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Word Puzzles Produce Distinct Patterns of Activation in the Ventrolateral Prefrontal Cortex and Anterior Cingulate Cortex

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Abstract

This research reports two studies that use word puzzles that required participants to find a word that satisfied a set of constraints. The first experiment used a remote associates tasks where participants had to find a word that would form a compound word with three other words. The second experiment required participants to complete a word fragment with an associate of another word. Both tasks produced distinct patterns of activity in the ventrolateral prefrontal cortex (VLPFC) and the anterior cingulate cortex (ACC). In both experiments activity in the VLPFC continued only as long as the participants were trying to retrieve the solution and disengaged as soon as the solution was obtained, while activation in the ACC increased upon the retrieval of a solution reflecting the need to process that solution. An ACT-R model was fit to the data of the second experiment. This theory attributes the activity in VLPFC to retrieval operations and the activity to ACC to setting of control states or subgoals. The data confirm these interpretations over alternative interpretations that have been offered in the literature for the function of these two regions.

Studies of cognitive neuroimaging have consistently shown that medial and lateral areas of the prefrontal cortex are critically active when participants are engaged in cognitively demanding tasks (e.g., Botvinick et al., 2001; Bunge & Wallis, 2007; Fincham & Anderson, 2006; MacDonald et al., 2000; Schneider & Cole, 2007). However, the field is still trying to articulate the precise roles of different prefrontal regions. The current work uses event-related functional magnetic resonance imaging (fMRI) to investigate two particular components of cognitive demand: the need to retrieve specific information and the need to control the direction of cognition. The studies reported will test whether a region in the ventrolateral prefrontal cortex (VLPFC) reflects memory retrieval demand and an ROI in dorsal anterior cingulate cortex (ACC) reflects goal-relevant control demand. They will use special properties of a pair of word puzzle tasks to separate the functions of these two regions.

Our understanding of these regions is informed by the ACT-R cognitive architecture (Anderson et al., 2004; Anderson, 2005; Anderson, 2007) that is capable of making explicit the computations underlying performance of a task. According to the ACT-R theory, cognition emerges through the interaction of a number of relatively independent modules. Figure 1 identifies these modules and their brain associations. Later the paper will describe an ACT-R model that involves 6 of these modules, but the principal focus is on the VLPFC region and the ACC region (regions 6 and 7 in Figure 1).

Theories of the Ventrolateral Prefrontal Cortex and the Anterior Cingulate Cortex

The human prefrontal cortex is a large structure and consists of many distinct areas, both in terms of structure and function (e.g. Miller & Cohen, 2001; Petrides, 2005). The ventrolateral region has been associated with retrieval factors in imaging studies (e.g., Buckner, 1999; Cabezza et al., 2002; Fletcher & Henson, 2001; Wagner, 2001). It is also active in many tasks particularly those involving language. As Badre & Wagner (2007) note, this involvement in such tasks can be understood in terms of accessing the information needed to perform the tasks.

The hypothesis in ACT-R is that this region serves the role of maintaining the retrieval cues for accessing information stored elsewhere in the brain. The longer it takes to complete the retrieval successfully, the longer the cues will have to be maintained and the greater the activation. Focused studies that manipulate retrieval difficulty produce systematic differences in the activation of this region. This region and not other regions in Figure 1 tends to respond to manipulations of fan or associative interference (Sohn et al., 2003, 2005), retention delay (Anderson et al., in press), and repetition (Danker et al., in press). All these are factors that influence the duration of a single retrieval from declarative memory.

Perhaps the major competing interpretation of this prefrontal region is that it is activated in conditions that require difficult selections among retrieved information (e.g., Moss et al., 2005; Thompson-Schill et al., 1997). On the other hand, it has been argued that these effects are due to greater retrieval demands in the more difficult conditions (Martin & Cheng, 2005; Wagner et al., 2001). The research reported here will be relevant to adjudicating this difference.

The ACC region is associated with ACT-R's goal module that is responsible for setting subgoals or control states that enable different courses of information processing to be taken when conditions are otherwise equal. It thus enables internal control of cognition independent of external circumstances. The subgoals determine which branch is taken at decision points in the information processing. This sense of “control” is basically the same as in computer science where it indicates how the state transitions within a system are shaped and is similar to some theories of the ACC (e.g., Desposito et al., 1995; Posner & Dehaene, 1994; Posner & DiGirolamo, 1998;). However, other theories relate ACC activity to error detection, (e.g., Falkenstein et al., 1995; Gehring et al.), response conflict (Botvinick et al., 2001; Carter et al., 2000; Yeung et al., 2004), or the likelihood of an error (Brown & Braver, 2005). Again the research to be reported here will be relevant to distinguishing among these various possibilities.

Exposing the Cycle of Central Cognition using Word Puzzle Problems

Any task involving significant internally controlled cognition tends to involve a cycle of cognition that requires repeated retrieval of new information. The system will be in some state (for instance, in the midst of solving an equation like $2x - 3 = 5$) and make a request for retrieval of a declarative fact (such as what is the sum of 5 plus 3?). With the retrieval of this information the system may need to change its internal state (e.g., change the mental representation of the equation to $2x = 8$ and set a subgoal to perform division). This then in turn can evoke another retrieval request (e.g., what is 8 divided by 2?). Thus, the cycle is one in which the current state of internal representations evoke requests for declarative retrievals and the system may change its state to reflect the retrieved information. The mappings in Figure 1 imply that the retrieval operations will be reflected in the activity of the VLPFC, the changes to the problem representation in the activity of the posterior parietal region, and the subgoal changes in the activity of the ACC. Many researchers have noticed that these regions tend to activate together and this is what ACT-R would expect given this information-processing cycle (e. g., Cabezza et al., 2003; Dorsenbach et al., 2006; Schneider & Cole, 2007).

The research to be reported here will capitalize on a feature of certain word puzzles that allow us to pull apart the retrieval from the goal module. The first experiment will use remote association problems introduced by Mednick (1962). Participants saw three words (e.g., *pine*, *crab*, and *sauce*) and attempted to produce a single solution word (i.e., *apple*) that can form compound words with each of the problem words (i.e., *pineapple*, *crabapple*, and *applesauce*). In the ACT-R model for this task a goal is set to find a solution and the retrieval module is continuously engaged until the problem is solved. The important characteristic about these problems is that it takes a long time to retrieve a solution if one is retrieved at all. This produced a sustained demand on the retrieval module while the goal module is dormant in a fixed state. In terms of predictions for the BOLD single this implies that activity should be increasing in the VLPFC (retrieval module) while it is falling off in the ACC (goal module). However, once the problem is solved, activity will stop in the retrieval module while activity will re-emerge in the goal module to set the subgoals in the expression of the answer. Then the patterns of BOLD activity should reverse and activity should increase in ACC while it decreases in VLPFC. This is the same cycle as in many tasks but because the retrieval phase can be so long it should be possible to see the separation of the stages despite the limited temporal resolution of the fMRI.

Experiment 1

In imaging research Jung-Beeman et al. (2004) and Kounios et al. (in press) used the remote compound solutions in Bowden & Jung-Beeman (2003), adapted from the work of Mednick (1962). Their main research interest was in the contrast between solutions that were solved with a reported experience of insight and those that were not. In contrast the current experiment will simply contrast solutions with non-solution. If they could find imaging effects reflecting the rather subtle difference between problems solved with a feeling of insight and problems solved without, this experiment should be able to detect differences based on the contrast between solution trials and non-solution trials and so it follows their procedures fairly closely.

Participants

Twenty right-handed members of the Pittsburgh community (11 females) aged 18 to 32 years old (M = 23.2 years) completed the study.

Procedure

Participants were presented with 3 hint words that could be combined with a common word and participants had to produce this common word. For example, the words *print*, *berry*, and *bird* can all be combined with *blue* (i.e., *blueprint*, *blueberry*, *bluebird*). In this study, as in the Beeman-Jung et al. study, the participants were presented with the three hint words for up to 30 s. If at any time they were able to identify the word, they pressed a button on a data-glove and were taken to a solution screen. They were then given 5 s in which to speak the target word. After this they were presented with a screen that asked them if they had solved the problem with insight and they had up to 5 s to respond. The insight screen instructed them to respond yes by pressing their index finger button and no by pressing their middle finger button. During instruction, the participants were given the following definition of insight (taken from Beeman-Jung et al., 2004):

> A feeling of insight is a kind of 'Aha!' characterized by suddenness and obviousness. You may not be sure how you came up with the answer, but are relatively confident that it is correct without having to mentally check it. It is as though the answer came into mind all at once - when you first thought of the word, you simply knew it was the answer. This feeling does not have to be overwhelming, but should resemble what was just described.

After making their insight response, they were presented with a fixation for 9.5 to 11.5 s (to the start of a new 2 sec. scan) and then a new trial began.

If unable to solve the problem in the 30 s, the participant was then taken to a screen that presented the target word as well as the three hint words. This screen lasted for 5 s, and was followed by an 11 s fixation before the next set of hint words was presented.

The instruction included one example of three cue words and a solution word. Participants were given instruction and 20 practice trials during structural scans. Participants were asked to solve 63 problems during one scan session, which were broken into blocks of 9 to 10 min. These 83 problem/solution combinations were randomly selected from the pool of 144 Bowden & Jung-Beeman (2003).

FMRI Data Acquisition and Analysis

Images were acquired using gradient echo-planar image (EPI) acquisition on a Siemens 3T Allegra Scanner using a standard RF head coil (quadrature birdcage), with 2 s repetition time (TR), 30ms echo time (TE), 70° flip angle, and 20cm field of view (FOV). The experiment acquired 34 axial slices on each scan using a 3.2mm-thick, 64×64 matrix. The anterior commissure-posterior commissure (AC-PC) line was on the 11th slice from the bottom scan slice.

Acquired images were analyzed using the NIS system. Functional images were motion-corrected using 6-parameter 3D registration (AIR, Woods et al., 1998). All images were then co-registered to a common reference structural MRI by means of a 12-parameter 3D registration (AIR, Woods et al.) and smoothed with an 8 mm full-width-half-max 3D Gaussian filter to accommodate individual differences in anatomy. Spatial F maps were generated using random effects analysis of variance (ANOVA).

Results

Behavioral Results

60.2% of the problems were solved. Of those solved 54% were reported as solved with insight. Of the 20 participants, one never reported a solution with insight and another participant never reported a solution without insight. For the 18 participants that reported both solutions with insight and without insight, the mean solution time was 11.98 s for non-insight solutions and 9.24 s for insight. The difference in times was marginally significant – $t(17) = 1.74$; $p < .10$; 2-tailed. These are relatively comparable numbers to those reported in Beeman-Jung et al. (2004) including the marginally significant difference in latencies.

Imaging Results

The principal interest is in comparing trials with solution and those without solution but the end of this section will briefly report the results associated with insight. Although the average time for a solution was about 11 s, there was distribution of times with a standard deviation of over 7

s. A response-locked analysis was used to deal with this variability. We set the scan of the response as scan 0 and looked for the 5 scans (10 sec) before and the 5 scans (10 sec) after.   We used this scan designation to average all solution trials for each participant to get an average 11 scan BOLD response that began 5 scans before the response.   The analyses are based on the participant BOLD responses for the left hemisphere version of each region designated in Figure 1.

To have a contrast with solution trials, a baseline is needed from the trials on which no solution was produced.   On these trials the participant goes through 15 scans without a response.   Which scan should correspond to scan 0 in the response-locked analysis for the solution trials? We averaged these non-solution scans together for each participant and then produced a weighted averaging of them to reflect a comparable set positions for scan 0 as in the solution trials. We calculated the proportion p_n of the responses that occurred on the nth scan from onset on solution trials.   We then calculated the average baseline, B_i for the ith scan of that participant's non-solution trials as

$$B_i = \sum_{n=1}^{15} p_n S_{i+n}$$

where i varies from -5 to 5 and S_{i+n} is the average response during scan i+n. Thus, the mean location of the baseline B_i for non-solution trials is the same in the as its mean location in the solution trials.

Figure 2 shows the contrast between solution and baseline for each of the 8 predefined regions (see Figure 1). For each region we performed a t-test of the difference between the solution and baseline conditions for the 4 scans from -7 s. through -1 s. (which reflects processing before the solution is announced) and for the 4 scans from 3 s. through 9 s (which largely reflects processing subsequent to the solution). The former test reflects effects before announcing a solution and the latter effects after announcing a solution[1]. These tests are reported in the figures. Most regions showed quite significant and interpretable effects. The motor areas associated with the hand (Figure 2c) and the mouth (Figure 2d) show strong effects after the solution reflecting the key press and word generation. The aural region (Figure 2b) also shows a post-solution response reflecting processing of the speech. In each of these three cases, the difference between solution and baseline is significantly greater ($p < .0001$) after solution than before solution. The parietal (Figure 2e) and VLPFC (Figure 2f) regions do not show significant effects of solution either before solution or after solution. In the case of the VLPFC, however, the difference between solution and baseline is positive before solution, negative afterwards, and the difference of these differences is significant ($t(19) = 2.72$, $p < .05$). The ACC (Figure 2g) and caudate (Figure 2f) show a stronger response for solutions both before and after the solution is announced. The effect in the ACC is stronger post-solution than pre-solution ($t(19) = 7.13$ $p < .0001$) while the difference between the two differences is marginal in the case of the caudate ($t(19) = 1.89$, $p < .10$).

With respect to the major topic of the difference between VLPFC and ACC, the patterns are quite different. Reflecting a residual correlation with task structure, the correlation between Figure 2f and 2g is still positive but a modest .56. A three-way ANOVA using the factors of region (VLPFC or ACC), time (before or after solution), and condition (solution or baseline)

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[1] We ignore scans centered on the response and just after because they would reflect both factors given the lagged character of the hemodynamic response.

finds a highly significant 3-way interaction ($F(1,19) = 52.80$; $p < .0001$) such that the difference between solution and baseline turns from positive early to negative late in the VLPFC while it grows in the ACC. So this experiment has succeeded in strongly separating the behavior of these regions. Moreover, it is in the direction predicted. The effect in the VLPFC reverses because the participants are no longer engaged in retrieval in the solution condition while their retrieval efforts continue in the baseline condition. In contrast, with the emergence of a solution the ACC activity spikes reflecting the change in control states associated with response generation.

To provide comparison with Jung-Beeman et al., we will report the effects associated with the report of an insight, although this is not the interest of the current research. In contrast to the strong contrasts between solution and baseline, none of the predefined regions showed a significant contrast between solutions that were reported with the feeling of insight and those that were not[2]. However, none of these regions correspond to the regions that Beeman-Jung et al. found in their exploratory analysis. Exploratory analyses looked for regions that would show significant interactions between insight and non-insight. Even using a liberal threshold (10 contiguous voxels at .05 significance) the only significant region was an area that overlapped with the predefined left motor area. Somewhat inexplicably, post-response signal is greater in the non-insight condition. Finally we examined the response in the 7 regions reported in Beeman-Jung et al. and none of these showed significant effects of insight versus non-insight or a significant interaction between insight and scan.

Discussion of Experiment 1

[2] These analyses were restricted to the 18 participants who reported both solving some problems with insight and other problems without insight.

The differences between VLPFC and ACC were highly significant and qualitatively as predicted. However, the ACT-R theory does more than make qualitative predictions about the effects in these two regions. It makes predictions for the exact BOLD responses observed in all 8 of these predefined regions. Unfortunately, such predictions are difficult to test this experiment with its highly variable response times. Also, the fact that a response was generated immediately upon solution made it difficult to separate effects associated with solution and effects associated with response generation. Therefore we did a second experiment with less variable response times and which included a delay between solving the problem and generating a motor response.

Experiment 2

The second experiment involves a somewhat different word puzzle task and so tests how well the results of the first experiment generalize. Participants were shown a word fragment like *–a-a-a* and an associate like *hockey* and were given 10 s to complete the fragment – the intended answer is *Canada*. Only after this second 10 s interval did they have to generate a response. In a behavioral pilot participants were asked to generate the response as soon as they thought of it were able to solve about 32% of the problems in 10 s. When they solved the problem with a hint they took an average of 2.98 s to solve the problems with a standard deviation of 1.77 s. Thus, while these problems took multi-seconds to solve they were not as long or variable as the problems in the previous experiment. The 90th percentile for solution times was 5.43 s and the 95th percentile was 6.72 s. Therefore, we felt confident that most of the solutions would occur early in the 10 s interval before the response was required and also show their effect within that interval. A comparison of activity during that interval for successful trials versus unsuccessful trials would offer a test that was free of effects of response generation.

Participants

Twenty right-handed members of the Pittsburgh community (10 females) aged 19 to 30 years old (M = 22.4 years) completed the study.

Procedure

Participants were presented with a fragment of a word that was between 5 and 11 letters long, with approximately half the letters replaced by hyphens, always including the first letter. The participants would then have 10 s to study this word and try to identify the word. If the participants could solve the puzzle within the 10 s period, they would press a button on the data-glove and be taken to a solution screen. This first 10 s period was included to eliminate any problems that could be solved without the cue word. If the participants could not complete the fragment, they would then be presented with the fragment and a cue word for 10 s. After that 10 s, the participants would be asked if they believed they knew the answer to the word fragment, which they would indicate by pressing a button on the data-glove. The participants had 2 s in which to respond. Independent of how they responded, the participants would be taken to a solution screen, which presented the puzzle word along with five choices for its first letter. The participants would have 2 s in which to select the letter that they believed to be the first letter of the word, with 1 corresponding to the thumb button, 2 to the index finger, etc. Following this, the participants were given feedback on their response and the correct word was presented. This screen remained for 6 s, before returning to the first screen with a new word to solve.

Participants were presented with 68 randomly ordered words. They solved these problems in scan blocks that lasted from nine-and-a-half to ten minutes. During structural scans, participants were trained both on responding with the data-glove to the numbers 1-5 correctly, and given 10 practice problems drawn from a different set of words.

The same scanning parameters were used as in the first experiment.

Results

94% of the problems were not solved when just shown the word fragment. Of those that were not solved, 38% were solved with the hint and of those solved with the hint and 90% of these were solved with the intended word. Our analysis will compare those that were solved with the intended word in the second interval with those that were not solved at all. Figure 3 presents the results for the same 8 regions as Figure 2. Figure 3 uses as a baseline the average of the two scans before the appearance of the cue. It plots the percent increase from this baseline for the 10 scans that involve 10 s to process the cue and the 10 s to process the respond and process the feedback. Figure 3 also includes the predictions of an ACT-R model described later.

For each region we performed a t-test of the difference between the solution and no-solution conditions for the 4 scans before the response (i.e. the 4 scans from 3 to 9 s which reflects processing before the solution is announced) and for the last 4 scans from starting with the second scan after the response (i.e. the 4 scans from 13 s to 19 s after the response, which reflect largely processing subsequent to the solution). These tests are reported in the figures. Most regions showed quite significant and interpretable differences. To complete the comparison with Figure 2, Figure 3 includes the vocal and aural regions, but as there is no speech in this experiment these regions are not active. Otherwise, the differences between the solution and no-solution conditions before the response (3 to 9 s in Figure 3) in this experiment are largely consistent with the differences between solution and baseline before response in Figure 2 for Experiment 1. On the other hand, some of the patterns are different after the response (13 – 19 s. in Figure 3) in this experiment than in Experiment 1 because participants in this experiment see the same displays and engage in comparable actions whether they solve the problem or not. So, for instance, the manual motor region shows a rise in the no-solution condition of this experiment whereas it did not in the baseline condition of the previous experiment.

With respect to the major topic of the paper, this experiment again shows major differences in the BOLD response of the VLPFC and ACC. Reflecting a residual correlation with task structure, the correlation between Figure 3f and 3g is a rather small .30. A three-way ANOVA using the factors of region (VLPFC or ACC), time (before or after solution), and condition (solution or baseline) finds a significant 3-way interaction ($F(1,19) = 6.29$; $p < .05$) such that there is a significant difference between solution and no-solution early in the ACC but no effect in the VLPFC, while there is a significant difference late in the VLPFC but no effect in the ACC. Moreover, the significant early effect in the ACC is greater activation in the solution than no-solution condition while the significant effect late in the VLPFC is greater activation in the no-solution condition. These are the predicted effects. The achievement of a solution evokes control activity in the ACC before the response. The failure to achieve a solution means that retrieval efforts will continue in the VLPFC and produce sustained activation. Below we describe the ACT-R model that predicts these effects and the effects for the other regions.

The ACT-R Model

The ACT-R model involves a minimal set of processes to perform the task[3]. Figure 4 compares a trace of this model solving a problem with a trace of the model not solving the problem. The figure represents the activity of six relevant modules for performance of the task. The four that take the longest times are indicated by boxes –a visual module encoding the information that is presented on the screen, a retrieval module that tries to retrieve a solution, an imaginal module that updates the problem representation with each significant development, and a manual module for programming hand movements. In addition, the horizontal lines in Figure 4 reflect the firing of productions that are responsible for selecting cognitive actions and the brackets reflect periods of time when the model is operating under a single subgoal. The time is traced down the figure from presentation of the critical cue (e.g., hockey for _a_a_a) to the end of processing the feedback. Long periods of no interesting change are grayed out; otherwise the time representation is to scale.

There are only three types of differences between solution and no solution but these differences each is critical:

1. **Retrieval Activity.** Based on the pilot data we estimated a 2.5 s time to retrieve an answer on a success trial, which with encoding and response generation would produce the observed 3 s solutions. We estimated that participants gave up on trying to retrieve after 7 s. The other retrieval difference is that we assumed participants resumed their

[3] A running version of this model may be downloaded from

retrieval efforts when they were queried for an answer if they had not yet retrieved an answer.

2. **Goal activity.** Upon successful retrieval of a solution, the goal state was changed and the problem representation updated.
3. **Manual activity**. We assume that participants initiated a trial by preparing themselves to press the key indicating no answer, but if they retrieved an answer they changed this programming. When the menu was presented, participants who knew the answer had to program the pressing of the appropriate finger whereas participants who did not know the answer could just press any key. Thus, the manual activity is longer when there is a solution, reflecting the need to program a specific response.

The model in Figure 4 largely reflects default ACT-R parameters. The only parameters estimated were activation parameters that determined the time of a successful retrieval and the time to give up on an unsuccessful retrieval.

Anderson (2007) describes how to take a pattern of module activity like that in Figure 4 and predict the BOLD response in each of the predefined regions of interest. From Figure 4 one can extract for each module a demand function *d*(x), which has a value of 1 when the module associated with that region is active and a value of 0 when it is inactive. Whenever there is demand for a module this demand will drive a hemodynamic response described by *b*(t), which is a standard gamma function used in previous studies to represent the hemodynamic response (Boyton et al., 1996; Cohen, 1997; Dale & Buckner, 1997; Glover, 1999):

$$b(t) = m\left(\frac{t}{s}\right)^{a} e^{-(t/s)} .$$

In this function, *m* is the magnitude of the response, *s* is a time scaling parameter, and *a* determines the steepness of the BOLD response—the greater the value of *a*, the steeper the function. We used values of $a = 6$ and $s = .8$ s for all regions and just estimated different magnitude parameters on a per region basis.

We then convolved functions *d*(x) and *b*(t) to produce the complete BOLD response function:

$$B(t) = \int_0^t d(x)b(t-x)dx\,.$$

We fit the BOLD responses in Figure 3 by estimating values for the magnitude parameters for each region[4]. The deviations from predicted can be evaluated according to the following chi-square statistic:

$$\chi^2(df) = \sum_i (\hat{Y}_i - \overline{Y}_i)^2 / s^2_{\overline{Y}_i}$$

which is a sum of the squared deviations divided by the variance of the participants around that data point.. There are 24 data points for each region (12 scans by success-versus-no-success). Since a single magnitude parameter is estimated for each region the chi-square statistic has 23 degrees of freedom. A chi-square value greater than 36 reflects significant deviations at a threshold of p = .05.

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[4] It is worth keeping in mind that there is some processing of the word fragment in the 10 seconds before Figure 4 begins and the BOLD response from this activity has not entirely fallen back to baseline at the point where Figure 4 begins.

Table 1 presents the magnitude parameters, the chi-square statistics, and the correlations between predictions and observed responses for each of the 6 regions:

1. The predictions for the fusiform capture the general fluctuation with the presentation of material on the screen but only achieve a modest correlation with the data. The major deviation is that participants show a fusiform response to the presentation of the cue on the screen one scan later than the model predicts. Also, the model fails to predict the small difference that occurs early between the solution and no solution conditions.
2. The manual module does a good job of predicting the response in the motor region, achieving a high correlation. The chi-square is still significant and reflects the failure to predict the magnitude of the difference between the solution and no-solution scans late. The model does predict a difference due to the need to program a selection from the menu in the solution condition, but this is smaller than what is observed.
3. The imaginal module does a satisfactory job in predicting the fluctuations in activity in the parietal including the early difference in favor of the solution condition. This is difference is produced by the representation of the solution.
4. The fit of the retrieval module to the VLPFC region is particularly good. It captures the facts that the BOLD response will initially show the same rise whether there is a solution or not, but that the BOLD response will drop off upon retrieval of a solution.
5. The fit of the goal module to the ACC is also good although the residual differences are significant. It does successfully predict greater early activity in the case of a solution but it does not completely predict the magnitude of the BOLD response in the early period.
6. The response in the caudate is weak and the correlation with predictions of the procedural module is only modest. The principal problem with the predictions are that they fail to

predict when the response in the caudate dips below the baseline.

The model predictions generally correspond with the data. Probably, the residual deviations reflect the fact that the model engages in the minimum of activity while actual participants may do other things as well. Of most relevance to the topic of this paper, the match up with predictions is quite good for the VLPFC and ACC.

Discussion

The experiments succeeded in producing distinct responses in the VLPFC and ACC regions and these effects were as predicted. Activity in the VLPFC region continued only as long as the participants were trying to retrieve the solution and disengaged as soon as the solution was obtained. In contrast, activation in the ACC increased upon the retrieval of a solution reflecting the need to process that solution. These results support the ACT-R conception of the function of these regions over alternative conceptions.

The principal alternative interpretation of this VLPFC area is that it supported selection among retrieved alternatives. If this was a correct interpretation activation should only have increased close in time with the identification of a solution when there might be the need to select among alternatives. Rather, activation dropped off upon identification of a solution and continued to rise in absence of a solution.

In both experiments the ACC was more active when the problem was solved. This fact causes difficulty for alternative theories of the ACC. The fact that the ACC response was stronger in the presence of success is particularly hard to reconcile with a view that claims ACC activation is associated with errors – either the actual occurrence of errors or the likelihood of errors. With respect to the response-conflict view, one could argue that in the first experiment, since participants only generated a response if they solved the problem, response conflict could only occur in solution cases. However, since the responses were equated in the second experiment, this cannot be the cause of the difference in that experiment. Moreover, a difference appeared in ACC activation before the generation of a response.

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Table 1

Summary Statistics for Fits of the ACT-R Modules to the 6 Relevant Regions

Region (Module)	Magnitude	Correlation	Chi-Square
Fusiform (Visual)	0.0138	0.753	129.85
Motor (Manual)	0.0149	0.968	39.95
Parietal (Imaginal)	0.0027	0.874	29.44
Prefrontal (Retrieval)	0.0006	0.956	15.11
ACC (Goal)	0.0012	0.927	45.00
Caudate (Procedural)	0.0036	0.665	55.24

Figure Captions

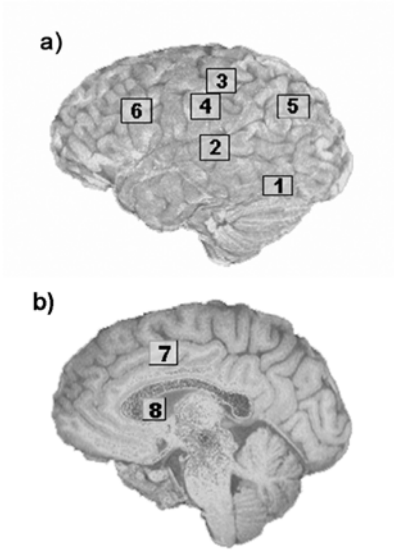
Figure 1. An illustration of the locations of the 8 brain regions associated with ACT-R modules. In part (a) are the regions close to the surface of the cortex and in part (b) are the regions deeper in the brain. Most of the regions are cubes 5 voxels long, 5 voxels wide, and 4 voxels high. The exceptions are the procedural (caudate), which is 4 x 4 x 4; the goal (ACC), which is 5 x 3 x 4; and the fusiform, which is 5x5x3. A voxel is 3.125 mm long and wide and 3.2 mm high.

Figure 2. Response-locked responses in Experiment 1 for the 8 predefined regions illustrated in Figure 1.

Figure 3. Results in Experiment 2 for the 8 predefined regions illustrated in Figure 1. Solid lines reflect the predictions of the ACT-R model in Figure 4 and dotted lines connect the data points.

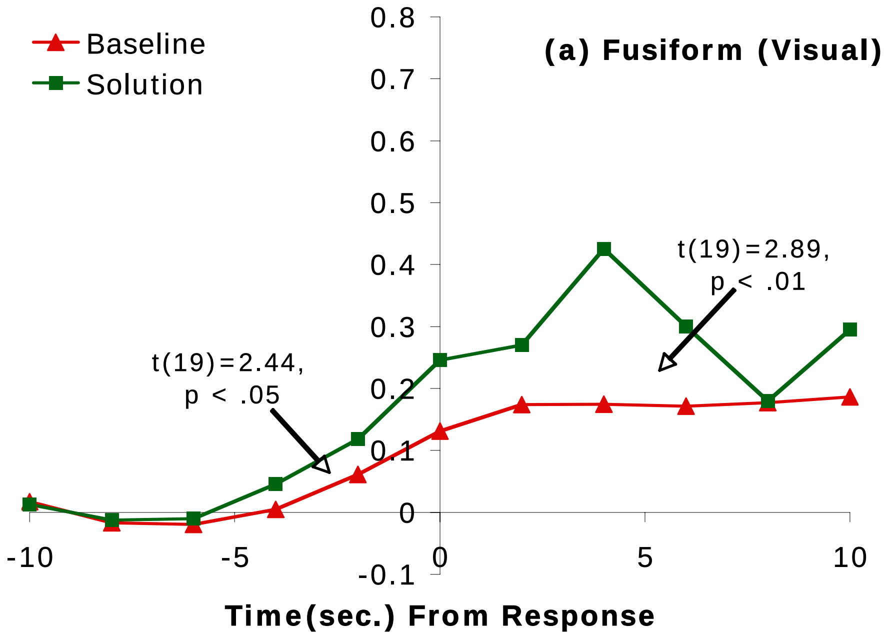
Figure 4. Activation of the modules in the ACT-R model for Experiment 2.. Time is given in seconds. Lengths of boxes (for visual, retrieval, imaginal, and manual modules) reflect approximate times the modules are engaged. The horizontal lines represent the firing of production rules. Brackets indicate subtasks of activity controlled by a setting of a goal. Periods of time that are compressed are indicated by graph bars.

Figure 1



	X	Y	Z	Region
1. Visual	42	-61	-9	Fusiform
2. Aural	46	-22	9	Auditory
3. Manual	41	-20	50	Motor
4. Vocal	43	-14	33	Motor
5. Imaginal	23	-63	40	Parietal
6. Declarative	43	23	24	Prefrontal
7. Goal	7	10	39	ACC
8. Procedural	14	10	7	Caudate

Figure 2


Baseline
Solution
(a) Fusiform (Visual)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
-10
-5
0
5
10
t(19)=2.89,
p < .01
t(19)=2.44,
p < .05
Time(sec.) From Response

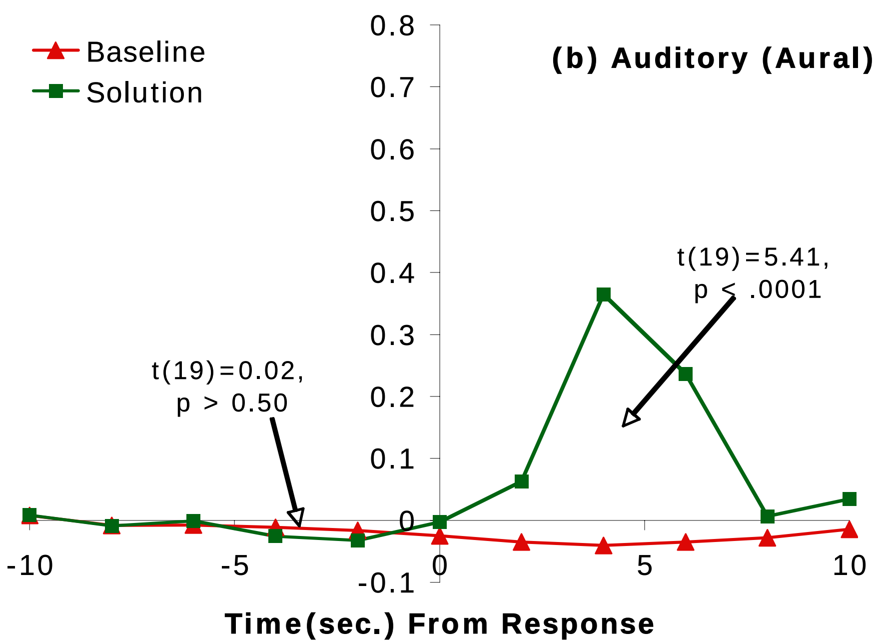

Baseline
Solution
(b) Auditory (Aural)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
-10
-5
0
5
10
t(19)=5.41,
p < .0001
t(19)=0.02,
p > 0.50
Time(sec.) From Response

Figure 2 continued

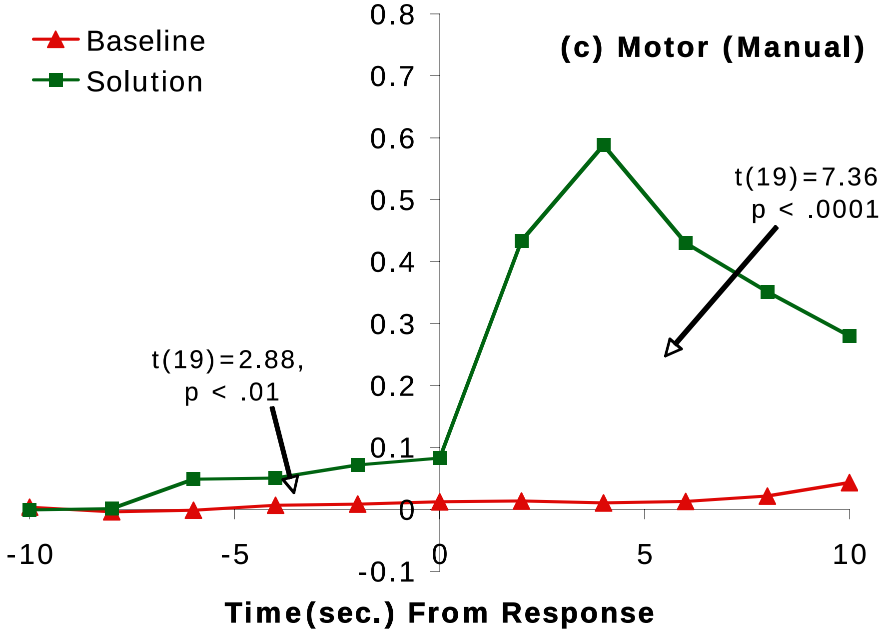
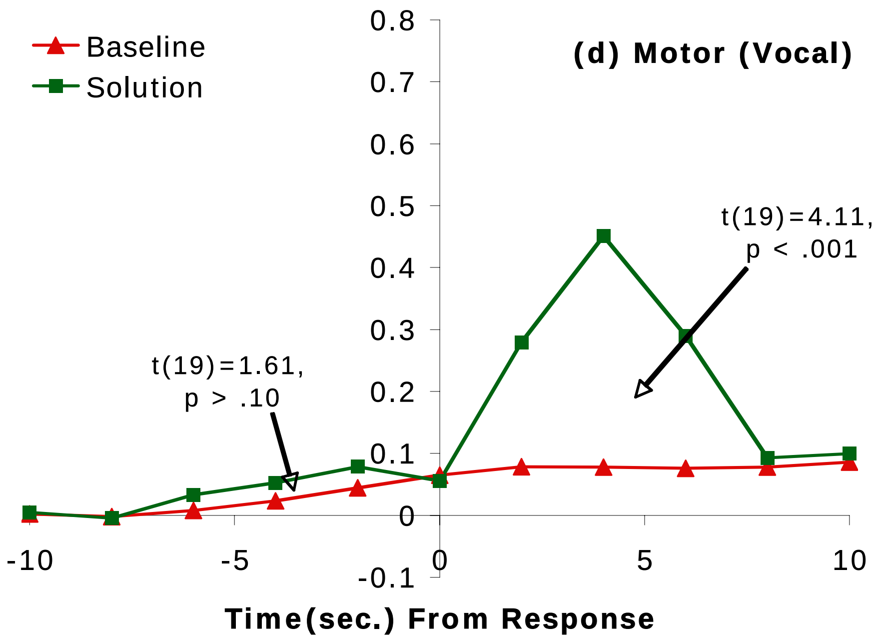


Figure 2

continued



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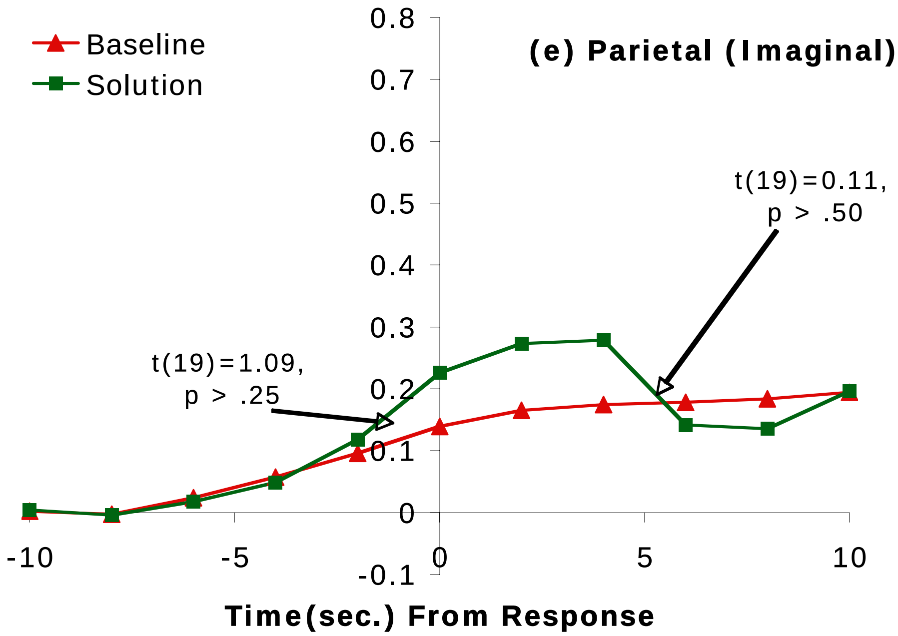


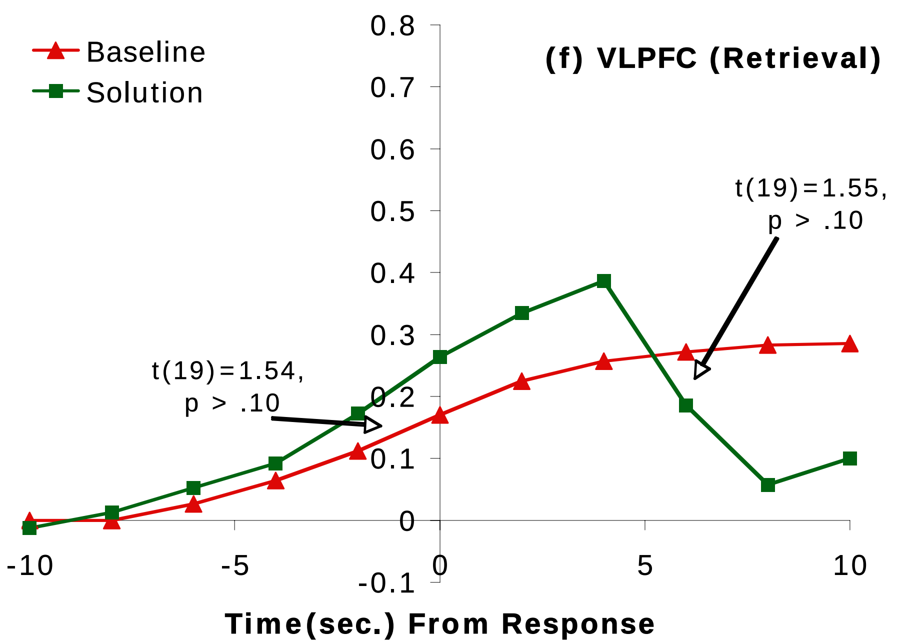
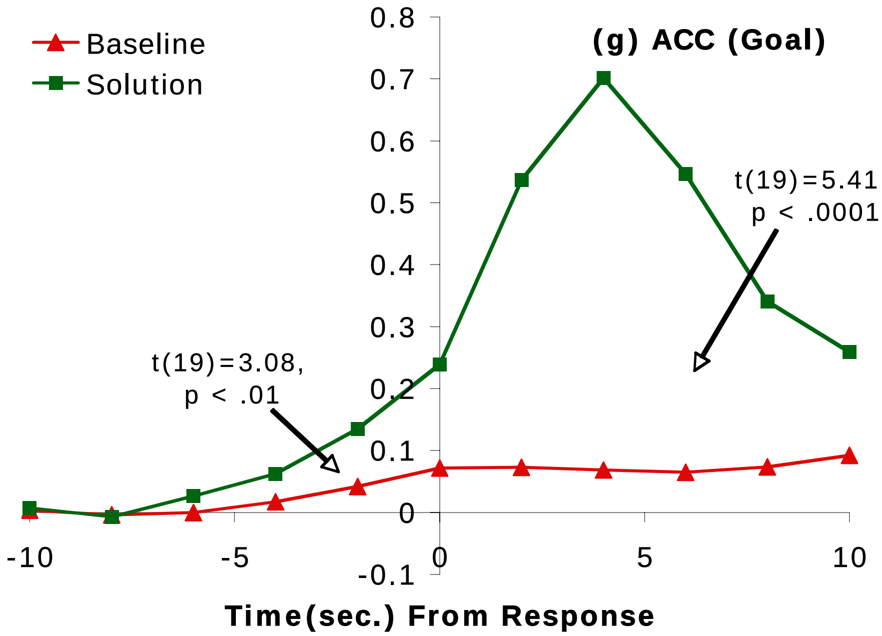


Figure 2 continued



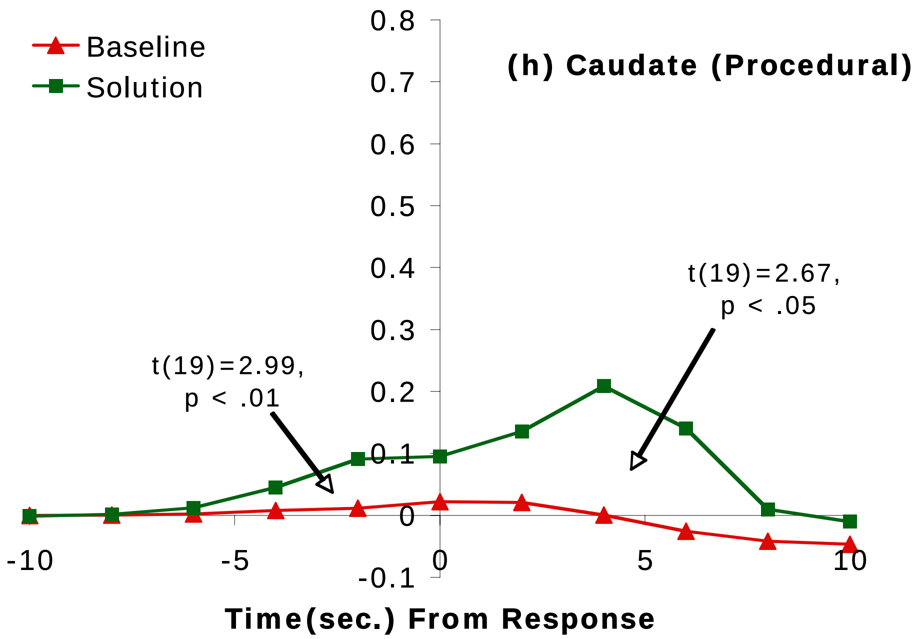
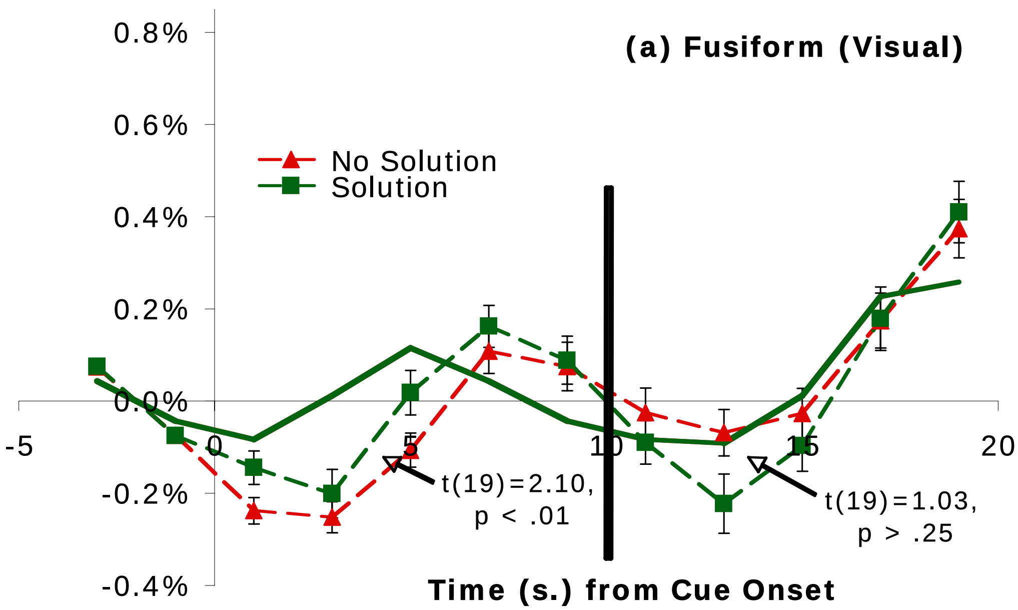
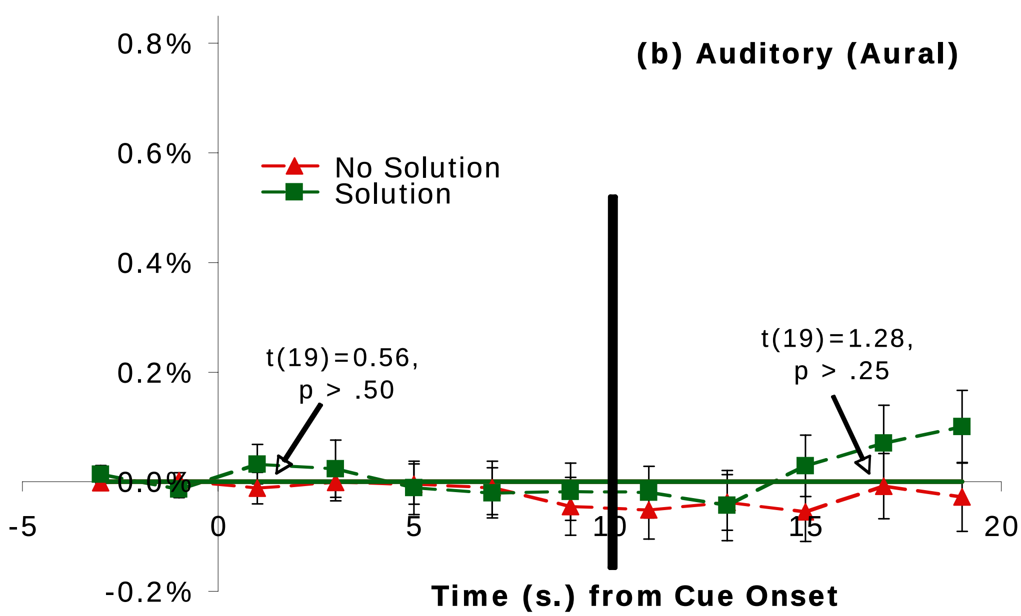


Figure 3



(a) Fusiform (Visual)
No Solution
Solution
0.8%
0.6%
0.4%
0.2%
0.0%
-0.2%
-0.4%
-5
0
5
10
15
20
t(19)=2.10,
p < .01
t(19)=1.03,
p > .25
Time (s.) from Cue Onset

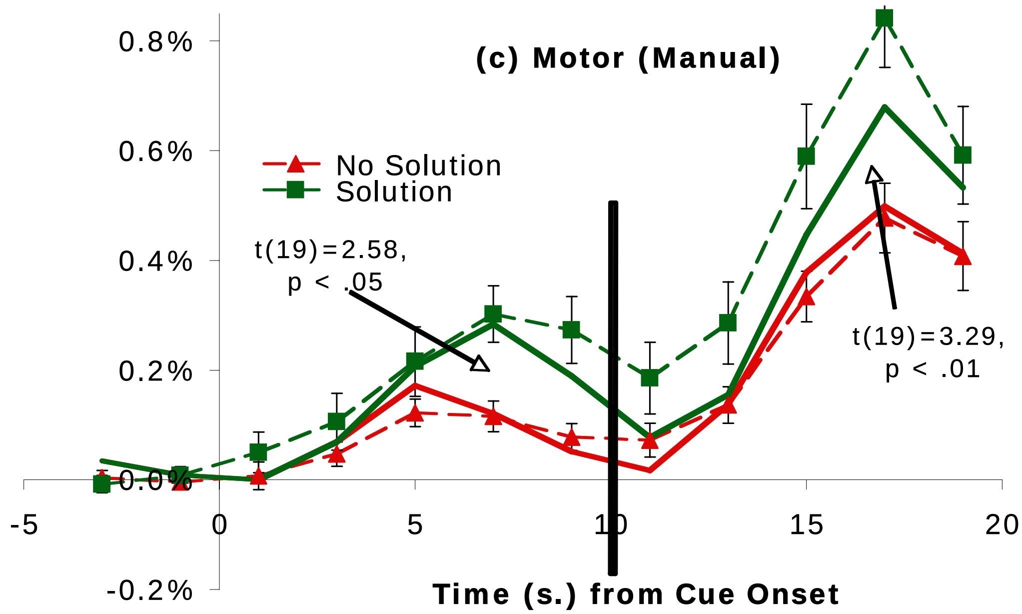


(b) Auditory (Aural)
No Solution
Solution
0.8%
0.6%
0.4%
0.2%
0.0%
-0.2%
-5
0
5
10
15
20
t(19)=0.56,
p > .50
t(19)=1.28,
p > .25
Time (s.) from Cue Onset

Figure 3

Continue

d



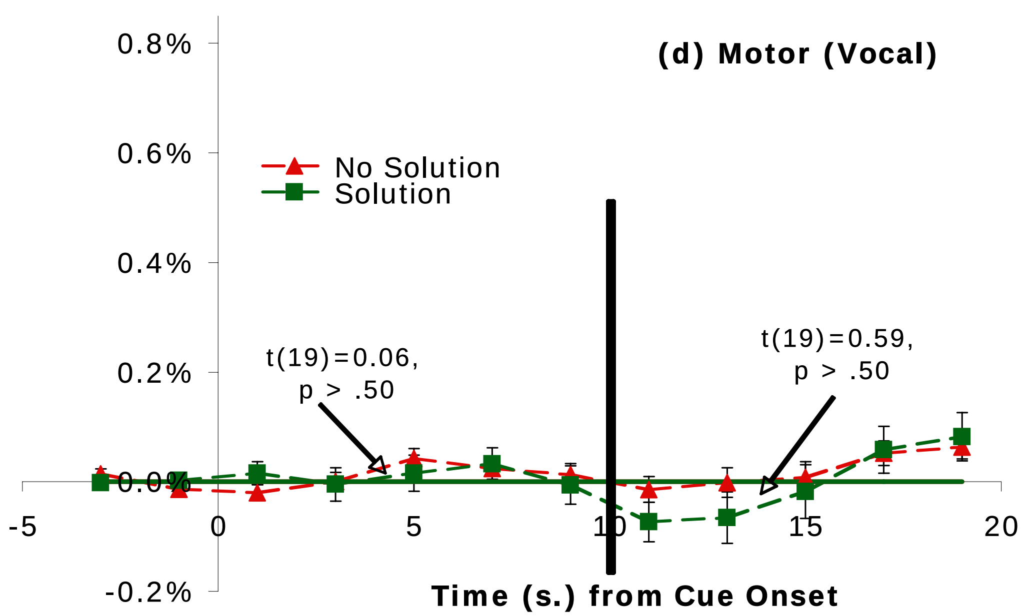
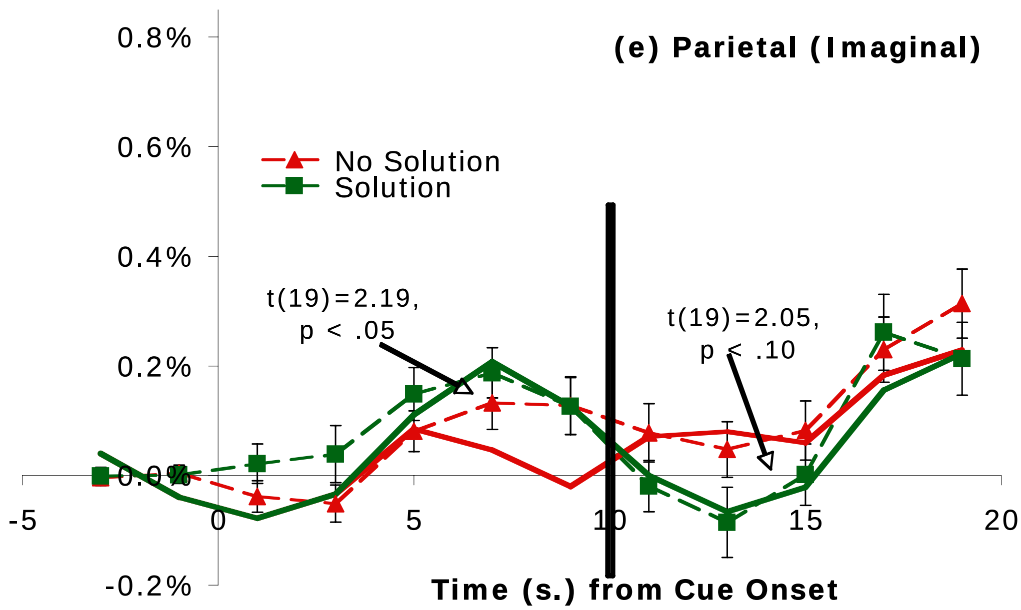


Figure 3 continued



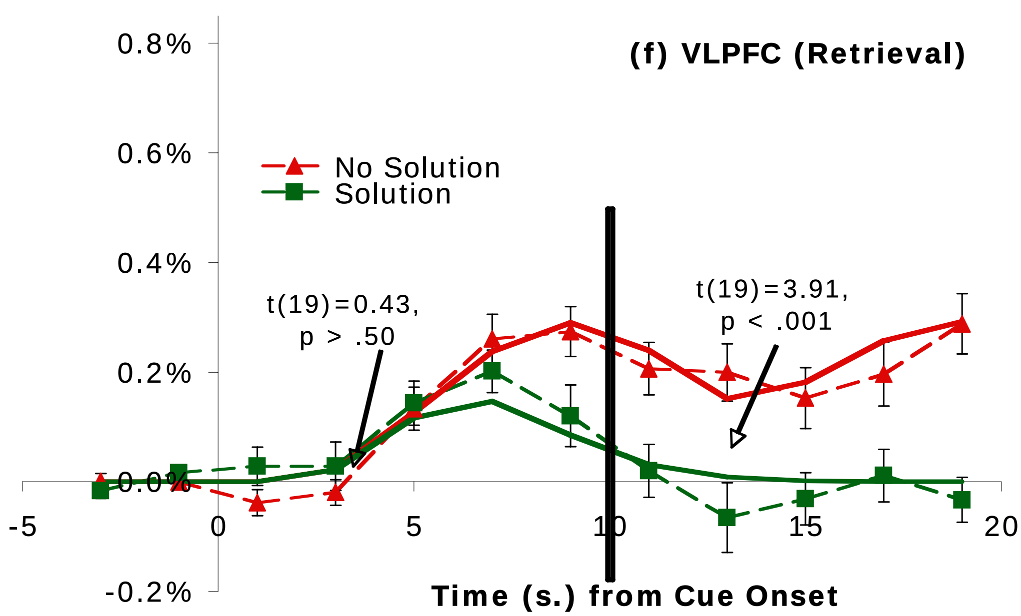
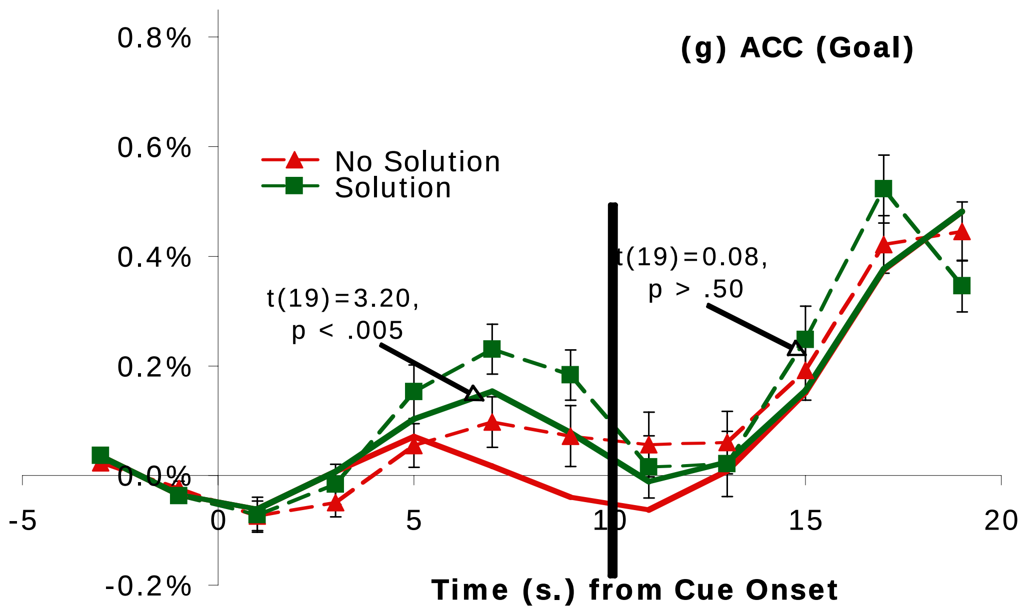


Figure 3 continued



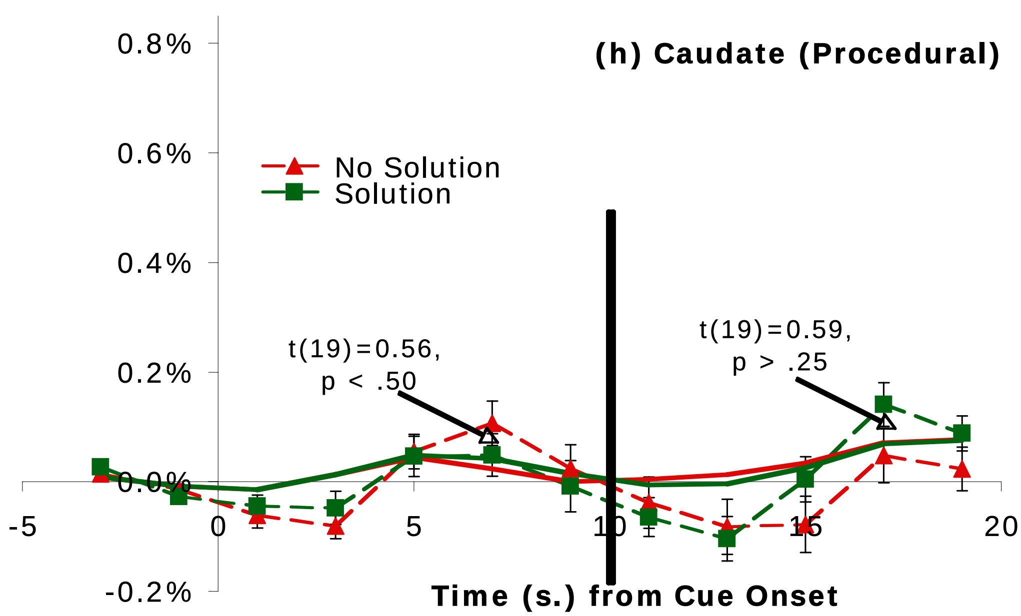
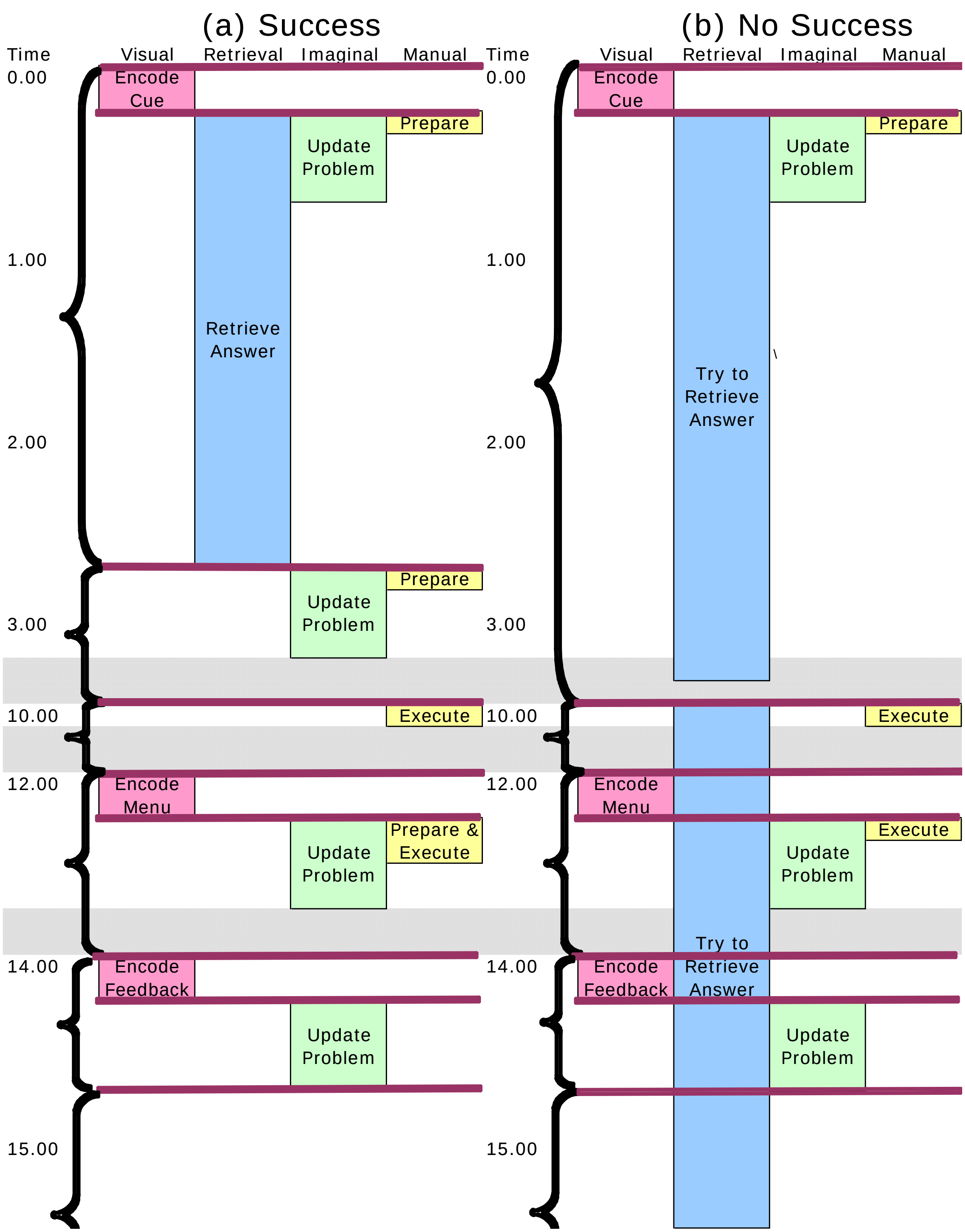


Figure 4


(a) Success
Time
Visual
Retrieval
Imaginal
Manual
0.00
Encode Cue
Prepare
Update Problem
1.00
Retrieve Answer
2.00
Prepare
Update Problem
3.00
10.00
Execute
12.00
Encode Menu
Prepare & Execute
Update Problem
14.00
Encode Feedback
Update Problem
15.00
(b) No Success
Time
Visual
Retrieval
Imaginal
Manual
0.00
Encode Cue
Prepare
Update Problem
1.00
Try to Retrieve Answer
2.00
3.00
10.00
Execute
12.00
Encode Menu
Execute
Update Problem
Try to Retrieve Answer
14.00
Encode Feedback
Update Problem
15.00