Dissociating the Neural Correlates of Planning and Executing Hierarchical Task Sets

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Abstract

Task processing and task representation, two facets of cognitive control, are both supported by lateral frontal cortex (LFC). However, processing and representation have largely been investigated separately, so it is unknown if they are distinguishable aspects of control or if they are complementary descriptions of the same mechanism. Here, we explored this by combining a hierarchical task mapping with a pre-cueing procedure. Participants made match/non-match judgments on features of pairs of stimuli. Cues presented at the start of each trial indicated the judgment domain (spatial/non-spatial), the response hand, both, or neither, giving variable amounts of information to the subject at each time point in the trial. Our results demonstrated that regions throughout LFC supported task processing, indicated by an influence of time point on their BOLD activity levels. A subset of regions in left caudal LFC also supported task representation, indicated by an interaction between time point and cue information; we termed this subgroup the "CuexTime" group. This interaction effect was not seen in the remaining LFC regions, which only showed a main effect of time consistent with involvement in task processing; we termed this subgroup the "Time" group. These results suggest that task representation is one component of task processing, confined to the "CuexTime group" in left caudal LFC, while other regions in our task support other aspects of task processing. We further conducted an exploratory investigation of connectivity between regions in the "CuexTime" and "Time" groups and their potential relationship to networks that support distinct cognitive control functions.

Dissociating the neural correlates of planning and execution in hierarchical task sets

Cognitive control refers to the set of psychological processes and representations that allow us to formulate goals based on our current internal mental state and to use those goals to guide our perception of and interactions with the external world. Two intertwining aspects of cognitive control are our capacity to 1) rapidly and flexibly construct a mental representation of a given task, i.e., task representation; and 2) to use information in the environment to prepare for and execute that task, i.e., task processing. While both of these facets of cognitive control are known to be supported in part by regions in the lateral frontal cortex (LFC; Badre & D'Esposito, 2009; Schumacher et al., 2007; Waskom & Wagner, 2017), their literatures are largely separate. Research on task processing has shown that we can use partial information about a task to select and prepare a subset of that task a priori, which is supported by LFC regions that are largely distinct from those involved in executing the response (Cookson et al., 2016; Dixon et al., 2014). In parallel, research on the representation of tasks has revealed that we represent tasks with a multi-level hierarchical structure, and that distinct LFC regions organized along a rostrocaudal axis represent progressively more abstract levels of the task within this hierarchy (Badre, 2008; Koechlin & Summerfield, 2007). Here, we present a novel task that aims to investigate the LFC correlates of preparation and execution, two components of task processing, at distinct levels of hierarchical abstraction, a key facet of task representation.

There is a long and broad history of research on task processing on both its psychological and neurological mechanisms. A common procedure for investigating task processing is the cueing procedure, which presents information about a task sequentially at two different times that can be statistically separated by way of a variable delay period. This separation in time allows researchers to distinguish the processes that select and prepare a response from those involved in executing that response. Early work with the cueing paradigm demonstrated that participants could prepare subsets of motor responses prior to having full knowledge of the required response, which resulted in a response time (RT) benefit for

informative relative to uninformative cues (Adam et al., 2003; Miller, 1982, 1985; Reeve & Proctor, 1984). The cumulative results of this work clearly indicate that preparation and execution encompass distinct and dissociable components of task processing.

Hopfinger, Buonocore, and Mangun (2000) used event-related functional magnetic resonance imaging (fMRI) to investigate whether these processes had similarly distinct neural bases. On each trial of the task, the authors presented a directional followed by a pair of horizontally aligned checkerboard stimuli. Participants then made a discrimination decision on the checkerboard presented on the cued side. The results showed marked differences in the activation patterns between the preparation and execution phases of the experiment. This distinction was especially apparent in LFC, where preparation showed widespread left-lateralized frontal activation in superior and middle frontal gyri, while execution showed a more constrained left-lateralized activation of inferior frontal gyrus coupled with bilateral activation of the motor cortices.

Beyond simple distinctions between preparation and execution, research using the cueing procedure further aimed to understand the nature of the cue benefit itself. Rosenbaum (1980) first demonstrated that the magnitude of the behavioral benefit afforded by a cue was dependent on the number of distinct pieces of information given about the upcoming response, independent of the type of information given. Participants were instructed to make movements specified by three independent dimensions: hand (left/right), direction (toward/away from the body), and extent (short/long). They were then presented a cue on each trial that could indicate one, two, all three, or none of the values of the upcoming movement along these three dimensions. The RTs showed a main effect of the number of dimensions remaining to be specified at the time of stimulus presentation. That is, participants responded faster the more dimensions that were cued prior to the time of response. This suggested that participants made use of the cues to prepare sets of potential movements given whatever partial information they received about the upcoming response.

Deiber and colleagues (1996) reported one of the earliest studies of the neural correlates of this cueing benefit. They recorded PET images while participants conducted a variation of Rosenbaum's (1980) finger extension task. To maximize the rCBF signal, the authors reduced the task to two-dimensions, having participants make large movements on all trials. They therefore could present cues for the upcoming movement that gave no information, one dimension (partial information), or both (full information). Their behavioral results recapitulated Rosenbaum's finding a stepwise increase in RT the number of dimensions specified at the cue increased. The authors further indicated that this cueing benefit was associated with left lateralized activity in the premotor cortex of LFC, as well as activity in the sensorimotor cortices and the supplementary motor area. While they did not find differences in rCBF as a function of the level of information provided, the use of PET necessitated that the authors collapse across preparation and action, which could have obscured phasic differences in activation between the cue and the stimulus.

Though interest in the cue benefit originated from research on task processing, it has since become a cornerstone of the task representation literature. The idea that participants can select between subsets of stimulus-response associations, and even subsets of subsets, is formalized in the task file hypothesis, which proposes that task processing is guided and bounded by the structure of our internal representation of a task’s structure. An extension of the event file hypothesis (Hommel, 2004), The task file hypothesis posits that tasks are represented as hierarchical associations of stimuli, responses, task contexts, and other goal-related factors (Schumacher & Hazeltine, 2016). These task files are highly flexible, allowing stimulus-response associations to be rapidly grouped together into meaningful subsets bound to distinct contextual triggers according to current task context and selected between on demand. These set-context representations are referred to as "task sets" (Sakai, 2008). Task sets can be further extrapolated to increasingly abstracted structures that add hierarchically nested layers of additional context associations, allowing for the selection between entire task sets as a whole.

As in motor cueing experiments, participants can benefit from cue information that allows them to select between task sets based on current contextual information when the task structure encourages participants to form subgroupings within the task (Adam et al., 2003). Recent work from our group has demonstrated a benefit of cue information that is specific to task structure (Cookson et al., 2019). In this design, participants learned stimulus-response mappings that either segregated different stimulus categories to different hands ("Separated") or interleaved them across the fingers ("Interleaved"). the group that learned the Separated mapping showed a larger benefit of cue information than the group that learned an Interleaved mapping, suggesting a benefit of preparing a coherent task set above and beyond the benefit of information that simply restricted the total number of potential stimulus-response options. In other words, there appear to be distinct selection mechanisms operating at different levels of a task's representational hierarchy.

Work on understanding how hierarchical task set representations support and bound task processing has remained largely behavioral thus far. However, investigations of the role of LFC regions in cognitive control outside of the task set literature suggest that the division of task representations in the brain follows a similarly hierarchical structure (Badre, 2008). The areas of activation seen in these studies are strongly left-lateralized and are connected to one another along a rostrocaudal axis (Badre & D'Esposito, 2007; Koechlin & Summerfield, 2007). These regions are organized in a functional hierarchy, such that mid-LFC regions have outbound influence on the activity of both more rostral and more caudal regions (Nee & D'Esposito, 2016). These regions appear to be distinguished by the level of abstraction at which they represent a given task. Caudal areas represent the task-relevant, concrete associations between stimuli and responses; mid-frontal areas represent context-dependent rules; and rostral areas maintain schema that organize and contextualize the set of potential task rules and action sequences that apply to the task (Badre & Nee, 2018).

Studies relating LFC regions to different levels of task abstraction often use tasks that manipulate the number of levels in a pseudo-hierarchical response mapping structure. Badre and D'Esposito (2007; see also Koechlin & Summerfield, 2007 for an alternative hypothesis with similar design and results) reported one such task that distinguished between four levels of abstraction. At the lowest level, participants selected responses to presented stimuli (colored squares) based on a learned mapping. The next level used cue-dependent responses, in which participants might have to respond to one of a number of potential target features based on the cue presented (e.g., respond to the texture of a target when the cue color was red or to its orientation when the cue color was blue). At the third level, participants were shown pairs of stimuli and instructed to make match/non-match decisions on the feature dimension indicated by the cue, rather than making a response based on the value of the feature itself. For example, participants might have to decide if the textures of two stimuli were the same when the cue color was red, and if they were at the same orientation angle when the cue color is blue. Finally, the fourth level implemented the same third level task, but with block-level switching of the mappings between cues and dimensions. At each level of abstraction, then, the design added another layer of contingencies that had to be resolved in order to correctly execute the task. Functional magnetic resonance imaging (fMRI) recordings taken during the execution of this task demonstrated progressively more rostral activation in LFC for tasks at higher levels of abstraction.

The multiple layers of contingencies used in the task above are highly reminiscent of the hierarchical task set structures described in the task file hypothesis (Schumacher & Hazeltine, 2016). However, because imaging studies investigating the frontal organization of cognitive control have mainly relied on trial-related or mixed-block designs, little is known about how preparation and execution may be instantiated in the brain across distinct levels of representation. Conversely, imaging studies investigating task preparation and execution are limited and have mainly relied on simple stimulus and motor cues rather than the abstract cues

that are used in hierarchical task set cueing. In another study from our group (Cookson et al., 2016), we explored the neural correlates of preparation and execution for cued and uncued task sets using the same "Separated" mapping task in the experiment above and presenting cues that either gave information about the upcoming stimulus category or response hand ("informative") or neither ("noninformative"). In this way, when participants were given an informative cue, it indicated one set or the other for the upcoming stimulus; the noninformative cue, on the other hand, would indicate that either set could be relevant. Importantly, the cue did not allow participants to select a specific response; nonetheless, fMRI data recorded during the presentation of the cue showed greater LFC activity to informative cues of both types relative to noninformative cues, suggesting that participants prepared the individual task sets at the cue when possible. Alternatively, this may have also been an indication that participants were processing the information contained in the cue. Because this design only included one level of informative cues, it is still not clear how cue-related preparation and subsequent execution may be instantiated in the brain for more complex task hierarchies.

More generally, it is unknown the extent to which task representation and processing may be two sides of the same coin versus distinct entities in regard to their instantiation in the brain. If distinct brain regions support distinct psychological functions of task processing and representation, two distinct subsets of task-related regions should emerge, one that shows general differences in activation between the cue and stimulus time point, and one that shows time-independent sensitivity to cue information. This may emerge as a distinction between cue-sensitivity in the LFC regions previously identified by policy abstraction studies and time sensitivity in other task-related regions, such as motor cortex and SMA. On the other hand, task representations may be the static scaffolding on which time-dependent processing takes place. In this hypothesis, distinct LFC regions along the rostrocaudal axis may show sensitivity to cue information that is further dependent on time. The specific patterns of this interaction along the

rostrocaudal axis would then further provide evidence for potential mechanisms by which these two facets of cognitive control relate in the brain.

Here, we present a novel task that blends a cueing paradigm with a hierarchical response mapping structure to investigate the neural correlates of preparation and execution for multiple levels of task representation, illustrated in Figure 1. During the experiment, participants were presented with pairs of simple stimuli and instructed to make a match/non-match judgment on one of four possible dimensions of the two stimuli. The judgment domains could be categorized into two groups: two of the judgment dimensions related to spatial features of the stimuli, and two to object identity (i.e., non-spatial) features. Each judgment dimension was associated with a two-choice response mapping. The responses for one judgment dimension from each domain (i.e., spatial and non-spatial) were mapped to each hand, where each possible response was mapped to a different response finger. At the start of each trial, a cue was presented that gave participants information about either the upcoming domain of the relevant judgment dimension, the hand with which participants would make their response, both, or neither. Because judgment domain and response hand were crossed in this design, information about either could not be used to determine the other, though each would allow participants to prepare a subset of half the task structure; however, information about both would implicitly specify the judgment dimension for the upcoming trial. This allowed us to explore preparation versus execution in three levels of cue information. Notably, no combination of cues gave full information about the upcoming response, which means that any interaction between the level of cue information and activity at the cue and stimulus time points would be specific to task preparation rather than motor preparation.

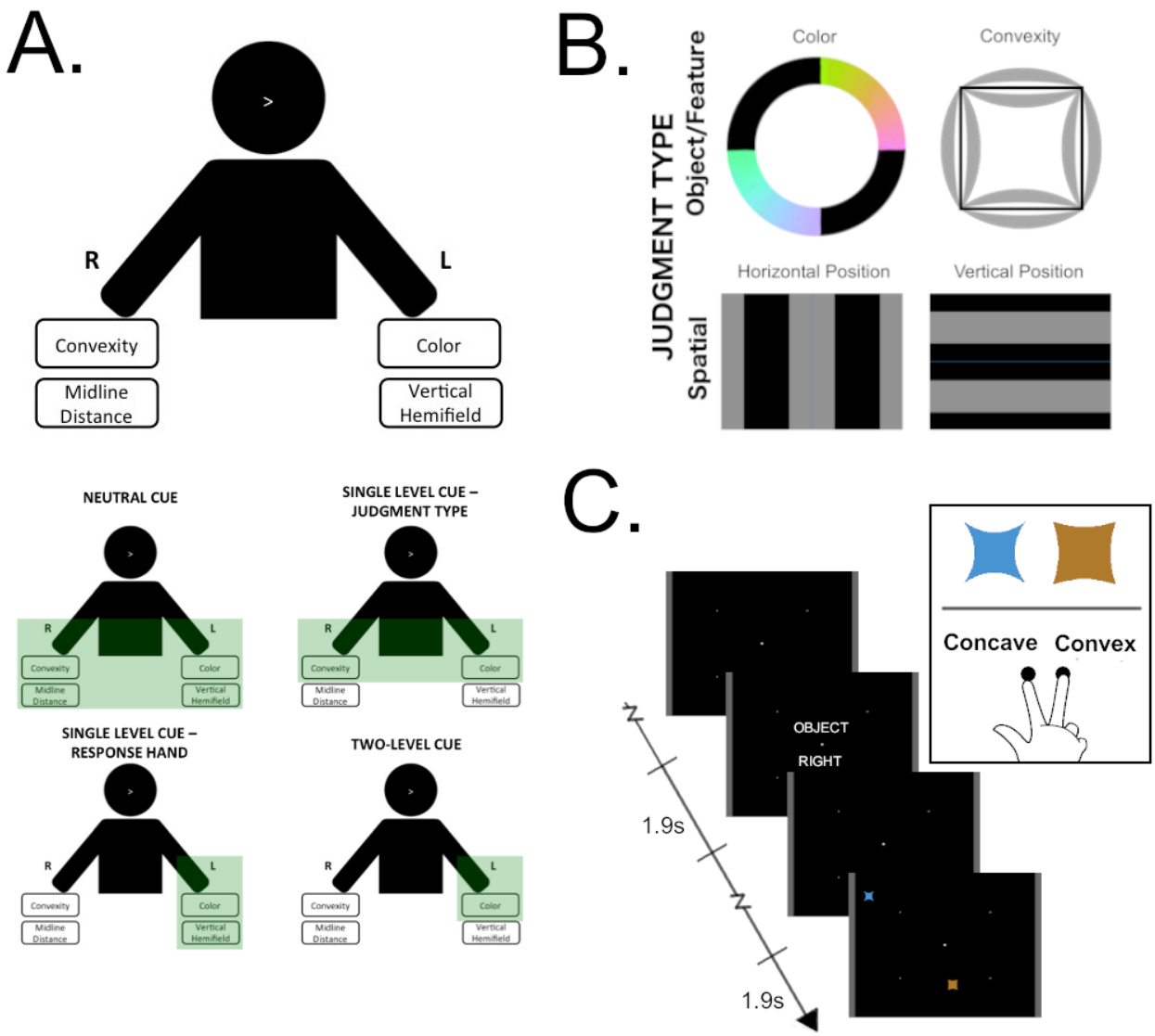

Figure 1. Illustration of experimental design elements. A) Participants learned a task mapping that mapped one each of two spatial (vertical hemifield and midline distance) and two object-based judgments (convexity and color) to each hand. Cues presented at the start of each trial could provide information about either the upcoming judgment dimension, response hand, both, or neither, which reduced the set to the subset highlighted in green for each cue. Cues with no information left the full task set remaining to be specified; cues for the Judgment type reduced the set by half but did not reduce the decision to a single hand; cues for response hand limited the set to one hand and reduced it by half; and cues for both pieces of information reduced the set to a forced choice task. B) Visual ranges of the four features that defined the stimulus pairs on each trial. Features were selected from two ranges that corresponded to different judgment decisions for that feature. C) Example trial. Participants saw a cue following a varied inter-trial interval for 1.9s. They then waited for a variable cue-stimulus interval before the stimulus pair for that

trial was presented. Participants determined which of the four features of the stimulus pair shared the same judgment decision for both stimuli – in this case, both stimuli are convex – and then make a response for that judgment decision based on their learned mapping.

Using this design, we defined a set of LFC regions that were involved in processing the task as a whole, then assessed how each region's activity varied between the cue and stimulus time points of each trial as a function of the amount of information contained in the cue. Regions that were differentially involved in preparation and execution during task processing should demonstrate activity that varied between the cue and stimulus presentations. Regions that manage representations of the task should show sensitivity to the amount of cue information as they prepare different subcomponents of the task on each trial. This design allowed us to test several key questions surrounding the relationship between task processing and task representation.

First, we asked whether distinct regions were involved in task processing and task representation, or if some or all regions would have overlapping involvement in both. If task processing and representation are supported by distinct mechanisms, regions should demonstrate sensitivity to the time point in the trial or the level of cue information, but not both. Conversely, if task processing and task representation share underlying mechanisms, some or all of the regions in our task should demonstrate an interaction effect between time point and cue information.

Second, we asked how different amounts of cue information might drive activity levels in cue-sensitive regions. If cue sensitive activity is the result of the preparation of a relevant task set, or alternatively a marker of the number of alternative potential responses being prepared, regions showing this cue sensitivity should have greater activity as a function of the size of the set made relevant at the cue. For example, for a noninformative cue, no stimuli or responses can be excluded and thus the full task set remains relevant. Thus, we would expect the greatest activity for these cues. On the other hand, a cue for both judgment type and response hand can

reduce the task to a simple two-alternative forced-choice decision. In this case, we would expect the least amount of activity, with cues for one or the other in between. Conversely, it is possible that activity in LFC regions represents the resolution of uncertainty as information becomes available. In this case, we would expect the reverse pattern; cues giving both the domain and response hand would allow for the resolution of two levels of task hierarchy, and would therefore show the most activation at the cue, whereas noninformative cues provide no resolution of uncertainty and would show minimal activity. Moreover, this alternative hypothesis further predicts a reversal of this pattern at the stimulus, at which point the remaining information of the task can be processed.

Following this investigation, we further asked how these patterns were distributed along the rostrocaudal axis in our left-lateralized frontal regions. Given our observations of the results of this latter analysis, we followed up with an exploratory investigation of the background connectivity among our task-relevant regions and with regions known to be involved in networks supporting cognitive control processing at different timescales (Dosenbach et al., 2007, 2008).

Methods

Participants

Twenty right-handed participants (10 female) ages 18-34 were recruited from the student population at the Georgia Institute of Technology. This sample size was selected to be consistent with the median sample size of fMRI studies at the time of collection (Poldrack et al., 2017). One participant was removed from analysis due to a technical issue with data collection and one participant was removed due to sub-criterion performance on session 2. Participants had normal or corrected-to-normal vision, and were not otherwise contra-indicated for an MRI protocol. Participants gave written informed consent under the Georgia Institute of Technology Institutional Review Board and were compensated with course credit.

Apparatus

Stimuli were presented using PsychoPy software (Peirce, 2007) via a personal computer (PC) connected to an Avotec Projector (mock and MRI scanners). Task code is available at http://www.github.com/savannahcookson/Hierarchical-Precue-Task. Responses were collected using two scanner-compatible PST button boxes. Participants wore covered protective earphones in both sessions, with earplugs in the MRI for additional protection from noise. In the MRI, head movement was restricted with soft padding. In the mock scanner, scanner noises were simulated using a standard CD player with sounds recorded during typical MRI sessions. All presentation, scanning, and response collection apparatus were available through the Georgia State University/Georgia Institute of Technology Center for Advanced Brain Imaging.

The screen was presented at a resolution of 1024x768px with a black background. Text, including the instructions, cues, feedback, and fixation screens, was presented in white font. To provide a fixation point and additional spatial reference points for the task decisions, a square marker (80px) was shown in the center of the screen. This marker was surrounded by four smaller (40px) square points arranged in a rectangle centered around the fixation point such that each of the four points marked a corner of the rectangle. Each of these four points was exactly halfway between the center and outer edges of the screen in both directions. Grey bars were shown on the left and right edges of the screen to delineate the outer bounds of the horizontal aspect of the screen. Screen center is defined as point (0,0) for pixel ranges.

Target stimuli and cues

Stimuli consisted of warped, colored squares presented in locations that varied both vertically and horizontally (Figure 1.B). Descriptions of each of these four features, and the judgments participants made for each, are described below; precise value ranges for each of the four features of the stimuli are presented in Table 1.

Table 1. Value ranges for stimulus features by judgment type.

Judgment Type	Dimension	Value		Lower	Upper
Object-Based	Color Temperature (Degrees)	Warm		0	90
		Cool		180	270
	Shape Convexity (Deflection Radius, px)	Concave		-75	-25
		Convex		25	75
Spatial	Vertical Location (px from center)	Above		35	349
		Below		-349	-35
	Horizontal Location (px from center)	Inside	Left	-221	-35
			Right	35	221
		Outside	Left	-477	-291
			Right	291	477

Note: px: pixels.

Color temperature. The color of each stimulus was defined along Derrington-Krauskopf-Lennie (DKL; Derrington et al., 1984) color space. In this space, the range of observable colors are plotted as a color wheel oriented orthogonally to the luminance of the observed color; here, luminance was held constant at 0˚ to approximate isoluminance across our color ranges. Degree ranges along this plane were set for "warm" and "cool" color judgments such that "warm" colors include reds, oranges, yellows, and a limited range of yellow-greens; "cool" colors, likewise, include a subset of dark greens, blues, and purples.

Shape convexity. The shape of each stimulus was derived from a square 200 pixels (px) on each side. The sides of the template square were warped so that the center of each line was deflected toward or away from the center to form a quadratic parametric curve with the corners of the square maintained in their original positions. The deflection range in each direction varied with a resolution of 1px. Such warping allowed participants to judge the shape as a "concave" (deflected inward) or "convex" (deflected outward) shape. These stimulus images were resampled to a size of 70px square for experiment presentation.

Vertical location. The vertical location dimension established the y-coordinate of the presentation location for each stimulus, independent of the horizontal location (x-coordinate). Vertical location was defined as a function of the height of the presentation window (1024px). Stimuli could be presented at a range of distances from the horizontal midline of the screen with resolution of 1px, where stimulus position was determined by the location of the center point; the vertical location of the stimulus could then be judged as "above" or "below" the midline. Horizontal location. Horizontal location was defined as a function of the width of the presentation window (1280px). Stimuli could be presented at a range of distances from the vertical midline with a resolution of 1px, again determined by the location of the center point, with discrete windows in the outer and inner halves of the screen; stimuli could be judged as appearing toward the "inside" or "outside" of the screen.

Cues. Cues consisted of two words or letter blocks presented in capital letters, with one presented above and one below the central fixation (Figure 1.C). Cues for judgment type ("SPATIAL" or "OBJECT") appeared above the center fixation, and cues for response hand ("LEFT" or "RIGHT") below. When information was not to be given for a particular cue type on a given trial, "XXXXX" served as the placeholder in the relevant cue position.

Procedure

The experiment proceeded in two sessions; the first session was completed in the mock scanner, and the second in the MRI scanner. When participants arrived for the first session of the experiment, they completed the informed consent process and were assigned to a mapping structure. In each mapping, one dimension from each judgment type (object, spatial) was mapped to each hand; i.e., one object-based and one spatial judgment each were mapped to each hand (Figure 1.A). Index and middle finger mappings for judgments were assigned for each of the two decisional options of the mapped dimension. These mappings were partially counterbalanced between participants for a total of 8 mapping sets. Participants were trained on

their assigned mapping at the start of session 1, as described below, and complete session 2 using the same mapping.

Once the consent process was complete in session 1, the participant was oriented to and assisted into the mock scanner. They then began the training phase of the task, which took approximately 30 minutes. Next, the participant completed between 6 and 12 experimental runs. The number of runs completed by each participant was determined by the how quickly the participant reaches a criterion performance; specifically, an average accuracy of 90% over the three most recent blocks. At the start of the first of these runs, the participant was informed that the experimenter would start playing the MRI sounds, and that they should remain as still as possible. The MRI sounds were played for the duration of each experimental run, and were stopped between runs while the experimenter checked in with the participant.

The second session took place 1-7 days after the first. Upon arrival, participants were assisted into the MRI scanner. Once the participant was ready to begin, they completed a shortened version of the training procedure described below. Finally, they completed 16 experimental runs. The experimenter checked in with the participant briefly in between runs. Upon completion of the task, participants were extracted from the scanner and brought back to the lab, where they completed a debriefing questionnaire.

Experimental runs in both sessions consisted of 32 trials. Runs presented all possible combinations of cue types, judgment types, response hands, and decision values. In both sessions, participants were given overall feedback for their accuracy and RT across the run at the end of that run. In addition, during session 1, feedback was given at the end of each trial. If participants gave the correct response, they were shown the fixation screen; if they gave an incorrect response, they were told what the correct response should have been.

Training. To learn the task, participants completed a series of progressive training blocks in session 1. First, participants familiarized themselves to the four possible responses in the task (index or middle finger press; the left or right hand) by responding to explicit instructions, e.g.,

"Press the RIGHT MIDDLE finger." This practice block contained 8 trials, counterbalanced across the four possible response options.

Next, participants completed a set of mapping training blocks that progressively introduced the mapping for each judgment dimension. These blocks instructed participants on the responses required for each of the four judgment dimensions based on their assigned mapping. At the start of each block, participants were presented with instructions that indicated: 1) what judgment was to be made for that particular dimension; 2) the hand that would be used to respond to that dimension; and 3) what responses corresponded to each of the two possible judgment decisions. Following the instructions for a given dimension, participants completed 16 practice trials for that dimension, in which they performed the instructed judgments on a single stimulus. In all participants, the mapping blocks introduced the dimensions in the following order: color temperature, shape convexity, vertical location, and lastly horizontal location. For the color temperature training block squares presented in the center of the screen bearing a particular color. As participants progressed through the mapping training phase, the stimuli gained values along each of the new dimensions while continuing to present with random values along the already-learned dimensions. This allowed participants to incrementally familiarize themselves with the nature of the stimuli they would see on-screen. When the vertical location dimension was introduced, participants were further instructed to maintain fixation on the center of the screen at all times during the task. The instruction to maintain fixation on the center of the screen was emphasized at the beginning of each subsequent block and run.

Once the mapping training was complete, participants were introduced to the experimental task, without cues. They were instructed that they would see stimuli appear in pairs, and that these pairs of stimuli would share a judgment decision value along exactly one of the four possible dimensions. They were then instructed to identify the shared dimension and respond with the appropriate response for the judgment decision value shared by the pair, according to their previously learned mapping. They then completed a practice block consisting

of 32 trials in which they respond to pairs of stimuli as they were presented onscreen. Trials were counterbalanced across judgment types, response hands, and judgment decision values. Finally, participants were introduced to the cueing aspect of the task. They were instructed that each trial would be preceded by a cue that may give some information about the upcoming trial. The instructions explained the information that could be contained in the two parts of the cue and describe how these two parts could combine into the different cue levels (no information, hand-only, judgment-only, or both). Participants were instructed to use the cues to the best of their ability to help their performance during the task. Following these instructions, participants completed a full practice run of the experimental procedure, as described below.

Trial structure. On each trial, participants made judgments of pairs of stimuli based on the feature that the two stimuli shared. First, the cue was presented for 1.9s. This was followed by a fixation screen for a cue-stimulus interval (CSI) that was jittered as described below. Following this interval, the two stimuli were presented simultaneously on the screen, one in the left half and one in the right, for 1.9s. The stimuli had different judgment values for each of the four dimensions described above except for one; participants were instructed to make a judgment about this shared dimension and to make the appropriate index or middle finger response on the hand associated with that judgment decision value. Participants were able to make their response for the interval that the stimuli were on-screen; this was followed by a fixation screen with a inter-trial interval (ITI) that was jittered in the same manner as the CSI. Participants were instructed to respond as quickly and accurately as possible on each trial, and to use the cues presented at the beginning of each trial to prepare the possible upcoming responses to the best of their ability. An illustration of the trial structure is found in Figure 1.C.

The CSI and ITI durations were jittered using the Analysis of Functional NeuroImages (AFNI; Cox, 1996) optimization algorithm. This algorithm produces a random experimental timing given the desired trial types (i.e., the factor combinations for the cue and stimulus time points), the desired average duration of the CSI and ITI events (1.9s each), and a set of bounding

parameters (minimum duration: .25s; step: .25s.). An estimate of the unexplained variance for this design can then be calculated. Here, for the experimental runs in each session, this process was iterated 1000 times, comparing the unexplained variance for each design and keeping the design that minimized this value. The same process was completed over 100 iterations to produce the timings for cue practice blocks in the training.

fMRI parameters. Images were collected on a Siemens 3T MRI scanner using a standard 32-channel radio-frequency head coil. At the beginning of the session, a 3D MPRAGE structural scan (1mm isotropic voxels) was collected, followed by a three-plane localizer. The blood-oxygen level-dependent (BOLD) signal was recorded during each experimental run using an interleaved echoplanar T2* sequence (TR=2000ms, TE=30ms, 3mm isotropic voxels). Each functional volume contained 37 axial slices, with 130 volumes/run.

Analyses

Behavioral analyses. RT values included correct trials only. Mean RTs and arcsine-transformed accuracies on the experimental blocks for session 2 were calculated for each subject as a function of three within-subjects factors (cue type, 4 cells; judgment domain, 2 cells; response hand, 2 cells) as well as a between-subjects factor for the congruency of each participant's horizontal judgment response mapping (2 cells; viz, whether the "inner" judgment was mapped to the index or middle finger). This latter factor was included to assess a potential confound of congruency effects due to participants' natural tendency to map fingers closer to the body to stimuli presented closer to the midline of a display. A four-way repeated measures ANOVA was performed on the RT and accuracy data for the three factors. Post-hoc comparisons were conducted using Tukey's HSD procedure.

fMRI processing and whole-brain analysis. Data preprocessing and analysis were conducted using AFNI (Cox, 1996). Preprocessing procedures included despiking, slice timing, volume registration, 6-parameter rigid-body motion correction, structural-functional alignment and

registration to standard Montreal Neurological Institute (MNI) space. The data were scaled to an intensity range of 0 to 100 to reflect percent signal change.

Data were analyzed using typical general linear modeling techniques. Nuisance regressors were included for constant, linear, and quadratic trends, as well as the 6 motion parameters extracted from preprocessing. Events were defined for the cue and stimulus time points (1.9s each) of each trial, labeled for the cue type, judgment type, and response hand. Contrasts were then defined for all effects of interest, including task (all cue and stimulus timpoints) versus baseline.

Region of interest definition and activation analysis. To define our regions of interest (ROIs) for analysis, we started by generating a set of 6mm-radius spherical regions across the brain using the coordinates published by Power and colleagues (2011). We then masked this set of regions to the FDR-corrected (q = .05) whole-brain contrast for task versus baseline, restricting final inclusion to those regions that retained at least 10 voxels after thresholding. Average beta values for each within-subjects condition (i.e., cue type, 4 cells; judgment type, 4 cells; response hand, 2 cells) at each time point (i.e., cue or stimulus event) were extracted for each ROI and each participant. The average beta values for each region were then subjected to a four-way repeated measures ANOVA across subjects. Where necessary, violations of the sphericity assumption were corrected for using the Hyunh-Feldt method.

While the factors of judgment domain and response hand were involved in some effects, they were few (9 terms across 5 ROIs) and with small effect sizes (Mean η_p^2: 0.205; Range: [0.191 : 0.400]). As such, we focus on the main effects cue type and time point as well as their interaction in the results of this report. More specifically, further analyses categorized ROIs based on whether they exhibited either a cue type by time point interaction ("CueXTime ROIs") or a main effect of time point ("Time ROIs"). These follow-up analyses excluded one region in ventral caudal frontal cortex, which was the only ROI that showed significant effects for both the main effect of time point and the cue type by time point interaction.

Network connectivity analysis. That our two categories of regions were distinguished by two distinct effect patterns involving time was intriguingly reminiscent of the time-based distinctions between the frontoparietal (FPN) and cinguloopercular (CON) networks described by the Dual-Networks model of cognitive control. Thus, in an exploratory follow-up analysis, we assessed how the distinct patterns of effects seen in each group of ROIs might relate to their connectivity with each other and with known cognitive control networks according to the dual-networks model (Dosenbach et al., 2007, 2008). To define ROIs for the dual-networks model, we calculated 6mm spherical regions centered on the point coordinates reported for each region identified in the original model (MNI-translated), generating 18 ROIs. We excluded any ROIs from the dual-networks model that overlapped with any of the ROIs defined in our task data at any point, which removed the left and right Frontal Cortex regions, the left dorsolateral prefrontal cortex region, and the superior dorsal anterior cingulate/medial superior frontal cortex region; this left left 14 ROIs, for a total of 34 ROIs across both the dual-networks model and the current task.

Next, we extracted a z-scored time-series correlation matrix across all 34 ROIs using AFNI's 3dNetCorr function (-fish_z option) applied to the residual time-series generated by the first-level GLM analysis for each subject. This residual time-series which is used as an estimate of "background" activity that has had task-related effects removed. The use of this background activity during correlation gives a measure of latent connectivity between regions that has been isolated from concurrent activation due to mutual involvement in the task (Otten et al., 2002; Tompary et al., 2018). Correlations were calculated across the concatenated time-series of all runs.

Within each resulting correlation matrix, the ROIs were labeled according to their membership in the FPN or CON in the case of the dual-networks regions or their characteristic effect pattern in the case of the task-related ROIs. These labels could then be used to define how pairs of correlated regions contributed to different within- and between-network connectivity

values. For example, the correlation value of two regions from the FPN would contribute to the value of the within-FPN connectivity, whereas the correlation value of a region from FPN with a region from CON would contribute to the value of the FPN to CON between-network connectivity. Correlation values across ROIs from each network pairing were averaged within each subject to yield a network-level correlation matrix for each subject.

Three comparisons were made between values within this network-level correlation matrix. First, we conducted two paired t-tests between the FPN-CON between-network connectivity values and each of the FPN and CON within-network connectivity values to confirm that the current data demonstrated higher connectivity within versus between networks as has been seen in prior literature. We next replicated these paired t-tests for the two sets of task-related ROIs to explore whether the differences in activity-related effects were likewise associated with correlations reflecting a dual-network structure. Finally, to explore how each set of task-related ROIs were directly connected to the FPN and CON, we conducted a 2x2 repeated measures ANOVA with factors for network (FPN vs CON) and effect pattern (CueXTime vs Time). If the time-based effect patterns that distinguished our two categories of regions are reflective of the distinct timescales at which the FPN and CON instantiate cognitive control, the connectivities within and between regions of our two effect categories should mirror the connectivity patterns seen in regions of the FPN and CON, and the connectivity between regions of our two effect categories and those of the dual-networks model should show an interaction between effect category and connecting network.

Results

Behavioral results

Accuracies and RTs are presented in full in Table 2 as a function of condition.

Table 2. Behavioral results across subjects summarized by condition.

			Congruent Mapping		Incongruent Mapping	
Cue Type	**Judgment**	**Hand**	**Accuracy**	**RT (ms)**	**Accuracy**	**RT (ms)**
None	Object-Based	Left	0.95	972.51	0.92	941.20
		Right	0.95	929.99	0.94	901.27
	Spatial	Left	0.90	939.43	0.92	974.05
		Right	0.93	970.78	0.91	992.98
Hand	Object-Based	Left	0.96	881.60	0.93	914.80
		Right	0.98	832.42	0.97	856.23
	Spatial	Left	0.98	873.57	0.94	893.02
		Right	0.96	874.08	0.94	924.29
Judgment	Object-Based	Left	0.95	906.22	0.93	899.26
		Right	0.96	845.02	0.96	856.17
	Spatial	Left	0.93	906.59	0.92	911.70
		Right	0.94	889.97	0.95	959.44
Both	Object-Based	Left	0.98	739.62	0.98	779.10
		Right	0.97	712.45	0.97	784.77
	Spatial	Left	0.98	697.69	0.98	732.64
		Right	0.97	700.78	0.99	782.59

Note: Within-subject factors are presented by row; between subject factors are presented in separate columns. RT: reaction time. ms: milliseconds.

Accuracy. Accuracies approached ceiling (Overall average = 95.1%). The ANOVA revealed a main effect of cue type, $F(3, 48) = 15.37$, $p < .001$, $\eta_p^2 = .49$; in general, participants were more accurate when cues provided more information about the upcoming trial. There was also a significant interaction between cue type and judgment domain, $F(3, 48) = 2.83$, $p = .048$, $\eta_p^2 = .15$; that is, the cue-related performance differences above varied based on whether participants were making a spatial or object-based judgment. No other effects for accuracy were significant.

Reaction time. The ANOVA revealed a main effect of cue type, $F(3, 48) = 307.04$, $p < .001$, $\eta_p^2 = .95$; in general, participants responded faster the more information the cue provided, illustrated in Figure 2. There were also interactions between cue type and two other factors: 1)

judgment domain, $F(3, 48) = 8.69$, $p < .001$, $\eta_p^2 = .35$, indicating that RT differences between cue types further depended on whether participants were making a spatial or object-based judgment; and 2) between-subjects congruency, $F(3, 48) = 5.08$, $p = .004$, $\eta_p^2 = .24$, indicating that RT differences by cue type also depended on whether participants' inner-outer judgment was mapped anatomically congruently or incongruently. In both cases, these interaction effects did not impact the qualitative pattern of the influence of the amount of cue information on RT.

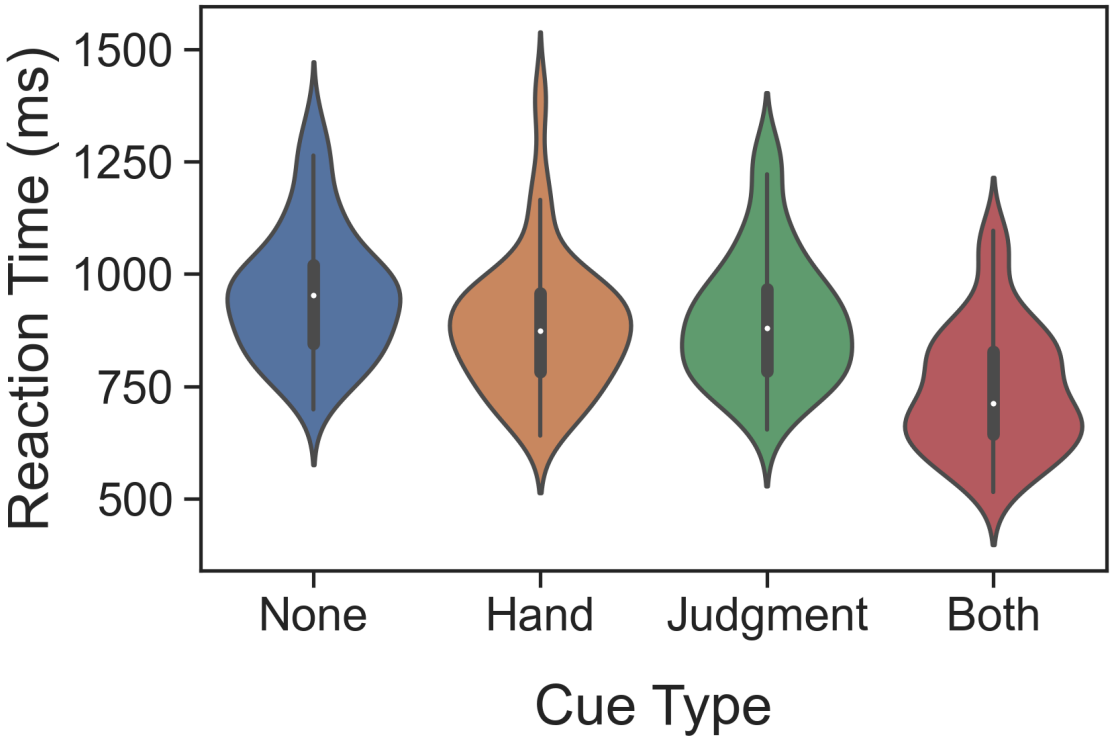

Figure 2. Reaction time (RT) as a function of cue type. Subject-level variability is presented as violin plots within each condition. The center white dot is the mean RT across subjects for that condition. Thick center lines in each violin plot show the 50% inter-quartile range (IQR) and thin lines extend to 1.5*IQR.

Regional Activity Results

ROI distribution. Ten ROIs were generated for this analysis, summarized in Table 3 and shown in Figure 3. Seven of these ROIs were located in left LFC, making these seven ROIs and their relative positioning of particular interest for relating the current results to previous investigations of rostrocaudal organization in the lateral frontal cortex (Badre, 2008; Badre &

D'Esposito, 2007; Koechlin & Summerfield, 2007). Four were located in caudal LFC, arranged roughly along the dorsoventral axis and curving rostrally toward the ventral end. The remaining three were positioned rostral to these and were distributed rostrocaudally along the inferior frontal gyrus.

Two ROIs were located in right LFC; one each in caudal dorsal and ventral LFC. Finally, one ROI was located subcortically in the putamen.

Table 3. Summary of ROI characteristics and effects.

			Center (pre-T, MNI)			Volume	Effects		
Hemisphere	**Region**	**Atlas Index**	**x**	**y**	**z**	**(post-T, vx)**	**Cue**	**CuexTime**	**Time**
Left	dcFC	261	-32	-1	54	31	X	X	
	mdcFC	174	-44	2	46	32	X	X	
	mvcFC	187	-41	6	33	32	X	X	
	vcFC	176	-47	11	23	24		X	X
	cPFC	201	-42	25	30	30	X	X	
	mPFC	188	-42	38	21	11			X
	rPFC	198	-42	45	-2	13			X
Right	vPFC	186	47	10	33	21			X
	dPFC	193	32	14	56	18			X
Subcortical	Putamen	186	-22	7	-5	16			X

Note: Atlas indicies refer to index numbers of original published atlas from Power et al, 2011. T: Threshold; vx: voxels; Cue: Main effect of cue type; CuexTime: Interaction effect between cue type and time point; Time: main effect of time point; FC: frontal cortex; PFC: prefrontal cortex; d: dorsal; v; ventral; c: caudal; m: mid; d: dorsal.

ROI Analysis. The effects for each ROI are also summarized in Table 3 (and example effects are shown in Figure 4). Four ROIs demonstrated a significant main effect of cue type, including the left dorsal caudal frontal cortex (L-dcFC; $F(3,51) = 6.18$, $p = .001$, $\eta_p^2 = .27$), left mid-dorsal caudal frontal cortex (L-mdcFC; $F(3,51) = 3.52$, $p = .021$, $\eta_p^2 = .17$), left mid-ventral caudal frontal cortex (L-mvcFC; $F(3,51) = 4.48$, $p = .007$, $\eta_p^2 = .21$), and left caudal prefrontal cortex (L-cPFC; $F(3,51) = 4.86$, $p = .005$, $\eta_p^2 = .22$), indicating that these regions' activity varied as a function of the amount of information contained in the cue. This effect appeared to be primarily driven by lower activity to noninformative cues overall relative to the informative cues.

All four of these ROIs also demonstrated an interaction between cue type and time point (L-dcFC: $F(3,51) = 15.34$, $p < .001$, $\eta_p^2 = .47$; L-mdcFC: $F(3,51) = 7.67$, $p < .001$, $\eta_p^2 = .31$; L-mvcFC ($F(3,51) = 9.83$, $p < .001$, $\eta_p^2 = .37$; L-cPFC: $F(2.341,39.803) = 5.88$, $p = .004$, $\eta_p^2 = .26$) as well as the left ventral caudal frontal cortex (L-vcFC $F(3,51) = 9.46$, $p < .001$, $\eta_p^2 = .36$), indicating that the activity differences in these ROIs by the amount of information contained in the cue further varied as a function of time point within the trial. That is, the cue time point showed generally increasing activity in these ROIs with more cue information, whereas the stimulus time point showed generally decreasing activity with more cue information.

Of all of these ROIs, only the L-vcFC also exhibited a main effect of time ($F(1,17) = 9.88$, $p = .006$, $\eta_p^2 = .37$), indicating that activity in this region differed overall between the cue and stimulus time points. The remaining ROIs consistently and only demonstrated this main effect of time, including the left middle prefrontal cortex (L-mPFC: $F(1,17) = 6.52$, $p = .021$, $\eta_p^2 = .28$); left rostral prefrontal cortex (L-rPFC: $F(1,17) = 19.97$, $p < .001$, $\eta_p^2 = .54$); right ventral frontal cortex (R-vFC; $F(1,17) = 20.86$, $p < .001$, $\eta_p^2 = .55$); right dorsal frontal cortex (R-dFC: $F(1,17) = 10.43$, $p = .005$, $\eta_p^2 = .38$); and putamen ($F(1,17) = 23.93$, $p < .001$, $\eta_p^2 = .58$).

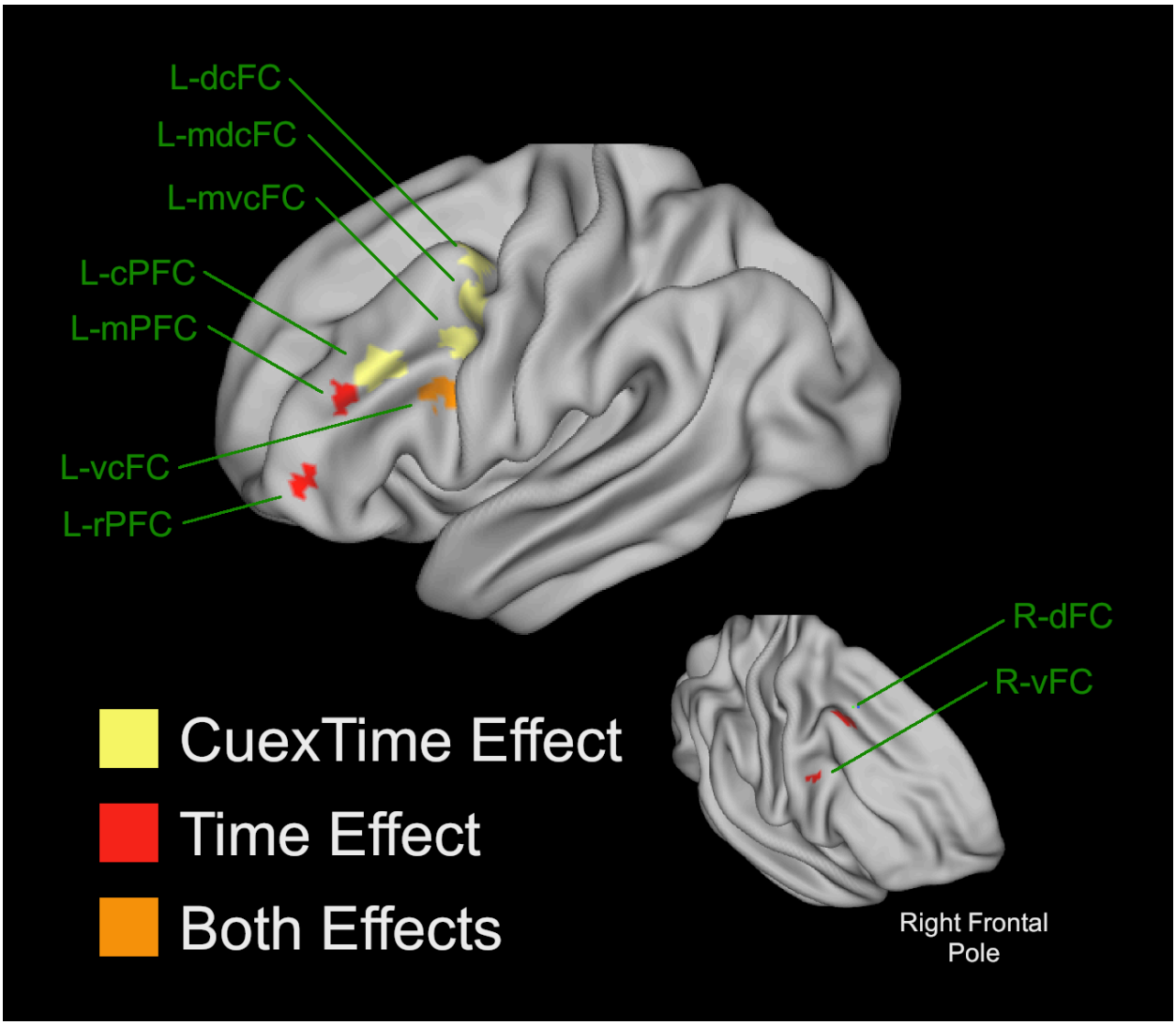

Figure 3. Topographic distribution of frontal ROIs and their associated effects. Left caudal ROIs demonstrated an interaction effect between cue type and time point. Left rostral LFC and right LFC/subcortical ROIs (putamen not shown) demonstrated a main effect of time point. L-vcFC was the only ROI to show both effects.

Generally, these results indicate an interaction between cue type and time point or a main effect of time, but not both (with the exception of L-vcFC). Based on these results, we categorized our ROIs by their pattern of effects, with L-dcFC, L-mdcFC, L-mvcFC, and L-cPFC falling in the "CueXTime" category, and L-mPFC, L-rPFC, R-vFC, R-dFC, and putamen falling in the "Time" category. The left LFC ROIs illustrated in Figure 3 are colored by their effect category; of particular interest, left-hemisphere regions in the "CueXTime" category were located more caudally, whereas those in the "Time" category were located more rostrally. In

other words, regions whose activity differences between time points were dependent on the amount of information contained in the cue were located in areas of frontal cortex associated with lower task abstractness, while those whose activity differences were independent of cue information were located in areas associated with higher task abstractness. To illustrate the difference in effects between these two groups, the percent signal change from baseline for an exemplar ROI from each category – the LdcFC for the CuexTime group and the LrPFC for the Time group – have been plotted as a function of cue type and time point in Figure 4. Because it demonstrated both effects of interest, L-vcFC was excluded from further analysis.

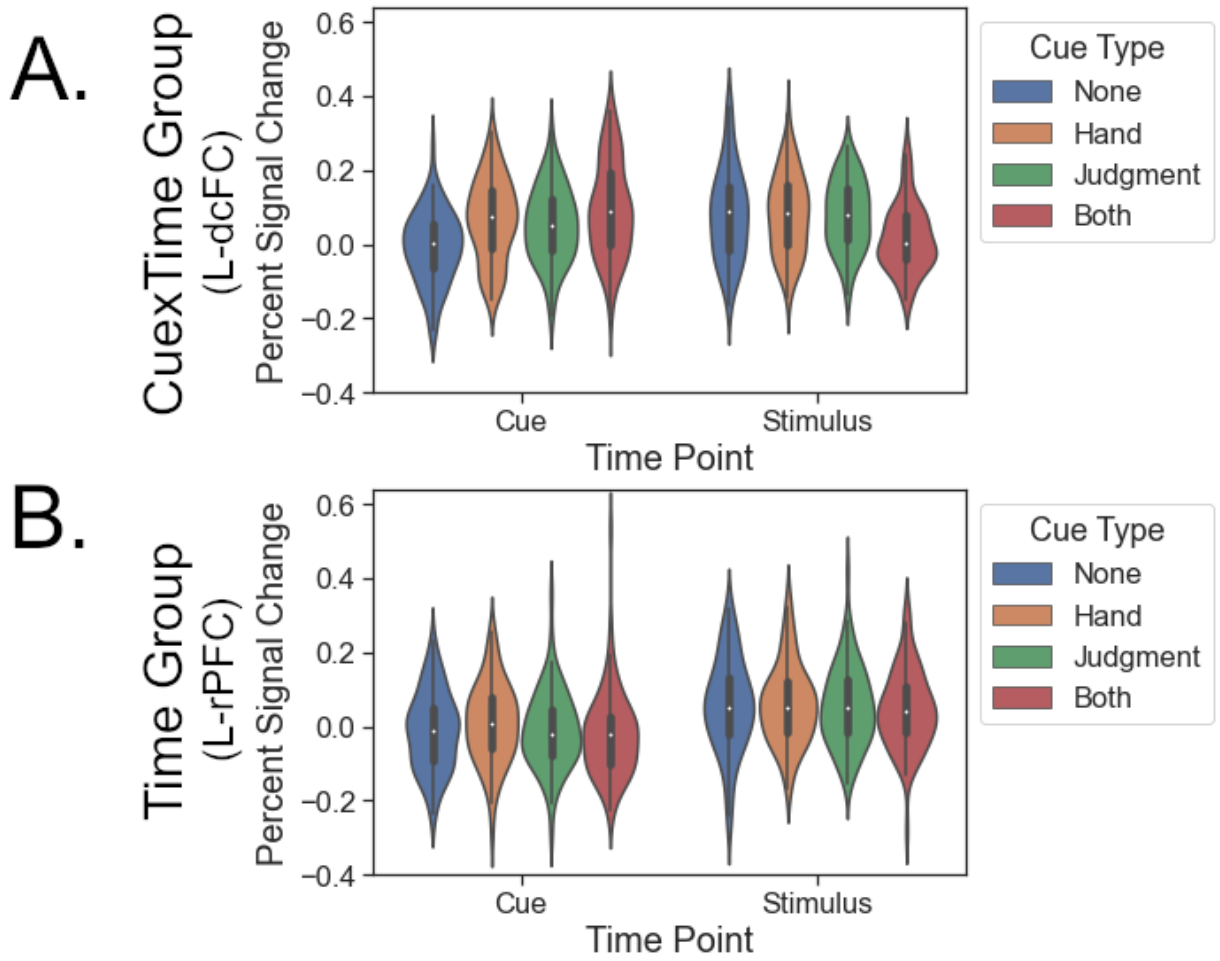

Figure 4. Representative illustrations of effects of cue type and time point on percent signal change in the CuexTime and Time group ROIs as measured by the BOLD signal. The CuexTime group demonstrated an interaction between cue type and time point such that activity in these ROIs increased with increasing cue information at the cue time point and decreased with increasing cue information at the stimulus time point. The Time group demonstrated only a main effect of time, such that activity was generally higher at the stimulus than the cue across cue types. Subject-level variability is presented as violin plots within each condition. The center white dot is the mean percent signal change across subjects for that condition. Thick center lines in each violin plot show the 50% inter-quartile range (*IQR*) and thin lines extend to 1.5**IQR*.

Network Connectivity Results

The FPN and CON from the dual-networks model (Dosenbach et al., 2007) both demonstrated significantly higher within-network connectivity relative to their between-network connectivity across the session (FPN: $t(17) = 9.388$, $p < .001$, Cohen's $d = 2.213$; CON: $t(17) = 9.857$, p

< .001, Cohen's d = 2.323). Connectivity also varied in the two sets of regions identified above. However, while the "CueXTime" regions showed greater connectivity to each other than with the "Time" regions ($t(17) = 4.862$, $p < .001$, Cohen's d = 1.146) as expected, the "Time" regions showed the opposite pattern ($t(17) = -3.011$, $p = .008$, Cohen's d = -.710). That is, the "Time" regions were more strongly connected to the other regions identified in the task than they were to each other. These results are contrasted in Figure 5.A.

The ANOVA assessing the "CueXTime" and "Time" regions' connectivities with FPN and CON further revealed main effects of network ($F(1,17) = 46.600$, $p < .001$, $\eta_p^2 = .733$) and of effect category ($F(1,17) = 28.659$, $p < .001$, $\eta_p^2 = .628$). Overall, our regions demonstrated greater connectivity with FPN than CON, and "CueXTime" regions had stronger connectivity than "Time regions" across both networks. The interaction between these factors was not significant ($F(1,17) = 2.421$, $p = .125$). These results are illustrated in Figure 5.B.

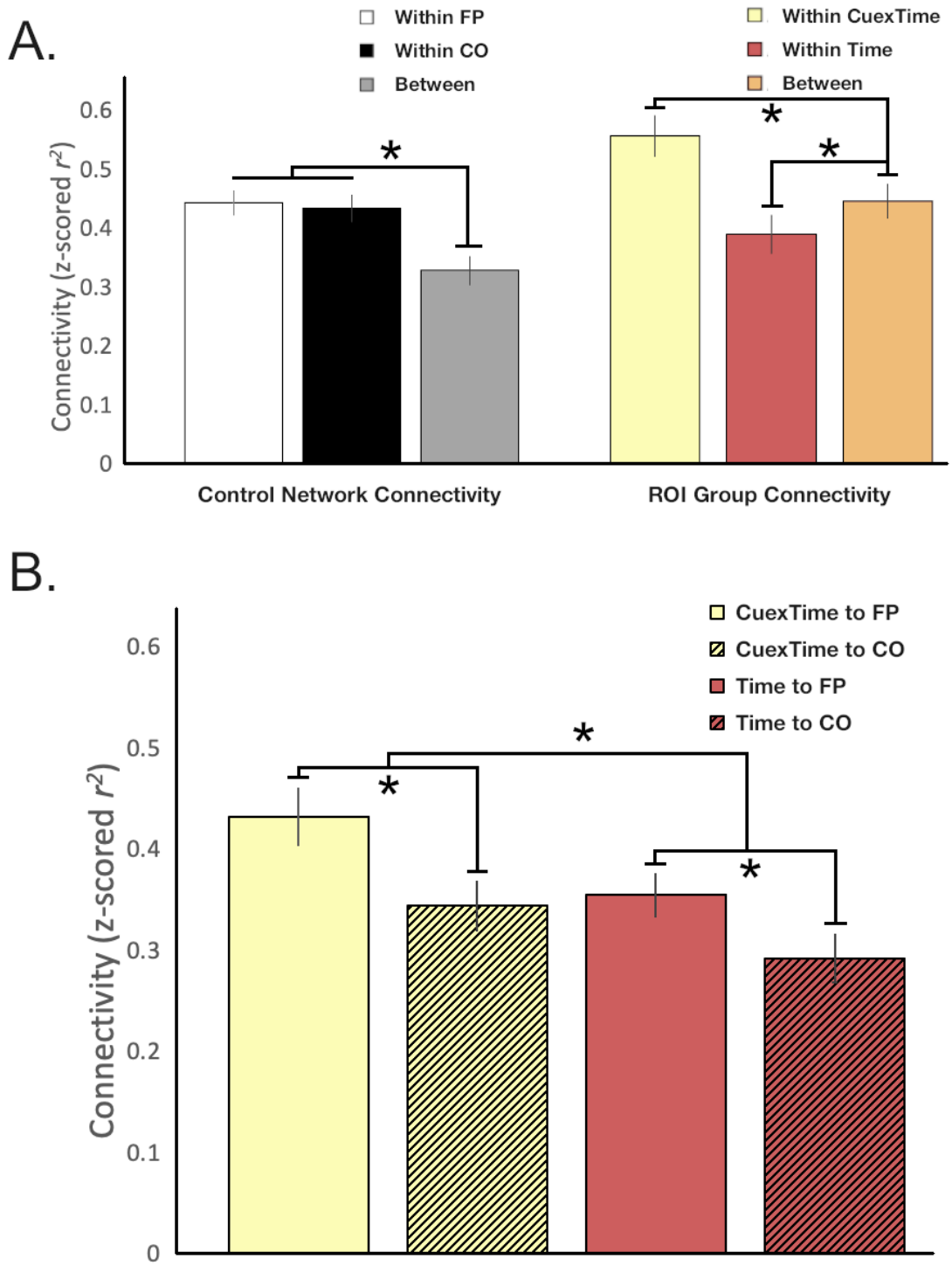

Figure 5. Results of exploratory connectivity analyses. A) Comparison of connectivity patterns seen in known cognitive control networks with those seen in the CuexTime and Time groups of ROIs from the current study. Between = between-network/group connectivity. B) Connectivity between the ROIs from the current study and each of the two cognitive control networks. Error bars in all graphs represent the standard error within conditions.

Discussion

The current study is, to our knowledge, the first investigation of how hierarchical task set representations may be implemented across trial events using a cueing procedure to distribute task processing across events in time. Through this design, we aimed to determine the neural correlates of task processing and task representation and the potential relationships between them. Regions that differentially support preparation and execution processes should show activity that varies from one time point in the trial to another; those that are involved in task representation should show activity that varies with the amount of information contained in the cue. First, we asked whether task processing and task representation were supported by distinct or overlapping mechanisms; in the former case, regions would be sensitive to one factor or the other, whereas in the latter some or all regions should demonstrate an interaction of both. Next, we asked whether cue-sensitive regions showed changes in cue-related activity that reflected preparation of sets of different sizes or reduction of different amounts of uncertainty, based on whether they showed decreasing or increasing activity at the cue time point. Finally, based on differences in the effect patterns that we observed in left caudal frontal regions relative to other task related regions, we further conducted an exploratory analysis that aimed to relate these different sets of effects to network-level connectivity.

Our data indicate that amount of cue information and time point did indeed interact in a number of our task-relevant regions (viz., L-dcFC, L-mdcFC, L-mvcFC, L-vcFC, and L-cPFC; see Figure 3), clearly indicating overlap between the mechanisms of task processing and representation. Interestingly, all regions that demonstrated an effect of cue information also showed this interaction, while most regions demonstrating a main effect of time point did not (viz., L-mPFC, L-rPFC, R-dFC, R-vFC, putamen). Thus, the mechanisms of task processing appear to be inextricably interlinked with task representation - but left caudal frontal regions may uniquely mediate these shared mechanisms.

Our behavioral results may provide some insight into how these mechanisms interact. The current results demonstrated a stair-step effect as a function of the amount of information provided by the cue, such that participants responded more quickly and with higher accuracy based on how many pieces of information they were given, independent of what those pieces of information were. This mirrors similar effects seen for specification of individual components of a motor response (Rosenbaum, 1980), despite the use of abstract cues in the current experiment. This suggests that preparation of motor responses and more abstract task sets may involve the same general mechanism implemented at different levels of representation. Badre and Frank (2012; see also Frank & Badre, 2012, for computational model) have previously demonstrated a similar distribution of a reinforcement learning mechanism across distinct task levels. This mechanism is supported by progressive cortico-subcortical loops between frontal regions distributed along the rostrocaudal axis and similarly organized subregions of the basal ganglia. Each loop implements gating mechanisms at a given level of representation to learn probabilistic associations at that task level; the results of that selection process then cascade from the top levels of abstraction to the most concrete to coordinate across levels. Gating mechanisms are critical for cognitive control (Chiew & Braver, 2017; Ott & Nieder, 2019) and specifically for task preparation (Ruge & Braver, 2007); this distributed gating mechanism, then, likely also supports selection between task representations at each level as a function of the representational content maintained in LFC within each level of cortico-subcortical loops along the rostrocaudal axis.

Accordingly, of our task-related regions, those demonstrating an interaction between cue information and time point were restricted to left-lateralized mid-caudal to caudal LFC. The pattern of activity seen for different types of cues was relatively similar across these regions. At the cue, regions generally showed the least activity for a noninformative cue, roughly equal levels of activity for each of the cues giving one piece of information, and the most activity for cues for both pieces of information; this pattern was reversed at the stimulus. This mirrors the

stair-step effect seen in the behavioral data, suggesting that this activity may be a neural correlate of the cue benefit itself. Activity in these regions may reflect the integration of new cue information with the existing task representation to reduce uncertainty about the upcoming task at the cue, where the processing of more information demands greater activity. At the stimulus, then, processing demand in these regions is likewise greater when more of the task remains to be processed. Lower cue information thus causes increased demand at the stimulus that may require longer processing time, resulting in the stair-step effect seen both in the current reaction time data and likewise in previous behavioral studies (Rosenbaum, 1980). Previous research on reward motivation at different levels of task representation used a psychophysiological interaction (PPI) analysis to demonstrate a positive relationship between frontal activity and reward-based performance benefits that was specific to task representation level (Bahlmann et al., 2015). This may hint at a similar relationship for frontal activity and cue benefits. While the current study does not have the power to assess the relationships between our frontal activation and cue benefit at each task representation level, future work using the hierarchical pre-cue design could remove noninformative cues, to allow for a direct, more powerful comparison between two different cue levels.

Beyond the relationship between cue benefits and cue information, the pattern of activity seen in these regions also indicates that the level of activity seen at each event during task processing in the cueing procedure is related to the amount of information being actively represented, or alternatively the amount of uncertainty being resolved at that time point, rather than the size of the task set being prepared at the time of the event. At the cue, participants showed less activity with lower cue information. This is perhaps expected for noninformative cues, which have previously shown lower activity in frontal cortex relative to informative cues in standard cueing procedures (e.g., Cookson et al., 2016). More interesting is that this pattern is also seen between different levels of informative cues. In our design, cues for one piece of task information reduced the task set to half the total possible decision options (i.e., two 2-alternative

forced choice tasks), while cues for both pieces reduced the task to a single 2-alternative forced choice task. That there is greater frontal activity at the cue for cues giving both pieces of information suggests that participants are using the additional information to process more of the task during this time point. This is further supported by the reversal of the pattern at the stimulus; as participants have processed more of the task a priori, there is less remaining at the stimulus, so cues for both pieces of information have the least activity.

A third intriguing observation from these activity patterns is that they do not appear to vary with rostrocaudal position. The regions in left LFC demonstrating an interaction between cue information and time point roughly align with regions previously associated with the lower two levels of a policy abstraction task (Badre & D'Esposito, 2007), suggesting that a two-level task set representation was employed by participants in this study. The question then remains what aspects of the task structure are represented at each level, and how the cue information influences processing at each level. That the activity in the caudal and mid-caudal regions in this study followed the same patterns of activity across cue types indicates that cues were informative at both levels of representation. This may be a reflection of the nature and flexibility of task abstraction in the brain. Coding of tasks in LFC is highly flexible (Cole et al., 2014; Stokes et al., 2017), and tasks can be represented with a wide variety of task features (Badre & D'Esposito, 2007; Cookson et al., 2019; Huang & Awh, 2018). This includes cue information, even if it is presented during distinct time points (Grant et al., 2020; Hazeltine et al., 2011). Because the cue is always presented first in this experiment, it is possible that participants represented the highest level of the task as a distinction of the amount of information contained in the cue. Then, based on the type of cue presented, they could then determine what kind of reduction, if any, they would be able to make in the upcoming task, and prepare accordingly. Future research should explore this type of content-independent meta-task representation and its relationship to policy abstraction and the rostrocaudal axis.

As a final point, we are struck by the stark contrast between the groups of regions that were involved in representational aspects of task processing, evidenced by an interaction between cue information and time point ("CueXTime" group) and those that were involved in other aspects of task processing, exhibited by a main effect of time point ("Time" group). Specifically, we were interested in the rostrocaudal distribution of these effect patterns in left LFC. Our "CuexTime" regions are located in more caudal LFC whereas "Time" regions are located more rostrally. This is similar to the distribution of distinct sets of regions involved in two different networks related to cognitive control, as described by the Dual Networks model (Dosenbach et al., 2007, 2008). Our "CueXTime" regions are located in areas similar to those regions in the FPN of the dual-networks model, while our "Time" regions are in areas similar to those regions of the CON. Moreover, the FPN is hypothesized to facilitate moment-to-moment processing, whereas the CON supports tonic maintenance of active representations. This parallels the distinctions in processing and representation effects found for the regions in this study; the interaction between cue information and time-point may capture moment-to-moment processing of cue information, while the main-effect of time may indicate the activation of the task representation during response execution regardless of the specific information being processed. Thus, we conducted an exploratory analysis to assess whether the connectivity of our two groups of regions mirrored that of regions in the FPN and CON.

However, our background connectivity analysis did not support this hypothesis. Connectivity patterns between FPN and CON regions in our data reflected typical network patterns, where connectivity within both networks is greater than connectivity between the two networks (Cohen et al., 2014). In contrast, the connectivity between "CuexTime" and "Time" regions was in fact higher than the connectivity within our "Time" regions, suggesting that the regions supporting non-representational task processing do not form a cohesive and separate network from those supporting representational task processing. Additionally, both sets of regions were more strongly connected to FPN than CON regions, with "CueXTime" regions

showing greater connectivity with both networks than "Time" regions. Overall, this generally indicates that the two effect patterns found in this study were not drawn along network boundaries. Rather, it suggests that regions involved in all aspects of task processing in this study are more strongly associated with the FPN than the CON, i.e., with moment-to-moment processing. In other words, the results presented here are preliminary evidence of a rostrocaudal distinction of regional functions in LFC that appears to occur within the FPN; future research should further explore how these rostrocaudal distinctions fit within the more general functional framework of the dual-networks model.

Taken together, the results of this study clarify the relationship between task processing and task representation, and provide new insights into the progression of task processing as information about a task is made available. Furthermore, they begin to draw new parallels between the task preparation and execution literature and the representational abstraction literature, giving us a more complete and cohesive understanding of the implementation of cognitive control in the brain. We hope that making this procedure open-sourced will encourage others to continue to explore this design and learn more about task processing and representation in the brain.

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