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Research Report
Brain activation evidence for response conflict in the exclude recognition task
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ABSTRACT

How do memory retrieval processes (i.e., familiarity and recollection processes) interact with motor and control processes to bring about an appropriate response? Our parallel task-set model predicts, and behavioral and electromyographic data support, the hypothesis that under some circumstances familiarity and recollection processes activate competing responses. Combining predictions from the parallel task-set model and the conflict monitoring hypothesis, this competition should lead to response conflict and corresponding activity in anterior cingulate cortex (ACC). However, ACC activity in response to competing familiarity and recollection retrieval processes is inconsistently reported in the literature. We tested this prediction directly by measuring brain activation with functional magnetic resonance imaging while participants performed an exclude recognition task (i.e., respond one way to one set of familiar stimuli and another way to new and to a different set of familiar stimuli). As predicted by our model, overriding a familiarity-based response led to increased activity in ACC. These data suggest that recognition, motor, and control processes interact in strategic retrieval tasks.

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1. Introduction

Familiarity and recollective memory processes often lead to the retrieval of complementary knowledge. When you see someone who looks familiar, recollective processes may retrieve the person's name and information about where you met them. Other times, however, recollection may fail — and a person may look familiar, but you may have no idea how you know them. Still other times, familiarity and recollective processes may lead to competing responses such as when a criminal attempts to hide privileged knowledge that he or she has about a crime. This leads to the question addressed by the

current research: How do we control the interaction between familiarity and recollective processes to produce recognition responses appropriate to our current task goals?

A commonly used procedure for studying strategic processes in recognition memory and examining whether familiarity and recollective memorial processes compete with one another is the *exclude recognition* task (e.g., [Jacoby et al., 1989a](#)). In this task, participants study two lists of items and then perform an old/new judgment task in which they respond “old” to items from one of the lists (*targets*), and “new” to items from the other list (*probes*) and to new (i.e., *filler*) items. Typically, participants are slower and less accurate when

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rejecting familiar probes as “new” compared to accurately demonstrating their familiarity of target and lack of familiarity of filler items (Allen et al., 1992; Farwell and Donchin, 1991; Jacoby et al., 1989a,b; Jacoby, 1991; Seymour et al., 2000; Seymour, 2001; Seymour and Kerlin, 2008; Seymour and Schumacher, 2009). The key question is why, despite understanding the goal of responding “new” to familiar probe items, do participants have difficulty doing so?

Many theories of exclude recognition performance focus on the recognition memory components (i.e., familiarity and recollection; see Yonelinas, 2002). Such dual-process models posit a complementary system in which fast familiarity and slower recollection (or search) processes can both contribute to responses. Performance is explained as either a result of familiarity alone, or a combination of both familiarity and recollection. In some cases, the familiarity process is sufficient, but other times a recollection or search process using episodic information is necessary to identify previously studied items (e.g., Atkinson and Juola, 1974; Gillund and Shiffrin, 1984). In other dual-process variations, both processes are typically involved unless recollection fails, leaving familiarity to drive the response alone (e.g., Jacoby, 1991; Jacoby et al., 1993). Although familiarity is logically sufficient for target (familiar = “old”) and filler (unfamiliar = “new”) items, a familiarity-based “old” response would guarantee an error on probe trials. Thus, such models focus on the relative contribution of recollection and familiarity memory processes on each trial and have successfully accounted for accuracy effects in exclude recognition and related procedures (for a review, see Yonelinas, 2002).

The *parallel task-set* (PTS) model (Seymour, 2001) extends this dual-process approach by accounting for the memory, motor, and executive control processes that interact in strategic recognition tasks. Because it offers a detailed stage model for each response and uses the production rule formalism of the *executive-process/interactive-control* (EPIC; Meyer and Kieras, 1997), the PTS model is able to produce quantitative accounts of both reaction time (RT) and accuracy data in the exclude recognition procedure (Seymour, 2001). In particular, the model suggests that a pair of task-sets (c.f., Monsell, 1996) are automatically initiated on each trial. Each task-set consists of processes for memory retrieval, response selection, response preparation, and motor execution. One task-set initiates a response based on the familiarity of the stimulus. The other initiates a response based on the item’s source (i.e., target list or probe list). These task-sets operate asynchronously and in parallel. On target and filler trials, both task-sets initiate preparation of the same response (“old” for targets, and “new” for fillers). However, on probe trials, the familiarity task-set initiates an incorrect “old” response and the recollection task-set initiates a correct but conflicting “new” response. Based on the assumption that the slower prepared response is the intended one (i.e., a correction), a set of task-invariant executive control processes attempts to abort the familiarity-based response and facilitate the recollection based one. If successful, a slow but correct “new” response is made; otherwise, a fast but incorrect “old” response is made. In this way, the PTS model can account for both the RT and accuracy effects in the exclude recognition procedure. Although most of the accuracy effects are

accounted for by failed aborts, some probe errors and most target errors are accounted for by *misrecollections* (viz., probes are incorrectly remembered as targets, or vice versa; Seymour, 2001). Misrecollections are particularly likely when target and probe study contexts are similar (Dodson and Johnson, 1996; Dodson et al., 1998; Dodson et al., 2007).

Unlike dual-process recognition models, which imply that competing response representations (i.e., old vs. new) are resolved prior to response initiation,¹ the PTS model proposes that, on probe trials, a familiarity-based response is initiated, aborted, and followed by a recollection-based response. Thus, the PTS model predicts that response conflict will lead to an alternating “old”-then-“new” activation in the motor system. Although the main prediction is that such conflict on probe trials will be more prevalent than on filler trials, the existence of misrecollections also predicts conflict on target trials, as well. However, because conflict can only occur when targets are misrecollections as probes, target trials involving response conflict should be less common than on probe trials.

The PTS model’s main structural assumption that there exist two processing streams, one of which is automatic and may need to be aborted prior to execution, has been previously used to model stimulus-response compatibility effects (Kornblum et al., 1990). Unlike the PTS model, the abort in Kornblum et al.’s model is triggered by whether the more automatic process will lead to a correct response or not. The PTS model assumes that the slower of the two task-sets is the correct one and attempts to facilitate it, even if this assumption is false (which can occur on trials in which recollection is faster than familiarity). Thus, the aborted response may be the correct one. This mechanism allows the PTS model to predict accuracy as well RT effects.

The PTS model has been used successfully to simulate behavior in the exclude recognition task with only the durations of the familiarity and recollection processes as free parameters (Seymour, 2001). This simulation yielded a particularly close quantitative fit with average root mean squared errors of 23 ms ($R^2 = .99$) for RT and 2% ($R^2 = .97$) for accuracy. Indeed, data from an include recognition task (similar to the exclude version except that all familiar stimuli, probes and targets, require an “old” response) can be accounted for equally well without changing parameter values. For further detail on the PTS model and its fit of both exclude and include recognition data, see Seymour (2001).

Despite its success in accounting for behavioral data, there may be an advantage to verifying the assumptions of the PTS model using electrophysiological and brain imaging measures. Although studies have been quite consistent in demonstrating RT and accuracy differences between probe trials (mostly involving conflict) and filler trials (rarely involving conflict), as well as between target trials (sometimes involving conflict) and filler trials, these measures have not consistently revealed the predicted difference between probe and target trials. Seymour and Kerlin (2008), for example,

¹ We use “imply” here because it is uncommon for dual-process recognition models to distinguish between response selection and response initiation. Typically, predictions stop at the response selection stage (for a review of dual-process models, see Yonelinas, 2002).

reported significant differences between probes and targets when the stimuli were faces, but not with verbal stimuli. These behavioral measures may reflect the sum of all cognitive processes involved on each trial and thus may not exclusively represent the conflicting memory and response processes under investigation.

Recently, two of the current authors (Seymour and Schumacher, 2009) measured behavioral and electromyographic data while participants performed a verbal phrase-based exclude recognition task similar to the one used by Seymour and Kerlin (2008). Consistent with previous experiments using this procedure (Allen et al., 1992; Farwell and Donchin, 1991; Jacoby et al., 1989a,b; Jacoby, 1991; Seymour et al., 2000; Seymour, 2001; Seymour and Kerlin, 2008), and predicted by the PTS model, Seymour and Schumacher reported that responses to probe phrases were slower and less accurate than responses to target phrases, which were in turn slower and less accurate than responses to filler phrases. The more novel result came from the electromyographic data. Seymour and Schumacher found significantly more partial errors (i.e., subthreshold muscle activity associated with the incorrect responses prior to suprathreshold activity associated with the correct response) on probe than target trials, and a similar relationship between target and filler trials. This pattern of results suggests that participants were overriding their incorrect familiarity-based response to produce the correct recollective-based one (c.f., Burle et al., 2002, 2004; Coles et al., 1985, 1995).

Though RT differences may have multiple causes (e.g., stimulus or response confusion), partial errors are incontrovertibly related to motor response processing; and they have previously been taken as evidence of conflict processing in more canonical conflict tasks such as Stroop and Flanker (Botvinick et al., 2001; Burle et al., 2008). In the present study we explore another opportunity to examine a measure previously tied to response conflict in Stroop, Flanker, and other tasks (viz., activity in anterior cingulate cortex, ACC).

Many influential theories for how response conflict is resolved in the brain postulate a role for ACC and prefrontal (PFC) cortices for monitoring and controlling response conflict (Botvinick et al., 2001, 2004; Miller and Cohen, 2001; Schneider and Chein, 2003). The conflict monitoring hypothesis states that processes in ACC indicate the presence of multiple competing responses. This monitoring signal induces control processes in other brain regions to activate and resolve the conflict and produce the correct response. A key difference between the conflict monitoring and PTS models is what triggers conflict. According to conflict monitoring theory, conflict arises when multiple competing responses are simultaneously activated in memory. The PTS model defines conflict as attempting to prepare and execute an overt motor response while a different response initiation is already underway. Thus, the temporal locus of conflict in the PTS model is after response selection has occurred. Conflict monitoring theory was developed through consideration of a vast amount of neuroscience data implicating ACC and other medial PFC regions in situations high in response conflict (e.g., Stroop and Flanker tasks) and has been very successful modeling response conflict in a wide variety of tasks (Botvinick et al., 2001).

However, two functional magnetic resonance imaging (fMRI) studies of the exclude recognition task have produced little evidence of ACC involvement, and thus little evidence for response conflict (Henson et al., 1999; Rugg et al., 2003). During fMRI scanning of the retrieval phase of their experiment, Henson, Shallice and Dolan required participants to make one response to a presented word if it appeared to one side of a fixation stimulus (either left or right) during the study phase; and to make a different response if a presented word appeared to the other side of fixation during study or if it had not been studied previously. Performing this exclude recognition task produced activity in ACC (x, y, z coordinates: 6, 36, 31)² compared to a baseline condition. However, the authors reported no ACC activity when an exclude condition was compared to an include condition, in which participants responded to all studied words in one way and new words in another. This may suggest that ACC is involved in both recognition procedures and therefore mediates memory retrieval processes more generally in this task, rather than processes specific to monitoring for response conflict (c.f., Cabeza et al., 1997). Consistent with this hypothesis, Nyberg et al. (2003) reported activity in ACC and medial PFC across two experiments in a variety of episodic retrieval tasks (e.g., include recognition, cued-recall, autobiographical memory) that do not obviously involve response competition. In another experiment using the exclude recognition task, Rugg et al. (2003) reported no ACC activity for a comparison between include and exclude recognition tasks overall. Additionally, they reported no ACC activity in the exclude task when comparing probe and filler trials. This comparison should show maximum response conflict. Thus, contrary to our predictions, these fMRI studies provide little support for ACC activity (and corresponding response conflict) in the exclude recognition task.

However, none of these studies was designed specifically to address the issue of response conflict during memory retrieval, and the ACC activity reported was ancillary to the primary focus of these reports. Additionally, there exists other evidence to suggest that ACC may yet play a role in monitoring for response conflict during memory retrieval. Finally, the exclude-include comparison reported by Henson, Shallice, and Dolan (1999) may not have been sensitive to the effects of conflict because it included all trial types in the exclusion task (i.e., probe, target, and filler), not all of which would be expected to produce response conflict. Furthermore, whole-brain analyses were used in the Henson, Shallice and Dolan and Rugg et al. (2003) studies. This leaves open the possibility that the ACC activity was not sufficient to survive the statistical threshold correction required for the whole-brain analyses.

Some evidence for ACC activity and response conflict in memory retrieval comes from studies of false memory (e.g., McDermott et al., 2000; Slotnick and Schacter, 2004), which often show more ACC activity for false memories (i.e., unstudied items similar to studied ones) than for true memories. For example,

² All activations are shown in MNI coordinates. When the original source used the Talairach coordinate system, the coordinates were converted to the MNI system using the Matthew Brett's conversion function (<http://imaging.mrc-cbu.cam.ac.uk/downloads/MNI2tal/tal2mni.m>).

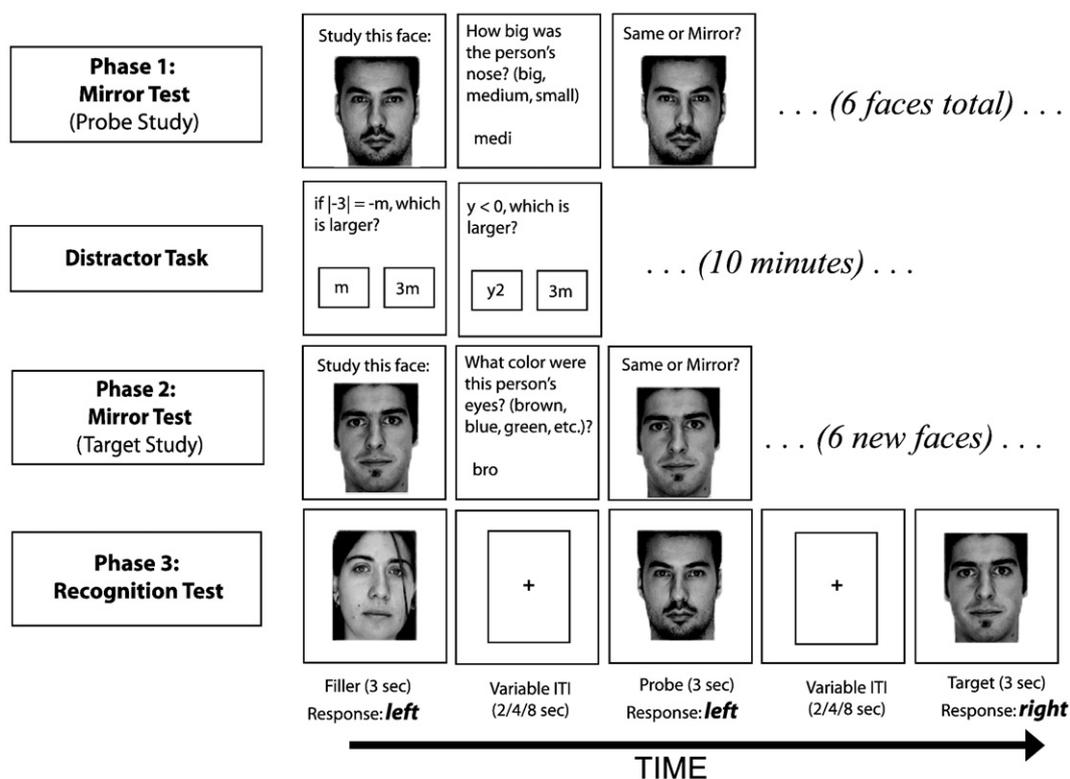


Fig. 1 – Overview of the experimental procedure. Faces appeared in natural color during the experiment.

McDermott et al. performed an include recognition experiment in which participants studied lists of compound words (e.g., *nosebleed* or *skydive*) prior to scanning. Memory retrieval was tested during fMRI scanning during which participants discriminated between compound words from the studied list and new compound words. The new words are of particular interest here. Some of them were unrelated to the studied list (e.g., *lifeguard*); others were conjunctions of the lexical subunits from the studied list (e.g., *nosedive*). McDermott et al. reported significant ACC activity (x, y, z coordinates: 1, 19, 47; $-3, 28, 34$) for conjunction lures relative to unrelated words. This activity is consistent with the existence of response conflict. Conjunction lures may have led to activity on the incorrect response “old” before that response is overridden by the correct response “new.”

In light of the inconsistent support for ACC activity in the exclude recognition task as predicted by the PTS model (Seymour, 2001; Seymour and Schumacher, 2009), and because of the possible limitations of analyses used in those studies, further investigation is warranted. To achieve this, we had participants study two lists of faces prior to fMRI scanning (see Fig. 1). During the fMRI scan, participants made one response to faces from List 2 (the target faces) and a different response to faces from List 1 (probe faces) and new faces (fillers). This procedure allows us to investigate directly the PTS model prediction that response conflict occurs in the exclude recognition task using a different dependent measure of response conflict (viz., activity in ACC) than we tested in Seymour and Schumacher (2009). We predicted increased ACC activity on probe trials relative to fillers because familiarity and recollection-based memory retrieval processes lead to conflicting responses for probe (like the color and the word responses on incongruent Stroop trials) but not filler trials. We

also predicted increased activity on probe trials relative to target trials, some of which involve response conflict due to misrecollections. Additionally, we also investigated activation to target and probe faces in other brain regions related to episodic memory (e.g., dorsal PFC, DPFC; ventral PFC, VPFC; anterior PFC, APFC), which may identify how cognitive control mechanisms respond to signals of conflict from ACC. We also expected to replicate the behavioral result typically found using this procedure in which responses on probe and target trials (both of which involve at least some response conflict overall) are slower and less accurate than on filler trials (which should involve no conflict).

2. Results

2.1. Behavioral results

Mean correct RTs and accuracies were analyzed with separate within-subjects analyses of variance with Stimulus Type (target, probe, filler) as a factor. The effect of Stimulus Type had a marginally significant effect on correct RT, $F(2, 16)=2.93, p=.08$ and a significant effect on mean accuracy, $F(2, 16)=4.39, p<.05$. As shown in Fig. 2, planned comparisons show that probe trials were slower ($t(8)=2.19, p<.05$, one-tailed³) and less accurate ($t(8)=3.30, p<.005$, one-tailed) than filler trials and that target trials were slower ($t(8)=3.23, p<.01$, one-tailed) and less accurate ($t(8)=2.34$,

³ One-tailed tests are appropriate for probe vs. filler and target vs. filler comparisons because the PTS model (and all other theories) predicts a direction for this effect.

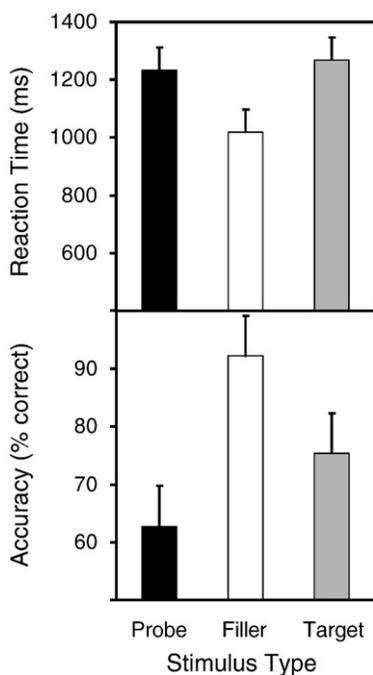


Fig. 2 – Mean reaction time and accuracy for probe, filler, and target trials. Error bars represent ±1 SEM.

$p < .05$, one-tailed) than filler trials; but that probe trials did not differ significantly from target trials (mean RT: $t(8) = .24$, $p = .82$; accuracy: $t(8) = .94$, $p = .38$, two-tailed).

2.2. ACC activation results

We used a small volume correction (Worsley et al., 1995) to investigate contrasts of interest (viz., probe vs. filler, target vs. filler, and probe vs. target) in ACC. This analysis reveals regions of significant activity within a proscribed brain region and is appropriate because of the anatomically well-defined hypothesis tested here. As shown in Fig. 3, there were two clusters in ACC in which activity was greater in probe than filler trials (peak t -value=7.00; cluster size=6; voxels, $x = -8$, $y = 36$, $z = 14$ and peak t -value=5.65; cluster size=4; voxels, $x = 10$, $y = 38$, $z = 24$); and one cluster in ACC in which activity was greater in probe than target trials (peak t -value=4.87; cluster size=12; voxels, $x = -10$, $y = 38$, $z = 24$). No other contrasts produced significant activity in ACC.

2.3. PFC activation results

To investigate activity in PFC regions implicated in memory retrieval (for a review see Fletcher and Henson, 2001; Simons and Spiers, 2003; Skinner and Fernandes, 2007) we used the combined experimental condition (viz., target, probe and filler) vs. baseline contrast to identify activity in regions-of-interest (ROIs) ($p < .05$, FDR) in left and right APFC, VPFC, and DPFC (regions often activated in studies of recollection and source memory). This analysis is appropriate for the PFC because of the large number of sulci and gyri spanned by, and the heterogeneous nature of, the PFC. The coordinate of peak activation, extent of these ROIs, and activation patterns are shown in

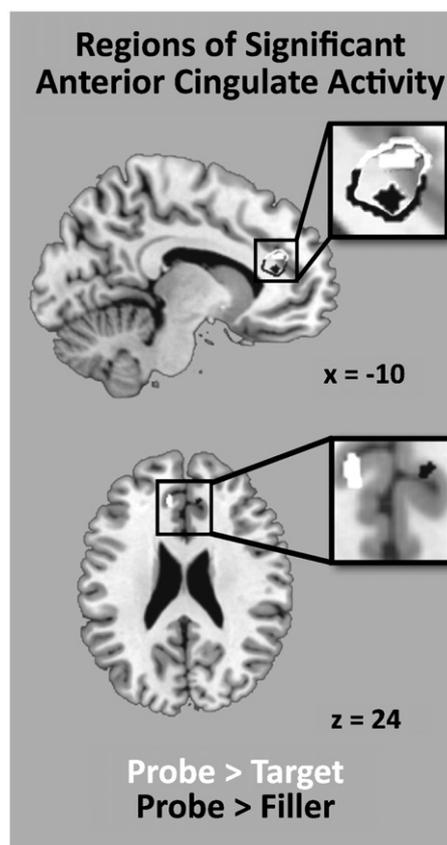


Fig. 3 – Sagittal and axial slices showing significantly active clusters in anterior cingulate cortex (ACC) for the probe vs. target (white) and probe vs. filler (black) contrasts. No other contrast showed significant activity. The white and black outlines show the extent of activity in these regions at $p < .01$, uncorrected. The overlap in the extent of activity suggests that these peaks represent increased underlying ACC activity for the probe condition in general and not distinct regions mediating each specific contrast.

Table 1 and Fig. 4. The β -values from each experimental condition relative to baseline for the ROIs for each of the prefrontal regions (left and right APFC, VPFC, and DPFC) were analyzed with separate within-subjects analyses of variance

Brain region	Brodmann area	MNI coordinates	t-value	Cluster size
<i>Dorsal prefrontal</i>				
Left	45	-44, 28, 30	5.38	70
Right	45	40, 28, 20	7.78	115
<i>Ventral prefrontal</i>				
Left	Insula	-26, 10, -2	12.19	302
Right	47	32, 22, 0	6.61	198
<i>Anterior prefrontal</i>				
Left	10	-30, 50, 8	4.83	13
Right	11	32, 52, 4	4.92	5

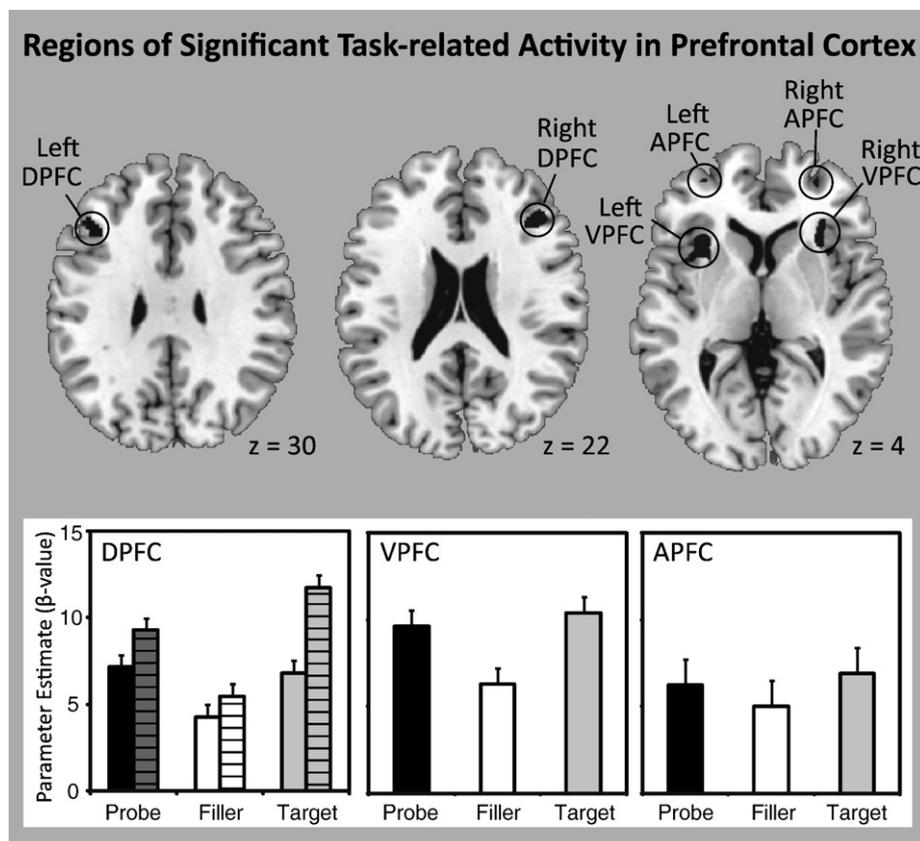


Fig. 4 – Bar graphs show mean brain activation for probe, filler, and target trials in the dorsal prefrontal (DPFC), ventral prefrontal (VPFC), and anterior prefrontal (APFC) regions-of-interest (ROIs). For DPFC, the solid bars represent the left hemisphere and the striped bars represent the right hemisphere. Because there was no effect of hemisphere in VPFC and APFC, these data were combined in these graphs. Error bars represent ± 1 SEM. Example axial brain slices, showing these ROIs, are also depicted.

with Hemisphere (left, right) and Stimulus Type (target, probe, filler) as factors. There were no significant main or interacting effects in APFC (Hemisphere: $F(1, 8) = .74, p = .42$; Stimulus Type: $F(2, 16) = 1.84, p = .19$; Hemisphere \times Stimulus Type: $F(2, 16) = .49, p = .62$). In VPFC, the main effect of Stimulus Type was significant: $F(2, 16) = 8.06, p < .005$. Post-hoc tests revealed that the only significant effect was that activity for targets was significantly greater than fillers ($p < .001$). Neither the main effect of Hemisphere ($F(1, 8) = 1.76, p = .22$) nor the interaction between Hemisphere and Stimulus type ($F(2, 16) = .25, p = .78$) were significant. In DPFC, both main effects and their interaction were significant (Hemisphere: $F(1, 8) = 9.18, p < .05$; Stimulus Type: $F(2, 16) = 6.90, p < .01$; Hemisphere \times Stimulus Type: $F(2, 16) = 5.95, p < .05$). Post-hoc tests revealed that the only significant effect was that activity for targets was significantly greater than fillers (left hemisphere: $p < .005$; right hemisphere: $p < .05$).

3. Discussion

These data provide substantial support for the involvement of response conflict in the exclude recognition task. The RT and accuracy results replicate the most consistent finding from previous reports using similar procedures (Allen et al., 1992; Farwell and Donchin, 1991; Jacoby et al., 1989a,b; Jacoby, 1991;

Seymour et al., 2000; Seymour, 2001; Seymour and Kerlin, 2008; Seymour and Schumacher, 2009) in that responses to probe stimuli were slower and less accurate than filler responses. The novel contribution of the present experiment is the inclusion of brain activation results from the ACC. Consistent with our prediction that this task involves response conflict, we found significantly more ACC activity on probe than on filler trials. These results are consistent with literature on response conflict. The significant ACC activity reported here fall within the region typically activated by studies of response conflict, although they are anterior and inferior to most sites of peak activity (Ridderinkhof et al., 2004). The results are also consistent with the PTS model and other strategic recognition models that assume familiarity and recollection processes lead to incompatible responses on probe but not filler trials (c.f., Yonelinas, 2002).

Although our main prediction involves comparing trials with high response conflict with those with low conflict (viz., probe vs. filler trials), we also compared probe trials with target trials and target trials with fillers because the PTS model predicts that conflict may sometimes occur on target trials due to misrecollections. Here the results are more equivocal. Anterior cingulate cortex showed significantly more activity to probe than target trials, consistent with the hypothesis that conflict is greatest on probe trials, but ACC was not significantly more active for target than filler trials. This may suggest, contrary to the prediction of

the PTS model, that misrecollections do not produce much, if any, response conflict on target trials. However, the behavioral data show a different pattern: target trials were slower and less accurate than filler trials (and not significantly different than probe trials).

It is not clear why the behavioral data in the present experiment did not replicate the pattern for longer RTs and reduced accuracy in probe than target trials as reported in previous experiments (Allen et al., 1992; Farwell and Donchin, 1991; Jacoby et al., 1989a; Jacoby, 1991; Seymour et al., 2000; Seymour and Kerlin, 2008; Seymour and Fraynt, 2009; Seymour and Schumacher, 2009). Although, the comparison between RTs for probe and target is reported inconsistently in the literature. For example, Seymour and Kerlin (2008; visual stimuli) and Seymour and Schumacher (2009) found a significant difference, but Seymour and Kerlin (2008; verbal stimuli) did not. We suspect the lack of a significant effect in the present data may be due to increased intra-subject variability in the MRI subjects compared to the other behavioral tests. We note that the effect on accuracy was in the predicted direction (viz., probe < target).

This inconsistency leads to an important question, however: Does the lack of a behavioral effect suggest that the ACC activity was due to some process other than response conflict? We think this is unlikely. No other existing theories of ACC function predict the present difference between behavioral and brain activity data. If, for example, ACC mediates familiarity (Leveroni et al., 2000; Maddock et al., 2001; Wang et al., 2005), memory retrieval (Fleck et al., 2006; Kuhl et al., 2008), task difficulty (Paus et al., 1998), or stimulus ambiguity (Jones et al., 2002; Van Veen et al., 2001), then the activity in ACC should follow the behavioral data patterns (and the activity patterns in all other areas). Only the ACC shows increased activity for probe trials relative to targets. This is consistent with our interpretation that memory retrieval leads to response conflict in this task. Unfortunately, this conflict did not propagate (significantly) to the behavioral dependent measures. This may suggest that neuroscientific dependent measures (e.g., electromyographic and fMRI data) are more sensitive to response conflict than behavioral measures. This may be because the behavioral effects are affected by additional processes besides response conflict (e.g., stimulus and/or response ambiguity; c.f., Sternberg, 2001). Indeed, this was one motivation for this and our previous study (Seymour and Schumacher, 2009). More research is necessary to distinguish the neurocognitive processes underlying target performance in the exclude recognition task.

We also note that the current data and interpretation do not suffer from a reverse inference problem (Poldrack, 2006). We are not inferring the existence of response conflict because we found ACC activity. We proposed, based on predictions of the PTS model, that memory retrieval in the exclude recognition task may produce response conflict. We then looked for evidence for response conflict in the area of the brain (viz., ACC) hypothesized to mediate conflict. ACC may mediate other processes as well, but our experiment specifically targets its role in monitoring for response conflict.

The activity in DPFC and VPFC also replicates previous activation studies of recollection memory (see Fletcher and Henson, 2001; Simons and Spiers, 2003; Skinner and Fernandes, 2007). Each of these regions showed increased activity for items that engaged recollective processes (i.e., the studied faces) relative to items that could not be retrieved from memory (i.e., the new

faces), though this effect was only significant for target trials. Additionally, the effect of hemisphere suggests that right DPFC was more involved in memory retrieval than the left DPFC — especially for the targets. This is consistent with research suggesting that right DPFC mediates recollective and familiarity episodic retrieval processes (e.g., Fletcher and Henson, 2001; Skinner and Fernandes, 2007). Yet, other research suggests a role for left DPFC (Dobbins et al., 2002; Nolde et al., 1998). The present study was designed to investigate response conflict in the exclude recognition task, not the neural correlates of memory retrieval. Therefore, additional research is necessary to distinguish between specific memory processes mediated by distinct PFC regions. Finally, the activity in APFC did not replicate previous results suggesting this region is involved in recollection memory. However the activity trends in this region were in the expected direction (viz., probe and target greater than filler trials). Therefore, we are hesitant to draw any conclusions from these null results. Nevertheless, the significant memory-related activity in DPFC and VPFC suggests that our participants were engaged in memory retrieval processes during the probe and target trials, thus validating our search for retrieval-related conflict in ACC.

These data have implications for another area of cognitive neuroscience: namely, investigations of how the brain mediates lying. The exclude recognition task is conceptually similar to the *concealed knowledge test* (also called the *concealed information test* and the *guilty knowledge test*) used in the detection of deception (e.g., Farwell and Donchin, 1991; Rosenfeld et al., 2004; Seymour et al., 2000; Seymour and Kerlin, 2008). In the concealed knowledge test, participants are instructed to misrepresent (or attempt to misrepresent) their knowledge about some information (probes) but not other information (targets). This and related tasks have been used to investigate the neural correlates for deception — and the possibility of using them in applied forensic contexts (Farwell and Donchin, 1991; Langleben et al., 2002; Rosenfeld et al., 1988; Rosenfeld et al., 2004). Activity in ACC, DPFC, VPFC and APFC in conditions where participants are required to conceal knowledge is often interpreted as the brain network underlying deception. In our task, during which no lying was required, the activity in these regions suggests that they may mediate memory and control processes more generally, rather than specifically relate to a deception-related processes as commonly suggested (for a similar interpretation and a review of the neural effects of lying see Sip et al., 2008).

Overall, the data reported here show that strategic recognition procedures like the exclude recognition task involve motor response conflict. As such, typical models that account for accuracy performance in these tasks by focusing on memory processes only (c.f., Yonelinas, 2002) may need to adopt components of models typically used to account for canonical response conflict tasks (Botvinick et al., 2001, 2004) in order to account for both accuracy and RT effects. One attempt is the PTS model (Seymour, 2001; Seymour and Schumacher, 2009), which suggests that performance on exclude recognition tasks (and presumably other conflict tasks as well) is best explained as an integration between memory, response, and additional control processes responsible for mediating behavior. We show that the assumptions of this model can be tested using behavioral data such as RT and accuracy, as well as physiological measures like brain activity. These data provide substantial support for the PTS

model. However, more work is needed to distinguish it from other integrative models of response conflict.

4. Experimental procedures

4.1. Participants

Ten right-handed volunteers (ages 19–27; 4 females) participated in this experiment. All participants were recruited from the Georgia Institute of Technology community and gave their informed consent. One participant did not respond correctly to any of the probe faces and was therefore excluded from all analyses.

4.2. Behavioral procedure

The experimental procedure was similar to one used previously (Seymour and Kerlin, 2008; Seymour and Schumacher, 2009). It consisted of three phases and a distractor task (shown in Fig. 1). In the first two phases, participants studied separate sets of six faces. These study phases were separated by 10 min during which participants performed a distractor math task. Participants performed both study phases just prior to entering the MR scanner. The faces from the first study phase later served as probe items. Faces from the second phase later served as target items. This categorization of stimuli was not revealed to participants who were simply asked to study one set of faces and then the other. In addition to probe and target items, 24 filler faces were randomly selected for each participant for a total stimulus set of 36 faces.

The stimulus set for all phases of the experiment consisted of 68 color pictures of human faces (32 male and 36 female) taken from the Aberdeen Psychological Image Collection at Stirling (Hancock, 2004). These pictures featured the subject of the picture from about shoulder-height and included hair. Each picture was 324 pixels in height and 250 pixels in width, and subtended a horizontal visual angle of 12.5° and a vertical angle of 16.2° at a viewing distance of 18". Stimuli were presented on a black background and were matched for expression (neutral), luminance and background color. A random subset of 36 images was sampled from this set for each participant with the restriction that half were female. The presentation and randomization of stimuli, as well as the recording of manual response data (RT and accuracy) were handled by E-Prime experimental presentation software (Schneider et al., 2002) running on a desktop computer.

In each study phase, participants studied a set of six faces. On each trial, a face appeared in the center of the computer monitor. Participants were instructed to study the face and told that they would subsequently be questioned about it. Participants then viewed each face until they advanced the experiment by pressing the spacebar. Immediately after studying a face, participants typed an answer to a question about some aspect of the face they just studied (e.g., *How big was the person's nose?*). There were six possible questions concerning the nature and style of the hair, facial hair, and eyebrows, as well as the shape of face, nose and lips. Facial feature questions were randomly selected with replacement

to prevent participants anticipating which facial feature would be queried next. Following the question, participants viewed either the same face or its mirror image. They pressed the "j" key with their right index finger if the face was identical to the one they studied, and the "f" key with their left index finger if it was a mirror image. Participants studied each set of faces three times. The order of presentation within a set was randomized.

The subsequent phases of the experiment were conducted in the MR scanner. Stimuli were projected onto a screen viewed by participants through a mirror mounted on the head radio-frequency (RF) coil while lying supine in the scanner. Participants made their responses with the thumbs of their left and right hands using the middle two buttons on an MR compatible 4-button response pad (Current Designs, Inc.).

Participants performed six fMRI runs of an exclude recognition task (216 trials). Each run consisted of 36 trials (one for each stimulus face) that began with a fixation warning stimulus for 1000 ms. After the warning stimulus, a face appeared for 3000 ms followed by a variable inter-trial interval (ITI). The ITI consisted of the warning stimulus frame without the fixation cross. The ITI lasted 2 s on 18 trials, and 4 and 8 s on 9 trials each. The ITI duration was randomized across trials without regard to stimulus trial type. Each of the six faces from the two study phases appeared once per fMRI run, along with an additional 24 filler faces. The stimuli presented on each trial were counterbalanced such that an equal proportion (1/6 target, 1/6 probe, 2/3 filler) of trials with each stimulus type occurred on the three previous trials.

On each trial, participants made speeded "old/new" judgments. They were asked to press a button with their right thumb if the face had been studied during the second study phase (target faces, referred to as "one of the faces you just studied"). Otherwise they were to respond with a left thumb button press (viz., to new filler faces and to familiar faces studied in the first study phase, probe faces). Participants were encouraged to respond both quickly and accurately. When responses exceeded a 3000 ms deadline, the warning frame displayed during the ITI was displayed in red, otherwise the frame was green. This was the only feedback given during each fMRI run. At the end of each 36 trial run, participants viewed a screen indicating their proportion of correct responses and the number of "too slow errors" (the number of times their response time had exceeded the deadline).

4.3. fMRI procedure and analysis

Images were acquired using a Siemens 3 T Trio MR scanner. A standard RF head coil was used with foam padding to restrict head motion comfortably. An echoplanar sequence (TR=2000 ms, TE=30 ms) was used to acquire data sensitive to the blood oxygen level dependent signal. Each functional volume contained 33 axial slices of 3.4 mm isotropic voxels and lasted about 4:48 min (148 volumes/run). A high-resolution 3D MPRAGE structural scan (1 mm isotropic voxels) was collected at the end of the MRI session.

4.4. fMRI data processing and analyses

Data reconstruction, processing and analyses for each participant were performed using SPM5 (<http://www.fil.ion.ucl.ac.uk/spm/>).

After reconstruction, head-motion artifacts were corrected to the last functional scan with a least squares approach using a six-parameter, rigid-body transformation algorithm (Friston et al., 1995); slice acquisition timing differences were corrected; and the data were smoothed with a 6 mm full-width half-maximum Gaussian kernel.

Data were analyzed using modified general linear models (Worsley and Friston, 1995). We created design matrices for each participant with the covariates of interest (viz., target, probe, and filler). These covariates were convolved with an idealized hemodynamic response function. A high-pass filter removed frequencies below .0078 Hz. Contrast images were computed for each participant for all three of the experimental conditions combined vs. baseline (i.e., the ITI) as well as for each experimental condition vs. baseline, separately. These images and each participant's structural image were normalized to the Montreal Neurological Institute reference brain.

The experimental question addressed here (viz., does response conflict occur in the exclude recognition task) involves investigating activity across our three stimulus types (i.e., target, probe and filler) in brain regions previously implicated in response conflict. Therefore, we used a small volume correction (Worsley et al., 1995) to investigate activity in contrasts of interest (probe vs. filler; target vs. filler; probe vs. target) in ACC.

We were also interested in activity in regions previously implicated in the recollection memory processes involved in this experiment (for a review see Fletcher and Henson, 2001; Simons and Spiers, 2003; Skinner and Fernandes, 2007). Many studies of recollection and source memory activate regions in the DPFC, VPFC, and APFC. Activity in these regions is sometimes lateralized (e.g., Dobbins et al., 2002; Nolde et al., 1998; Nyberg et al., 1996; Rugg et al., 1999), but often bilateral activity occurs. Henson, Shallice, and Dolan (1999), for example reported bilateral activity in these prefrontal regions for an exclude recognition task involving words presented to the left or the right of fixation. Simons et al. (2005) also reported bilateral activity in these regions in a task investigating source memory. To investigate the activity in these ROIs in our experiment, we used the combined experimental condition (viz., target, probe and filler) vs. baseline contrast to identify regions of activity ($p < .05$, FDR) in left and right anterior, ventral, and dorsal prefrontal cortices. The β -values from each experimental condition relative to baseline were then extracted from these ROIs for subsequent analysis. This approach has been used successfully to investigate response selection by one or more of the authors previously (Nagel et al., 2008; Schumacher and D'Esposito, 2002; Schumacher et al., 2003, 2005, 2007; Schwarb and Schumacher, 2009; Stelzel et al., 2006). The coordinate of peak activation and extent of these ROIs are shown in Table 1 and Fig. 4. The assumptions for sphericity were not violated in any analysis so no correction was applied.

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REFERENCES

- Allen, J.J., Iacono, W.G., Danielson, K.D., 1992. The identification of concealed memories using the event-related potential and implicit behavioral measures: a methodology for prediction in the face of individual differences. *Psychophysiology* 29, 504–522.
- Atkinson, R.C., Juola, J.F., 1974. Search and decision processes in recognition memory. In: Krantz, D.H., Atkinson, R.C., Lucke, R.D. (Eds.), *Learning, Memory, and Thinking*. Freeman, San Francisco.
- Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S., Cohen, J.D., 2001. Conflict monitoring and cognitive control. *Psychol. Rev.* 108, 624–652.
- Botvinick, M.M., Cohen, J.D., Carter, C., 2004. Conflict monitoring and anterior cingulate cortex: an update. *Trends Cogn. Sci.* 8, 539–546.
- Burle, B., Possamai, C., Vidal, F., Bonnet, M., Hasbroucq, T., 2002. Executive control in the Simon effect: an electromyographic and distributional analysis. *Psychol. Res.* 66, 325–336.
- Burle, B., Vidal, F., Tandonnet, C., Hasbroucq, T., 2004. Psychological evidence for response inhibition in choice reaction time task. *Brain Cogn.* 56, 141–152.
- Burle, B., Roger, C., Allain, S., Vidal, F., Hasbroucq, T., 2008. Error negativity does not reflect conflict. A re-appraisal of conflict monitoring and anterior cingulate cortex activity. *J. Cogn. Neurosci.* 20, 1637–1655.
- Cabeza, R., Kapur, S., Craik, F.I.M., McIntosh, A.R., Houle, S., Tulving, E., 1997. Functional neuroanatomy of recall and recognition: a PET study of episodic memory. *J. Cogn. Neurosci.* 9, 254–265.
- Coles, M.G.H., Gratton, G., Bashore, T.R., Eriksen, C.W., Donchin, E., 1985. A psychophysiological investigation of the continuous flow model of human information processing. *J. Exp. Psychol. Hum. Percept. Perform.* 11, 529–553.
- Coles, M.G.H., Scheffers, M.K., Fournier, L., 1995. Where did you go wrong? Errors, partial errors, and the nature of human information processing. *Acta Psychol.* 90, 129–144.
- Dobbins, I.G., Foley, H., Schacter, D.L., Wagner, A.D., 2002. Executive control during episodic retrieval: multiple prefrontal processes subserved source memory. *Neuron* 35, 989–996.
- Dodson, C.S., Johnson, M.K., 1996. Some problems with the process-dissociation approach to memory. *J. Exp. Psychol. Gen.* 125, 181–194.
- Dodson, C.S., Holland, P.W., Shimamura, A.P., 1998. On the recollection of specific- and partial-source information. *J. Exp. Psychol. Learn. Mem. Cogn.* 24, 1121–1136.
- Dodson, C.S., Bawa, S., Slotnick, S.D., 2007. Aging, source memory, and misrecollections. *J. Exp. Psychol. Learn. Mem. Cogn.* 33, 169–181.
- Farwell, L.A., Donchin, E., 1991. The truth will out: interrogative polygraphy (“lie detection”) with event-related brain potentials. *Psychophysiology* 28, 531–547.
- Fleck, M.S., Daselaar, S.M., Dobbins, I.G., Cabeza, R., 2006. Role of prefrontal and anterior cingulate regions in decision-making processes shared by memory and nonmemory tasks. *Cereb. Cortex* 16, 1623–1630.
- Fletcher, P.C., Henson, R., 2001. Frontal lobes and human memory: insights from functional neuroimaging. *Brain* 124, 849–881.
- Friston, K.J., Ashburner, J., Frith, C.D., Poline, J.B., Heather, J.D., Frackowiak, R.S.J., 1995. Spatial registration and normalization of images. *Hum. Brain Mapp.* 3, 165–189.
- Gillund, G., Shiffrin, R.M., 1984. A retrieval model for both recognition and recall. *Psychol. Rev.* 91, 1–67.
- Hancock, P., 2004. *Psychological Image Collection at Stirling*, vol. 2000. University of Stirling Psychology Department.
- Henson, R., Shallice, T., Dolan, R.J., 1999. Right prefrontal cortex and episodic memory retrieval: a functional MRI test of the monitoring hypothesis. *Brain* 122, 1367–1381.
- Jacoby, L.L., 1991. A process dissociation framework: separating automatic from intentional uses of memory. *J. Memory Lang.* 30, 513–541.

- Jacoby, L.L., Kelley, C., Brown, J., Jasechko, J., 1989a. Becoming famous overnight: limits on the ability to avoid unconscious influences of the past. *J. Pers. Soc. Psychol.* 56, 326–338.
- Jacoby, L.L., Woloshyn, V., Kelley, C., 1989b. Becoming famous without being recognized: unconscious influences of memory produced by dividing attention. *J. Exp. Psychol. Gen.* 118, 115–125.
- Jacoby, L.L., Toth, J.P., Yonelinas, A.P., 1993. Separating conscious and unconscious influences of memory: measuring recollection. *J. Exp. Psychol. Gen.* 122, 139–154.
- Jones, A.D., Cho, R.Y., Nystrom, L.E., Cohen, J.D., Braver, T.S., 2002. A computational model of anterior cingulate function in speeded response tasks: effects of frequency, sequence, and conflict. *Cogn. Affect. Behav. Neurosci.* 2, 300–317.
- Kornblum, S., Hasbroucq, T., Osman, A., 1990. Dimensional overlap: cognitive basis for stimulus-response compatibility — a model and taxonomy. *Psychol. Rev.* 97, 253–270.
- Kuhl, B.A., Kahn, I., Dudukovic, N.M., Wagner, A.D., 2008. Overcoming suppression in order to remember: contributions from anterior cingulate and ventrolateral prefrontal cortex. *Cogn. Affect. Behav. Neurosci.* 8, 211–221.
- Langleben, D.D., Schroeder, L., Maldjian, J.A., Gur, R.C., McDonald, S., Ragland, J.D., O'Brien, C.P., Childress, A.R., 2002. Brain activity during simulated deception: an event-related functional magnetic resonance study. *Neuroimage* 15, 727–732.
- Leveroni, C.L., Seidenberg, M., Mayer, A.R., Mead, L.A., Binder, J.R., Rao, S.M., 2000. Neural systems underlying the recognition of familiar and newly learned faces. *J. Neurosci.* 20, 878–886.
- Maddock, R.J., Garrett, A.S., Buonocore, M.H., 2001. Remembering familiar people: the posterior cingulate cortex and autobiographical memory retrieval. *Neuroscience* 104, 667–676.
- McDermott, K.B., Jones, T.C., Petersen, S.E., Lageman, S.K., Roediger, H.L., 2000. Retrieval success is accompanied by enhanced activation in anterior prefrontal cortex during recognition memory: an event-related fMRI study. *J. Cogn. Neurosci.* 12, 965–976.
- Meyer, D.E., Kieras, D.E., 1997. A computational theory of executive cognitive processes and multiple-task performance: I. Basic mechanisms. *Psychol. Rev.* 104, 3–65.
- Miller, E.K., Cohen, J.D., 2001. An integrative theory of prefrontal cortex function. *Annu. Rev. Neurosci.* 24, 167–202.
- Monsell, S., 1996. Control of mental processes. In: *Unsolved Mysteries of the Mind: Tutorial Essays in Cognition*. Vol. V. Bruce, eds. Erlbaum, Taylor and Francis, Hove, England, pp. 93–148.
- Nagel, I., Schumacher, E.H., Goebel, R., D'Esposito, M., 2008. Functional MRI investigation of verbal selection mechanisms in lateral prefrontal cortex. *Neuroimage* 43, 801–807.
- Nolde, S.F., Johnson, M.K., D'Esposito, M., 1998. Left prefrontal activation during episodic remembering: an event-related fMRT study. *NeuroReport* 9, 3509–3514.
- Nyberg, L., McIntosh, A.R., Houle, S., Nilsson, L.-G., Tulving, E., 1996. Activation of medial temporal structures during episodic memory retrieval. *Nature* 380, 715–717.
- Nyberg, L., Marklund, P., Persson, J., Cabeza, R., Forkstam, C., Petersson, K.M., Ingvar, M., 2003. Common prefrontal activations during working memory, episodic memory, and semantic memory. *Neuropsychologia* 41, 371–377.
- Paus, T., Koski, L., Caramanos, Z., Westbury, C., 1998. Regional differences in the effects of task difficulty and motor output on blood flow response in the human anterior cingulate cortex: a review of 107 PET activation studies. *NeuroReport* 9, R37–R47.
- Poldrack, R.A., 2006. Can cognitive processes be inferred from neuroimaging data? *Trends Cogn. Sci.* 10, 59–63.
- Ridderinkhof, K.R., Ullsperger, M., Crone, E.A., Nieuwenhuis, S., 2004. The role of the medial frontal cortex in cognitive control. *Science* 306, 443–447.
- Rosenfeld, J.P., Cantwell, B., Nasman, V.T., Wojdac, V., Ivanov, S., Mazzeri, L., 1988. A modified, event-related potential-based guilty knowledge test. *Int. J. Neurosci.* 24, 157–161.
- Rosenfeld, J.P., Soskins, M., Bosh, G., Ryan, A., 2004. Simple, effective countermeasures to P300-based tests of detection of concealed information. *Psychophysiology* 41, 205–219.
- Rugg, M.D., Fletcher, P.C., Chua, P.M., Dolan, R.J., 1999. The role of the prefrontal cortex in recognition memory and memory for source: an fMRI study. *Neuroimage* 10, 520–529.
- Rugg, M.D., Henson, R., Robb, W.G.K., 2003. Neural correlates of retrieval processing in the prefrontal cortex during recognition and exclusion tasks. *Neuropsychologia* 41, 40–52.
- Schneider, W., Chein, J.M., 2003. Controlled and automatic processing: behavior, theory, and biological mechanisms. *Cogn. Sci.* 27, 525–559.
- Schneider, W., Eschman, A., Zuccolotto, A., 2002. *E-Prime User's Guide*. Psychology Software Tools, Pittsburgh, PA.
- Schumacher, E.H., D'Esposito, M., 2002. Neural implementation of response selection in humans as revealed by localized effects of stimulus-response compatibility on brain activation. *Hum. Brain Mapp.* 17, 193–201.
- Schumacher, E.H., Elston, P.A., D'Esposito, M., 2003. Neural evidence for representation-specific response selection. *J. Cogn. Neurosci.* 15, 1111–1121.
- Schumacher, E.H., Hendricks, M.J., D'Esposito, M., 2005. Sustained involvement of a frontal-parietal network for spatial response selection with practice of a spatial choice-reaction task. *Neuropsychologia* 43, 1444–1455.
- Schumacher, E.H., Cole, M.W., D'Esposito, M., 2007. Selection and maintenance of stimulus-response rules during preparation and performance of a spatial choice-reaction task. *Brain Res.* 1136, 77–87.
- Schwarb, H., Schumacher, E.H., 2009. Neural evidence of a role for spatial response selection in the learning of spatial sequences. *Brain Res.* 1247, 114–125.
- Seymour, T.L., 2001. A EPIC model of the “guilty knowledge effect” Strategic and automatic processes in recognition. *Dissertation Abstracts International: Section B: The Sciences and Engineering.* 61, 5591.
- Seymour, T.L., Fraynt, B.R., 2009. Time and encoding effects in the concealed knowledge test. *Appl. Psychophysiol. Biofeedback* 34, 177–187.
- Seymour, T.L., Kerlin, J.R., 2008. Successful detection of verbal and visual concealed knowledge using an RT-based paradigm. *Appl. Cogn. Psychol.* 22, 475–490.
- Seymour, T.L., Schumacher, E.H., 2009. Electromyographic evidence for response conflict in the exclude recognition task. *Cogn. Affect. Behav. Neurosci.* 9, 71–82.
- Seymour, T.L., Seifert, C.M., Shafto, M.G., Mosmann, A.L., 2000. Using response time measures to assess “guilty knowledge.” *J. Appl. Psychol.* 85, 30–37.
- Simons, J.S., Spiers, H.J., 2003. Prefrontal and medial temporal lobe interactions in long-term memory. *Nat. Rev. Neurosci.* 4, 637–648.
- Simons, J.S., Gilbert, S.J., Owen, A.M., Fletcher, P.C., Burgess, P.W., 2005. Distinct roles for lateral and medial anterior prefrontal cortex in contextual recollection. *J. Neurosci.* 25, 813–820.
- Sip, K.E., Roepstorff, A., McGregor, W., Frith, C.D., 2008. Detecting deception: the scope and limits. *Trends Cogn. Sci.* 12, 48–53.
- Skinner, E.I., Fernandes, M.A., 2007. Neural correlates of recollection and familiarity: a review of neuroimaging and patient data. *Neuropsychologia* 45, 2163–2179.
- Slotnick, S.D., Schacter, D.L., 2004. A sensory signature that distinguishes true from false memories. *Nat. Neurosci.* 7, 664–672.
- Stelzel, C., Schumacher, E.H., Schubert, T., D'Esposito, M., 2006. The neural effect of stimulus-response modality compatibility on dual-task performance. *Psychol. Res.* 70, 514–525.
- Sternberg, S., 2001. Separate modifiability, mental modules, and the use of pure and composite measures to reveal them. *Acta Psychol.* 106, 147–246.

- Van Veen, V., Cohen, J., Botvinick, M.M., Stenger, V.A., Carter, C., 2001. Anterior cingulate cortex, conflict monitoring, and levels of processing. *Neuroimage* 17, 1562–1571.
- Wang, C., Ulbert, I., Schomer, D.L., Marinkovic, K., Halgren, E., 2005. Responses of human anterior cingulate cortex microdomains to error detection, conflict monitoring, stimulus–response mapping, familiarity, and orienting. *J. Neurosci.* 25, 604–613.
- Worsley, K.J., Friston, K.J., 1995. Analysis of fMRI time-series revisited — again. *Neuroimage* 2, 173–182.
- Worsley, K.J., Poline, J.B., Vandal, A.C., Friston, K.J., 1995. Tests for distributed, nonfocal brain activations. *Neuroimage* 2, 183–194.
- Yonelinas, A.P., 2002. The nature of recollection and familiarity: a review of 30 years of research. *J. Memory Lang.* 46, 441–517.