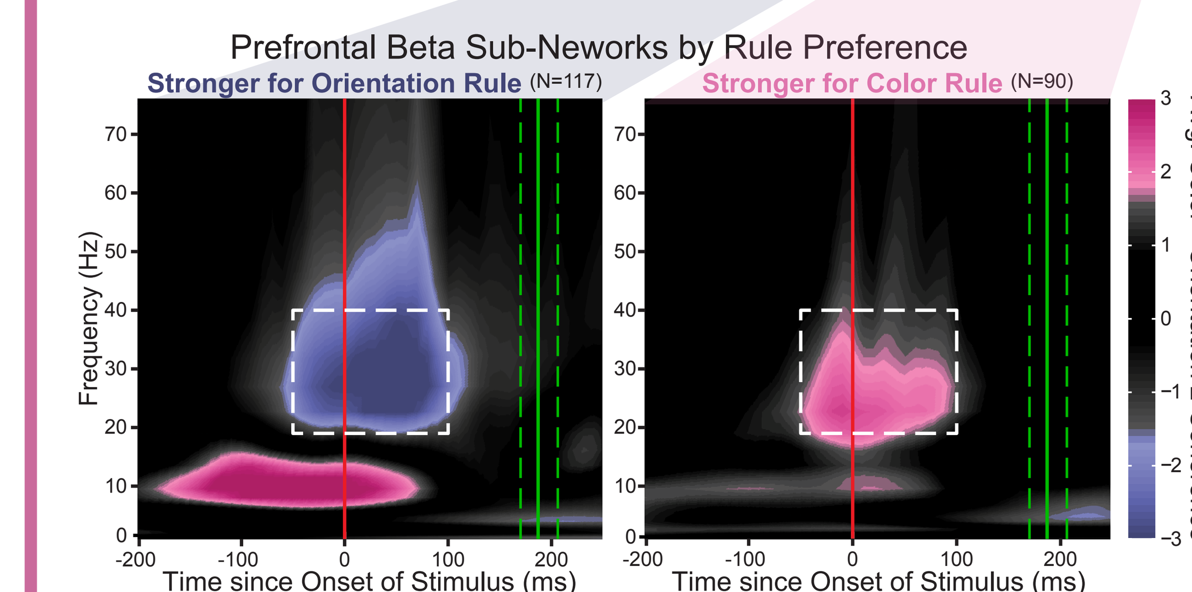
Sub-Networks within PFC Support Each Rule



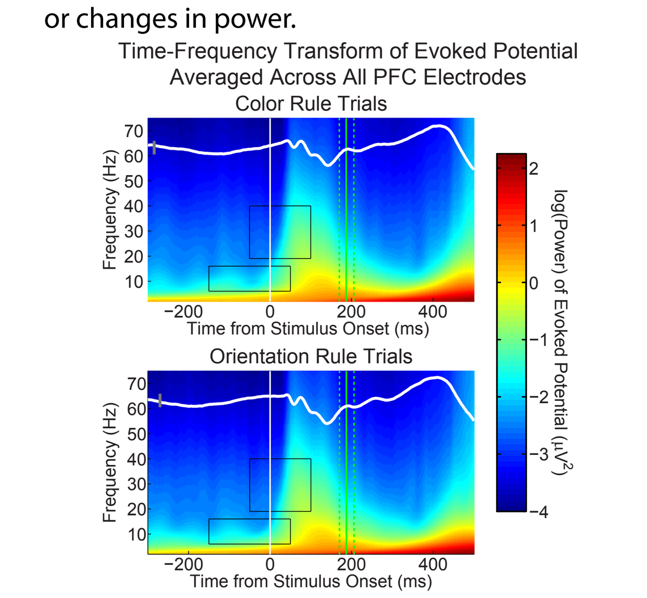
Local field potentials in PFC showed rule-selective changes in coherence in the 'alpha' (6-16 Hz) and 'beta' (19-40 Hz) bands, suggesting **changes in synchrony between local neural ensembles within PFC depending on the rule**. ACC showed no such changes.

Differences in alpha coherence followed the onset of the rule cue and primarily resulted from electrode pairs showing stronger synchronization during the color rule. In contrast, beta coherence differences occurred around the test stimulus presentation and resulted both from electrode pairs with greater synchronization during the orientation rule and from electrode pairs with greater synchronization during the color rule (beta sub-networks).

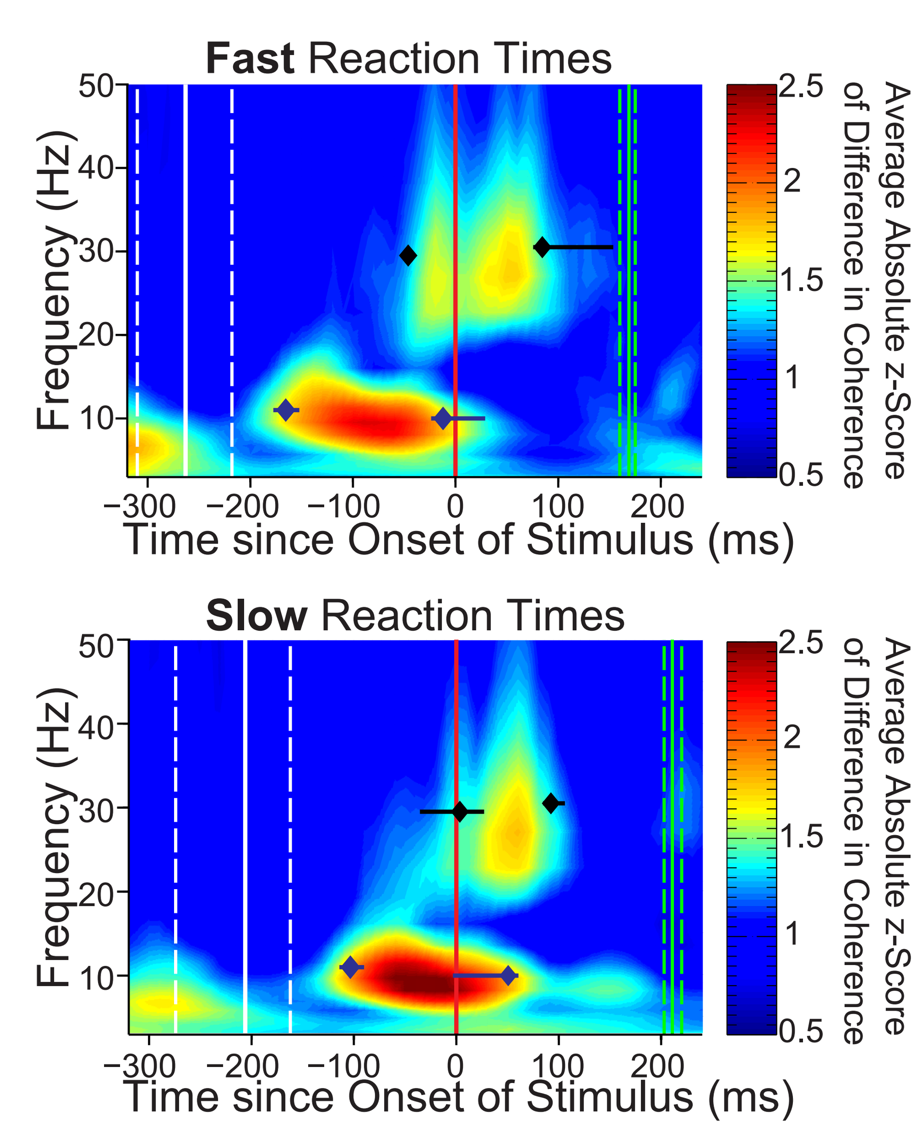
Interestingly, the electrode pairs that preferred the orientation rule during beta were also the electrode pairs that preferred the color rule during alpha (bottom left). **Since the alpha band is associated with inhibition and inattention, the alpha may reflect suppression of the dominant orientation beta sub-network during the color rule.**



Rule-selective differences in coherence were not due to differences in the evoked potential or changes in power.



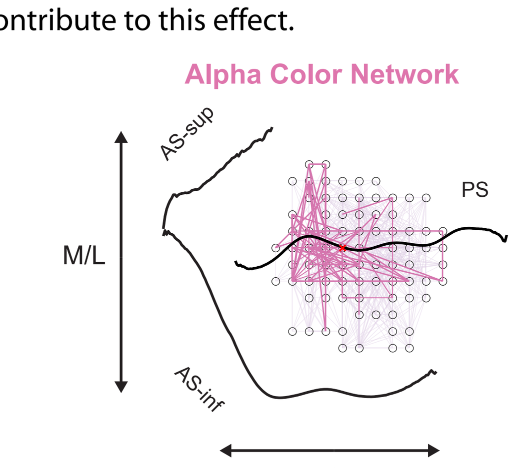
Synchrony in Rule Sub-Networks Correlates with Reaction Time and Topological Structure of Sub-Networks are Not Random



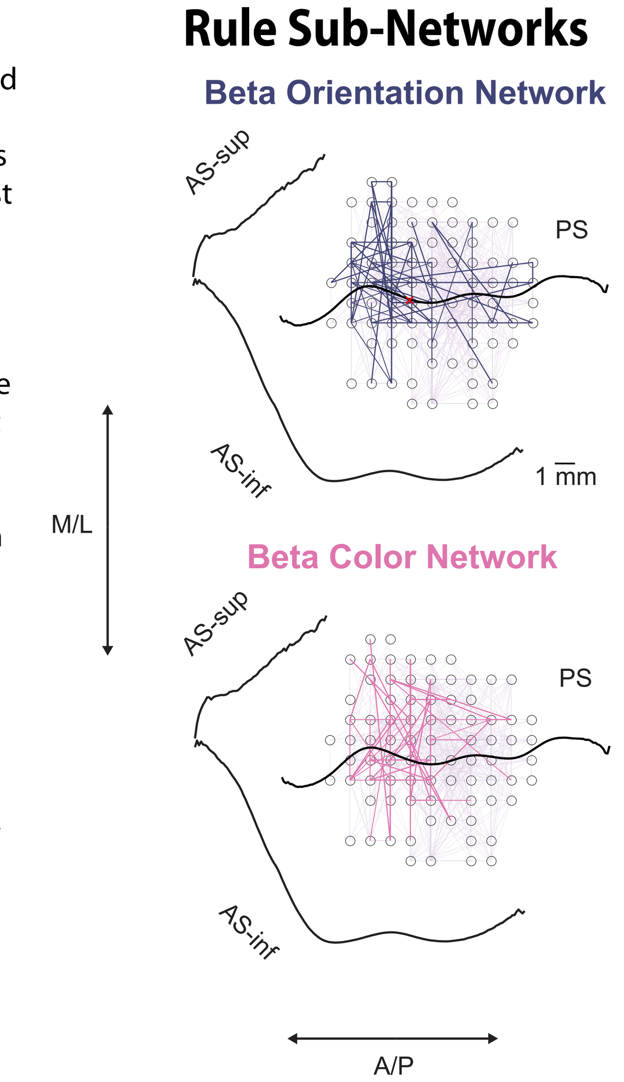
Trials in which the animals responded quickly showed earlier onset of alpha and beta coherence than trials in which the animals responded slowly (alpha: 166 ms and 104 ms before stimulus onset for fast and slow trials, beta: 46 ms before and 3 ms after stimulus onset).

Moreover, the alpha coherence ended later in trials where the animals' response was slower (12 ms before stimulus onset on fast trials, 51 ms after on slow trials).

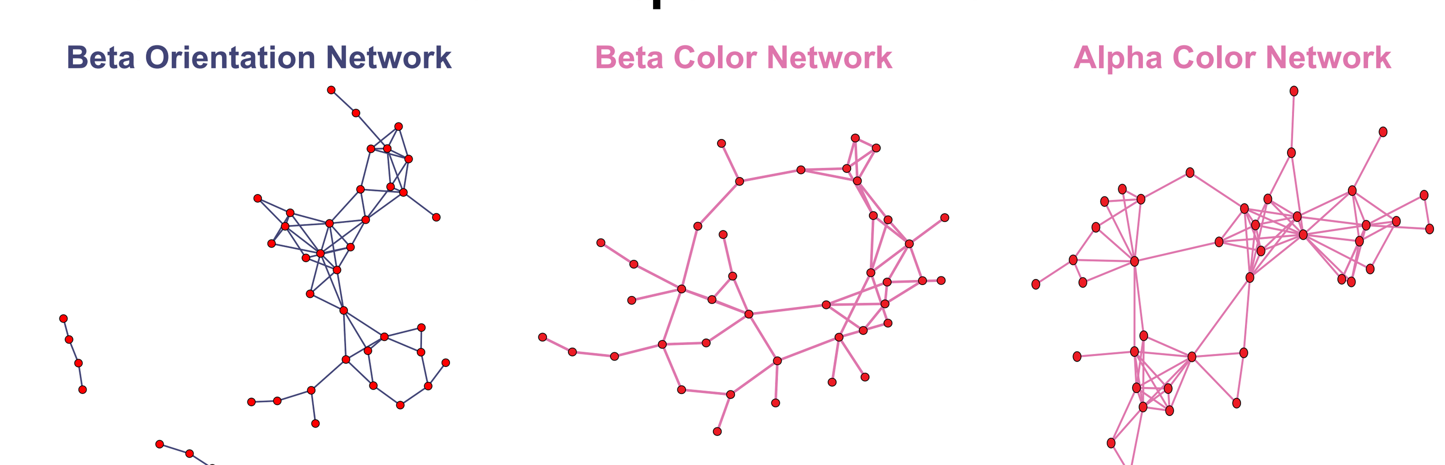
Faster reaction times are associated with longer preparatory periods, which may contribute to this effect.



Spatial Distribution of PFC Rule Sub-Networks



The structure of the rule-dependent sub-networks is not random



Prefrontal Rule Sub-Network Topology

Summary

1. Neurons in PFC, and not ACC, play a **leading role** in maintaining and switching between rules. ACC is only engaged around the time the stimulus is applied and only around the rule switch. This supports a model where ACC signals, and becomes involved in the task, during moments of rule conflict.
2. **Synchronous sub-networks** within PFC support each rule. These networks organized task-selective neural activity and correlate with behavior. This ability to dynamically bring together task-relevant neural activity may be key to behavioral flexibility. These results suggest a "push-pull" mechanism underlying cognitive competition whereby beta selects the relevant rule and alpha suppresses the dominant rule.