Figures and figure supplements

Cascade of neural processing orchestrates cognitive control in human frontal cortex

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Figure 1. Experimental task and behavioral performance. (A) Subjects were presented with one of three words (Red, Blue or Green); each word was randomly colored red, blue, or green. Trials were incongruent (I) when the word and color did not match, and were congruent (C) otherwise. The word-color combinations were counter-balanced and randomly interleaved. Subjects performed the Stroop task (name the color), and the Reading task (read the word) in separate blocks. (B) Distribution of z-scored behavioral reaction times (speech onset) across all subjects (n = 15) for congruent (black) or incongruent (brown) trials during the Stroop task. Bin size = 0.2. Dashed lines indicate average reaction times. (C) Distribution of z-scored reaction times during the Reading task. (D) Z-scored reaction time across subjects for different trial histories during the Stroop Task (cI: incongruent trial preceded by congruent trial; iI: incongruent trial preceded by incongruent trial; iC: congruent trial preceded by incongruent trial; cC: congruent trial preceded by congruent trial). Error bars indicate s.e.m.

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The following source data is available for figure 1:

Source data 1. Behavioral data.
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Figure 1—figure supplement 1. Behavioral data for each subject. (A-B) Percent correct for each subject for the Stroop task (A) or Reading task (B) during congruent (black) or incongruent (brown) trials. Subjects made more errors for incongruent trials compared to congruent trials during the Stroop task ($P < 0.001$, signed-rank test). One subject (Subject 6) did not participate in the Reading task. (C-D) Average behavioral reaction time (speech onset) for each subject for the Stroop task (C) or Reading task (D). Error bars indicate s.e.m. Subjects had delayed responses for incongruent trials compared to congruent trials during the Stroop task ($P < 0.001$, signed-rank test).

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**Figure 2.** Example electrode in left Anterior Cingulate Cortex.  
(A) Average gamma power signals aligned to the stimulus onset from an electrode during the Stroop task, for congruent (black) or incongruent (brown) stimuli. For display purposes only, we z-scored the gamma power by subtracting the average and dividing by the standard deviation of power during the baseline period (500 ms prior to stimulus onset). Shaded areas indicate s.e.m. The total number of trials for each condition is indicated in the upper right. (B) Single-trial data for congruent (left) and incongruent (right) trials. Each row is a trial, and the color indicates the z-scored gamma power (color scale on upper right). Trials are sorted by behavioral response time (black line).  
(C) Same as (A), but showing data from the Reading task. (D-F) Same as in A-C, but aligning the data to behavioral response time. Gamma power was better aligned to the behavioral response, and was stronger for incongruent compared to congruent trials. The dashed line indicates the response-aligned latency, defined as the first time point at which incongruent and congruent trials can be discriminated.  
(G) Signals elicited by each of the 9 possible stimulus combinations.  
(H) There was a correlation between the maximal z-scored gamma power and behavioral reaction times during incongruent trials (Pearson correlation coefficient = 0.25, P = 0.02, permutation test). Each point in this plot represents a single trial.

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The following source data is available for figure 2:

**Source data 1.** Conflict-selective electrode data.

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Figure 2—figure supplement 1. Example conflict-selective electrode in the right dorsolateral Prefrontal Cortex. Here we show a different conflict selective electrode, located in the dlPFC (format as in Figure 2).

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Figure 2—figure supplement 2. Example conflict-selective electrode in the Orbitofrontal Cortex comparing responses in the Theta and Gamma Bands. (A-F) Responses in the theta power frequency band, z-scored. Same format as Figure 2—figure supplement 1. (G-L) Responses in the gamma power frequency band, z-scored. Same format as Figure 2—figure supplement 1.

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Figure 3. Electrode locations. (A) Location of conflict-selective electrodes (black/gray) shown on a reference brain, with each region colored (Materials and methods). Electrodes from the right hemisphere were mapped to the left hemisphere for display purposes. For more detail, see Supplementary file 2. (B) Percent of total electrodes in each region that were selective for conflict. Chance levels were computed using a permutation test (black line). The number of observed electrodes was significantly above chance for all regions ($P < 0.01$, permutation test, Materials and methods).

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The following source data is available for figure 3:

Source data 1. Population gamma-power data.
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Figure 4. Gamma power in frontal cortex correlates with behavior. (A) Distribution of gamma power log-ratio (Incongruent/Concurrent) for the Stroop task (blue) and Reading task (green). Bin size = 0.05. Gamma power showed a significant interaction between Congruency and Task ($P = 0.002$, multilevel model, Materials and methods). Power was larger for incongruent versus congruent trials during the Stroop task ($P < 0.001$, $n = 51$ frontal cortex electrodes) but not during the Reading task ($green$, $P = 0.56$). The statistical analyses directly compare the gamma power, we show the log-ratios here for display purposes only. (B) Normalized gamma power log-ratio averaged across electrodes from each of the four different frontal cortex regions during the Stroop task. We divided the power during incongruent trials by the power during congruent trials, then computed the log and finally averaged across electrodes. Data are aligned to the behavioral response onset ($t=0$). (C) Distribution of Pearson correlation coefficients between the maximal gamma power and behavioral reaction time during incongruent trials for $n = 51$ frontal cortex electrodes. These correlations were significantly positive ($P < 10^{-5}$, sign-rank test). Bin size = 0.1. (D) For incongruent trials, there was a significant interaction between trial history and task ($P = 0.03$, multilevel model). Gamma power was larger for incongruent trials preceded by congruent trials (cl) compared to incongruent trials preceded by incongruent trials (ii), particularly during the Stroop task (blue, $P = 0.001$), compared to the Reading task (green, $P = 0.72$). Data beyond the range of the x-axis are shown in the first or last bins. (E) For congruent trials, there was no interaction between trial history and task ($P = 0.17$, multilevel model). Gamma power was similar in congruent trials preceded by incongruent trials (iC) compared to congruent trials preceded by congruent trials (cC) during the Stroop task (blue, $P = 0.16$) and during the Reading task (green, $P = 0.19$).

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The following source data is available for figure 4:

Source data 1. Population gamma-power data.
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### Figure 4—figure supplement 1

Theta and Beta band population results. (A) Distribution of theta power log-ratio (Incongruent/Congruent) for the Stroop task (blue) and Reading task (green). Bin size = 0.05. *P* values in black denote interaction statistics whereas *P* values in blue and green denote the statistics for the Stroop and Reading tasks respectively. As discussed in Figure 4, the average log-ratios are presented here for display purposes only and the statistical tests are based on the raw power values. (B) Distribution of the gamma power log-ratio between incongruent trials preceded by congruent trials (cI) compared to incongruent trials preceded by incongruent trials (iI). (C) Distribution of the gamma power log-ratio between congruent trials preceded by incongruent trials (iC) compared to congruent trials preceded by congruent trials (cC). (D-F) Same as (A-C), but for power in the beta band.

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Figure 4—figure supplement 2. Cross-frequency coupling analyses. For the anterior cingulate cortex electrode in Figure 2: (A) Phase-amplitude distribution during the Stroop task for the example electrode shown in Figure 2 (see Materials and methods for calculation of cross-frequency coupling). (B) The observed Modulation Index (MI, black arrow) is significantly greater than the surrogate distribution generated by adding a lag between the phase and amplitude measurements, demonstrating that the amplitude of the gamma band is strongly coupled to the phase of the theta band. (C) During the Stroop task, the difference in Modulation Index between congruent and incongruent trials (black arrow) was not significantly different from 0 (\(P = 0.61\)). The null distribution (gray bars) was generated by randomly permuting the congruent and incongruent labels. Across the population of electrodes: (D) The percent of total electrodes in each region (Frontal cortex or non-frontal cortex) that had significant phase-amplitude coupling. Shown on the right is the percentage of the \(n = 51\) conflict selective electrodes that showed significant coupling. (E) The MI of congruent compared to incongruent trials for all Frontal cortex electrodes (gray dots) and the subset that were conflict-selective in the gamma band (blue dots). For both groups, there was no significant difference in the MI between congruent and incongruent trials (Frontal Cortex, \(P = 0.45\); Conflict-selective, \(P = 0.52\); signed-rank test). For this comparison, the number of congruent and incongruent trials was equalized before computing the MI.

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Figure 4—figure supplement 3. Stimulus-aligned population averages. Same as in Figure 4B, but data are aligned to the stimulus response onset (t=0).
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Figure 5. Responses during self-corrected error trials. (A) An example self-correction trial from the ACC electrode in Figure 2 when the word Green colored in red was presented. The single trial gamma power is shown on top, with the speech waveform below. The dashed lines indicate the onset of the initially incorrect response (‘green’) and the following corrected response in bold (‘no – red’). Note the increased gamma power after an error response. (B) Average gamma power aligned to the onset of the initial error response (blue) and the onset of the corrected response (black) for n = 11 self-correction trials. Shaded areas indicate s.e.m. The post-response power was significantly greater after the error (P = 0.001, signed-rank test). (C-D) Same as (A-B) for another example electrode in the dorsolateral prefrontal cortex. The post-response power was significantly greater after the error response (P = 0.002, signed-rank test). (E) Across the n = 7 electrodes with n = 10 or greater self-correction trials, the z-scored gamma power during the initial error response was larger than during the corrected response. Electrodes with significant differences (P < 0.05, signed-rank test) are colored black. Letters mark the examples in (A) and (C).

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The following source data is available for figure 5:

Source data 1. Data for self-correcting trials.

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Figure 6. Latency Comparisons across regions. Latency differences between different regions computed from all pairs of simultaneously recorded electrodes. \( n_p \) denotes the number of electrode pairs. Because we only consider simultaneously recorded electrodes here, not all the electrodes modulated by conflict can be paired with any other electrode. Supplementary file 3 shows the number of electrodes modulated by conflict in each area and subject. There was only one electrode pair between ACC and OFC and therefore we do not show the latency difference between these two regions here. Significant latency differences (\( P < 0.05 \), permutation test, Materials and methods) are shown in black, and non-significant differences in gray. ACC leads both mFC (\( P = 0.001 \)) and dIPFC (\( P = 0.02 \)), with OFC following dIPFC (\( P = 0.009 \)).

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The following source data is available for figure 6:

Source data 1. Data for region latency comparisons.
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