

CONTROL AND REPRESENTATION IN ALGEBRA

Endogenous Control and Task Representation

An fMRI Study in Algebraic Problem Solving.

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Abstract

The roles of prefrontal and anterior cingulate cortices have been widely studied, yet little is known on how they interact to enable complex cognitive abilities. We investigated this issue in a complex yet well defined symbolic paradigm: algebraic problem solving. In our experimental problems, the demands for retrieving arithmetic facts and maintaining intermediate problem representations were manipulated separately. An analysis of functional brain images acquired while participants were solving the problems confirmed that prefrontal regions were affected by the retrieval of arithmetic facts, but only scarcely by the need to manipulate intermediate forms of the equations, hinting at a specific role in memory retrieval. Hemodynamic activity in the dorsal cingulate, on the contrary, increased monotonically as more information processing steps had to be taken, independent of their nature. This pattern was essentially mimicked in the caudate nucleus, suggesting a related functional role in the control of cognitive actions. We also implemented a computational model within the ACT-R cognitive architecture, which was able to reproduce both the behavioral data and the time course of the hemodynamic activity in a number of relevant ROIs. Therefore, imaging results and computer simulation provide evidence that symbolic cognition can be explained by the functional interaction of medial structures supporting control and serial execution, and prefrontal cortices engaged in the on-line retrieval of specific relevant information.

Introduction

Humans are set apart from other species by their ability to perform sequences of arbitrary operations over complex representations. Such activities include planning, problem solving, and the wide range of symbol-manipulation abilities that probably underlie language and certainly enable mathematical and logical reasoning. These capabilities are usually credited to an increased capacity for cognitive control—i.e., the ability to voluntarily coordinate the ongoing cognitive processes in order to achieve a certain goal.

A large part of the literature on this topic has been concerned with basic experimental paradigms, like the Stroop or the Flanker task, or Task Switching (e.g., Pardo, Pardo, Janer, & Raichle, 1990, Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Sohn, Ursu, Anderson, Stenger, & Carter, 2000; Yeung, Nystrom, Aronson, & Cohen, 2006). But even under such controlled conditions, it is often difficult to distinguish control functions from the processing of task-relevant information. In Task Switching, for instance, the so-called switch cost is usually assumed to reflect the additional control effort for reconfiguring the response set. However, the same effect has been also interpreted as a cost paid in retrieving appropriate information from memory (Altmann & Gray, 2002; Logan & Bundesen, 2003), a lack of benefit from successive task repetitions (Sohn & Anderson, 2001), and as the interference between the alternated task representations (Yeung et al., 2006). Also, the contribution of different cognitive strategies to accomplishing the same task might be confounded with executive control. As an example, Lovett (2005) presented a model of the Stroop task that was capable of reproducing most of the effects reported in the literature as the result of an internal competition between alternative procedures. As another example, the strategy-conflict model of Peebles and Bothell (2004) succeeded in reproducing participant's performance in the Sustained Attention to Response Task.

By using both computational modeling and brain imaging, our research group has previously succeeded in tracking the maintenance of temporary representations and the adoption of cognitive strategies in more complex domains (Fincham, Carter, Van Veen, Stenger, & Anderson, 2002; Anderson, Albert & Fincham, 2005), and the effects of practice and learning (Fincham & Anderson, 2006; Qin et al., 2003). In this paper, the same approach is used to examine the interplay between task-related and control-related information in algebraic problem solving, a domain which had been investigated in a series of previous imaging studies (e.g., Anderson, 2005; Qin et al., 2003; Qin et al., 2004).

The Role of Anterior Cingulate Cortex and Lateral Prefrontal Cortex in Cognitive Control

Two brain regions have been mainly characterized as underlying cognitive control: the lateral part of the prefrontal cortex (LPFC) and the anterior cingulate cortex. Although the contribution of LPFC in cognitive control and executive functions is commonly agreed upon (e.g., Miller & Cohen, 2001), the consensus is less on its exact functional role. Braver, Cohen and Barch (2002) pointed out that there are at least two issues at the stake: whether PFC is seen as a passive memory buffer or an active controller, and, in the latter case, whether its functions are inhibitive or attentive. The less controversial finding probably is its contribution to memory, and especially working memory (e.g., Nolde, Johnson, & D'Esposito, 1998; Wagner, Paré-Blagoev, Clark, & Poldrack, 2001).

The anterior part of the cingulate gyrus is a complex structure involved in several functions. Its most dorsal part (dACC), however, has been repeatedly found to correlate with internal control demands (e.g., Bush, Luu, & Posner, 2000). Three major views have been put forward: according to the earliest theory, the dACC is responsible for the orienting of attention, and particularly for recruiting the brain regions required for the execution of a particular task

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(Pardo et al., 1990; Posner & Dehaene, 1994). A subsequent hypothesis was that ACC was monitoring behavior and detecting errors, providing fundamental feedback for correcting one's own actions (Dehaene, Posner & Tucker, 1994). A third view has been recently gaining prominence, according to which the dACC detects conflicts among competing responses (Botvinick et al., 1999; Carter et al., 2000). Botvinick, Cohen & Carter (2004) suggested a two-step framework, where dACC detects conflict and, before a selection among competing responses is made, it alerts prefrontal cortex to adjust the amount of top-down control. The balancing of control between the two regions has been empirically supported (MacDonald, Cohen, Stenger, & Carter, 2000), and can also explain the same data supporting the error detection hypothesis (Yeung, Botvinick & Cohen, 2004).

The conflict-monitoring hypothesis is noteworthy because it fractionates cognitive control into two subsystems, one for detecting conflict and one for resolving it through top-down selection, making one important step towards a more mechanistic explanation of control. However, it must be noted that the anterior cingulate has been found to be sensitive to a wide range of control demands, not limited to conflict monitoring (e.g., Badre & Wagner, 2004). Additionally, lesion studies in humans have brought forth inconsistent results: some authors (Swick & Turken, 2002; Di Pellegrino, Ciaramelli & Làdavas, 2007) found evidence of reduced ability in adapting to control demands in patients with focal damage to the anterior cingulate, while others (Fellows & Farah, 2005; Baird et al., 2006) did not.

Cognitive Control within a Cognitive Architecture

Our experiment and our predictions were based on the ACT-R (Adaptive Control of Thought–Rational) cognitive architecture (Anderson et al., 2004). In ACT-R, representations are temporarily held in independent information-processing modules, corresponding to different

cortical regions. Communication between modules is made possible by a central, procedural module, which detects the onset of particular conditions through the incoming pathways from the cortex and routes the relevant information to the appropriate regions. The action of relaying information among modules corresponds to the minimal cognitive steps, and is computationally encoded as production rules. The activity of this central module has been related to functions of the basal ganglia (Anderson, 2005; Anderson et al., 2004). While the basal ganglia are involved in several cognitive and non-cognitive functions (e.g., Graybiel, 2000), this interpretation is consistent both with their role in procedural knowledge acquisition (Knowlton, Mangels & Squire, 1996) and with existing computational models stressing their role as a gating system to the prefrontal cortex (O'Reilly & Frank, 2006).

Being a production system, ACT-R implicitly assumes a definition of control that does not correspond to the hierarchical models we have reviewed. From a purely computational perspective, control is achieved by the serial execution of production rules—this being all that determines the transitions of the system from one state to another. Instead of a hierarchy of controllers, a production system achieves flexible behavior by building upon progressively more articulated representations, therefore banishing the need for a control homunculus. Correspondingly, dichotomies such top-down vs. bottom-up control, or controlled vs. automatic behavior, scarcely make any sense, since representations lay on a continuum of complexity.

The role of appropriate representations in the control of action has been increasingly appreciated in recent years. For instance, Botvinick and Plaut (2004) presented a neural network whose capability for coordinating routine sequences of actions depends on the number of layers and how remote they are from (and, therefore, less interfered with by) immediate sensory units. When units were removed, the model produced patterns of errors that closely mimicked those

found in frontal patients. Similarly, Koechlin, Ody, and Kouneiher (2003) provided evidence that, moving from the caudal to the rostral part of the frontal lobe, prefrontal regions encode increasingly complex information (from simple sensory input to contextual signals to episodic memory). Also, Schneider and Logan (2005) presented a task switching model that can fully account for the various types of switch cost by relying only on memory processes involved in the retrieval of appropriate response representations.

Specialized Control Information and the Role of Anterior Cingulate Cortex

Previous studies have been able to identify distinctive brain regions whose hemodynamic activity could be related to different ACT-R modules (Anderson et al., 2004; Anderson, 2005). In particular, one part of the LPFC located within the inferior frontal gyrus was found to correlate with the demands for memory retrievals. These demands correspond to the activity of a *retrieval module* in ACT-R. Also, a posterior parietal region has been mapped onto ACT-R's *imaginal module* that holds and updates problem-state information, and a region in the motor cortex to the *manual module* that programs manual output. As previously noted, the *procedural module* has been associated with the basal ganglia, and in particular with the activity of the caudate nucleus.

One ACT-R component is of special interest for our purposes: it is the so-called *goal module*, which has been mapped onto the dACC (Anderson, 2005; Fincham & Anderson, 2006). Its functional role is to hold control-relevant information that relates to the ongoing process. Special control information is necessary to make a selection whenever more than one basic behavioral action is compatible with the current state of the modules. This happens in situations of response conflict but will also occur when there are no responses being selected. Control states do not need to have semantic content, and their role is often limited to providing introspective access to the internal states of cognitive processing modules. This view has the

advantage of reducing the gap between the cognitive functions of ACC and its involvement in monitoring and regulating somatic responses (e.g., Critchley et al., 2003).

In any case, the need for control information increases in complex tasks where more representations need to be processed and maintained in different modules. This very same factor also affects the procedural module, because more representations are usually needed when larger amounts of information are being relayed. In a cognitive-demanding task like algebra, the hemodynamic activity in the dACC and in the striatum should be similarly affected by manipulating the internal demands for maintaining and retrieving information.

The Experiment

Cognitive control has been traditionally studied with the paradigms we outlined before, which often contrast trials where an automatic response is appropriate with trials where voluntary actions are needed to inhibit them. Here, we tried to keep both task and stimuli constant, but to manipulate the amount control that is necessarily performed internally (“endogenous”) vs. the amount of control that is explicitly encoded in the stimuli themselves (“exogenous”: Monsell, 2003). The task we opted for was solving simple algebraic equations. Algebraic problem solving is complex and arbitrary enough to significantly engage control and specialized task representations, yet well enough understood to allow for mechanistic modeling. In addition, brain regions involved in representing different types of algebraic knowledge have been previously identified (Qin et al., 2003; Anderson, 2005).

Stimuli and Design

Our participants were presented with 128 equations¹, all of which were comprised of four

¹ A complete list of the equations is available as part of the supplementary model file at this URL: <<http://actr.psy.cmu.edu/publications/pubinfo.php?id=716>>

terms, two on the left and two on the right of the equal sign (“=”). Each equation was either entirely parametric or entirely numeric. An example of parametric equation is reported in (1):

$$a*x - a = a*b - a \quad (1)$$

while (2) gives one of the numeric type:

$$8*x - 2 = 36 - 6 \quad (2)$$

The leftmost term was always the only one containing the unknown quantity x . It always contained another factor, which either multiplied (e.g. “ $8*x$ ”, “ $a*x$ ”) or divided (e.g., “ $x/4$ ”, “ x/b ”) the unknown.

The solution of each equation required three steps: (a) Eliminating the addend on the left side by appropriately adding or subtracting a quantity; (b) Unwinding the unknown by applying the inverse operand of its factor; and eventually (c) Providing the correct result. Participants were required to perform these steps in this exact order. At each step, the correct action was selected by pressing the key corresponding to one out of four possible options. In the first two steps, the options were the four possible operators (“+”, “-”, “*” and “/”, respectively). In the last step, the options were either “2”, “4”, “6”, and “8” (for numeric equations) or “ a ”, “ b ”, “ $-a$ ” and “ $-b$ ” (for the parametric ones), which were also the only possible results of each equation. For instance, in solving (2), participants needed to select “+” (to get rid of the left addend “ -2 ”) and then “/” (to unwind the unknown in “ $8*x$ ”) from the list of operators, and eventually pick up the correct answer (“4”) among the possible results (see Figure 1).

Four conditions were obtained by manipulating two variables within subjects: (a) whether equations contained *parameters* or *numbers*, and (b) whether the equation was updated *internally* or *externally*. In the *external* condition, the software calculated and displayed the intermediate version of the equation resulting from the application of the selected option after each response

(see Figure 1). Conversely, when the update was *internal* the software kept displaying the initial version of the equation, forcing participants to represent the intermediate forms within their heads. All the problems were displayed in black characters. The background color was light blue when the update was external and yellow when it was internal (see Figure 1). Problems were randomly mixed and separated by variable-length blank screens with a white background.

Predictions

A large network of prefrontal and parietal areas is engaged by the execution of complex tasks (Hill & Schneider, 2006; Cole & Schneider, 2007). However, the increasing representational demands of our experimental conditions should affect *differently* certain regions. Our view is that the control of behavior is mainly due to the activity of medial frontal and subcortical structures (and in particular the basal ganglia and the anterior cingulate cortex), while prefrontal and parietal cortices are mostly engaged in maintaining specific types of task information. The current task relies on two kinds of representations: (a) arithmetic knowledge retrieved during numeric calculations; and (b) intermediate states of the problem that must be maintained and updated during the solution process, and which we assumed to be represented as imagery of how the equations would be written after each operation. Our experimental conditions pose different demands on these two types of representations. The two external conditions do not require any of them, since everything is taken care of by the software. Internal parametric problems, on the other hand, require storing and manipulating an inner representation of the equation in order to solve it. Finally, internal numeric problems require both the manipulation of intermediate equation forms and the retrieval of arithmetic knowledge.

Our expectations were as follows. We predicted that there should be no difference between the two types of equations when the update was external. Given our identification of the LPFC

with ACT-R's retrieval buffer, we expected it to be mainly sensitive to retrieval demands only, and therefore its hemodynamic response to be higher for the internal numeric problems than for the others. Therefore, our prediction for this prefrontal region was: internal numeric > internal parametric = external (numeric =parametric). In contrast, activity in both the ACC and the caudate nucleus should exhibit a monotonic increase in activation from the simplest to the most difficult condition. The reason for this is that both retrieving arithmetic knowledge and maintaining intermediate problem states increases the amount of control states required and the amount of information transferred during cognitive operations. Therefore, our predictions for both cingulate and caudate nucleus were: internal numeric > internal parametric > external (numeric =parametric).

Methods

Participants and Task

Participants were fifteen normal, right-handed college students (age 18-24, $M = 20.3$, $SD = 1.7$, seven female). Shortly before the beginning of the experimental session, they were given written instructions about the task and a short computer-based practice session consisting of eight equations. An additional practice of 16 equations was given at the beginning of the scanning session, while high-resolution structural images were acquired². None of the practice equations was later used in the experiment. During the experiment, participants were presented with 128 different problems (32 per condition) grouped into 8 consecutive blocks of 16 trials each, with a short pause between each block. The equations were presented in random order.

² A comprehensive practice of 24 equations might seem too short. However, an analysis of performance of early (1-3) vs. late blocks (5-8) found an effect of blocks on latencies but no effect on accuracies, and no reliable change in the hemodynamic activity was detected.

Participants' responses were recorded through a data glove attached to their right hand.

Stimuli presentation and response collection was done using the Eprime (Psychological Software Tools, Pittsburgh PA) software package.

Image Acquisition and Analysis

Imaging data were collected with a Siemens 3T Allegra Scanner using a standard RF head coil. Each functional volume contained twenty-nine oblique axial slices (3.2mm thickness, 200mm FOV, 64 by 64 matrix, 3.125 by 3.125mm in-plane resolution) parallel to the AC-PC plane, with the twenty-second slice from the superior centered at the AC-PC line. Functional images were acquired using a gradient echo-planar-image (EPI) acquisition sequence (1,500ms TR, 30ms TE, 73° flip angle, 200mm FOV, zero slice gap). Functional acquisition was event-related, with image acquisition synchronized to stimulus onset, such that 15 volumes, each with 29 slices, were acquired during each 22.5 second trial. There were eight functional imaging blocks, each containing 16 experimental trials.

Anatomical images were acquired using a standard T1-weighted spin-echo pulse sequence at the identical slice location as the functional images using a finer in-plane resolution (3.2mm thickness, 200mm FOV, 256 by 256 matrix, 0.78 by 0.78mm in-plane resolution).

Pre-processing of the functional imaging data included six-parameter rigid-body motion correction using AIR (Woods, Cherry, & Mazziotta, 1992). Data were spatially transformed into a common space using the transformation gotten from co-registering anatomical images to a common reference structural MRI image³ by means of a 12-parameter automatic algorithm AIR (Woods, Grafton, Holmes, Cherry, & Mazziotta, 1998), and then smoothed with a 6mm FWHM 3-D Gaussian filter to accommodate individual differences in anatomy.

³ The structural reference image is available at this URL: <<http://act-r.psy.cmu.edu/mri/>>

Behavioral Results

Data from one participant were discarded because his mean latencies were more than three standard deviations above the average in all conditions. The mean reaction time for each of the three responses was calculated for each condition and averaged over all participants. Only correct trials were included in the analysis. Figure 2 plots the average reaction times for the three responses in a trial, with the individual line plots representing the four conditions. Table 1 contains the comprehensive latencies (from the equation onset to the final answer) in the correct trials, as well as the average accuracy across all problems, for each condition.

Performance in the external numeric and external parametric problems was very similar, relative to the large differences among the other conditions. They differed in terms of latency ($t(13) = 2.82, p = .01$) but they did not on accuracies ($t(13) = 1.16, p = .26$). As expected, the additional representations that had to be processed in the other conditions exerted significant tolls. The internal parametric condition was more difficult than its external counterpart, as indexed by decreased accuracy ($t(13) = -2.36, p = .03$) and higher latencies ($t(13) = 10.42, p < .0001$). Similarly, the internal numeric condition was significantly more difficult than the internal parametric (reduced accuracy, $t(13) = -2.89, p = .01$; and higher latency: $t(13) = 4.97, p = .0003$).

Confirmatory Analysis

Five predefined ROIs were used in the confirmatory analysis, all of them located in the left hemisphere. These regions constitute a subset of larger group of 16 that had been previously mapped onto corresponding modules of the ACT-R architecture (e.g., Anderson et al., 2004; Anderson, 2005; 2007). They are marked in black in Figure 3 and listed in Table 2, together with their corresponding anatomical structure, their size, their computational counterpart, and the Talairach-Tournoux coordinates of their centroids.

It must be noted that, despite our design being apparently factorial, the retrieval of arithmetic facts was not supposed to take place in the external but only in the internal numeric problems. The two external conditions (parametric vs. numeric) were not predicted to differ, and, as expected, in none of the predefined regions was the hemodynamic activity significantly dissimilar between them. Therefore, instead of analyzing our data as 2 by 2 factor manipulation, we excluded the external numeric problems and concentrated on the three remaining conditions. These conditions vary monotonically in terms of behavioral difficulty and representational demands: the internal parametric condition differs from the external parametric because it requires the maintenance of intermediate equation forms, while the internal numeric differs from its parametric counterpart because it additionally requires the retrieval of arithmetic knowledge.

All the incorrect and the first trials of each block were excluded from the analysis. The blood-oxygenation level-dependent (BOLD) response for each trial was computed using the last data scan from the previous trial as the baseline from which percent change was calculated over the full time course of the trial. For each subject and for each ROI, trials belonging to the same condition were averaged together. As a measure of the overall activity elicited by different conditions in each brain region, the positive part of the area under the hemodynamic curve was also calculated for each subject. We adopted this measure because it is not compromised by pre- and post-peak negative dips that are frequently present in the BOLD response, and it is sensitive to both the absolute magnitude of the response and its duration (Anderson, 2005). The area under the curve was then used to calculate two critical contrasts for each region: (a) between the two parametric conditions (internal vs. external update), to examine its sensitivity to the update factor; and (b) between the two internal conditions (numeric vs. parametric), to examine its sensitivity to the retrieval factor. The results of these contrasts are listed in the last two columns

of Table 2, while Figure 4 displays the time course of the BOLD response (averaged across subjects) in the predefined regions.

The first of our predefined regions corresponds to the part of the left motor cortex that is responsible for hand movements, and has been mapped to ACT-R’s manual module. The varying difficulty across conditions should have no impact on its overall activity (since the amount of motor programming remains equal), but should be reflected in a significant Scan by Condition interaction, because of the increased lag between finger presses (see Figure 2). As expected, both our contrasts turned out to be non-significant ($t(13) > 0.66, p > .52$). A repeated measures ANOVA was run on the averaged BOLD responses, using Scan (16 values) and Condition (3 values) as within-subject factors. In this and all the subsequent analysis, subject was always treated as a random factor. The results conformed to our predictions (Effect of Condition: $F(2,26) = 0.72, p = .50$; interaction: $F(30,390) = 3.08, p < .0001$. See Figure 4, Plot 1).

Three other ROIs exhibited the pattern we predicted for control-related regions, with the hemodynamic response increasing monotonically across condition, and both contrasts being significant. These regions are located in the dorsal ACC, the posterior parietal cortex, and in the head of the caudate nucleus (See Table 3 and Figure 3, regions marked in black). The contrast between the internal numeric and the external parametric conditions was also significant ($t(13) > 3.78, p < .003$, uncorrected), as well as the main effect of Condition on the areas under the curve ($F(2,26) > 9.68, p < .001$).

The BOLD response in our predefined ACC and caudate regions conformed to our predictions (See Figure 4, Plots 2 and 5). A comparison between the BOLD responses in ACC and the caudate nucleus yielded a non-significant ROI by Condition interaction ($F(2,26) = 1.83, p = .18$), suggesting that they were similarly impacted by the increased demands for control.

The predefined left prefrontal region also conformed to our prediction, showing no significant difference between the two parametric conditions, but a significantly larger response for the internal numeric problems (See Table 3). This pattern is consistent with the increased demands for retrievals elicited in the internal numeric condition.

The difference between our lateral prefrontal and anterior cingulate regions was further tested by means of a Scan (16 values) by Condition (3 values) by ROI (2 values) ANOVA. A significant main effect of ROI ($F(1,13) = 5.36, p = .04$) and a significant interaction between ROI and Condition ($F(2,26) = 3.41, p < .05$) were found, confirming that different problem types had a different effect on those brain areas. The three-way interaction between Scan, Condition and ROI was also significant ($F(30, 390) = 1.89, p = .004$). The same interaction held when comparing the hemodynamic response in our predefined prefrontal region with the head of the caudate nucleus (Condition by ROI interaction: $F(2,26) = 7.04, p = .004$; Condition by ROI by Scan: $F(30,390) = 6.95, p < .0001$) and the left posterior parietal cortex (Condition by ROI interaction: $F(2,26) = 5.44, p = .01$; Condition by ROI by Scan, $F(30,390) = 4.29, p < .0001$).

Discussion

Our confirmatory analysis essentially supports our predictions. We found responses of identical magnitude in the motor region and the characteristic sensitivity of the lateral prefrontal cortex to arithmetic retrievals. Consistently with their involvement in cognitive control, monotonically larger responses were found in the dACC and the caudate nucleus,

Exploratory Analysis

An exploratory analysis was used to identify other regions reliably responding to the manipulations of the experiment. All the incorrect and the first trials of each block were excluded from the analysis. Functional imaging data were analyzed using mixed effects ANOVA models

(Braver et al, 1997) within the NIS system (<http://kraepelin.wpic.pitt.edu/nis/>). In the analysis, subject was treated as a random factor and within subject factors included Condition and Scan (16 values). This analysis was used to identify a number of brain areas that showed differential BOLD profiles in response to different conditions, indicated by a significant Condition by Scan interaction. The lower bound degree of freedom correction was applied to correct for non-sphericity due to non-independence of scans, using an alpha level of $p < .01$. To correct for multiple comparisons issues, only those regions having a contiguous cluster size of 20 or more significant voxels are reported (Forman et al., 1995).

A preliminary comparison between the two externally updated conditions (numeric and parametric) showed no reliable difference in our fMRI data. Therefore, we concentrated on three critical conditions: external and internal parametric and internal numeric. Here, eight different regions of interest (ROI) matched our criteria: they are marked in red in Figure 3 and listed in Table 3, together with their corresponding anatomical structure, their size, and the Talairach-Tournoux coordinates of their centroids.

For each of these regions, the average BOLD responses and the corresponding area under the curves were calculated for each condition, using the same method as in the confirmatory analysis. The areas under the curves were used to calculate the same two contrasts (external vs. internal parametric and internal parametric vs. numeric). These eight regions divide into two categories. Four of them (ROI 4, 5, 6 and 7) show the same pattern that we predicted for the lateral prefrontal cortex: a similar response for the two parametric conditions (whether the update was internal or external), but a significantly larger response for the internal numeric problems. The other four (ROI 1, 2, 3, and 8) exhibit a substantially monotonic pattern, showing higher peaks and larger areas under the curves as difficulty increased.

In the first group, two regions (ROI 4 and 5) are prefrontal clusters comprehending large portions of the left and right inferior and middle frontal gyri (BA9/46; the left one also extends to the precentral gyrus). The left region partly overlaps with our predefined prefrontal ROI (see Figure 3), and both their hemodynamic responses fully conform to our expectations for memory retrievals. The same pattern was also uncovered in the left and right insular region (ROI 6 and 7)

In three of the remaining four regions, both contrasts were significant at $p < .05$ (see Table 2), suggesting that these regions were sensitive to both factors. They consisted of a medial region in the prefrontal lobe, encompassing the Supplementary Motor Area and the dorsal part of ACC (ROI 1); a large parietal cluster (ROI 2), centered around the left Superior Parietal Lobule; and a region between the left middle occipital and the left inferior temporal gyri. The first two regions partly overlapped with two of our predefined ROIs (See Figure 3).

In the fourth region (ROI 3), centered in right Superior Parietal Lobule, the contrast between the two external conditions was only marginally significant ($t(13) = 2.06, p = .06$). This region was compared with its left counterpart (ROI 2) to see whether there was any significant difference. A Condition (3 values) by Region (right vs. left parietal) ANOVA on the areas under the curve uncovered no significant main effect of the Region ($F(1, 13) = 2.31, p = .15$) and no significant interaction ($F(2, 26) = 0.52, p = .60$). Given the substantial similarity of their hemodynamic responses, it was concluded that our right parietal particle exhibited the same monotonic pattern as its left counterpart.

Two distinct peaks of activity were found in our left parietal cluster: one in the left intra-parietal sulcus (Talairach coordinates: $x = -46, y = -44, z = 47$) and one centered in the left superior parietal lobule (Talairach coordinates: $x = -30, y = -72, z = 42$; See Figure 3). The first peak was located in close proximity to left horizontal portion of the intra-parietal sulcus (lHIPS).

This region is the most important of the three circuits identified by Dehaene, Piazza, Pinel and Cohen (2003), supposedly responsible for a modality-independent representation of numerical magnitude. The second spot was in close proximity of the left precuneus, which is responsive to both mental imagery and episodic memory retrievals (e.g., Fletcher et al., 1995).

The pattern of activation we found in our parietal ROI could actually be the sum of two distinct hemodynamic responses, one due to number processing and one due to mental imagery. To rule out this possibility, two sub-regions were identified and analyzed separately. The first region was a box of $3 \times 2 \times 2$ voxels (375mm^3) centered on the IHIPS peak, and the second one a box of $4 \times 4 \times 4$ voxels ($2,000\text{mm}^3$) centered on the precuneus. Their hemodynamic patterns turned out to be remarkably similar. No significant ROI by Condition interaction was found ($F(2,26) = 1.02, p = .38$), suggesting that these two sub-regions were not responding significantly differently to the same conditions. Similarly, a Condition by ROI ANOVA on the areas under the curves failed to uncover a main effect of the ROI ($F(1,13) = 1.48, p = 0.25$) and found just a marginally significant interaction ($F(2,26) = 3.01, p = .07$).

Discussion

The results of the exploratory analysis are consistent with the confirmatory analysis and conform to our expectations. First, in contrasting the two types of externally updated problems, no regions were reliably affected by the mere presence of numbers vs. parameters. Second, when comparing the three critical conditions, the activity in both the left and right prefrontal clusters conformed to our expectations for memory retrieval, being scarcely, if at all, affected by the extra effort in maintaining intermediate problem states, but strongly engaged when arithmetic retrievals were required. This pattern also seemed to be mirrored in the two insular regions.

Also, our medial prefrontal cluster, which crucially encompasses part of our predefined

cingulate ROI, conformed to our prediction of larger responses for more demanding problems, and its hemodynamic activity differed significantly from the prefrontal cortex. A very similar hemodynamic pattern was also exhibited by two parietal and one occipito-temporal region.

Computational Model of the Task

Although the strategy to solve an equation is well defined in general terms, a number of degrees of freedom remain—for example, in how to interleave arithmetic retrievals and problem manipulations. More detailed strategies were derived from a comparative analysis of the latency data.

The pattern in Figure 2 provides some informative clues. Reaction times follow almost identical patterns in the two external conditions, implying an identical strategy. Reaction times for the first response are similar in the two internal conditions, and in both cases larger than in the external problems: this suggests that participants are performing the same series of cognitive operations, which, in turn, rules out the retrieval of arithmetic facts, since it cannot occur in the parametric condition. The model assumes that participants use this first step not only to determine whether the response is an addition or a subtraction, but also to encode the right-hand side of the equation. It follows that, in the internal numeric problems, all the arithmetic retrievals must occur in the last two steps. In particular, it was hypothesized that the last two retrievals occur between the second and the third response, and only the first one (always an addition or subtraction) takes place between the first and the second, compensating for the larger number of mental manipulations occurring in this phase.

Given such constraints, three solution strategies were derived for the four types of equations and implemented in an ACT-R model⁴. A visual rendition of these strategies is

⁴ The model is available at this URL : <<http://act-r.psy.cmu.edu/publications/pubinfo.php?id=716>>

depicted in Figure 5⁵. The figure details the activity of three modules (retrieval, imaginal, and manual, whose contents are more clearly interpretable) while solving exemplificative equations of the three relevant types. In the figure, times flows down the chart, and individual module's periods of activity are represented by boxes on each module's track. The boxes' contents illustrate the operation being performed, while their vertical extent reflects the time needed to complete it.

The model replicates our behavioral results ($r = .959$, $RMSE = 116.65\text{ms}$; see the dotted lines in Figure 2). Two parameters were estimated: the first was the latency factor, which scales retrieval times from declarative memory (Anderson et al., 2004), and was set to 0.17. The second parameter was the time needed to complete each manipulation of the contents of the imaginal module, and was set at 50ms. This parameter contributed to account for the higher reaction times in the internal numeric condition, where the need to integrate the results of arithmetic calculations within the internal problem representation eventually required a larger number of manipulations in the imaginal buffer (see Figure 5).

Once the model was fit to the behavioral data, the predicted hemodynamic responses were calculated. The BOLD response $B(t)$ for a point event occurring at time $t = 0$ was approximated as a gamma function (Glover 1999):

$$B(t) = t^a e^{-t} \quad (3)$$

The *cumulative* BOLD response $CB(t)$ for a predefined region was calculated by convolving equation (3) with the corresponding module's demand function, as proposed by

⁵ The strategies for the two internal conditions are essentially similar, both requiring an initial encoding of the right-hand side of the equation, and a subsequent comparison with the addend on the left hand side. The strategy implemented only works for the restricted set of equation used in this experiment.

Anderson, Qin, Sohn, Stenger and Carter (2003) and Anderson (2005):

$$CB(t) = M \int_0^t D(\tau) B\left(\frac{t-\tau}{s}\right) d\tau \quad (4)$$

where $D(\tau)$ is the value of the demand function at time τ . Demand functions were calculated for each module by averaging the time course of its activity over all the trials belonging to the same condition. As in previous simulations (e.g., Anderson, 2005), the retrieval module was considered active between the initiation and the completion of a retrieval; the motor module was considered active from the initial preparation of a motor movement through its final realization; and the imaginal module was considered active from the beginning to the end of an internal problem manipulation. The goal module was considered active during the execution of any production rule that modified or tested for a control state. Differently from what has been previously done, activity in the procedural module was calculated as the amount of information relayed by each production being executed. Production rules transfer information by binding values to variables in their condition side, and relaying them to their action side. Therefore, the amount of information transferred was quantified as the number of variable bindings occurring within each production rule.

Both the parameters a in (3) and s in (4) concur in determining the shape of the response function and its peak onset, while M in (4) scales its amplitude. These parameters were estimated for each module, but remained identical across conditions. Although fit independently, their values were consistently similar across modules (see Table 4).

Figures 4 reports the estimated BOLD responses obtained for each module (dotted lines) together with the original hemodynamic data from our predefined ROIs (solid lines). The last two columns of Table 4 report the correlation coefficients and the root mean squared errors (*RMSE*) between the predicted and observed responses. The model's predictions correlated

significantly with the actual data ($r > .93$ for all ROIs) and were consistent with the different patterns observed in different regions.

General Discussion

This paper examined the effect of manipulating the amount of control required to solve algebraic equations by varying the amount and type of the internal representations needed. The lateral prefrontal regions were significantly affected only by increased demands for arithmetic retrievals, and not by other representational loads, even when the latter had significant and large effects on behavior and in other brain regions. This result is in agreement with previous studies where lateral prefrontal activity was dissociated from sheer difficulty (Barch et al., 1997) and its contribution to control was identified with holding on-line information (Cole & Schneider, 1997). On the contrary, the dorsal anterior cingulate cortex and the caudate nucleus were both affected by the amount of representations to be maintained, retrieved or processed during the task, independently of their nature.

The BOLD responses in the predefined cingulate and caudate regions were modeled as reflecting two computationally distinct aspects of control: the number of control states required, and the amount of information transferred during representational manipulations. This interpretation is crucial to our view of control, and was successful in reproducing the hemodynamic patterns and predicting the dissociation between these structures and the prefrontal regions. A number of alternative accounts, however, must be taken into consideration.

First, trial difficulty correlates with mental effort, which some authors consider the driving force (e.g., Critchley et al., 2003). Our results alone cannot rule out this explanation. Nonetheless, other studies indicate that dACC responses does not decrease with practice, which instead reduces difficulty and assuages mental effort (Fincham & Anderson, 2006)

Second, one could argue that, on a conflict monitoring perspective, the more difficult conditions have more opportunities for conflict among possible operations, in turn explaining the dACC responses within conflict-monitoring framework. On the other hand, the conflict detection should be followed by some compensative top-down control bias from prefrontal cortex. However, we failed to find a prefrontal region showing a difference between the internal parametric and external parametric conditions to match the difference in the anterior cingulate.

Third, activity in the dACC has also been proposed to reflect cognitive preparation, as distinct from the on-line processing occurring the prefrontal regions (Cole & Schneider, 2007). More complex equations certainly require more initial preparation. Nonetheless, BOLD responses in the ACC seem to extend throughout all the time needed to solve the equation, and not to be limited at an early stage where its difficulty is detected. It is conceivable to stretch this view and envision preparation at a finer-grained scale, essentially occurring before single cognitive operation. At this level, however, it becomes computationally undistinguishable from the control-state view outlined in this paper.

None of these explanations makes explicit predictions about the caudate nucleus, whose activity was also affected by condition difficulty. Brown and Braver (2005), however, suggested that dACC might contribute to preparation and control simply by reflecting learned task-specific error likelihoods, which can be used by other regions to adjust for control. Encoding of the error likelihood depends on error-related signals conveyed through the dopamine pathways originating in the basal ganglia, opening the possibility for a similar pattern in both regions. Since in our experiment the condition difficulty is correlated with error rates, this alternative explanation cannot be discarded on the basis of our results. However, there are subtle differences in the pattern of responses found in ACC and the caudate nucleus, which emerge naturally in our

modeling approach but are not explicitly predicted by this account.

The pattern of activation in both our predefined and exploratory parietal regions was consistently similar to that found in dACC and the caudate nucleus. Eventually, the hemodynamic responses in the parietal cortices were modeled as reflecting the costs of maintaining and updating intermediate representations of an equation. Our experimental task, however, does not allow for a tight control for these kinds of demands, and our mapping relied on previous experiments (e.g., Anderson, 2005; Anderson, Albert & Fincham, 2005). Alternatively, one can imagine parietal regions as playing a role in cognitive control. Furthermore, parietal responses might have been affected by other factors that were not controlled for (such as visual scanning strategies), or were concurrently manipulated in our design (such as memory retrievals).

A number of researchers (e.g., Dehaene, 1997) have suggested that human mathematical problem solving is grounded on specialized brain circuits supporting numerical representations. In fact, activity related to automatic number processing has been found to occur during arithmetic tasks (Dehaene et al., 2003) and even in response to subliminally primed stimuli (Naccache & Dehaene, 2001). When comparing the two externally updated conditions, however, we could not find any reliable effect due to the mere presence of numbers vs. parameters. We cannot rule out the presence of hemodynamic activity reflecting number processing, its effects must have been small compared with the larger ones due to the differences in representational demands. This suggests that, while algebraic problem solving might also be rooted in numerical abilities, it was made possible by those domain-general adaptations that achieved greater control over internal representations and underlie all complex mental activities.

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Table 1: Behavioral Results

		Equation			
		Numeric		Parametric	
Update	Internal	6,514ms	(242)	5,277ms	(216)
	Internal	0.75	(0.03)	0.87	(0.03)
	External	3,579ms	(125)	3,820ms	(162)
	External	0.96	(0.01)	0.95	(0.01)

Table 1. Mean latency in milliseconds (standard error) and, in the line below, mean accuracy (standard error) by equation and update type.

Table 2: Summary of Confirmatory Analysis

ROI	Grey matter (Brodmann Area)	Corresponding ACT-R Module	Size (Voxels)	T-T Coordinates	Areas Under the Curve		
					External Parametric	Internal Parametric (<i>T</i> value, vs. External)	Internal Numeric (<i>T</i> value, vs. Parametric)
1	Precentral gyrus (BA3)	Manual	5 x 5 x 4	-42, -20, 50	4.85	4.55 (-0.66)	4.88 (0.51)
2	Anterior cingulate cortex (BA24/32)	Goal	3 x 5 x 4	-6, 10, 39	4.09	5.11 (2.27*)	6.94 (2.54*)
3	Posterior parietal lobule, Precuneus (BA7/39)	Imaginal	5 x 5 x 4	-24, -63, 40	5.27	6.82 (3.15**)	7.98 (2.27*)
4	Middle frontal gyrus (BA9/46)	Retrieval	5 x 5 x 4	-42, 23, 24	2.69	2.60 (-0.35)	5.32 (5.51**)
5	Head of the caudate nucleus	Procedural	4 x 4 x 4	-13, 10, 7	1.99	2.66 (2.86*)	4.02 (3.61**)

Table 2: The five predefined ROIs (and their correspondent ACT-R modules) used in the confirmatory analysis. The last three columns contain the average positive areas under the curve for each condition, together with the *T* values obtained by contrasting the two parametric (internal vs. external update) and the two internal (numeric vs. parametric) conditions (**p* < .05; ***p* < .01, uncorrected, *DF* = 13).

Table 3: Summary of Exploratory Analysis

ROI	Gray matter (Brodmann Area)	Size in voxels	T-T coordinates	Mean (max) <i>F</i> value	Areas under the curve		
					External parametric	Internal parametric (<i>T</i> value, vs. external)	Internal numeric (<i>T</i> value, vs. parametric)
1	Left Anterior Cingulate (BA32)	240	-2, 14, 43	7.05 (14.14)	4.26	5.63 (3.36**)	8.27 (3.49**)
2	Left Superior Parietal Lobule (BA7)	678	-29, -58, 48	7.78 (17.98)	7.05	8.32 (2.15*)	10.51 (4.08**)
3	Right Superior Parietal Lobule (BA7)	237	27, -62, 45	6.33 (10.08)	7.35	8.46 (2.06)	10.56 (2.89*)
4	Left Middle Frontal Gyrus (BA9)	395	-40, 12, 31	6.65 (12.32)	4.24	4.36 (0.26)	7.82 (5.71**)
5	Right Inferior Frontal Gyrus (BA9)	46	48, 6, 32	5.57 (6.80)	5.37	5.64 (0.41)	8.75 (5.05**)
6	Left Insula	29	-28, 24, 6	7.14 (10.41)	2.74	3.08 (0.52)	5.63 (4.41**)
7	Right Insula	26	35, 15, 8	5.78 (6.90)	2.71	3.61 (1.98)	5.90 (2.45*)
8	Left Inferior Temporal Gyrus, Middle Occipital Gyrus (BA19)	64	-46, -58, -4	5.80 (7.25)	5.09	6.67 (4.63**)	8.13 (3.25**)

Table 3: List of brain regions showing a significant ($p < .01$) Scan \times Condition interaction

when comparing the three critical conditions (external parametric vs. internal parametric vs. internal numeric). The last three columns contain the average positive areas under the curves for each condition, together with the T values obtained by contrasting the two parametric (internal vs. external update) and the two internal (numeric vs. parametric) conditions (* $p < .05$; ** $p < .01$, uncorrected, $DF = 13$).

Table 4: Model's Parameters and Fit

Module	Parameter Values			Fit	
	a (eq. 3)	s (eq. 4)	M (eq. 4)	r	$RMSE$
Manual	4.0	1.0	0.14	0.968	0.062
Retrieval	3.7	1.5	0.13	0.932	0.058
Goal	3.7	1.1	0.23	0.982	0.045
Procedural	3.9	0.9	0.05	0.939	0.050
Imaginal	2.3	1.6	1.09	0.972	0.066

Table 4: The three parameters that were estimated independently for each module to simulate the hemodynamic responses in the corresponding regions (See main text for details), together with the corresponding measures of fit with the experimental data.

Figure Captions

Figure 1. Design of our experiment. The two series of panel represent the time courses of two possible trial types, with either internal (top panels, in grey) or external update (bottom panels, in black). Equations could be numeric or parametric (not depicted), and were always followed by a white panel whose duration was stretched to give each trial a fixed duration of 22.5 seconds. All the problems required exactly three behavioral responses in the form of right-hand finger presses, corresponding to the three steps needed to solve each equation (eliminating the left addends, eliminating the factor in the main term, and giving the result, respectively).

Figure 2. Participants' mean latencies by response and condition (solid lines), together with the correspondent predictions by our model (dotted lines).

Figure 3. Seven of the eight regions identified in our exploratory analysis (in red; ROI 8 is below the displayed slices) and the five predefined ROIs (in black) overlaid onto 18 axial slices of our reference brain. The AC-PC line passed through Slice 22 (not shown).

Figure 4. Time course of the BOLD response for the three critical conditions in our five predefined ROIs (solid lines), together with the corresponding hemodynamic responses predicted by the model (dotted lines). In each plot, the first scan is the baseline, while the following 15 belong to the trial.

Figure 5. A visual rendition of the strategies implemented by the model, together with their time course. Boxes represent the periods of time during three modules (retrieval, in light grey; imaginal, in dark grey; and manual, in black) were active while solving an example trial of each condition. The contents of the boxes illustrate the operations being performed by each module during each period of activity. The timeline starts at the onset of the equation: the fixation period (corresponding to the first scan) is omitted.

Figure 1

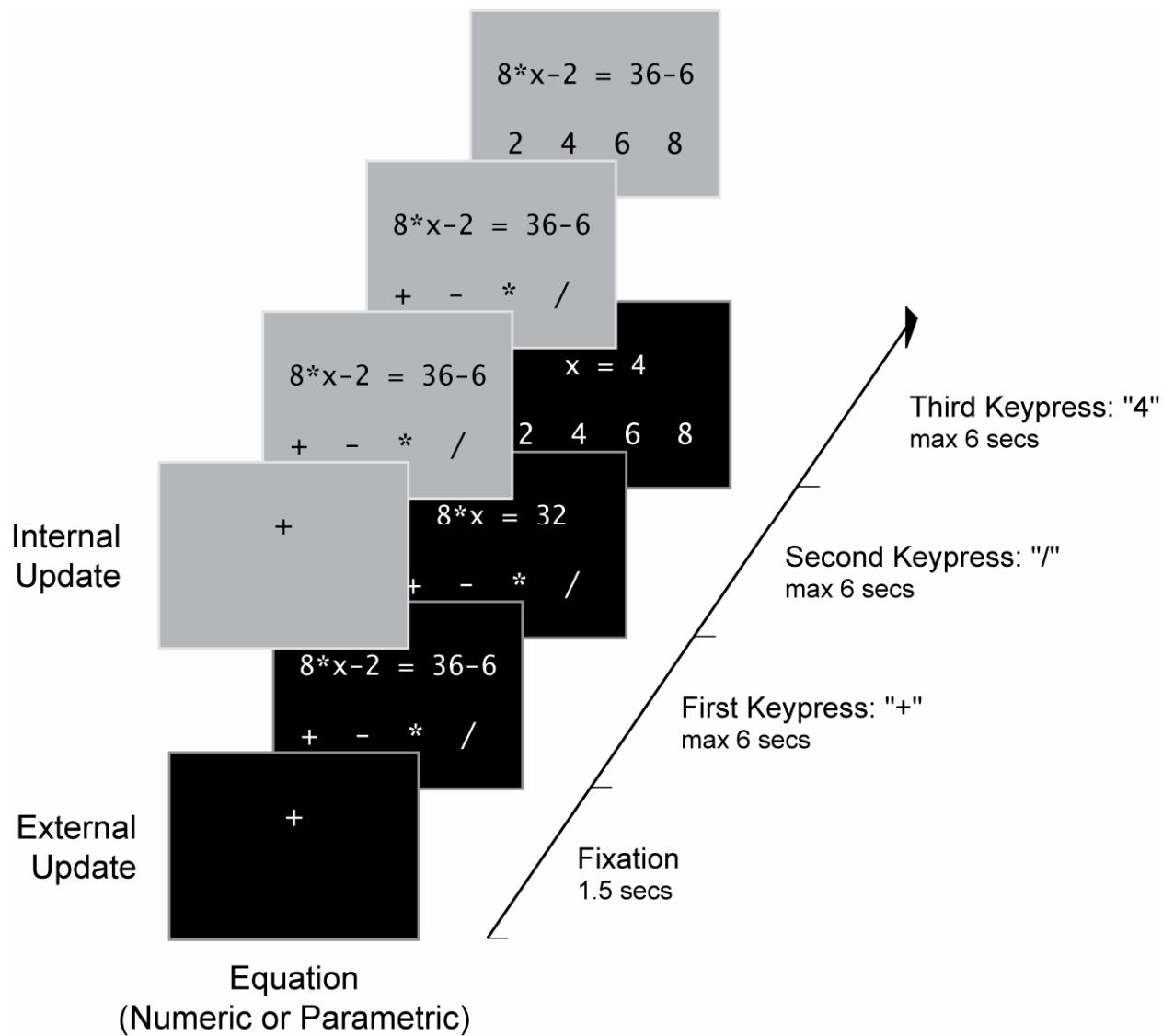


Figure 2

Reaction Times by Keypress and Condition

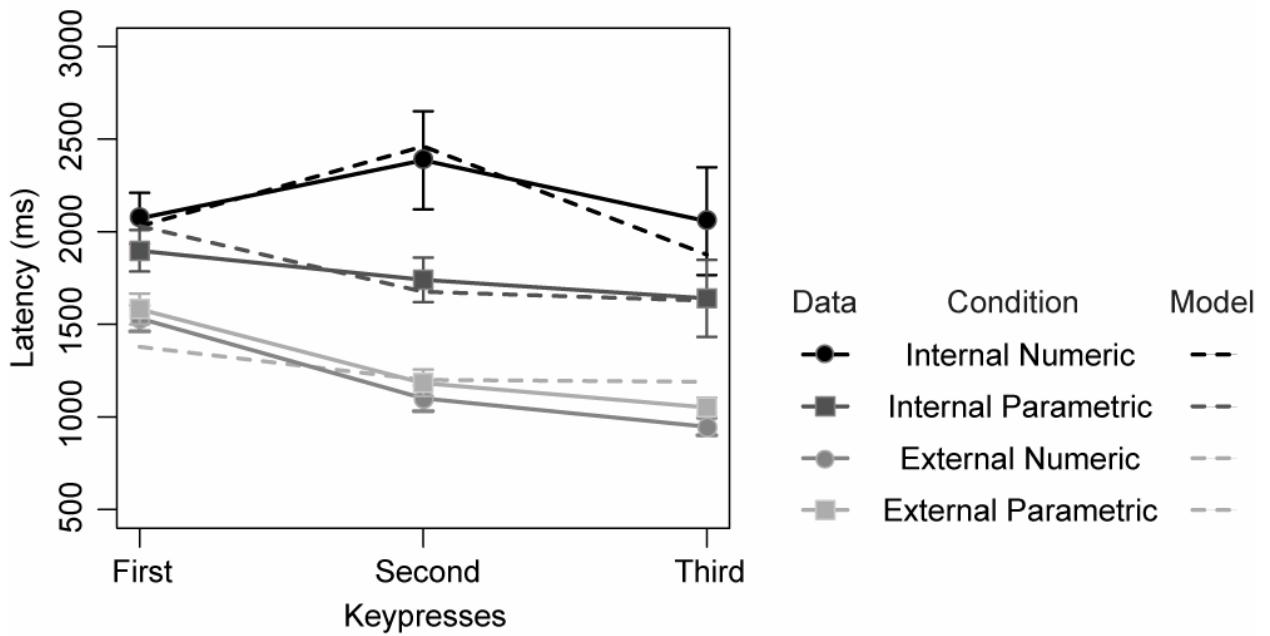


Figure 3

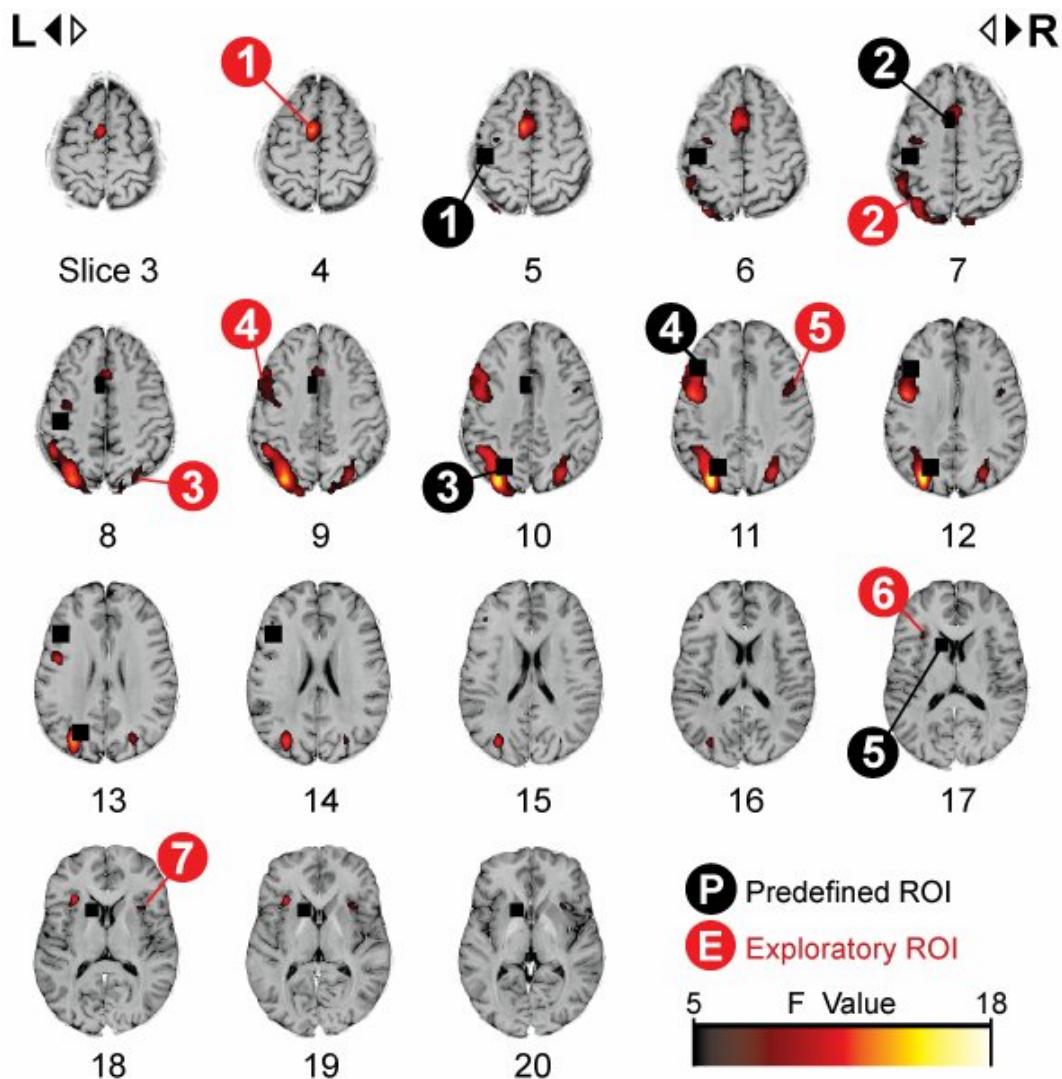
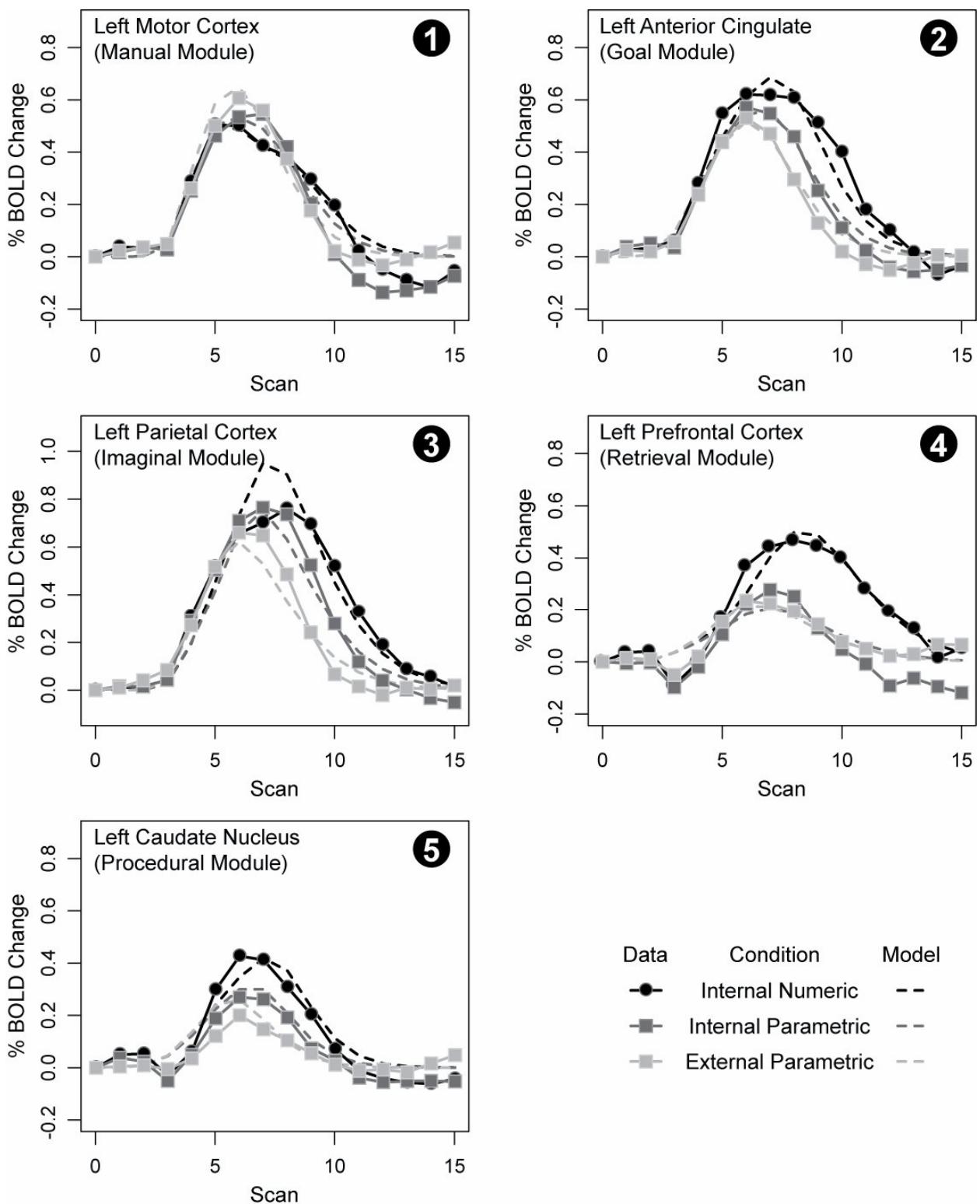


Figure 4



Data	Condition	Model
●	Internal Numeric	---
■	Internal Parametric	---
□	External Parametric	---

Figure 5

