Use of a Cognitive Architecture and fMRI to Mutually inform Each Other

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Abstract

Anderson et al (in press) performed a pair of fMRI studies that identified three cortical regions with three components of an information-processing model of algebraic problem solving. There is a left parietal ROI where the algebraic expression is represented and transformed, a left prefrontal ROI where information for solving the task is retrieved, and a motor ROI where hand movements to produce the answer are programmed. Here we describe an fMRI study of a more abstract symbol-manipulation task designed to articulate the characterization in Anderson et al. Participants learned to associate words with instructions for transforming strings of letters. The study manipulated the need to retrieve these instructions, the need to transform the strings, and whether there was a delay between calculation of the answer and the output of the answer. As predicted the left parietal ROI mainly reflected the need for a transformation and the left prefrontal ROI the need for a retrieval. Homologous right ROIs showed similar but weaker responses. Neither the prefrontal nor the parietal ROIs responded to delay but the motor ROI did respond to delay, implying motor rehearsal over the delay. Except for the motor ROI, these patterns of activity did not vary with response hand. In an ACT-R it was shown that the activity of an imaginal buffer predicted BOLD response of the parietal ROI, the activity of a retrieval buffer predicted the BOLD response of the prefrontal ROI, and the activity of a manual buffer predicted the BOLD response of the motor ROI. We also found an anterior cingulate ROI that responded robustly to all three factors – transformation, retrieval, and delay and we speculate about its possible interpretation.

Anderson, Qin, Sohn, Stenger, and Carter (in press) described how one can use fMRI to track different cognitive components in the execution of a complex task like solving an equation. Performing such a task involves a number of processes including retrieval of relevant information (such as arithmetic facts) from declarative memory, representing and transforming the problem (in this case, a mental representation of the equation), and programming motor actions (in this case, to produce the solved equation). There are cognitive architectures (Anderson & Lebiere, 1998; Meyer & Kieras, 1997a,b; Pew & Mavor, 1998) that give precise accounts of the involvement of various components in the performance of a task like this. Anderson et al (in press) show that, given an association of the components of such an architecture with brain regions, it is possible to make a priori predictions about the level of activation in these regions. fMRI imaging provides sufficiently precise and tractable methodology that one can test these predictions. Such an effort can be quite informative to the development of cognitive models for complex task. The purpose of this paper is to describe this methodology and show how it can be used to test the ACT-R theory (Anderson & Lebiere, 1998) and guide the development of models within that theory. However, this model-development methodology is not unique to the ACT-R theory nor are the conclusions. The methodology can be applied to any well specified architecture and we believe that it would force convergence among different architectures in terms of the characterizations they give of the cognitive processes involved in the performance of a task. We also suspect that the methodological program, if successful, would help bring convergence in the brain imaging literature on the function of different brain regions.

This paper will begin with a brief description of that architecture and the past studies that we have done testing the associations of components of that architecture with brain regions. Then it will describe a new experiment that was motivated to address some of the issues raised by the past experiments. After describing this experiment and its results the paper willdescribe a model that we developed for this task and how the development of an accurate model was informed by the results of the imaging study. We will show how this research resulted in a refinement of the ACT-R architecture and how it has advanced our understanding of the behavior of particular brain regions.

The ACT-R 5.0 Architecture and the BOLD Function

Figure 1 illustrates the basic architecture of ACT-R 5.0. There are a set of **modules** devoted to things like identifying objects in the visual field, controlling the hands, retrieving information from declarative memory, or keeping track of current goals and intentions. The central production system is not sensitive to most of the activity in these modules but rather can only respond to information that is deposited in the **buffers** of these modules. For instance, people are not aware of all the information in the visual field but only the object they are currently attending to. Similarly, people are not aware of all the information in long-term memory only the fact currently retrieved. Each module makes this information available as a chunk (an ACT-R declarative structure) in a buffer. As illustrated in Figure 1 the core production system can recognize patterns in these buffers and make changes to these buffers – as for instance, when it makes a request to perform an action in the manual buffer. In the terms of Fodor (1983) the information in these modules is largely encapsulated and they communicate only through the information they make available in their buffers.

This paper will be principally focus on the same three buffers that were of interest in Anderson et al (in press). The first buffer is an imaginal buffer that holds the representations of problems, like mental images of equations, while operations are being performed on these problems. In line with other work (Dehaene, Piazza, Pinel, & Cohen, submitted; Reichle, Carpenter, & Just, 2000) we found evidence for this buffer in the left parietal cortex. The second buffer holds information retrieved from declarative memory and is associated with a portion of the left prefrontal cortex close to a region that has also been identified by a number of other investigators (Buckner, Kelley & Peterson, 1999; Cabeza, Dolcos, Graham, & Nyberg, 2002; Donaldson, et al., 2001; Fletcher & Henson, 2001; Lepage, Ghaffar, Nyberg, & Tulving, 2000; Wagner, Maril, Bjork & Schacter, 2001; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001). The third is the manual buffer which is responsible for programming and execution of hand movements. It is associated with the region of the motor cortex that controls these movements (Roland, Larsen, Lassen, and Skinhoj, 1980)

Anderson et al performed a study of two algebraic tasks that served to test certain components of the architecture. The first experiment involved solution of real algebraic equations like $3x + 5 = 23$. The second, motivated in part to show that the imaging results did not depend on the involvement of arithmetic, used an artificial string transformation task which preserved many of the formal properties of algebra but did not involve arithmetic. ACT-R models (Anderson, Reder, & Lebiere, 1996 for real algebra; Blessing and Anderson, 1996, for artificial algebra) already existed for these two tasks. These models were updated to correspond to ACT-R 5.0 and to generate predictions about the fMRI signal. As we will describe later, it is possible to generate predictions for the exact form of the BOLD (blood oxygen level dependent) function. Here we will just describe the basic character of the predictions.

Figure 2 illustrates the three brain ROIs (regions of interest) that were identified in exploratory analysis in the study. All three regions were left lateralized. The same brain regions were used to predict the BOLD functions in both studies. The parietal ROI was associated with the imaginal buffer in ACT-R that was used to build up a representation of the equation and perform transformations on the equation. As such it responded to equations of all complexity but produced higher magnitude BOLD functions when more transformations were required. Figure 3a shows the response of this area as a function of number of transformations in the second study (and the predictions of the ACT-R model). Figure 3b shows the behavior of the prefrontal ROI (and the ACT-R predictions) for the same three levels of transformation. It is postulated to track memory retrievals. No information needs to be retrieved in the 0-transformation condition and so the function is basically flat. The degree of rise in the other conditions can be predicted by the number of facts that need to be retrieved. Figure 3c shows the behavior of the left motor ROI that corresponds to the region controlling the right hand. It basically produces identical BOLD functions in all conditions but the onset of these functions is differentially delayed in the different conditions corresponding to the different latencies in responding.

Qin, Sohn, Anderson, Stenger, Fissell, Goode, & Carter (submitted) did an follow up to this study. Rather than using the regions that accidentally came out in an exploratory study, they used predefined regions 5 voxels wide, 5 voxels long, and 4 voxels deep (approximately 16x16x13 mm) based on the regions found in Anderson et. al. In the case of the posterior parietal region, which was quite large in Figure 3, we chose to center on the posterior portion of this region.[1] The study involved the same artificial symbol system as the second study in Anderson et al (in press) but in this case participants received five days practice on this task and were imaged on the first and fifth day. Thus, it was possible to inspect the effect of practice on the BOLD function in these regions. There was very little effect in the parietal region, a result that was predicted since it is necessary to go through the same steps of transformation at all levels of practice. Practice had no effect on the shape of the BOLD functions in the motor region but the motor functions did move forward in time to reflect the more rapid responding on Day 5. In contrast to these regions, the BOLD function was considerable reduced with practice in the prefrontal region. Moreover, the degree of reduction could be predicted by the amount the ACT-R theory predicted retrieval of facts would be speeded by practice.

The Current Study

This study has a number of goals. The first was to ascertain better what the rise in the BOLD function reflects. The model we will propose assumes that these regions reflect active processing of critical information. For instance, each change to the image of the equation is predicted to produce an increase in the activity of the parietal region. However, the activity of these regions may just reflect how long the information is being maintained. To separate out the effects of active transformations from passive holding, we introduced a delay during which participants had to just hold the information. According to the ACT-R model, regions like the parietal should not be affected by this delay.

A second goal was to assess the degree to which these effects are left lateralized. Our original study that defined the regions involved high-school algebra, which one might assume is left lateralized. The research reported here will use a more abstract symbol-manipulation task that might not have the same degree of lateralization. It will examine the behavior of the right homologues of the regions used in the Qin et al study. Figure 4 shows the six prespecified ROIs, examined in this experiment. Also, to separate any effect of hand of responding, half of the participants responded with their left hand and half responded with their right hand.

Another goal was to more carefully separate retrieval from transformation. In the past studies they were confounded because number of retrievals increased with number of transformations. Here we wanted to perform a study in which retrieval and transformation were more independently manipulated.

A fourth goal was to minimize the effect of eye movements. The expressions used in the past research were rather large and subtended many degrees of visual angle. We used a string manipulation task in which all the critical information could be perceived in the fovea.

The experiment involved two phases. In the first phase (outside the magnet), participants memorized information that they would use in the second part of the experiment that took place in the magnet. The material to be memorized were associations between two-letter words and two-digit numbers such as:

$$\text{AT} \rightarrow 13 \text{ and BE} \rightarrow 26$$

Then in the second phase of the experiment, participants either saw these two-letter words or two-digit numbers paired with permutations of the letters A, B, C, and D. Table 1 illustrates the various conditions of the experiment. Participants were told that the two-digit codes that they had learned were instructions for transforming the 4-letter sequences. Thus, 13 means that the first and third letters should be transformed. Applied to CDAB it would produce ADCB. Some 2-digit sequences are "no-ops" such as 26 because one of the digits is greater than 4 and so in this case does not require a transformation. Participants can either be given the digit pair directly in which case no retrieval is required or be given a word from which they have to retrieve the digit pair.

Figure 5 illustrates the scanning procedure in these experiments. Each trial lasted 24 seconds and consisted of 20 1.2 scans in which we scanned the brain. During the first 1.2 seconds an asterisk appeared. Then the letter string appeared until the participant hit a thumb key indicating that they were ready to key the answer (the letters A B C and D were mapped to index, big, ring, and small fingers). The letter string could disappear but randomly the participant would have to wait 4 seconds before keying out the answer or could respond immediately.

Thus, the fundamental design of the experiment was a 2x2x2x2x20 design with choice of response hand a between-participant variable, and the within-participant variables being whether a delay was involved, whether a transformation was involved, whether retrieval of a paired associate was required, and scan (20 values).

Predictions

The following were our predictions for the experiment:

1. The parietal ROI would show a stronger effect of transformation than substitution since transformation requires more substantial changes to the problem representation.

2. The prefrontal ROI would show a stronger effect of substitution than transformation since substitution is associated with greater retrieval requirements.

3. The prefrontal ROI would show no response in the no-substitution, no-transformation condition (because no retrieval is required) but the parietal region would show a substantial effect because it is still necessary to build up a representation of the problem.

4. Neither the prefrontal nor parietal ROI would show an effect of delay.

5. Neither the prefrontal nor parietal ROI would be affected by the choice of response hand, but the dominant motor ROI would switch hemispheres according to the response hand.

6. Anchored for time of response, the motor region would not show an effect of substitution or transformation.

We did not have a priori predictions as to what region would show an effect of delay.

Results

Behavioral Results

Figure 6a shows the mean latencies of the thumb press (our measure of planning time) as a function of condition and Figure 6b shows the mean times for each of the subsequent key presses separately for delay and no delay. Response hand had no effect on any key time. With respect to planning time, participants show significant effects of transformation (F(1,20) = 78.70, p<.0001; MSE=.396) and of substitution (F(1, 20) = 156.60; p<.0001; MSE = .158) but no interaction between the two (F(1,20) = .47; MSE = .10). Note that the time in the substitution, no-transformation condition (4.21 sec) is almost identical to the time in the no-substitution, transformation condition (4.34 sec). Therefore, differences between these conditions in BOLD response are unlikely to be due to total time. With respect to subsequent keying times, participants average well under a half a second per key indicating that they must have planned their responses in advance. The times show an effect of key, indicating a basic speed up (F(3,60) = 54.47, p<.0001; MSE-.012). In the model, times are slower for key 1 because it must respond to the prompt to respond. The ACT-R predictions in the Figure 6b are a priori predictions based on the times for its perceptual-motor components. There is also a significant effect of delay (F(1,20) = 15.97; p<001; MSE = .021) and a significant delay-by-key interaction(F(3,60) = 11.84; p<.0001; MSE = .006). The model is faster for the first key with a delay because it can use the delay to prepare to respond. There is also a significant effect of substitution (F(1,20) = 19.83; p<.001, MSE = .0031) and a significant delay-by-substitution interaction (F(1,20) = 11.92; p<.01; MSE = .002). Participants are 6 msec slower to key in the substitution condition when there is delay and 28 msec when there is not. These effects are miniscule compared to the over one second effect of substitution on planning time.

Exploratory Analyses

We did separate exploratory analyses of the left and right responding participants. Analysis of fMRI data was also restricted to trials on which the participants were correct. ROIs were selected according to the interaction term in a 8 condition x 20 scans ANOVA. To have a conservative test that dealt with non-independence of successive scans we used the correction of assigning only 7 degrees of freedom to the numerator in the F-statistic for the interaction term (the Greenhouse-Geisser correction for non-independence of conditions). To avoid having distinct regions merged we defined two somewhat different but equally conservative tests. For the left-responding participants the selected regions met the criteria of minimum 15 contiguous voxels with significant interaction at p <= .01 (Forman, Cohen, Fitzgerald, Eddy, Minton, & Noll, 1995). For the right responding participants we used a .05 criteria but increased the number of contiguous voxels required to 23 (note $.05^{23} \approx .01^{15}$). Eleven ROIs met these criteria in the right-responding participants and 7 met the criteria in the left-responding participants. These are displayed in Figure 7 and Table 2 describes these ROIs.

To get a sense of the effects that these regions showed we calculated for each of the following conditions the mean percentage that the BOLD function over scans 3-18 rose above the baseline set by scans 1&2 and 19&20. This produces 8 effects corresponding to the 8 conditions for each ROI. Table 2 gives the average of these values over the 8 conditions as “Mean % Rise”. A positive value indicates a function that rises above baseline and a negative value indicates a function that dips below baseline. Table 2 also gives t-values that measure the average difference between the two sets of 4 conditions corresponding to each main effect. For instance, in the case of substitution we calculated the difference between the mean rise in the BOLD function when there was a substitution and the mean rise in the BOLD functions when there was no substitution. This difference was converted into a t-value by using the condition-by-scan-by error term in the analysis of variance. All of these t-tests have 1330 degrees of freedom which make them effectively z-scores.

Both the left-responding and right-responding participants have a large region of activation in the area that corresponds to that hand in the motor cortex (ROI 1 in Table 2 for both populations). This region only shows a significant effect of delay. A number of posterior parietal regions were identified in the exploratory analysis but these regions are much larger than the prespecified ROI in Figure 4 and only partially overlap with it. The exploratory regions that most overlaps with that prespecified ROI are ROI 6 in the right-responding participants and ROI 3 in the left-responding participants. Both regions show effects of all three factors. Only the right-responding participants showed an exploratory that corresponded to the prefrontal ROI in Figure 4. This is ROI 7 for these participants and it shows an effect of substitution and transformation but not delay.

Two other exploratory ROIs are consistent in the two populations. First, both show a large anterior cingulate region (ROI 3 in right-responding participants and ROI 2 in left-responding participants) that responds positively to substitution or delay. Second both show a right visual area (ROI 8 in right-responding participants and ROI 7 in left-responding participants that responds negatively to delay. Given the large and consistent anterior cingulate area and the fact that it does responds positively, we will offer some speculations about its function when we come to the model development.

In no case other than the motor area, is there a region in one population that is the hemisphere homologue of an area in the other population. Thus, it appears that when participants switch hands the pattern of activation remains constant except for the motor regions. The somewhat different exploratory regions obtained presumably reflect the accidents of statistical significance. With the exception of the failure to find a left prefrontal region in the left-responding participants, this exploratory analysis does support the hypothesis of activity in the left parietal and prefrontal areas, along with a motor area that switches between hemispheres depending on response hand. As the confirmatory analysis will show, the left prefrontal region is actually giving a reliable response in the left-responding participants, but it just failed to meet the conservative threshold in the exploratory analysis.

Confirmatory Analysis: The Prespecified Posterior Parietal Regions

Figure 8 reports the effects of substitution, transformation, and delay on the left and right parietal regions given a priori in Figure 4. These curves take as baseline the average of scans 1&2 (before the function begins to rise) and scan 20 (by which it has returned to baseline). Each point is defined as the percent rise above this baseline. We performed an analysis of the degree to which the curve defined by scans 3-19 rose above the baseline, which we measured as the area under the curve. There was no difference between left and right responding participants (F(1,20)

= .06, MSE = 24.77 percent) or between delay and no delay (F(1,20) = .43, MSE = 1.00 percent). However, the left side responds significantly more than the right (F(1,20)=8.34, $p < .01$, MSE = 6.15 percent), the functions rise more when there is a transformation than not (F(1,20) 26.67; $p < .0001$; MSE .89 percent), and more when there is a substitution than not (F(1,20) = 24.90, $p < .0001$, MSE = .89 percent). There were one significant interaction and one marginally significant interaction -- hemisphere-by-substitution (F(1,20) = 9.31, $p < .01$, MSE = .46 percent) and hemisphere-by-transformation (F(1,20) = 4.29, p = .05, MSE = .43 percent). Both of these interactions reflect the fact, apparent in Figure 8, that the effects are stronger in the left hemisphere. However, note that while the left hemisphere reflects both effects, there is only an effect of transformation and not an effect of substitution in the right hemisphere.

The fact that there was no effect of hand or of delay confirms the predictions about this region. The region seems to hold a problem representation and encode transformations to that representation. Once the solution has been obtained it is not affected by downstream factors like delay or response hand. We also had predicted that this region would show a larger effect of transformation than substitution. Comparing Figures 8a and 8b it does appear that at peak transformation has a larger effect than substitution, but the substitution effect maintains itself longer resulting in an equivalent difference in area between the transformation and no-transformation curves in Figures 8a and between the substitution and no-substitution curves in Figure 8b. A test looking at the differences in the heights of the two curves between scans 5 and 10, where they peak, does find the difference between transformation and no transforamtion significantly greater than the difference between substitution and no substitution, t(21) = 2.54, $p < .01$.

Confirmatory Analysis: The Prespecified Prefrontal Regions

Figure 9a shows the results for the left prefrontal region, collapsing over delay. Our prediction was that this region would show no rise in the condition of no substitution and no transformation. It would appear that our predictions have been exceeded in that there is a dip that appears to begin after the other curves have peaked. The other curves also appear to dip a below baseline. Other of our studies have found some suggestion for negativity in the prefrontal function (e.g., look carefully at Figure 3b) but nothing so strong as this. Actually, only half of the participants show this negative effect (5 left-responding and 6 right-responding). For purposes of model fitting we have chosen to adopt the no-substitution, no-transformation condition as reflecting baseline (zero) and to plot differences from this. This is the way in Figure 9b plots the data and it shows that there are systematic differences among the other conditions relative to this baseline. Subsequent analysis will work with transformed BOLD functions as in Figure 9b. We think the negativity in Figure 9a reflects some other process that occurs after the offset of the trial and view Figure 9b as reflecting the real process of interest.

Figure 10 displays the main effects of each factor using the recalculated BOLD functions for the left and right prefrontal regions. Again, we performed an analysis of the degree to which the curve defined by scans 3-19 rose above the baseline or the area under the curve. There was no difference between left and right responding participants (F(1,20) = 1.08, MSE = 10.17 percent) or between delay and no delay (F(1,20) = 0.40, MSE = 3.48 percent). The left side responds more than the right and this is marginally significant (F(1,20)=3.53, $p < .10$, MSE = 2.88

percent). The effect of substitution is significant (F(1,20)=8.98, $p < .01$, MSE = 3.20 percent) but not the effect of transformation (F(1,20)=1.35, MSE = 1.04 percent) as predicted. However, there is a significant region-by-transformation interaction (F(1,20)=6.09, $p < .05$, MSE = 0.36 percent) reflecting the fact that the left but not the right seems to respond to transformation. The interaction between region and substitution is marginally significant (F(1,20)=3.96, $p < .1$, MSE = 0.70 percent). These interactions may just reflect the greater sensitivity of the left prefrontal region to manipulations. There are no other significant interactions. The prediction of a greater effect of substitution than transformation seems confirmed. A contrast comparing the substitution, no-transformation condition with the transformation, no-substitution condition is significant – t(21) = 2.29, $p < .05$.

Confirmatory Analysis: The Prespecified Motor Regions

Figure 11 displays the average response of the left and right motor regions for the left and right responding participants. As would be expected, those participants who respond with their right hand show a large effect in the left motor cortex and those participants who respond with their left hand show a large effect in their right motor cortex. There is a suggestion of an interaction in the other hemisphere such that the BOLD response rises a little rise in the left hemisphere for participants responding with their left hands while it drops a little in the right hemisphere for participants responding with their right hands.

The graphs to this point are stimulus locked in that they begin with the onset of the stimulus. However, in the case of the motor regions it would be more informative to do a response-locked analysis where time zero was set to be when participants emitted their response. Figure 12 shows the data plotted this way with five scans before the response scan and the fourteen scans after. The baseline for these graphs are taken as the first three scans. The BOLD function is beginning to rise even on the scan before the response, indicating some preparatory motor behavior.

We performed an analysis of the degree to which the curve defined by scans –2 to 14 rose above the baseline define by scans –5 to -3. For purposes of analysis and display in Figure 12, we classified the left hemisphere for the right-responding participants as the major hemisphere and the right as the minor; this labeling was reversed for the left-responding participants. There was no difference between left and right-responding participants (F(1,20) = .93, MSE = 29.24 percent) but there was large difference between the major and minor hemispheres (F(1,20)=101.46, $p < .0001$, MSE = 16.98 percent). There was also an interaction between response hand and hemisphere (F(1,20)=5.52, $p < .05$, MSE = 16.98 percent), reflecting the fact that the two minor hemispheres react oppositely as noted with respect the Figure 11. As predicted there is no significant effect of transformation (F(1,20)=1.77, MSE = 2.43 percent) or substitution (F(1,20)=0.14, MSE = 14.33 percent). There is, however, a strong effect of delay (F(1,20)=22.38, $p < .0001$, MSE = 3.99 percent), which was not predicted. There is also a significant interaction between delay and region (F(1,20)=99.22, $p < .0001$, MSE = 3.08 percent), which reflects the fact that delay only has an effect on the major hemisphere. There are no other significant interactions.

Confirmatory Analyses: Summary

By way of summary, while the prefrontal and parietal behavior is strongly left-lateralized, there is a weaker response in the homologous right hemisphere region. As predicted the prefrontal region was more sensitive to substitution reflecting its role as a retrieval region. The parietal region is more sensitive to transformation than substitution in its peak response but not in its total area. Interestingly, in both cases the right hemisphere only responded to the more important factor (transformation in the case of the parietal region and substitution in the case of the prefrontal region) while the left hemisphere responded to both, but more strongly to the more important factor. Both prefrontal and parietial respond to actual information-processing engagement and not just time and so neither were sensitive to delay. Somewhat surprisingly, the motor region did respond to delay suggesting that people were rehearsing their motor responses over delay. Also the fact that the motor region started to rise before the overt response indicates anticipatory motor preparation before the thumb press. We used this behavior of the motor region to tune our model for this task.

Fit of the ACT-R Model to the BOLD Functions

Figure 13 illustrates the behavior of the ACT-R model in the most complex condition in the experiment, which involves substitution, transformation, and delay. Initially a representation of the string is built up in the imaginal buffer. Then the word-command (AT) is encoded and its number representation is retrieved from declarative memory. This number, 14, is added to the imaginal representation and then the letters in the critical positions (in the example D in first position and B in fourth position) are committed to temporary memory to guide the transformation of the string in declarative memory. Then the motor program for transmitting the string is encoded or rehearsed, a thumb key is pressed, the motor program rehearse during the delay, and then the four fingers pressed at the end of the delay. This differs from the ACT-R model we initially proposed before the imaging study that did not include motor rehearsal before the thumb press or during the delay. Guided by the BOLD function in the motor region we assumed the 4 keys were being rehearsed before the thumb press and an average of 5 keys were rehearsed in the interval. The addition of these motor rehearsals is an example of how imaging can inform model development.

Besides these rehearsals two parameters were estimated for the model in advance of trying to fit the BOLD functions. The retrieval of the paired associate was estimated at .79 seconds and the encoding and retrieval of the critical letters at .54 seconds. These parameters were estimated to fit the behavioral data in Figure 6. None of the other process times were estimated but all come from prior values in the model. In particular, the imaginal transformations take .2 seconds and each manual step (rehearsal or key press) takes .3 second. The .3 seconds for the manual step come from the well established motor module in ACT-R (which is derived from Meyer & Kieras's EPIC theory). The .2 seconds for the imaginal transformations comes from a generalization of the parameters in ACT-R's visual module for encoding an object. With the processes in Figure 13 and their durations set it is possible to predict BOLD functions for the three a priori regions.

Predicting the BOLD function

Anderson et al (in press) assumed that whenever an activity takes place in one of the ACT-R buffers, there is an increased hemodynamic demand and it is these hemodynamic demands that drive the BOLD function in the corresponding cortical regions. We developed a precise proposal for how the length of activity of a buffer mapped onto the predicted BOLD (Blood Oxygen Level Dependent) function in fMRI. A number of researchers (e.g., Boyton et al., 1996; Cohen, 1997; Dale & Buckner, 1997) have proposed that the BOLD response to an event varies according to the following function of time, t, since the event:

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

where estimates of the exponent *a* have varied between 2 and 10. This is essentially a gamma function that will reach maximum *a* time units after the event. We proposed that while a buffer is active it is constantly producing a change that will result in a BOLD response according the above function. The observed fMRI response is integrated over the time that the buffer is active. Therefore, the observed BOLD response will vary with time as

$$CB(t) = M\int_0^t i(x)B\left(\frac{t-x}{s}\right)dx$$

where *M* is the magnitude scale for response, *s* is the latency scale, and i(x) is 1 if the buffer is occupied at time x and 0 otherwise. Note because of the latency scale factor, the prediction is that the BOLD function will reach maximum at roughly t = a*s seconds.

The peak of the BOLD function reflects roughly when the buffer was active but is offset because of the lag in the hemodynamic response. The height of the BOLD function reflects the duration of the event since the integration makes the height of the function approximately proportional to duration over short intervals. While this relationship is only approximate for the height of the function, the total area under the curve will be precisely proportional to the total time that the buffer is active. If a buffer is active for a total period of time T, the area under the BOLD function will be M*Γ(a+1)*T where Γ is the gamma function (in the case of integer a, note that Γ (a+1) = a!).

Thus, we can use the length of duration of the buffer activities in Figure 11 to generate exact predictions for the BOLD function in each of the prespecified ROIs for each of the experimental conditions. In making these predictions we have to estimate three parameters that determine exact shape the BOLD function – the latency scale (s), the exponent (a), and the magnitude M. While these determine the exact shape of the BOLD function, they do not change the prediction that the area under the BOLD function is proportional to the time the buffer is active. Thus, given a commitment to timing of activity in a buffer across conditions of the experiment, the model is committed to predictions about the relative areas under the BOLD functions for the different conditions in the corresponding brain region. As the timing is set to fit the behavioral data, this becomes a parameter-free prediction of the theory.

Some strong assumptions underlie the application of this methodology. One is the BOLD function is exactly described by a gamma function. Another is that the effect of repeated use of a buffer is additive. A third is that the only thing reflected in the activity of a particular region is the behavior of the assumed buffer. We will return to discussing issues involving each of these assumptions at the end of the paper.

Note that this analysis does not reflect a frequent assumption in the literature (e.g., Just, Carpenter, & Varma, 1999) that a stronger BOLD signal reflects a higher rate of metabolic expenditure. Rather, the assumption is that it reflects a longer duration of increased metabolic expenditure. The two assumptions are relatively indistinguishable in the BOLD functions they produce but the time assumption more naturally maps onto an information-processing model that assumes stages taking different durations of activity. Since these processes are going to take longer they will generate higher BOLD functions without making any extra assumptions about different rates of metabolic expenditure.

The mathematics in this analysis is basically the same as what underlies the frequent image-analysis technique of correlating the BOLD signal with the temporal profile created by convolving the trial structure with a hypothetical hemodynamic function. Among the differences/elaborations are:

(1) The temporal structure generated by an ACT-R model (or any information-processing model) is more fine-grained, generated from the internal operations of different components of the cognitive architecture.
(2) Each condition has a natural baseline defined by the beginning of the trial before the BOLD function has begun to rise and the end of the trial after the BOLD function has come down – hence, there is no need to subtract out some neutral control condition.
(3) There is the additional assumption that the magnitude of the response reflects the duration of activation of that component. Combined with point (2) the theory becomes subject to strong parametric tests.
(4) There is an association of different regions of the brain with different components of the cognitive architecture.
(5) One can estimate the parameters $\underline{a}$ and $\underline{s}$ of the BOLD function for a specific region rather than having to fit a single assumed BOLD function to all regions.

With this mapping of activity of information-processing components onto BOLD functions one can derive predictions from a cognitive model test. Table 3 summmarizes the various fits, which we describe below.

Fit to Left Posterior Parietal Region

Figure 14a illustrates the ability of the imaginal buffer to predict the behavior of the left posterior parietal region. The overall quality of fit is good as indicated by a correlation of .990 and a chi-square of 90.59 with 157 degrees of freedom (160 observations minus 3 parameters).[2] Figure 14a collapses over delay because this did not have an effect on the behavior of this region, but the fit is to the data before collpasing. The heights of the curves reflect the numbers of visual operations performed. In the case of no substitution or transformation, 4 operations are required to encode the letter string. An additional operation is required to encode the result of transforming the word when substitution is required and two additional operations are required to transform the equation in the case of transformation. As predicted the transformation, no-substitution curve is higher than the no-transformation, substitution condition.

Fit to the Left Prefrontal Region

Figure 14b illustrates the ability of the retrieval buffer to predict the behavior of the left prefrontal region. As noted earlier we have made the no-substitution, no-transformation the baseline and so we are only predicting the other conditions. Again, because there is no effect of delay Figure 14b averaged over that factor. The overall fit is reasonable as indicated by a correlation of .939 and a chi-square of 68.21 with 117 degrees of freedom (120 observations minus 3 parameters). The model successfully predicts that the substitution, no-transformation condition will be higher than the no-substitution, transformation condition. However, there is a suggestion of a deviation in the data. Specifically, the model is underpredicting the height of these two curves and overpredicting the height of the substitution, transformation curve. Thus, even though the behavioral data (Figure 6a) display additivity, the BOLD functions may not. The actual deviation from additivity is only marginally significant – $t(21) = 1.86$, $p < .10$ in a test of whether the area under the substitution, no-transformation curve and the area under the no-substitution, transformation curve add to the area under the substitution, transformation curve.

Fit to the Major Motor Region

Figure 14c illustrates the ability of the manual buffer to predict the behavior of the major motor region – left motor cortex for right-responding participants and right motor cortex for left responding participants. This analysis is response-locked and Figure 14c collapses over the factors of substitution and transformation, which did not have significant effects. It assumes that there are nine events in the manual buffer in the no-delay condition (4 encoding/rehearsals of key presses and 5 finger presses) while there are 5 additional rehearsal events in the delay condition. As noted earlier, the assumption of motor rehearsal was not part of our original model but was suggested by the data. While the overall fit of the model is good as indicated by the correlation ($r = .977$) the chi-square measure (328.42 with 157 degrees of freedom) indicates that there are significant points of discrepancy. Looking at the curves, it can be seen where these are. First, the model does not rise above zero as quickly. This is particularly apparent on the scan on which the response is emitted – the participants' BOLD function has risen .10%, while the model is still almost at zero. On the other end, the empirical BOLD function goes down more rapidly and slightly undershoots zero, where the model predicts a more gradual approach to zero. These deviations suggest that use of the gamma function to model the shape of the BOLD function may not be exactly correct.

This is the only BOLD function whose form reveals something of the timing of the buffer actions – in particular, in the delay condition. The initial planning of the motor response produces the initial rise (and is the reason why in the model there is some rise even on the response scan). The rehearsal over the 4 seconds maintains the height of the BOLD function. The final execution of the response produces the second rise before the function goes back down to zero.

Anterior Cingulate Analysis

We noted in the exploratory analyses that the anterior cingulate cortex (ACC) evoked a strong response from the participants. It is a region that we have found active in a number of our studies and about which there have been numerous theories. The most prevalent theory is that it is involved in controlling cognition. For instance, Posner & Dehaene (1994) have described the ACC as "involved in the attentional recruitment and control of brain areas to perform complex tasks". D'Esposito et al (1995) have identified it with Baddeley's (1986) central executive and Posner & DiGirolamo (1998) have related it to Norman & Shallice's (1986) SAS. Another theory relates it to error detection. This is supported by the error-related negativity (ERN) in event-related potentials that has been observed when errors are made in speeded response tasks (e.g., Falkenstein, Holnsbein, & Hoorman, 1995). Dehaene, Posner, and Tucker (1994) where able to localize the ERN as residing within the ACC. However, ACC activity occurs in many more situations than just when there are errors and another interpretation of its activity is that it is just a reflection of task difficulty as indexed by errors or reaction time (Paus, Koski, Caramanos, & Westbury (1998). In this experiment we find it responding to all variables that make for increased task difficulty and this is the way it has behaved in past studies of ours (e.g., Anderson et al, in press). On the other hand, it does not always respond to task difficulty factors that increase latency. Carter, MacDonald, Botvinick, Ross, Stenger, Noll, and Cohen (2000) argue that the real function of the anterior cingulate is conflict monitoring and that other regions of the cortex actually respond to the conflict once detected. MacDonald, Cohen, Stenger, and Carter (2000) found that in a Stroop task, when participants are warned that it will be a difficult color trial, there is greater activation in the prefrontal region. In contrast, when the actual Stroop task is presented the ACC responds to a difficult color trial. Thus, they argue that, unlike the Posner and Dehaene proposal, the prefrontal cortex and not the ACC is responsible for control and that the ACC rather monitors for conflict, like that which occurs in the Stroop task. This conflict is often interpreted as conflict between competing responses and this interpretation is applicable to the Stroop task. However, in our more complex tasks ACC activity reflects transformations and retrievals that do not involve any overt responses. Thus, perhaps it is more appropriate to interpret the conflict more generally as occurring between competing steps of cognition.

We decided to create an anterior cingulate region like the prespecified regions used for the motor, prefrontal, and parietal regions. To give it an a priori character we centered it on the region that was found in the first experiment of Anderson et al. The anterior cingulate differs from the regions in Figure 4 in that it symmetrically straddles the midline. Nonetheless, we still tried to identify a left and right region. We looked at regions that were 5 voxels long, 3 voxels wide and 4 voxel deep on both sides of center. Their coordinates are x = 5/-5, y = 10, and z =39 and they overlap Brodmann regions 24 and 32. We had expected not to be able to really discriminate between these left and right regions and intended to collapse them into a single 5x6x4 voxel region.

Figure 15 displays the effects of substitution, transformation, and delay on the left and right anterior cingulate regions. As in the other confirmatory analyses we did an analysis of variance of the area under the curve (defined as amount scans 3-19 rose above the baseline defined by 1,2, and 20) in the various conditions. Again, there was no difference between right and left responding participants. There is a significant difference between regions and in this case the larger response is on the right side (F(1,20)=11.84, $p < .01$, MSE 5.52 percent). There is a significant effect of substitution (F(1,20)=24.01, $p <.0001$, MSE 2.42 percent), of transformation (F(1,20)=5.62, $p <.05$, MSE=1.74 percent), and of delay (F(1,20)=78.24,$p < .0001$, MSE-1.10 percent). The effect of substitution seems larger than transformation and a test was marginally significant (t(21)=2.10, $p< .05$) of whether the substitution, no-transformation condition produces a greater BOLD response than the no-substitution, transformation condition.

We were somewhat surprised to find a stronger right-sided response, particularly given the issues about accuracy of localization and the fact that we smooth the data and warp them into a common reference brain. However, both sides showed relatively strong robust results and in further analyses to average them to get a more reliable effect.

We looked for a construct in ACT-R that might predict the behavior in our anterior cingulate ROI. As we noted, a necessary condition for a successful predictor is that the area under the BOLD function and the time be proportional. Anderson et al introduced the following test for proportionality, which is the analog of an R^2 measure:

$$\text{Proportionality} = \frac{\left(\sum_i T_i A_i\right)^2}{\sum_i T_i^2 \sum_i A_i^2}$$

Note that in the definition of the standard R^2 one replaces the raw scores in the above by the deviations from the mean. Table 4 displays the measures of proportionality between four regions and four time measures. The four regions are the three prespecified regions (Figure 4) plus the amalgamated left and right anterior cingulate region. The four time measures are the times of the imaginal, retrieval, and manual buffer plus the total time the system is processing information. This latter measure, cognitive time, includes the time to generate the four keys after the thumb key is pressed and the 1.5 seconds during the delay that we estimated was spent in rehearsal (to fit the motor region). These measures of proportionality confirm our associations of buffers with ROIs. With respect to the anterior cingulate ROI its strongest proportionality is with cognitive time. The manual buffer is not as strongly associated because it does not show an effect of substitution or transformation, which the cingulate does. The imaginal buffer is not as strongly associated because it does not show an effect of delay which the cingulate does. The retrieval buffer is poorly associated because it predicts no response in the no-substitution, no-transformation condition while the cingulate shows a substantial response. One might wonder how well the anterior cingulate relates to just total time. The difference between total time and cognitive time is that delay has a 4 second impact on total time but only 1.5 seconds impact on cognitive time. If we use total time the measure of proportionality goes down from .996 to .983. Thus, both the motor region and the anterior cingulate agree that delay has an intermediate impact (neither 0 or 4 seconds) on their response.

This result is roughly consistent with the cognitive conflict interpretation of the cingulate. While the system is engaged it has to be choosing among productions to fire (a process called conflict resolution) and alternative facts to retrieve from declarative memory. During that portion of the delay in which the system is not active there is no effect on the BOLD function.

The results of trying to predict the response of the cingulate with cognitive time are displayed in Figure 16. While the fit is good there are some points of significant deviation as reflected by the chi-square of 224.16 with 157 degrees of freedom. One point of deviation, as reflected in Figure 16a is that, since slightly more time is spent in the no-substitution, transformation condition than the substitution, no-transformation condition, the model predicts a slightly larger response in the former condition. However, as we have already noted, the effect in the BOLD function appears to be in the opposite direction. The other point of deviation, apparent from Figure 16b is that there is a slight negative component to the end of the BOLD function in the no-delay condition, which the model cannot predict.

Discussion

The basic premise in this research is that we can map the duration of various components in an architecture like ACT-R onto the BOLD function obtained in various regions. The relative success in this paper supports this premise. However, it is worth noting some assumptions on which this effort depends and signs that these assumptions might have been somewhat stressed in our efforts.

1. It depends on the assumption that the BOLD function reflects just the duration a component is occupied and not the intensity of occupation. This uniform-intensity assumption seemed to have worked appropriately in most cases. However, one of the deviations we observed in our effort to model the anterior cingulate suggested a case where this might not be correct: Substitution produced an increase in activation greater than just the time associated with substitution would predict. Of course, we could be wrong in our association of the anterior cingulate with duration of cognitive engagement, but if we are correct then this indicates that some kinds of engagement produce more metabolic response per unit time than others.

2. It also depends on the assumption that the BOLD function is additive across multiple events. Again this has proven to be a relatively successful assumption but there was a suggestion that the BOLD response to substitution-plus-transformation in the prefontal ROI was less that the sum of the responses to substitution and transformation individually. While some people have found that the BOLD response is additive (e.g., Boyton, et al., 1996; Dale & Buckner, 1997) others have not (e.g., Glover, 1999).

3. A third assumption is that the BOLD function in a particular area reflects, at least for the current task, only a single postulated cognitive function. As a general assertion this seems an improbable assumption, but it might be true in specific tasks. The one place where we seemed to have the most problem with this assumption in the current task is in the prefrontal ROI where there seemed a post-response negativity overlaid on the stimulus-locked positive response to retrieval demands. In this case we had a neutral condition to serve as a base-line which we could subtract from the other BOLD functions. As a methodological point it might be worthwhile to try to maintain a condition that

deletes all the cognitive processes but retains simple stimulus and motor components. Such control conditions are typical of fMRI designs and this experience suggests that the current approach has not negated the utility of such a baseline.

4. The approach depends on the assumption that the gamma function correctly characterizes the BOLD response. We are able to parameterize the gamma function differently for different regions to accommodate regional differences. However, this approach still assumes it is exactly a gamma function everywhere. On the other hand, there was evidence for deviations from the assumed form in certain regions – such a small negativity at the end of the function. Others (e.g., Glover, 1999) have reported a small negative component to the BOLD response and proposed modeling the BOLD response as the difference of two gamma functions. This would greatly complicate the modeling but it is an approach that might be necessary.

This methodology should be judged not as absolutely true or false but rather as more or less fruitful. We think it has proven relatively fruitful. However, one needs to remain mindful of the potential pitfalls in using the methodology.

Given that the methodology was relatively successful, this paper does illustrate the profitable back and forth that is possible between a cognitive architecture and neuroimaging. Past research provided a priori hypotheses about the function of specific brain regions interpreted in ACT-R information-processing terms. The results of this study have been to largely confirm these assumptions but not without consequence for the modeling enterprise. In particular, the behavior of the motor region (surely the most obvious of our associations) told us that covert rehearsal was occurring and to incorporate this into our information processing model. Having done that and so recognized that the delay period was partially a period of cognitive activity, we were then in a position to assign an interpretation to the anterior cingulate as involving the period when the system is cognitive engaged selecting next actions and so dealing with conflict. While this interpretation awaits further verification, it is consistent with existing ideas about anterior cingulate function. The ACT-R production system offers one way of further operationalizing ideas like conflict monitoring. If the proposed association continues to be profitable we have another tool to measure processes of interest in ACT-R that heretofore had been incapable of being directly measured.

Method

Task and Procedure

The trial structure is illustrated in Figure 5. A trial began with a prompt, which was an asterisk. After 1.2 seconds, a 4-letter string was presented above a 2-digit number or a 2-letter word. Participants were instructed to extract the instruction represented by that number or word and apply it to transforming the string. Participants were instructed to solve the problem mentally, and press the thumb key when they were ready to key in the final solution, upon which the problem in the first rectangle disappeared. The thumb press provided a measure of the planning time. If the plan time exceeded 18 seconds, the trial was scored as incorrect. After the thumb press, they either had to enter the answer or wait 4 seconds. If there was a delay, the word “DELAY” appeared in the rectangle for the response and participants could only begin responding when the word disappeared. Once they began entering their answer, they had no more than 1.0 seconds to press a key for each of four symbols in the answer. This rapid responding was designed to prevent participants from postponing transformations until they gave their response. The letters A, B, C, and D were mapped to their index, big, ring, and little fingers in the response glove. After the participants typed the answer, the correct answer appeared for 1.6 seconds. Then the screen was blank for the remaining portion of the 24 second trial.

Pre-scan Practice

On the day before the scan day, there was a pre-scan session in which participants memorized the word-to-number correspondences (participants practiced until they could produce 3 consecutive trials without any errors), practiced finger-to-key mappings, and practiced actual problem solving. There were just two blocks (16 trials per block) of practice at the actual problem solving. This was just enough to familiarize them with the procedure before going into the scanner.

Parametric Design

Four binary factors were manipulated. First, half of the participants responded with their right hands and half responded with their left hands. The other factors were varied within participants. Half of the trials involved a 4 second delay and half did not. Half of the trials presented 2-letter words and half presented 2-digit numbers as instructions. Half of the trials required a transformation of the equation and half did not. These factors were totally crossed to created 16 conditions. The various within-participant conditions occurred in random order. Participants were tested in 6.5 minute blocks, in which two repetitions of each of the 8 within-participant conditions were tested in random order for a sequence of 16 trials.

Event-related fMRI scan

Event-related fMRI data were collected by using a single-shot spiral acquisition on a GE 3T scanner, 1200 ms TR, 18 ms TE, 70° flip angle, 20 cm FOV, 21 axial slices per scan with 3.2 mm thickness, 64 x 64 matrix (3.125 x 3.125 mm per pixel), with the AC-PC on the second slice from the bottom. Images acquired were analyzed using the NIS system.[3] Images first were realigned using 12-parameters AIR (Woods, Grafton, Holmes, Cherry, & Mazziotta, 1998) and then cross-registered to a common reference brain by minimizing signal intensity difference after which functional images were set to a standard mean intensity, smoothed (6mm FWHM 3D Gaussian kernel) and pooled across participants to improve signal-to-noise ratio. Spatial F-maps were generated using the condition-by-scan interaction that came from an ANOVA.

Participants

Participants were 22 right-handed, members of the CMU community (9 females). Their ages ranged from 18 to 24, with an average of 21.1. Half of the participants responded with their right hands and half responded with their left hands.

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Table 1
Illustration of the Four Conditions of the Experiment
(Assuming AT is associated to 13 and BE to 26)

	No Transform	Yes Transform
No Substitute	CDAB 26	CDAB 13
Yes Substitute	CDAB BE	CDAB AT

Table 2
Regions of Interest, Location of Centroids, Mean Rise in Bold Function and Main Effects

(a) Right-Responding Participants

Region of Interest	BA	Voxel Count	Stereotaxic Coordinates (mm)			Mean % Rise	z scores		
			x	y	z		Sub	Trans	Delay
1. Left Motor	3/4	590	-43	-22	45	0.23	-0.84	-0.24	7.25
2. Left Superior Frontal Gyrus	8	40	-18	27	48	-0.17	-0.51	-0.32	-1.06
3. Anterior Cingulate Gyrus	24/32	233	1	2	47	0.17	2.45	0.57	6.66
4. Precuneus, Left Posterior Parietal Cortex	7	119	-5	-60	48	0.27	3.63	7.02	3.75
5. Left Medial Frontal Gyrus	9	46	-2	55	27	-0.29	-1.45	-0.78	-1.23
6. Left Posterior Parietal Cortex	39/19	130	-36	-66	35	-0.24	0.45	1.23	-3.88
7. Left Frontal Gyrus	45/46	195	-40	25	15	0.01	5.09	3.97	0.05
8. Right Occipital Gyrus	19	27	25	-85	30	-0.20	0.47	0.80	-4.59
9. Posterior Cingulate Gyrus	30	25	1	-47	21	-0.12	2.17	0.93	-0.55

10. Right Thalamus		47	-8	-16	13	0.11	3.20	3.27	2.86
11. Left Thalamus		26	14	-16	13	0.06	2.53	2.59	1.99

(b) Left-Responding Participants

Region of Interest	BA	Voxel Count	Stereotaxic Coordinates (mm)			Mean % Rise	z scores		
			x	y	z		Sub	Trans	Delay
1. Right Motor	3/4	336	40	-19	49	0.23	-0.42	-0.53	6.76
2. Anterior Cingulate Gyrus	24/32	186	1	5	46	0.21	3.35	2.37	7.05
3. Left Posterior Parietal Cortex	40/39	373	-30	-42	47	0.22	2.94	6.07	5.84
4. Left Middle Frontal Gyrus	6	27	-24	-6	47	0.17	0.67	4.22	8.00
5. Left Middle Frontal Gyrus	9	26	-46	-2	40	0.25	1.72	3.94	3.91
6. Right Postcentral Gyrus	43	16	52	-15	22	0.04	-1.67	-0.38	2.17
7. Right Occipital Gyrus	19	19	28	-80	24	-0.11	0.81	0.16	-4.75

Table 3
Summary of Fits to Various Brain Regions

	Parietal	Prefrontal	Motor	Cingulate
Scale (s)	1.837	1.554	0.862	1.725
Exponent (a)	2.412	2.217	5.160	1.562
*Magnitude: $M\,\Gamma(a+1)$	2.219	1.319	1.502	.594
**Chi- Square	90.60	68.22	328.42	224.15
***Correlation	.986	.913	.971	.985

*This is a more meaningful measure since the height of the function is determined by the exponent as well as M.

** 157 degrees of freedom except for the prefrontal which has 117 since the no transformation, no substitution condition was defined as the zero baseline.

***Correlation with all 160 observations (rather than with the collapsed data in Figures 14 and 16).

Table 4
Proportionality between various ACT-R time measures and the area under the BOLD functions in various brain ROIs.

		Region			
		Parietal	Prefrontal	Motor	Cingulate
ACT-R Construct	Imaginal	0.991	0.837	0.918	0.967
	Retrieval	0.846	0.956	0.643	0.771
	Manual	0.909	0.705	0.996	0.973
	Cognitive Time	0.977	0.809	0.975	0.996

Figure Captions

Figure 1 The organization of information in ACT-R 5.0.Figure 1

Figure 2 Location of the posterior parietal ROI, the motor ROI, and the ventrolateral prefrontal cortex ROI as used in Anderson et al (in press).

Figure 3 BOLD response in Anderson et al as a function of scan for 0, 1, and 2 transformations: (a) posterior parietal ROI, (b) prefrontal ROI, and (c) motor ROI.

Figure 4 Localization of the 6 prespecified ROIs used in the study: Left and Right Prefrontal: BA 45/46 (centered on x = +/-40, y = 21, z = 21); Left and Right Motor: BA 3/4 (centered on x = +/-37, y = -25, z = 47); Left and Right Parietal: BA 39/40 (centered on x =+/-23, y = -64, z = 34).

Figure 5 The 24-second structure of an fMRI trial.

Figure 6 (a) Mean latencies for a thumb press as a function of whether a transformation or a substitution was required. (b) Mean interkey times for the subsequent 4 keys as a function of whether there is a delay or not. The solid lines indicates the predictions of ACT-R and the dotted lines indicate the data.

Figure 7 Activation map for right-responding participants (a) and left-responding participants (b) with a significant interaction between scan and condition. See Table 2 for identification of regions.

Figure 8 Effect of main factors on the BOLD response in the left and right parietal regions in Figure 4: (a) Substitution; (b) Transformation; (c) Delay.

Figure 9 The BOLD functions for the left prefrontal region: (a) each condition with its own baseline; (b) the no transformation, no substitution condition serving as the baseline.

Figure 10 Effect of main factors on the BOLD response in the left and right prefrontal regions in Figure 4: (a) Substitution; (b) Transformation; (c) Delay.

Figure 11 Stimulus-locked BOLD functions in the left and right motor regions for participants responding with the left and right hands.

Figure 12 Effect of main factors on the BOLD response in the left and right motor regions in Figure 4: (a) Substitution; (b) Transformation; (c) Delay.

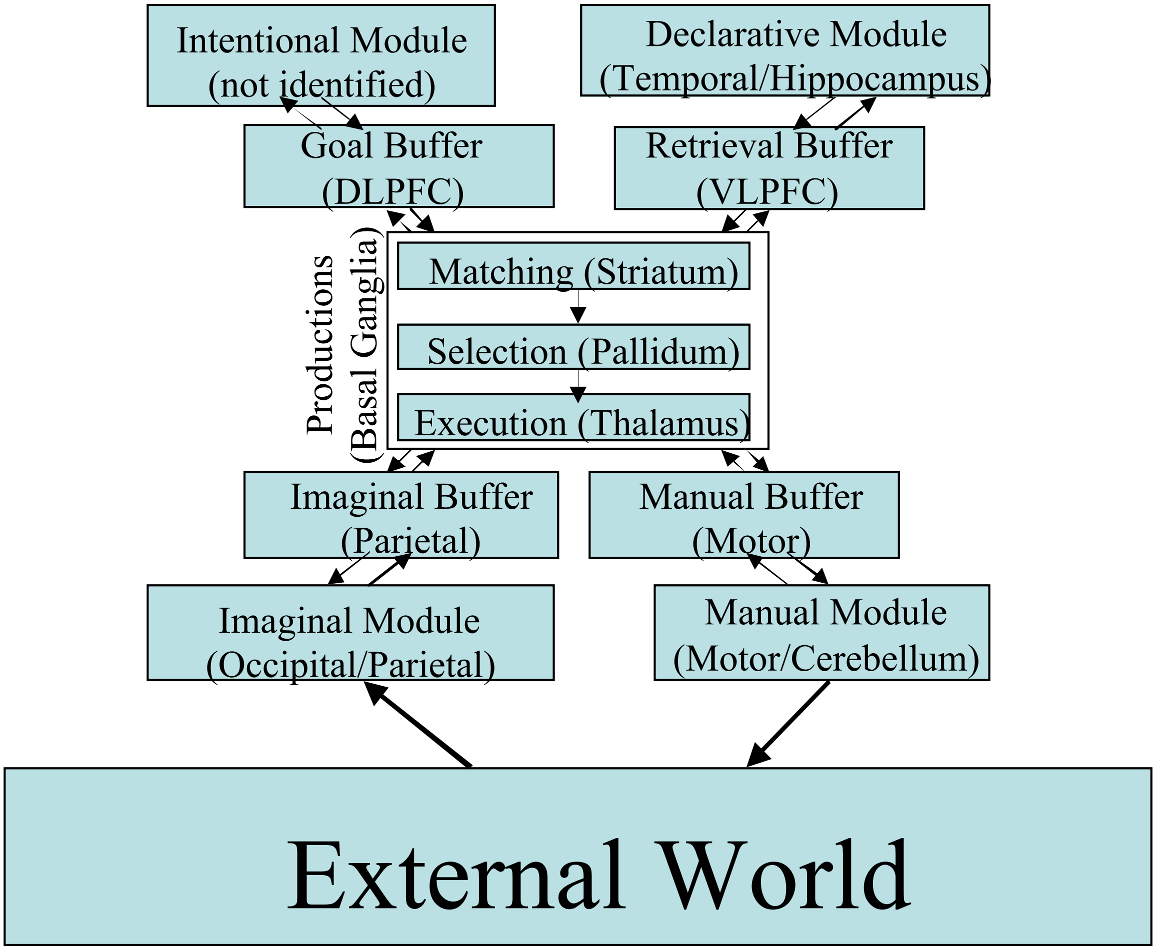
Figure 13 The approximate time line for the buffer activity in the ACT-R model

Figure 14 Predicted and observed BOLD functions: (a) posterior parietal ROI, (b) prefrontal ROI, and (c) motor ROI.

Figure 15 Effect of main factors on the BOLD response in the left and right anterior cingulate regions in Figure 4: (a) Substitution; (b) Transformation; (c) Delay.

Figure 16 Ability of Cognitive Time to predict the effect of transformation and substitution in the anterior cingulate; (b) Ability to predict effect of delay.

Figure 1



Intentional Module
(not identified)
Declarative Module
(Temporal/Hippocampus)
Goal Buffer
(DLPFC)
Retrieval Buffer
(VLPFC)
Productions
(Basal Ganglia)
Matching (Striatum)
Selection (Pallidum)
Execution (Thalamus)
Imaginal Buffer
(Parietal)
Manual Buffer
(Motor)
Imaginal Module
(Occipital/Parietal)
Manual Module
(Motor/Cerebellum)
External World

Figure 2

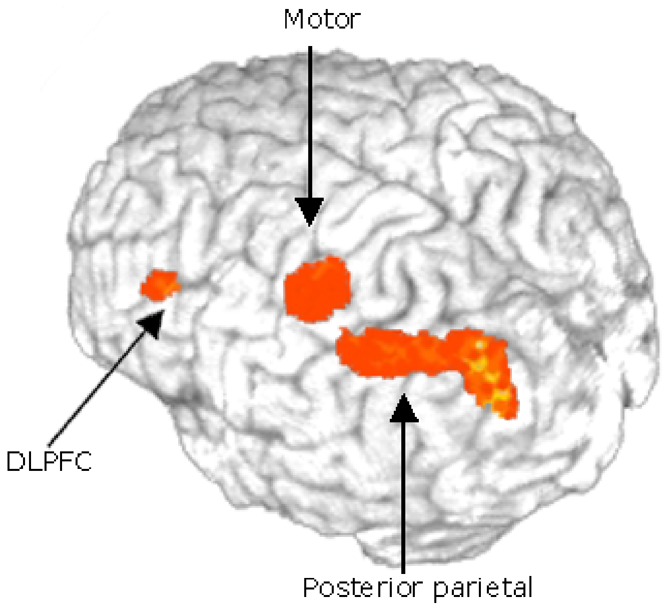
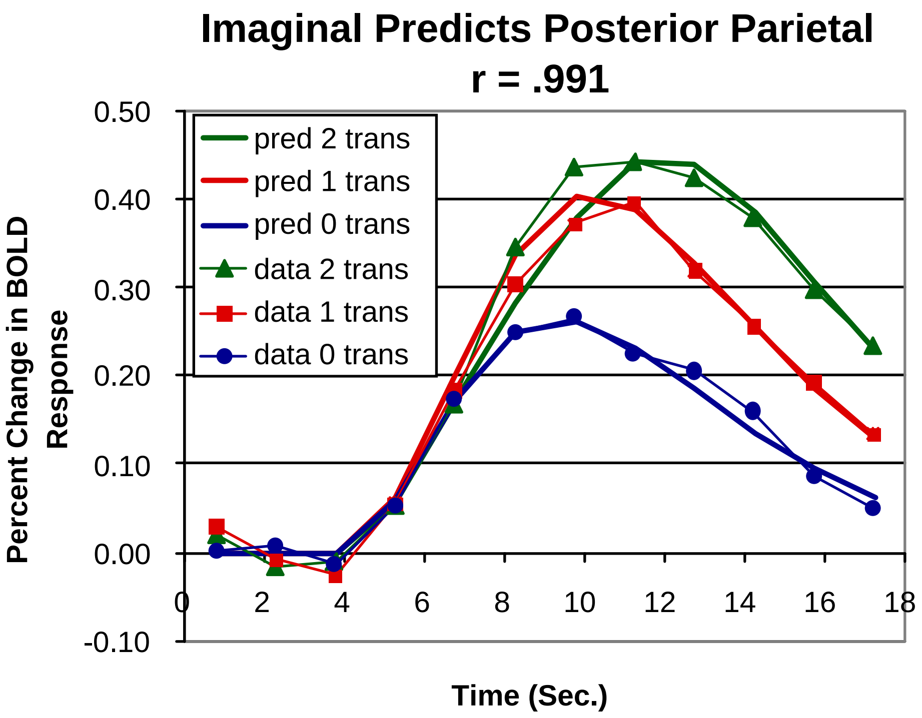
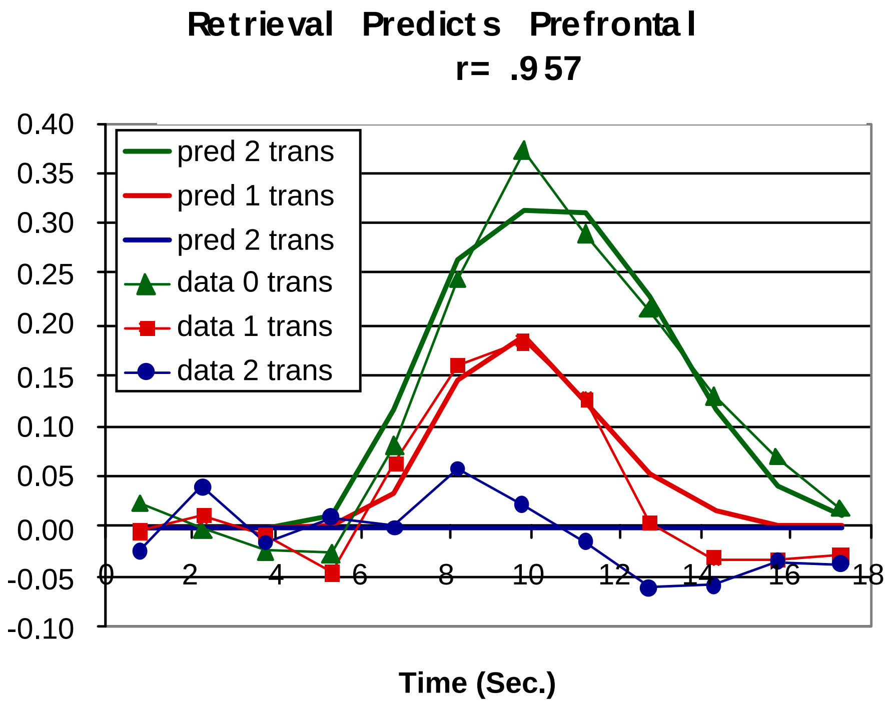


Figure 3
(a)


Imaginal Predicts Posterior Parietal
r = .991
Percent Change in BOLD Response
Time (Sec.)
0.50
0.40
0.30
0.20
0.10
0.00
-0.10
0
2
4
6
8
10
12
14
16
18
pred 2 trans
pred 1 trans
pred 0 trans
data 2 trans
data 1 trans
data 0 trans

(b)


Retrieval Predicts Prefrontal
r= .957
Time (Sec.)
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
-0.05
-0.10
0
2
4
6
8
10
12
14
16
18
pred 2 trans
pred 1 trans
pred 2 trans
data 0 trans
data 1 trans
data 2 trans

(c)

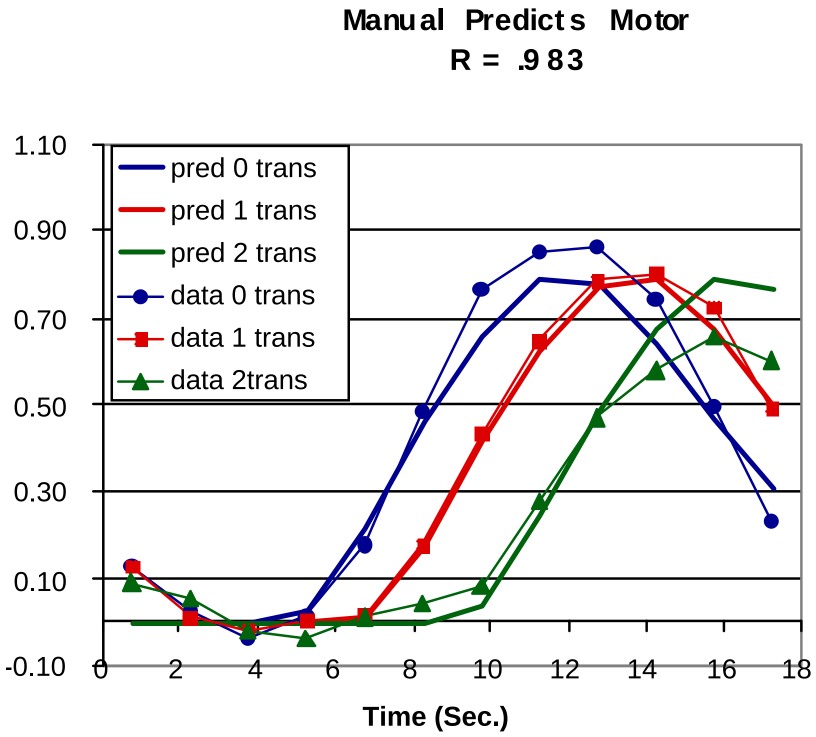
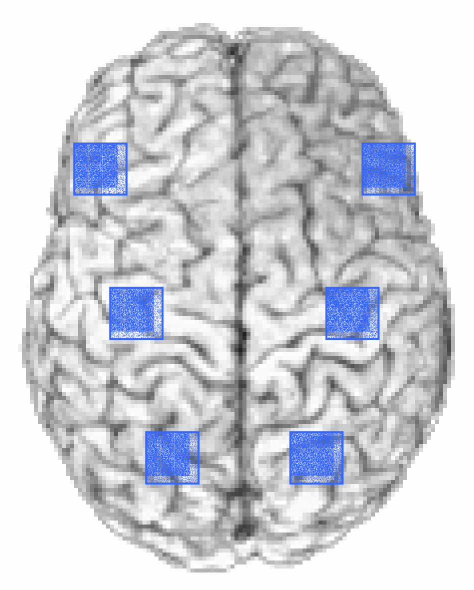

Manual Predicts Motor
R = .983
1.10
0.90
0.70
0.50
0.30
0.10
-0.10
0
2
4
6
8
10
12
14
16
18
Time (Sec.)
pred 0 trans
pred 1 trans
pred 2 trans
data 0 trans
data 1 trans
data 2trans

Figure 4

(a)



(b)

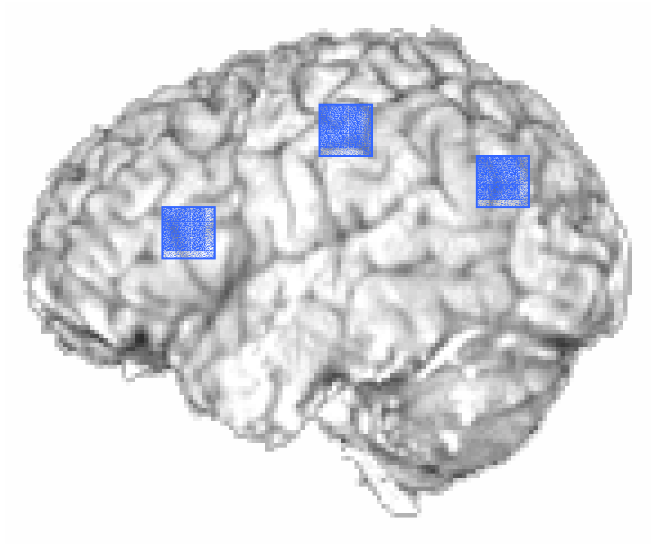


Figure 5

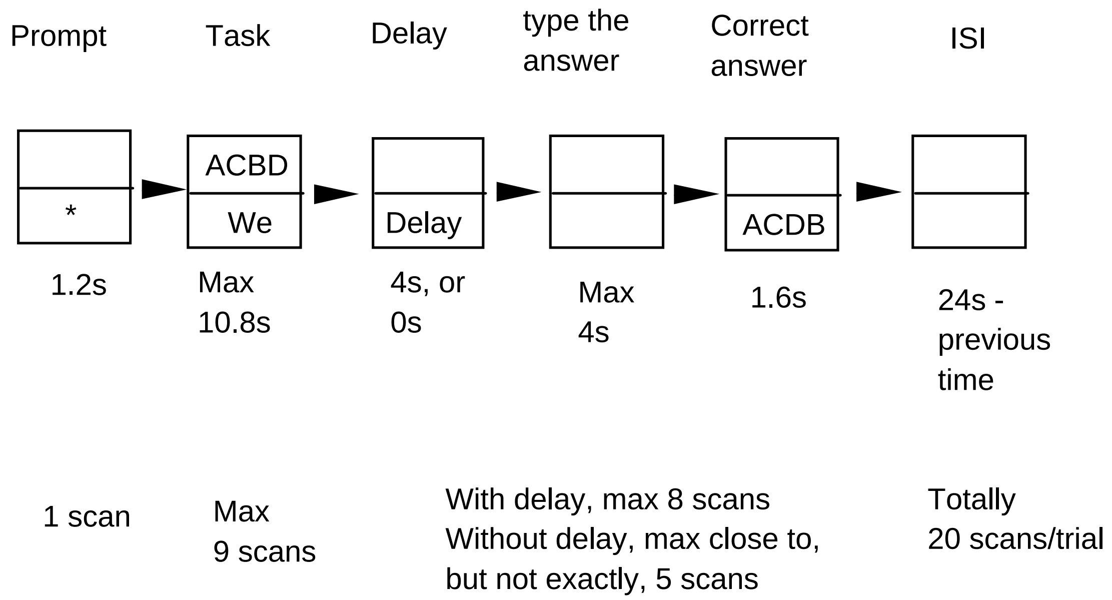

Prompt
Task
Delay
type the answer
Correct answer
ISI
*
ACBD
We
Delay
ACDB
1.2s
Max 10.8s
4s, or 0s
Max 4s
1.6s
24s - previous time
1 scan
Max 9 scans
With delay, max 8 scans
Without delay, max close to, but not exactly, 5 scans
Totally 20 scans/trial

Figure 6a

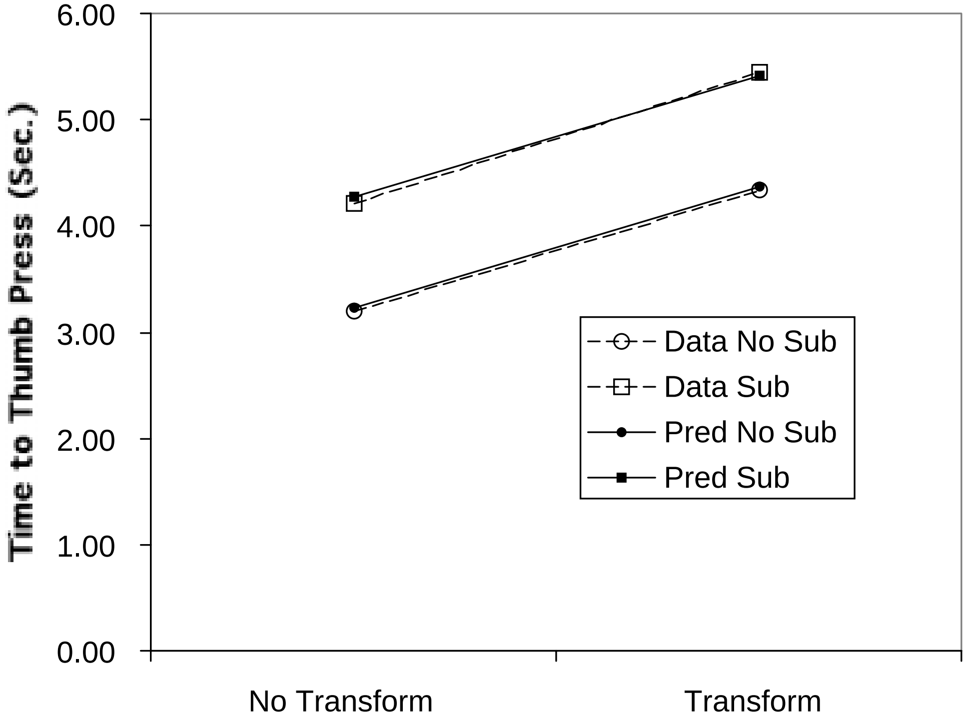


Figure 6b

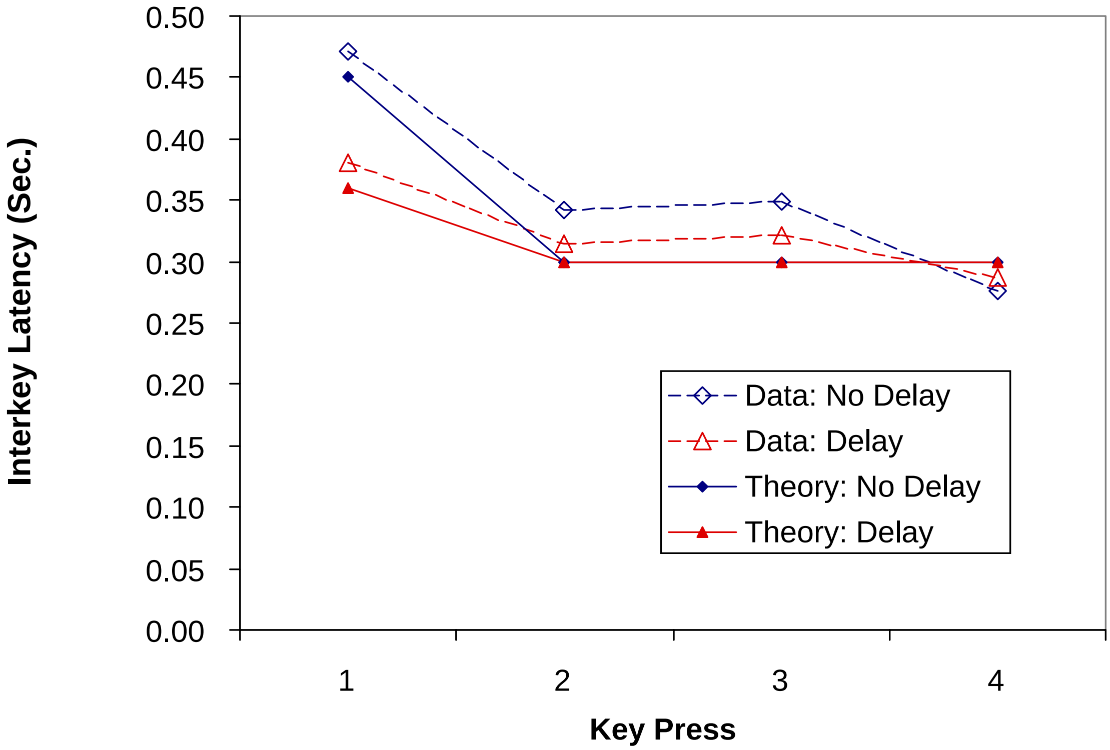


Figure 7

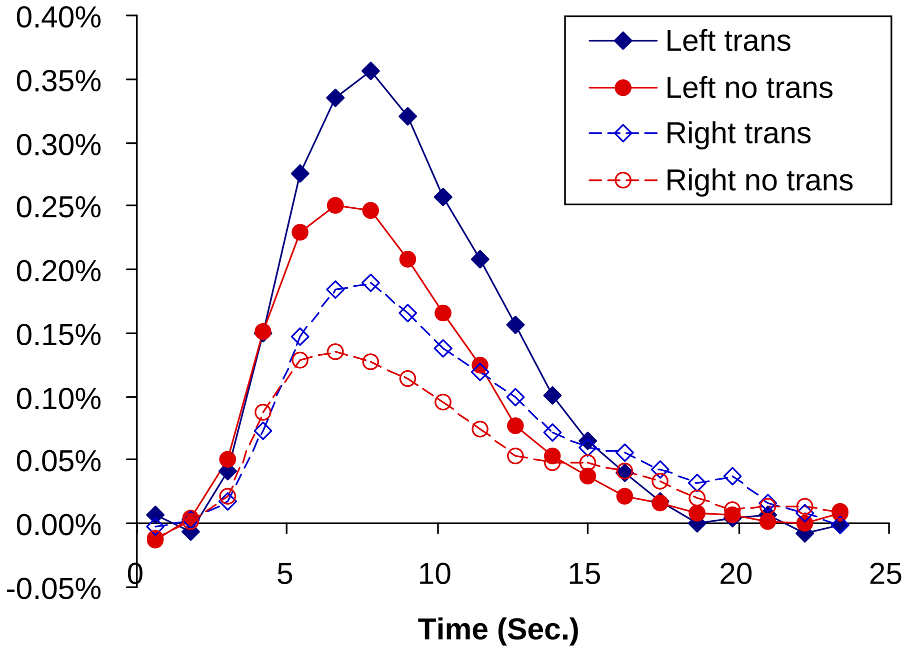
(a) Right-Responding Participants

QuickTime™ and a
Photo - JPEG decompressor
are needed to see this picture.

(b) Left-Responding Participants

QuickTime™ and a
Photo - JPEG decompressor
are needed to see this picture.

Figure 8a


0.40%
0.35%
0.30%
0.25%
0.20%
0.15%
0.10%
0.05%
0.00%
-0.05%
0
5
10
15
20
25
Time (Sec.)
Left trans
Left no trans
Right trans
Right no trans

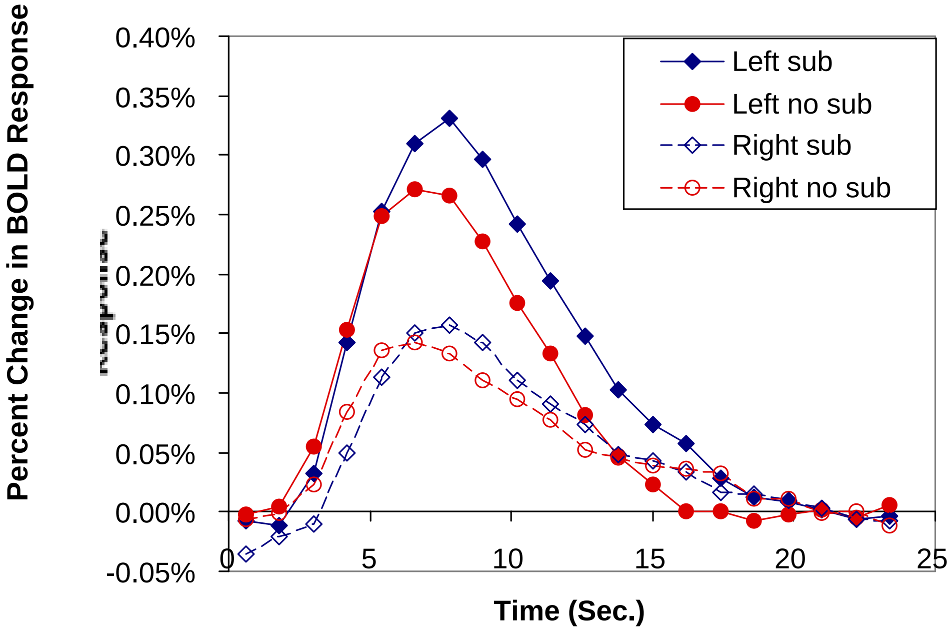


Figure 8b

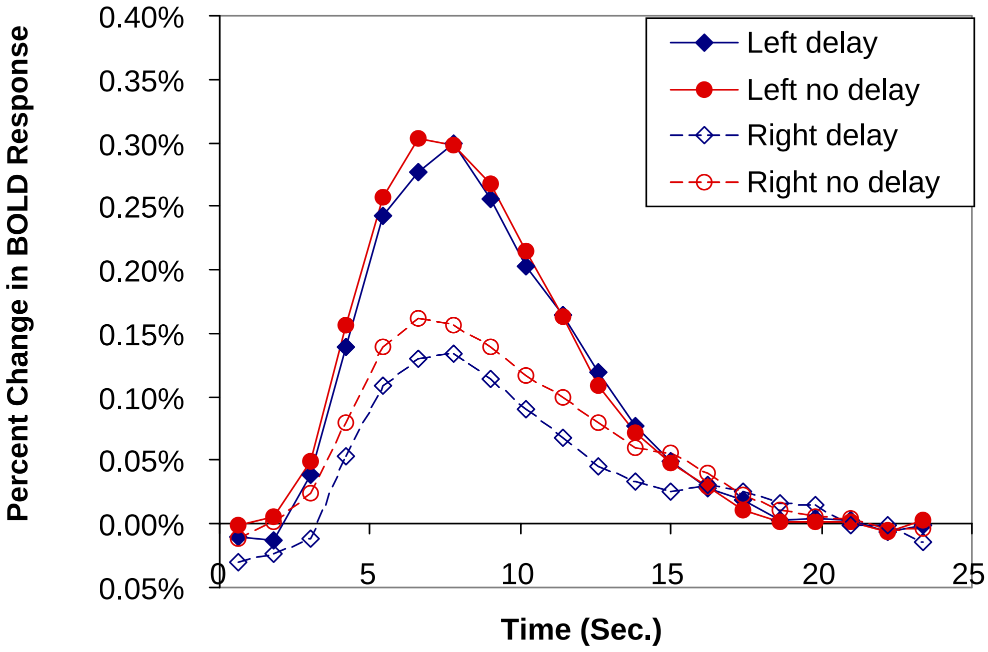


Figure 8c

Figure 9a

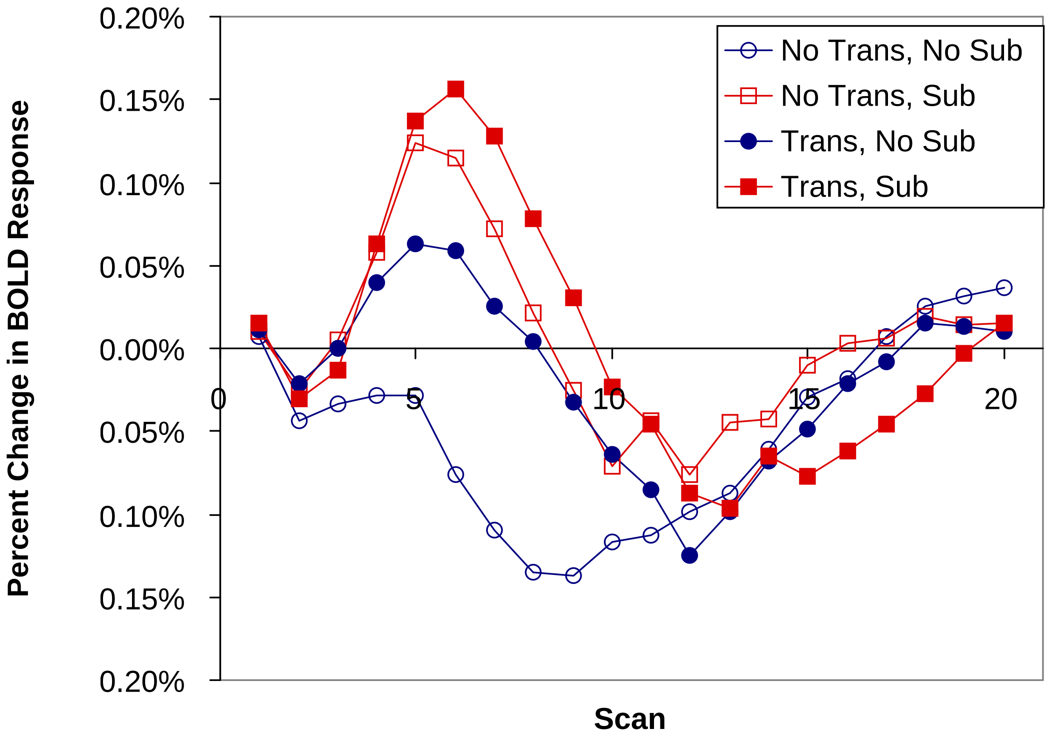


Figure 9b

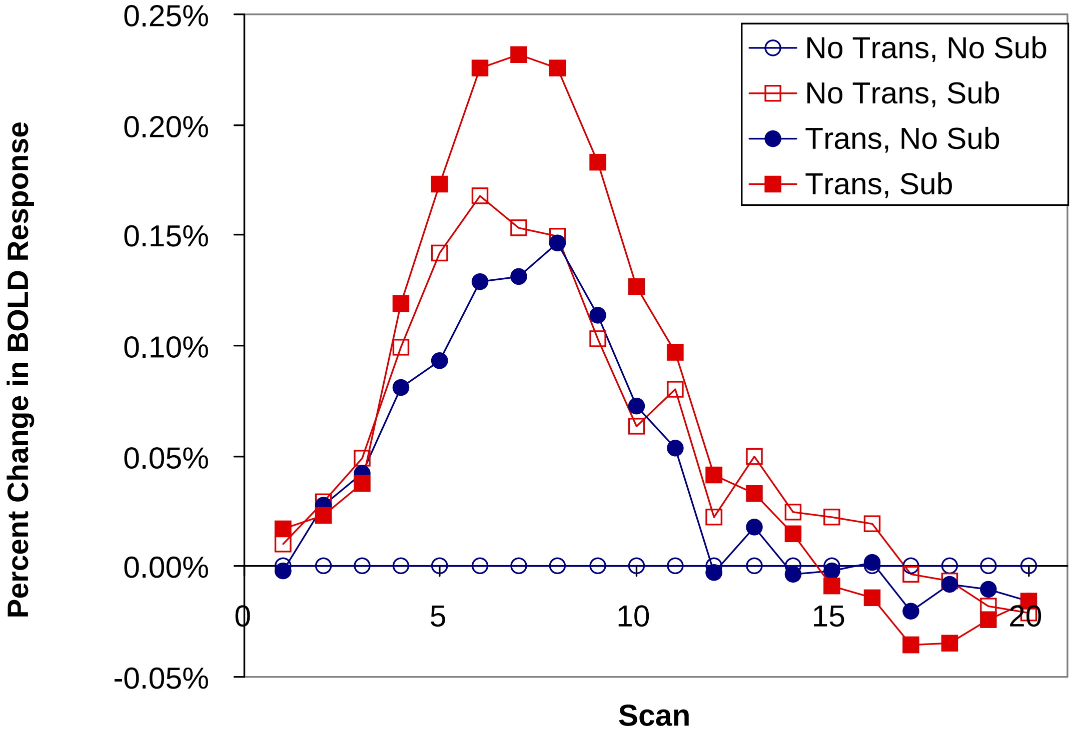


Figure 10a

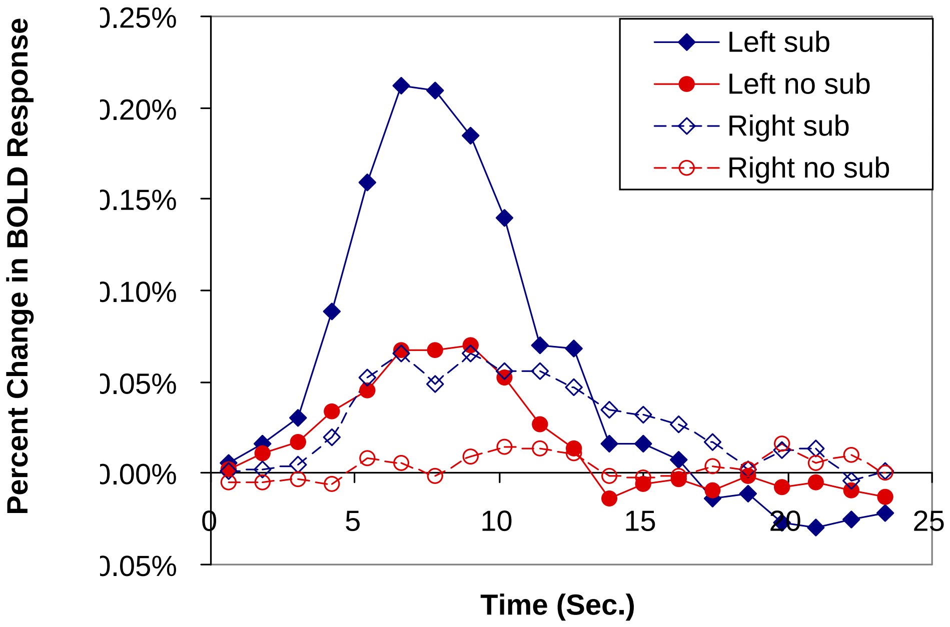


Figure 10b

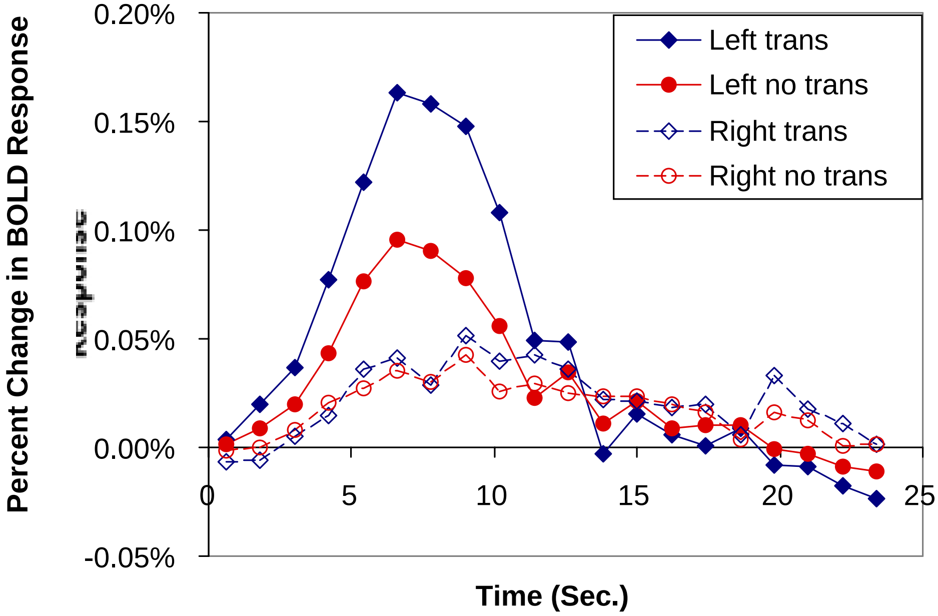
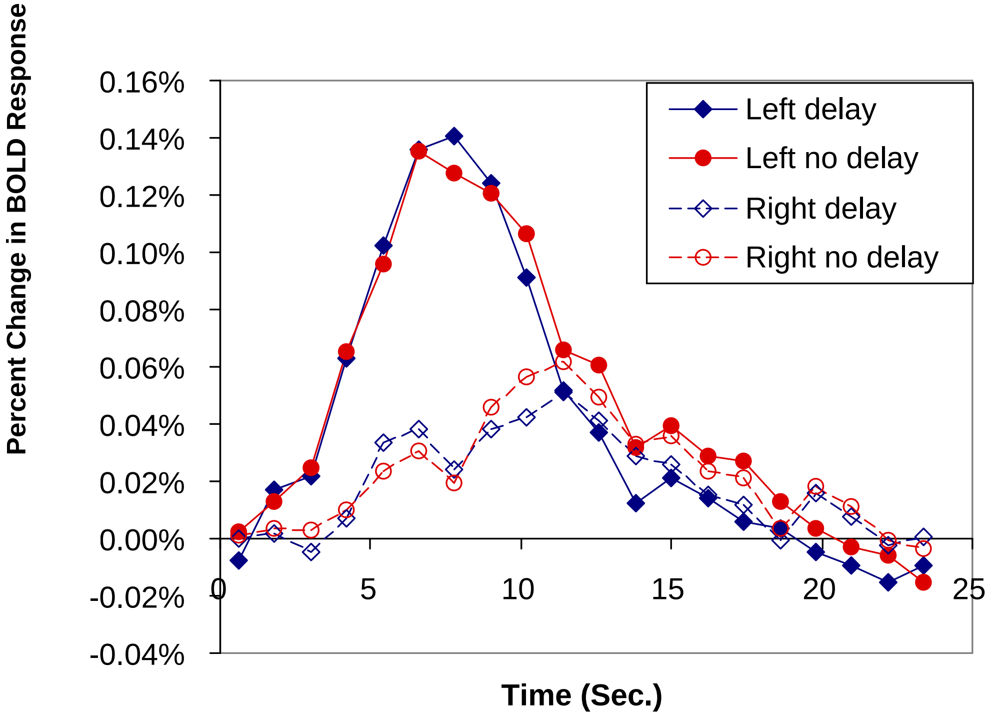


Figure 10c



Percent Change in BOLD Response
0.16%
0.14%
0.12%
0.10%
0.08%
0.06%
0.04%
0.02%
0.00%
-0.02%
-0.04%
0
5
10
15
20
25
Time (Sec.)
Left delay
Left no delay
Right delay
Right no delay

Figure 11

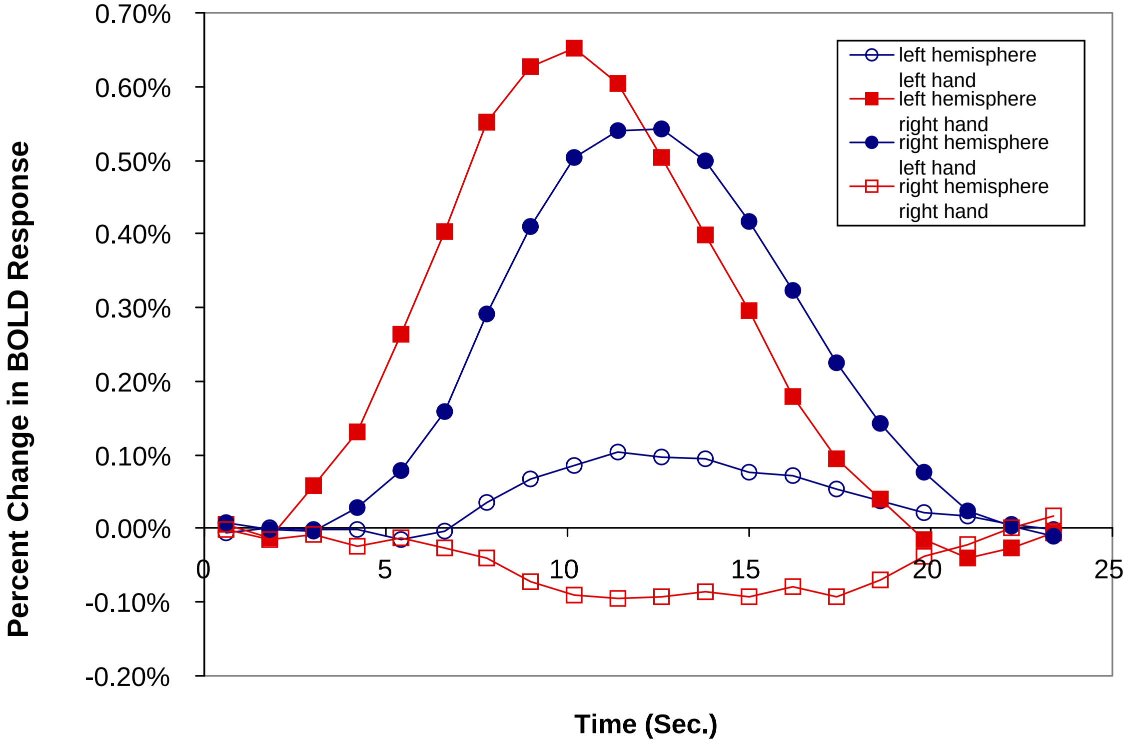

0.70%
0.60%
0.50%
0.40%
0.30%
0.20%
0.10%
0.00%
-0.10%
-0.20%
Percent Change in BOLD Response
0
5
10
15
20
25
Time (Sec.)
left hemisphere left hand
left hemisphere right hand
right hemisphere left hand
right hemisphere right hand

Figure 12a

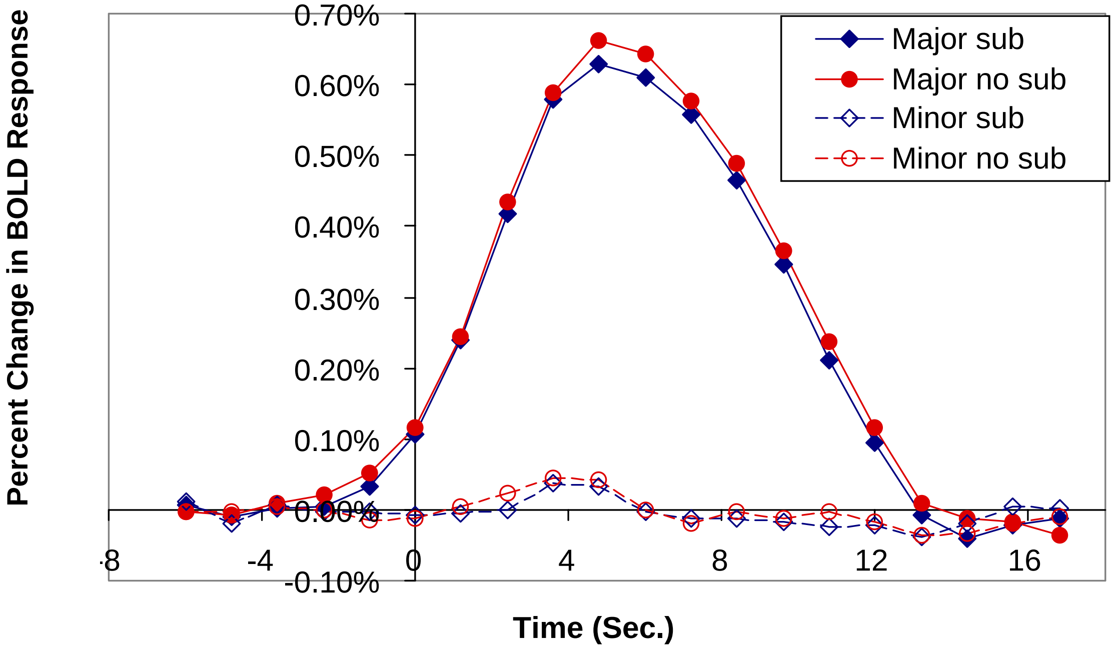


Figure 12b

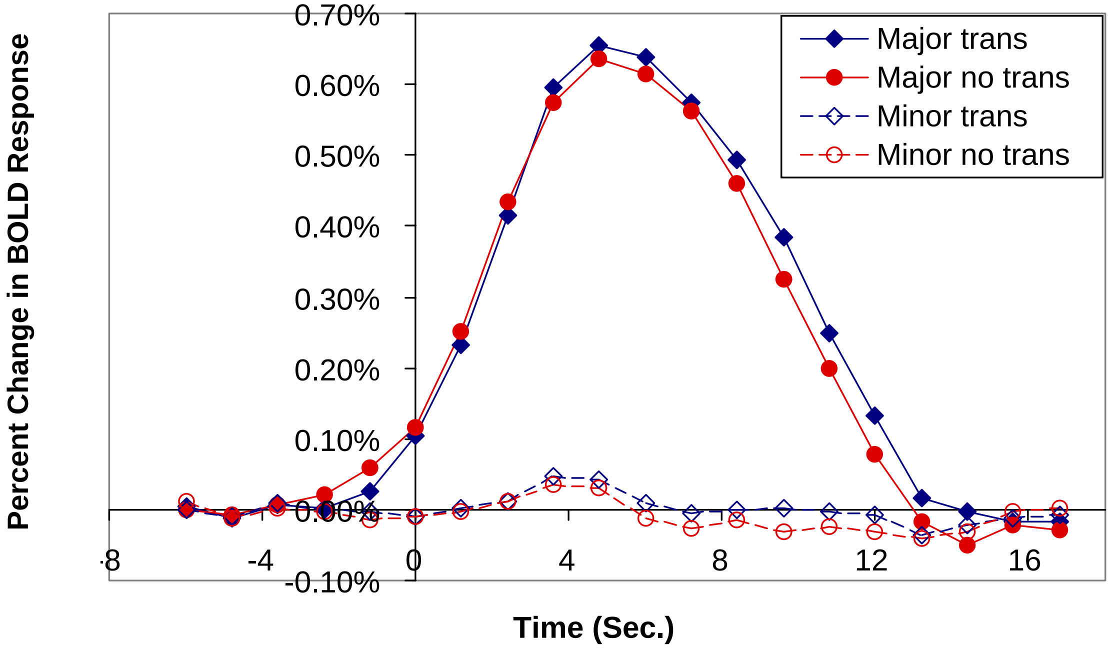
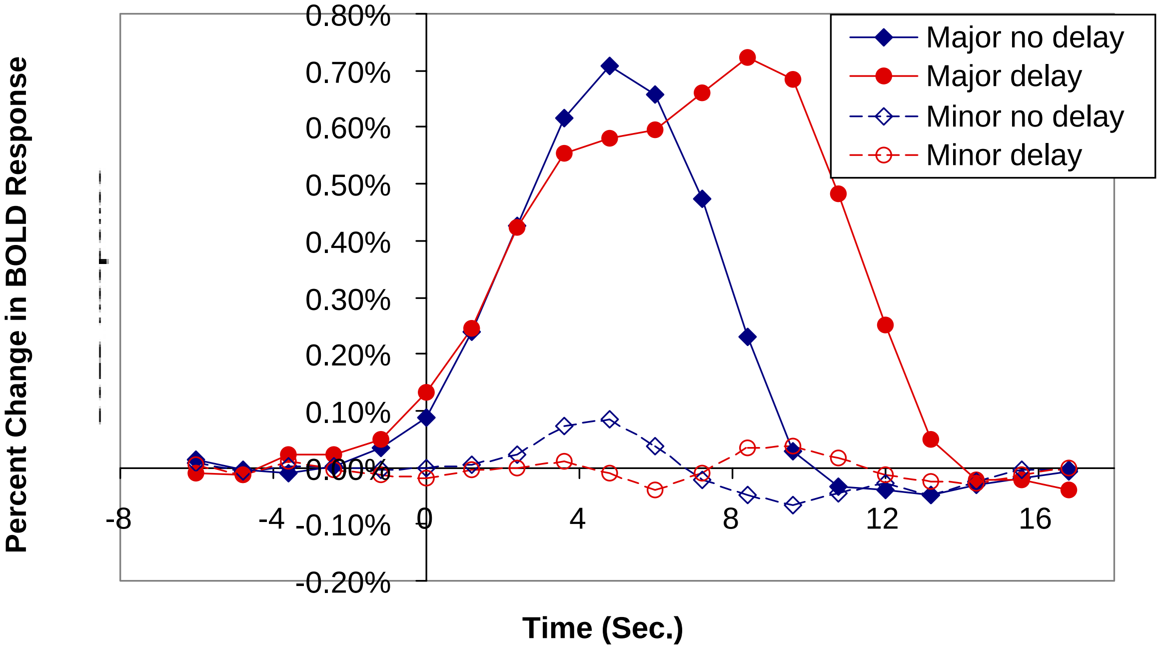


Figure 12c


Percent Change in BOLD Response
0.80%
0.70%
0.60%
0.50%
0.40%
0.30%
0.20%
0.10%
0.00%
-0.10%
-0.20%
-8
-4
0
4
8
12
16
Time (Sec.)
Major no delay
Major delay
Minor no delay
Minor delay

ı

Figure 13

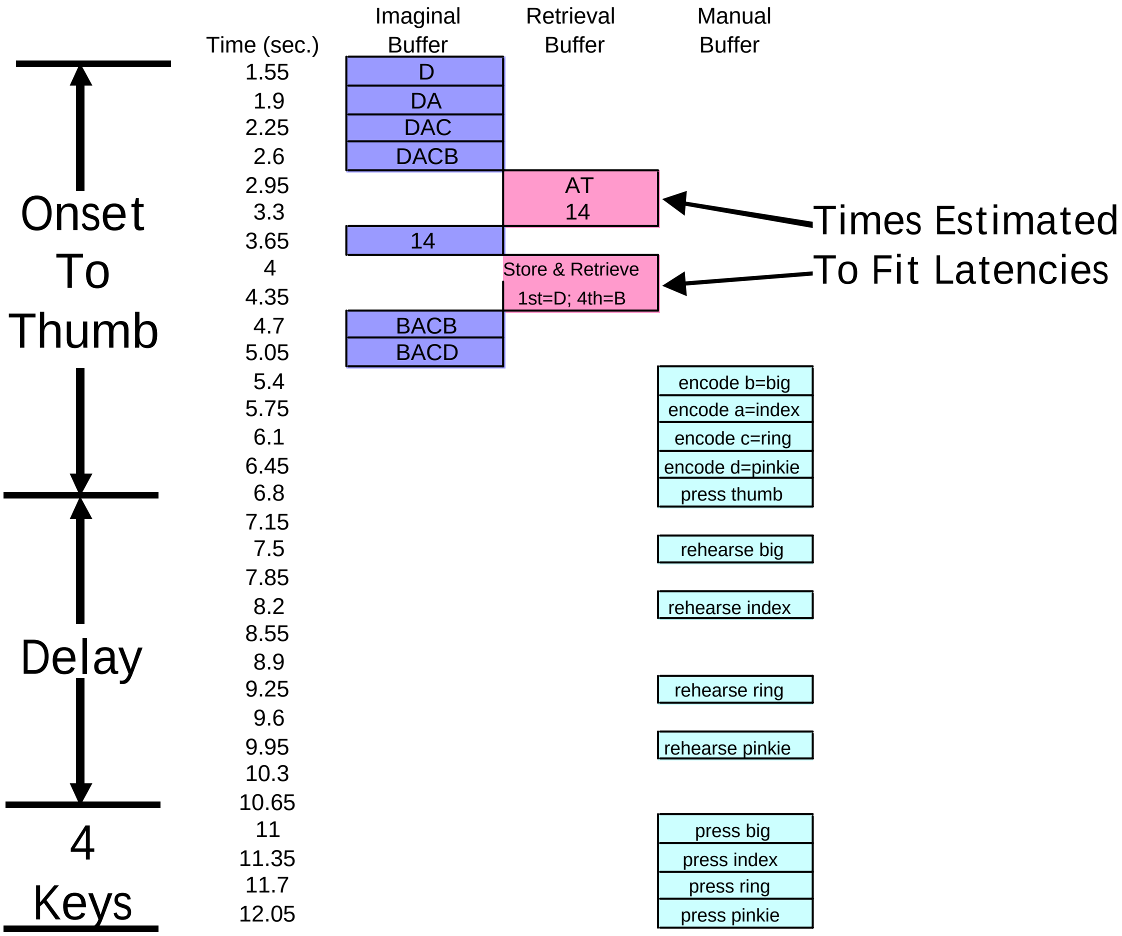

Time (sec.)
Imaginal Buffer
Retrieval Buffer
Manual Buffer
Onset To Thumb
Delay
4 Keys
1.55
1.9
2.25
2.6
2.95
3.3
3.65
4
4.35
4.7
5.05
5.4
5.75
6.1
6.45
6.8
7.15
7.5
7.85
8.2
8.55
8.9
9.25
9.6
9.95
10.3
10.65
11
11.35
11.7
12.05
D
DA
DAC
DACB
AT 14
14
Store & Retrieve 1st=D; 4th=B
BACB
BACD
encode b=big
encode a=index
encode c=ring
encode d=pinkie
press thumb
rehearse big
rehearse index
rehearse ring
rehearse pinkie
press big
press index
press ring
press pinkie
Times Estimated To Fit Latencies

Figure 14a

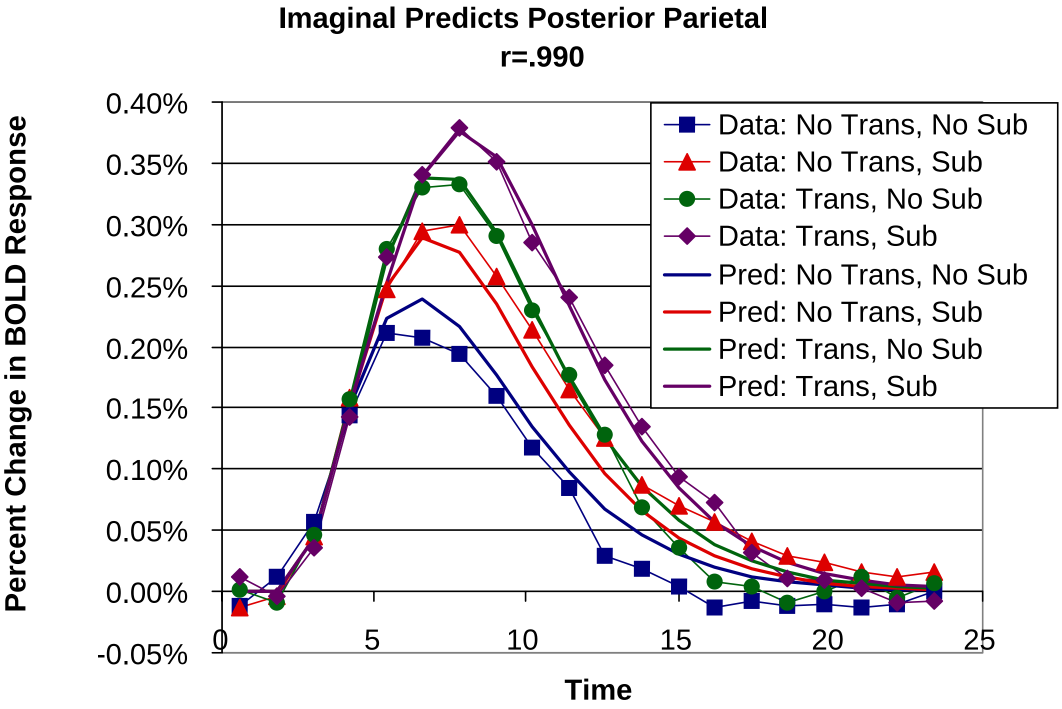


Figure 14b

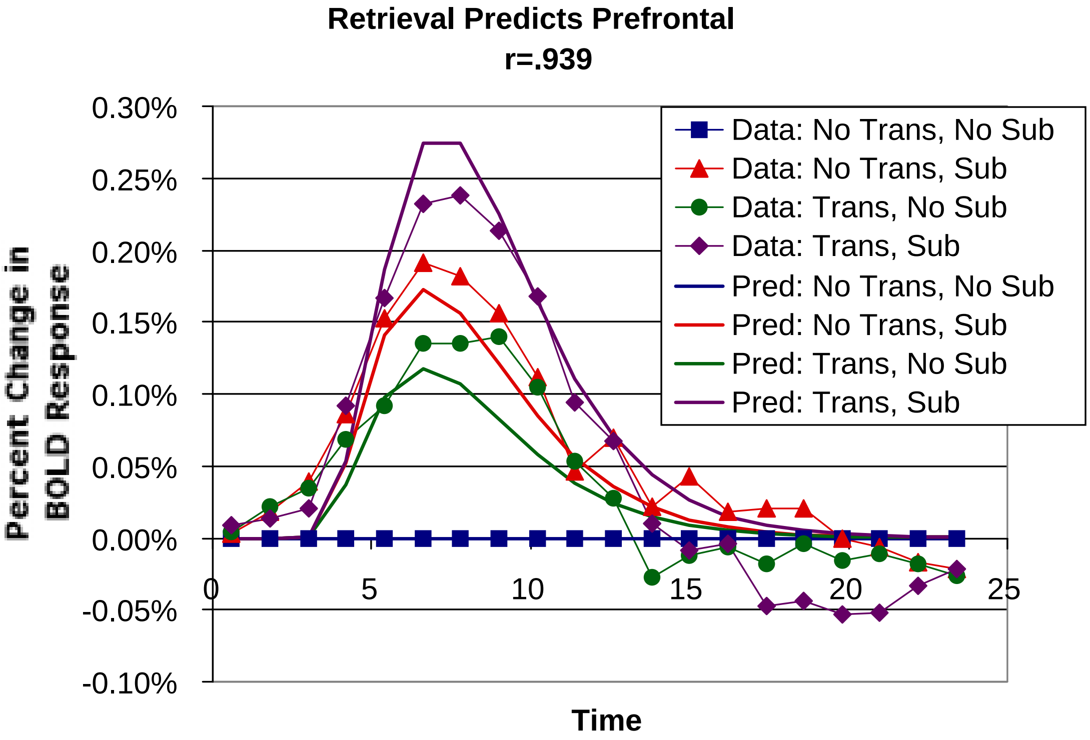


Figure 14c

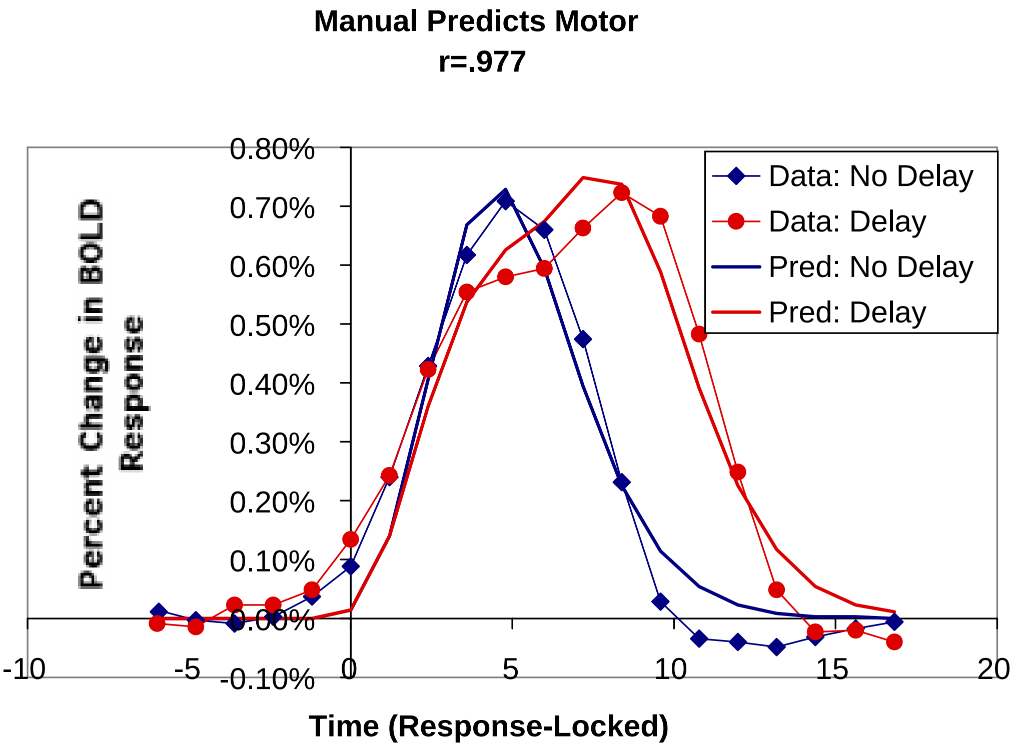

Manual Predicts Motor
r=.977
Percent Change in BOLD Response
0.80%
0.70%
0.60%
0.50%
0.40%
0.30%
0.20%
0.10%
0.00%
-0.10%
-10
-5
0
5
10
15
20
Time (Response-Locked)
Data: No Delay
Data: Delay
Pred: No Delay
Pred: Delay

Figure 15a

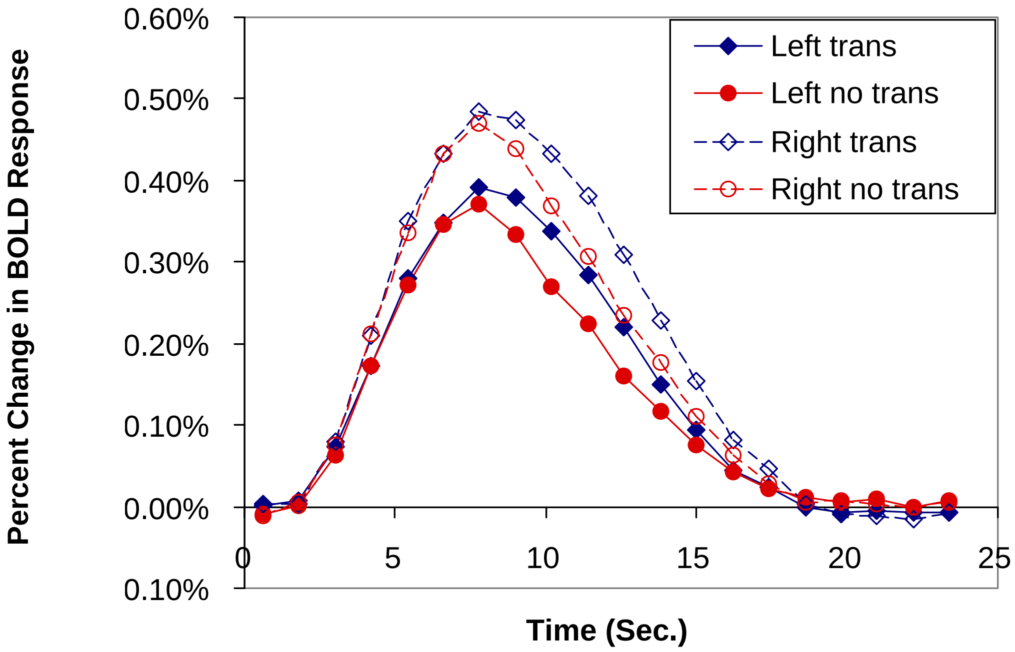
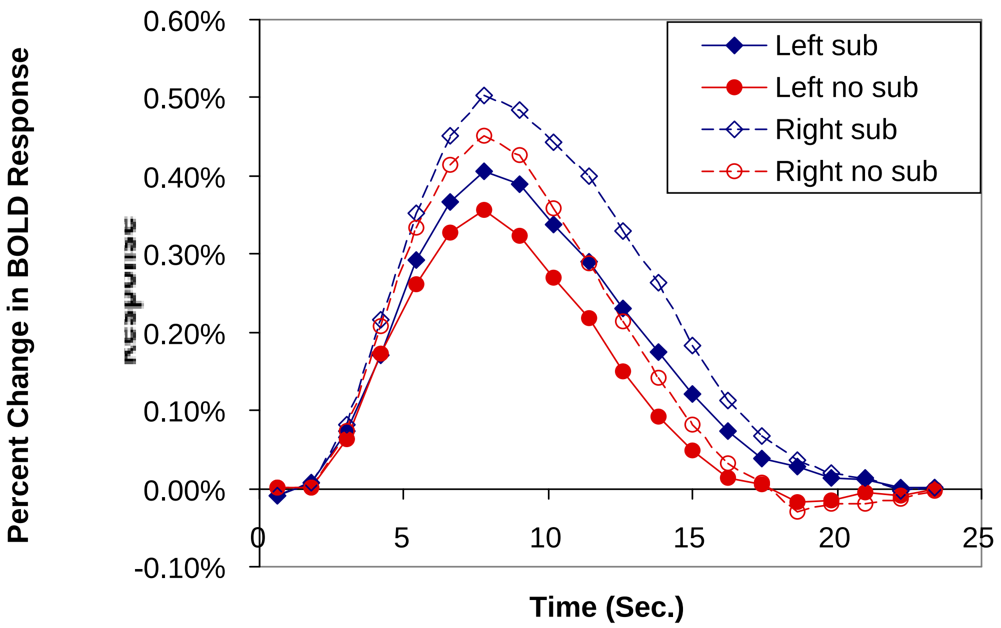


Figure 15b



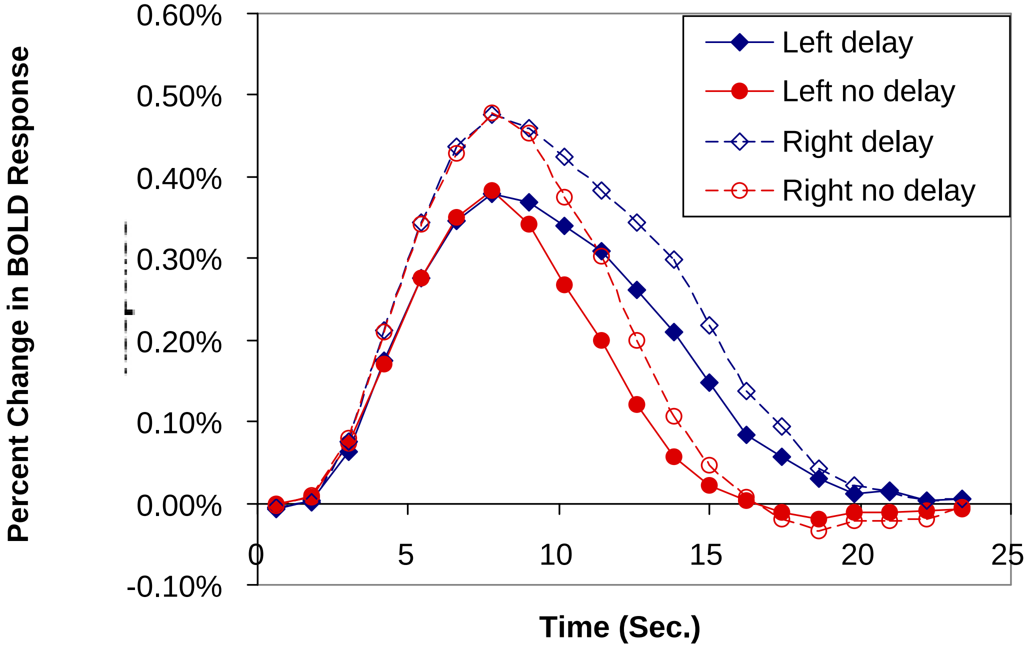

0.60%
0.50%
0.40%
0.30%
0.20%
0.10%
0.00%
-0.10%
Percent Change in BOLD Response
0
5
10
15
20
25
Time (Sec.)
Left delay
Left no delay
Right delay
Right no delay

Figure 15c

Figure 16a

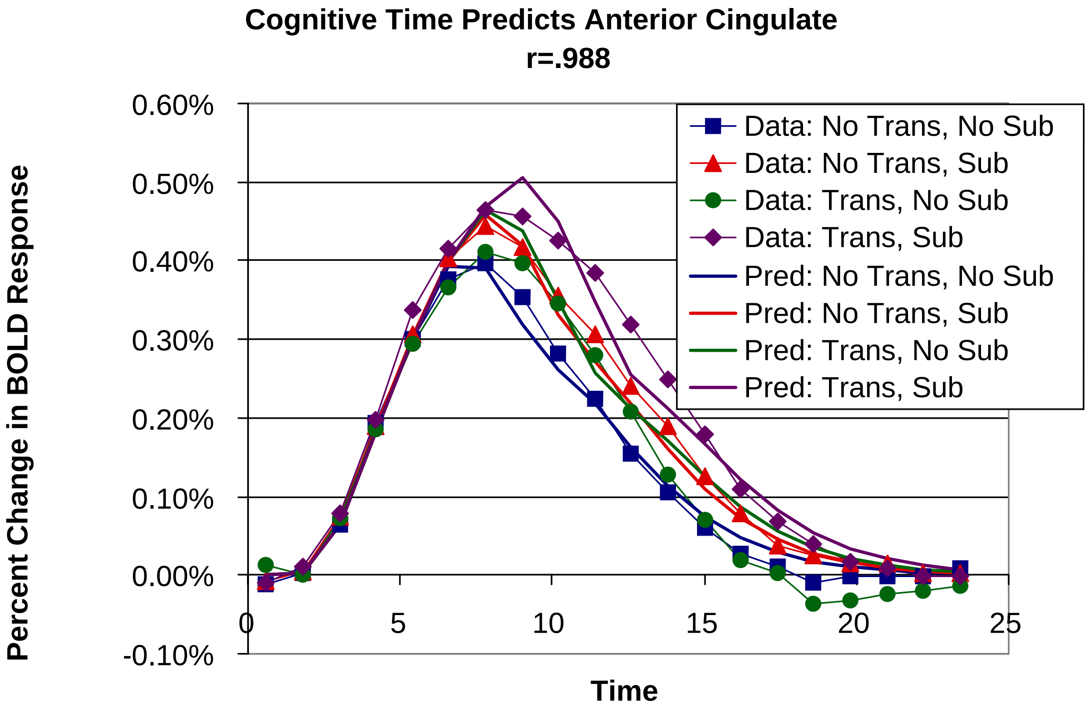
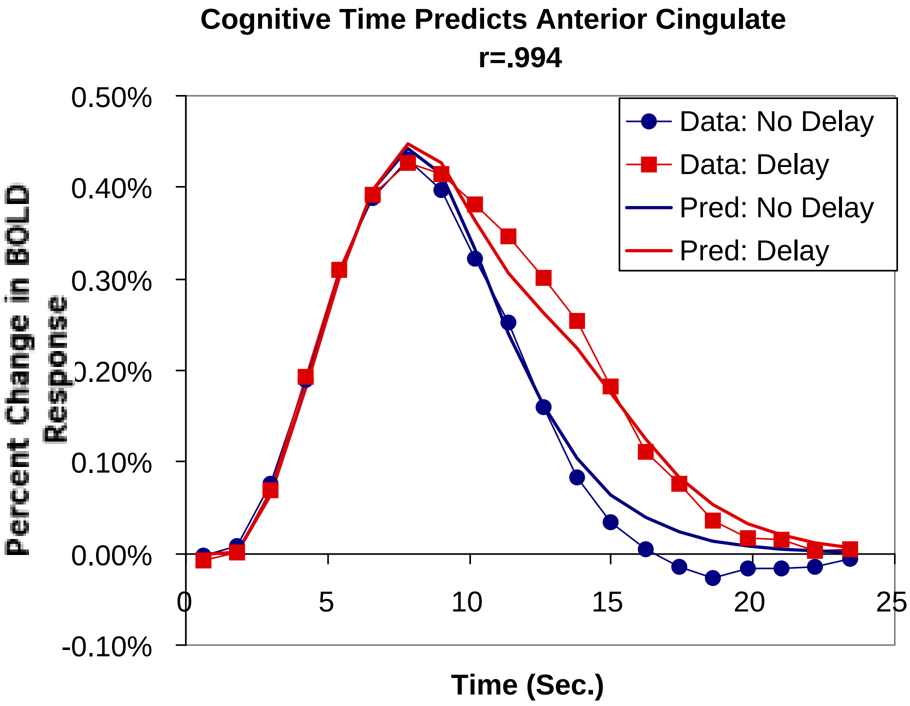


Figure 16b



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[1] This decision was made in consultation with Dehaene and his analysis of parietal regions (Dehaene et al, submitted). The more anterior portion of the parietal area may correspond to his HIPS (horizontal portion of the intraparietal sulcus) region which has arithmetic-specific functions. In contrast, the more posterior portion may correspond to his PSPL (posterior superior parietal lobe), which has a more purely visual representation function.

[2] In calculating these chi-squares, we divide the summed deviations by the variance of the means calculated from the condition-by-subject interaction.

[3] (http://kraepelin.wpic.pitt.edu/his/index.html)