

BRAIN MECHANISMS OF PROACTIVE INTERFERENCE IN WORKING MEMORY

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Abstract—It has long been known that storage of information in working memory suffers as a function of proactive interference. Here we review the results of experiments using approaches from cognitive neuroscience to reveal a pattern of brain activity that is a signature of proactive interference. Many of these results derive from a single paradigm that requires one to resolve interference from a previous experimental trial. The importance of activation in left inferior frontal cortex is shown repeatedly using this task and other tasks. We review a number of models that might account for the behavioral and imaging findings about proactive interference, raising questions about the adequacy of these models. © 2005 Published by Elsevier Ltd on behalf of IBRO.

Key words: left inferior frontal gyrus, proactive interference, executive function, neuroimaging, interference-resolution, inhibition.

What is it that limits our intellectual success? Clearly, there are large differences in performance on many tasks that engage cognitive skills. What is at the heart of these performance differences? Dating back to the very beginning of psychology, this has been a central issue in understanding the nature of human cognitive achievement. In the past 50 years, the concept of “capacity” has dominated discussions of cognitive success, and this concept has achieved an important status as an explanatory construct that might account for variations in cognitive performance. Although the idea of capacity varies in its conceptualization, one popular account describes capacity as the ability to use controlled attention to maintain information actively (Barrett et al., 2004). In particular, the capacity to store information in working memory has moved to center stage as an account of a host of important cognitive functions.

One reflection of the perceived importance of working memory is the sheer number of published studies that focus on this cognitive system. A count of papers in MEDLINE that cite “working memory” in their titles or abstracts reveals that this number has grown from 22 in 1984 to 137 in 1994 to 565 in 2004. Why is it that working memory has become so prominent an object of study? The reasons are two. First, working memory has been documented as an important basic component of such acclaimed human intellec-

tual achievements as reasoning, language-processing, and problem-solving (e.g. Just and Carpenter, 1999; Daneman and Merikle, 1996; Fry and Hale, 1996). Second, variation in working memory capacity has often been cited as a cause of variation among individuals in many cognitive tasks (Kyllonen and Christal, 1990). Related to this second issue, variation in working memory capacity has been considered a basic cause of the decline in cognitive skills with normal aging (e.g. Salthouse, 1996). Thus, if one can understand the mechanisms that determine working memory capacity, one will have a firmer understanding of an important component of many respected higher cognitive skills and a firmer understanding of why individuals differ from one another on these skills.

In this paper, we review the effect of a critical variable, proactive interference from previously relevant material (PI), which exerts significant control over the amount of information that can be retrieved from working memory. Specifically, we are concerned here with reviewing research on the brain mechanisms that are involved in the resolution of proactive interference. We concentrate on the resolution of proactive interference because it is not just an experimental curiosity. As the classic study by Keppel and Underwood (1962) demonstrated, it is possible that forgetting from working memory would be minimal or nonexistent were it not for the interference caused by prior material. Also, Whitney et al. (2001) have shown that a measure of susceptibility to proactive interference is a strong predictor of performance on the working memory span test, suggesting that span performance is at least in part a function of proactive interference effects. And, May et al. (1999) have shown that span performance on later trials is worsened by performance on earlier trials of the test, indicating that at least some of the variance in span performance is a function of susceptibility to proactive interference. Furthermore, it has been shown that working memory span is a good predictor of the ability to resolve proactive interference in a variety of tasks (e.g. Conway and Engle, 1994; Chiappe et al., 2000; Rosen and Engle, 1998; Whitney et al., 2001). In short, if working memory is critical to normal cognitive functioning, then proactive interference is an important determinant of the success of working memory.

Let us summarize: Working memory appears to be a critical ability underlying many higher cognitive functions, as revealed by the value of the working memory span test in predicting performance in language-comprehension, reasoning, and problem-solving tasks (Daneman and Carpenter, 1980; Just and Carpenter, 1999). Performance levels on the working memory span test, in turn, appear to be closely related to the ability to resolve proactive inter-

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Abbreviations: ACC, anterior cingulate cortex; gF, fluid intelligence; IFG, inferior frontal gyrus; PI, proactive interference from previously relevant material.

ference from previous information. In fact, people who are relatively successful on the working memory span test are also relatively successful in resolving interference of various types. Indeed, Engle (2005) has gone so far as to claim that “working memory is a system that evolved to deal with proactive interference.” All in all, then, resolving interference among items in memory appears to be a critical cognitive skill that has important implications for a host of other cognitive skills.

What brain mechanisms resolve interference? That is the focus of our review, and so we turn to this question now.

Brain mechanisms of proactive interference in working memory revealed by the recent-probes task

One experimental paradigm has dominated brain studies of the resolution of proactive interference in working mem-

ory. We shall call this the “Recent-Probes” task. The paradigm is due originally to the work of Monsell (1978) and is schematized in Fig. 1. The task is based on the item-recognition task of Sternberg (1966). Participants are given a series of trials in which they are presented a target-set of items to commit to memory (e.g. letters), and they store these items for a retention interval of several seconds, after which they are given a single probe item and must decide whether this probe matches one of the items in that trial’s target-set. Some probes will match one of the target-set items, thereby eliciting a positive response while some will not match and will elicit a negative response. Monsell (1978) introduced into this paradigm an opportunity for past trials to influence the current one. On some of the trials, a probe that had not been a member of the current trial’s target-set was drawn from the previous trial’s target-set (called “recent negative probes”). On other

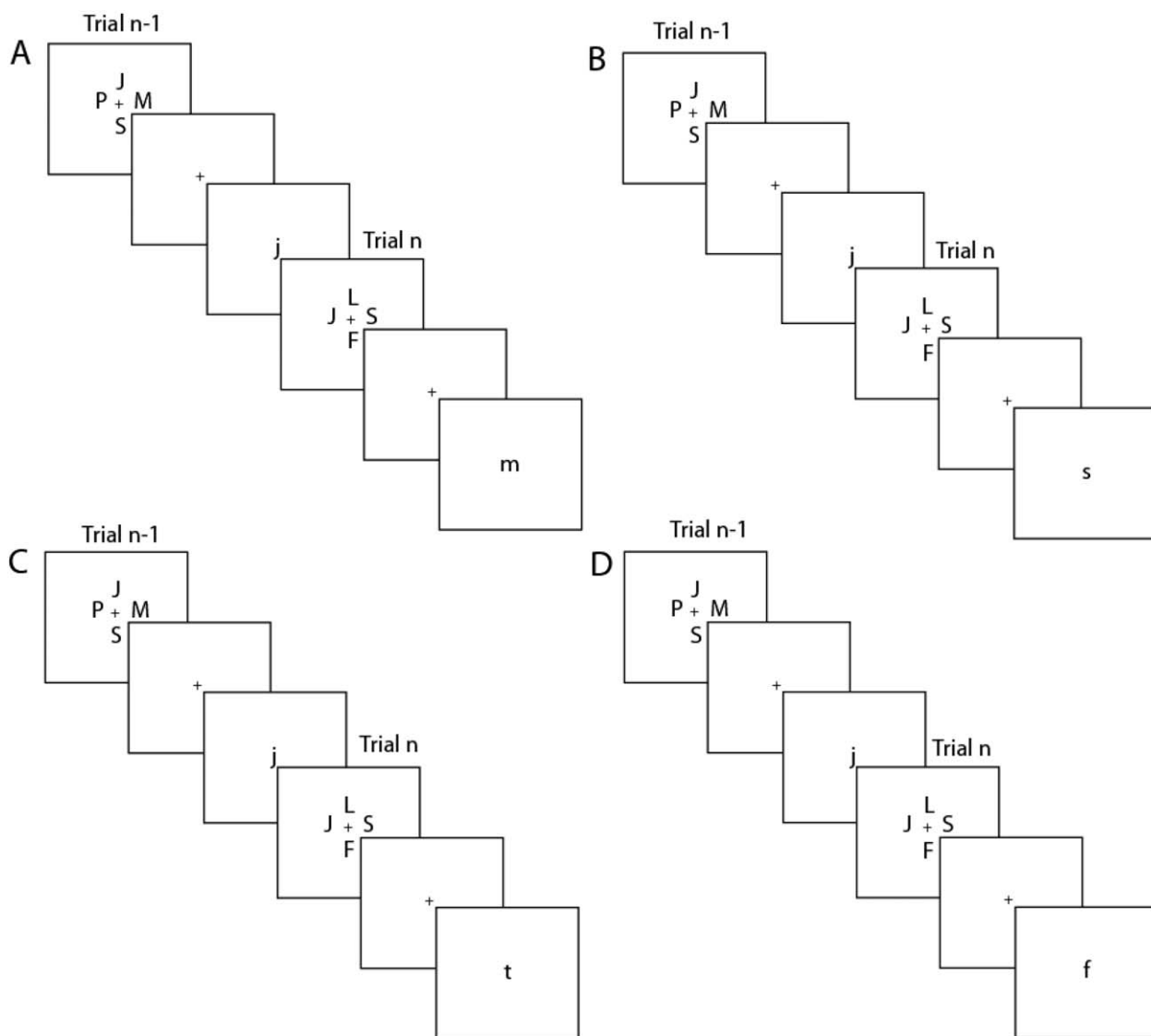


Fig. 1. A schematic of the Recent-Probes task. The four panels show the four central conditions. Panel A represents the recent-negatives; Panel B represents recent-positives. Panel C represents non-recent negatives; and Panel D represents non-recent positives.

trials, the negative probes had not appeared recently as members of other target-sets (“non-recent negative probes”). This manipulation was also applied to positive probes to yield recent and non-recent positive probes. For trials when the target-set included four items, Monsell (1978) showed that recent-negative probes yielded responses that were approximately 75 ms longer and 7% less accurate than non-recent negative probes. That is, there was proactive interference from the previous trial’s target-set on the current trial’s negative response. This extends a result shown previously by Atkinson and Juola (1974): A probe that demanded a negative response in an item-recognition task resulted in longer responses even if on the previous trial this same item had been presented as a probe and had also demanded a negative response. One account of these facts is that the recent presentation of an item causes a lingering familiarity for that item that persists into subsequent trials when that familiarity conflicts with a negative decision. Monsell offers support for this interpretation by showing that positive probes that occurred recently in the list of items in the target-set result in faster and more accurate responses, also consistent with the hypothesis that recency confers a higher familiarity code to an item. McElree and Doshier (1989) have demonstrated a similar effect.

This Recent-Probes paradigm is a useful model to study the effects of proactive interference in working memory because the behavioral effect of recent versus non-recent negative probes on response time and accuracy is quite robust. Also, as Brandon et al. (2003) have demonstrated, this paradigm is not an isolated curiosity; whatever this interference effect measures is correlated with a self-report measure of the dysexecutive syndrome. In addition, the paradigm minimizes the influence of strategic factors because participants are most often not aware of the interference effect that affects their responses (Bunge et al., 2001). Beyond this, the item-recognition task is a relatively simple one that does not load heavily on executive control mechanisms. Contrast it, for example, with another popular test of working memory, the *n*-back task. In this task, subjects see a string of single items (e.g. letters) and for each one, they must decide whether it matches the one *n*-back (say, 2-back) in the series. This task also taps interference processes as shown, for example, by Gray et al. (2003). However, it also engages other executive processes in addition to interference-resolution, processes such as those responsible for updating the contents of working memory (see Krawitz et al., 2004).

The brain mechanisms responsible for resolving interference in the Recent-Probes task were first documented in a study by Jonides et al. (1998). They compared activations for recent and non-recent negative probes using positron emission tomography to map brain regions that were sensitive to this difference. They found a behavioral interference effect reflected in both a time and an accuracy difference comparing blocks of trials with 50% of the trials containing recent negative probes to blocks with non-recent negatives only. Correspondingly, they identified a large swath of activation that peaked in the left inferior

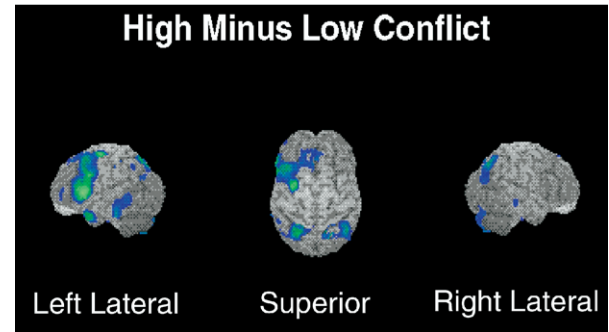


Fig. 2. Left lateral, superior, and right lateral views of a canonical brain on which are superimposed activations for recent-negative versus non-recent-negative blocks of trials from Jonides et al. (1998).

frontal gyrus, identified as Brodmann’s area 45, shown in Fig. 2. This was the only region that differentiated the trials of recent versus non-recent negative probes.

Of course, positron emission tomography is limited as an imaging tool in that it requires amassing activation over a block of trials. The consequence is that there is no opportunity to parcel out the various parts of a trial during which the activation differences for the two types of probes may appear. To ameliorate this problem, D’Esposito et al. (1999) conducted an event-related experiment that contrasted recent and non-recent negative probes within the same blocks of trials. They extended the epochs corresponding to presentation of the target-set, the retention interval, and the probe. So, this experiment offered the opportunity to determine whether the difference in activation due to recent and non-recent negative probes occurred at the time of presentation of the target-set, during the retention interval, or at the time of the probe. The experiment revealed that only when the probe was presented was there a reliable difference in activation in the left inferior frontal gyrus comparing the two types of probe. A similar trend was shown by Postle et al. (2004) across a variety of types of material.

By now, there have been various replications of the effect of interference-resolution in this task on brain activations in the inferior frontal gyrus (e.g. Braver et al., in press; Badre and Wagner, in press; Nelson et al., 2003; Mecklinger et al., 2003; Postle et al., 2004). Some of these experiments have also reported other regions of activation that appear in the comparison of recent with non-recent negatives for verbal stimuli. Although there is less consistency in the report of regions other than the left inferior frontal cortex, it does appear as if the original report by Jonides et al. (1998) may not have been sufficiently sensitive to reveal all the activations that are present in this task. Among the other regions that have been reported are intraparietal sulcus and precuneus (Mecklinger et al., 2003). In addition, there have been some reports of activation in right lateral prefrontal cortex (Bunge et al., 2001; Mecklinger et al., 2003; Badre and Wagner, in press) and in frontopolar cortex (Badre and Wagner, in press). These additional areas suggest that there is a network of regions responsible for interference-resolution in this task.

In spite of reports of additional regions of activation in the Recent-Probes task, the lion's share of attention has been paid to the left inferior frontal region in past studies (e.g. D'Esposito et al., 1999; Postle and Brush, 2004; Postle et al., 2004), at least in part because this region has been the most robust to emerge from these studies. These reports establish a relationship between resolving interference in this task and activation of this left inferior frontal region. However, they do not show that this activation is functional in resolving interference, merely that it is correlated with it. While Bunge et al. (2001) have documented a negative correlation between the amount of interference in this task and the amount of activation in left inferior frontal gyrus (see also Jonides et al., 2000), this correlation is far from conclusive. It is further testing with this paradigm that has made clear that the activation of inferior frontal gyrus is functional; this testing comes from two sources.

One source is patients who have damage to this region. Thompson-Schill et al. (2002) identified one such patient, R.C., who had damage to the same region of left inferior frontal gyrus identified by Jonides et al. (1998). At the time of testing, R.C. was a 51-year old male with damage to left inferior and middle frontal gyri as a consequence of surgery following a ruptured arteriovenous malformation some 20 years previous to his participation in the experiment. Thompson-Schill et al. (2002) compared R.C.'s performance on this task to performances of various control groups, most importantly other patients with frontal lesions in different regions and subjects who were demographically matched in age and education to the patient. R.C.'s performance on non-recent negatives and positive probes was well within the range of controls. So, R.C. did not have a general working memory deficit. However, R.C.'s interference-effect to recent negatives, as assessed by response time, was 4 standard deviations above the mean of his control group. Also, his error rate was 3 standard deviations above the mean of his control group. By contrast, none of the other frontal patients exceeded the standard-deviation criterion for their controls. Therefore it appears as though R.C. had a selective deficit in resolving interference in this task, likely owing to the damage in the left inferior frontal gyrus.

A second patient, M.L., has also been tested in the item-recognition task with recent negatives (Hamilton and Martin, 2005). At the time of testing, M.L. was a 62-year old male with a left-hemisphere lesion including the frontal operculum as a result of a stroke some 14 years prior. M.L. showed an interference effect in response time of some 5.9 standard deviations above that of control participants and almost 400 ms outside of the range of interference effects of the controls. In addition, his interference effect measured by accuracy was 25%, which was 12% outside the range of the controls against whom he was compared. Thus, the two patients with damage to the region identified by imaging studies both show substantial interference effects. Other studies of frontal patients also reveal substantial susceptibility to proactive interference, although these studies did not necessarily focus exclusively on the left inferior frontal gyrus (e.g. Smith et al., 1995).

The second source of evidence on the functionality of left inferior frontal gyrus in this task comes from studies of the effects of normal aging. Jonides et al. (2000) compared normal elderly adults to normal younger adults, examining differences in performance on recent-negative trials compared with non-recent negative trials. They found that the interference effect, as indicated by a combination of response times and errors, was larger for the elderly (see also Thompson-Schill et al., 2002 for a replication). This is consistent with much evidence that older adults have more difficulty resolving interference than younger adults (e.g. Hasher and Zacks, 1988; Chiappe et al., 2000; May et al., 1999). Having established that this is so for the Recent-Probes task as well, the stage was set to test whether participants who show a larger interference effect also show less activation in the left lateral prefrontal region. This prediction follows from the notion that if this region is critical for resolving interference, then participants who are less successful at resolving interference should show less activation. Indeed, this was so. While the older adults showed activation in this region that was close to reliable statistically ($P < 0.07$), the level of activation was reliably less than for younger adults. Taken together with the results of patients with damage to this region, the case appears to be strong that the left inferior frontal gyrus is critical to the resolution of interference in this task.

Content-specificity versus content-generality

Before turning to accounts of the function of left IFG, let us examine whether the activations in this task are specific to the content of the material (e.g. verbal) or are content-general. The results on this issue are mixed. Mecklinger et al. (2003) compared activations in the recent-negatives task using letters as stimuli versus abstract objects. Each target-set included just two memoranda, but otherwise the procedure for the experiment was largely the same as for other implementations of this task. Conveniently, the experimenters adjusted the experimental presentation times to equate interference effects measured by response time with the two types of material. For letters and objects respectively, the interference effects measured in response time were 34 and 38 ms. However, the accuracy scores were not also equated; the interference effect was larger for objects than for letters. Nonetheless, the interference effects behaviorally were at least somewhat similar for the two types of material. The imaging activations showed some similarities and some differences as a function of type of material. There was activation in intraparietal sulcus for interference effects with both types of material. However, there was reliably greater activation for recent negatives versus non-recent negatives in left inferior frontal cortex only for letters, not for objects. Also, the middle frontal gyrus and precuneus showed activations for interference using letters as stimuli, but not objects. Overall, the activations due to interference-resolution in this study were larger for letters than objects and included anterior and posterior regions, with some overlap. With respect to the region we have targeted as critical to interference-resolution, the left inferior frontal cortex, there was reliable acti-

vation in this region only for letters although it should be noted that the time-series of activation for objects was qualitatively similar, if not reliable.

A second study also compared memory for verbal and object material (Badre and Wagner, *in press*). The verbal materials were abstract words and the objects were fractal visual stimuli selected to minimize the extent to which they could be verbally coded. As with the data from Mecklinger et al. (2003), there were reliable interference effects comparing recent and non-recent negative probes. Activations due to resolving this interference were lodged in left IFG, right IFG and anterior frontal cortex, but these were statistically reliable only for the verbal stimuli, not for the objects. In this study, there were large performance differences between the two classes of stimuli, however, with the objects yielding much worse performance, especially in accuracy. In spite of these large differences, though, and despite of the lack of reliable overall imaging effects for interference with the objects, there was nonetheless a non-significant trend ($P=0.13$) of activation in left IFG for the objects as well as a significant activation in this region for the words.

Brandon et al. (2003) compared interference effects in the recent-negatives task using letters versus faces as stimuli and found quite robust effects with both types of material. In a follow-up study, Brandon et al. (2004) examined activation in left and right IFG to the face stimuli alone. They found activations in IFG in both hemispheres comparing recent to non-recent negatives, with the activation in left IFG correlating with the behavioral measure of interference.

Going beyond just two types of stimuli, Postle et al. (2004) investigated activations in the Recent-Probes task using as stimuli color patches, letters, polygons, digits, locations, words, and faces in different blocks of the task. They found behavioral interference effects for five of these stimulus-types, indicating some degree of generality over material. However, the activation in left IFG across types of material was only marginally reliable overall ($P<0.07$), thereby not permitting a strong comparison across material.

Overall, there is insufficient information as yet about whether different types of content engage different mechanisms of interference-resolution in the Recent-Probes task. One possible factor raised by Mecklinger et al. (2003) is that the extent to which stimuli can be verbalized may play a role in the amount of activation in left IFG that they elicit and possibly the amount of interference they produce in the Recent-Probes task. However, Brandon et al. (2003, 2004) have tested this hypothesis and found it wanting. They examined the amount of interference that arose from using faces as stimuli, and it was substantial. Of more importance, they had subjects rate the extent to which the faces were subject to verbal labeling. Although the overall error rate for faces did decrease with increased verbal labeling, the amount of recent-negatives interference was unaffected by verbal labeling. Furthermore, as Brandon et al. (2004) showed, the amount of left IFG activation in response to recent-negatives was also not influenced by the extent to which the faces could be verbally labeled.

Beyond the issue of verbal coding, though, there is little clarity yet about the effects of types of material, and so further work is required on this issue.

Individual differences in the recent-probes task

One of the advantages we cite above for the focus on the Recent-Probes task is that the interference effect it causes is apparently unknown to participants and so cannot come under strategic control (Bunge et al., 2001). However, it is possible to alter the task so that strategic control is possible, and in that case individual differences in interference-resolution emerge. Part of the work on this issue comes from Braver et al. (*in press*). They varied the probability of recent-negatives in blocks of trials, with some blocks containing only 20% and others containing 80%. They also tested subjects on the Raven's Advanced Progressive Matrices test, an assay that is used to measure fluid intelligence (gF). They found that subjects high in gF showed less interference than low gF individuals in blocks that contained high proportions of recent negatives. When there was a low probability of interference, however, there was no difference in interference comparing high and low gF individuals.

Braver et al. (*in press*) interpreted this result in a framework that makes a distinction between proactive and reactive control over interference. They argued that when interference can be expected, it is possible to prepare for it so that it intrudes on processing only minimally. Preparation is enhanced for individuals who are high in gF. This result is related to the rich literature of Engle and his colleagues who have shown that resistance to interference is a signature of individuals high in working memory capacity (e.g. Engle and Oransky, 1999; Rosen and Engle, 1998). In view of the fact that working memory span and gF are correlated approximately 0.50 (Carpenter et al., 1990), it is reasonable to suppose that span and gF both capture a similar skill. By Braver et al.'s (*in press*) account, this skill is preparing to deal with upcoming interference. This preparation, in turn, was reflected in higher activation in left inferior frontal cortex during the retention interval of the task for the high gF individuals in the condition that had high expectancy for recent-negative trials. Interestingly, this contrasts with the typical report of activation differences between recent and non-recent negatives which appear after presentation of the probe (D'Esposito et al., 1999; Badre and Wagner, *in press*). However, when Braver et al. (*in press*) collapsed across individuals and expectancy conditions, they also did find activation in left IFG in response to the probe on this task. So, the process of preparing for interference that apparently characterizes the high gF individuals must require some immunization against the upcoming interference before the probe appears.

Braver et al. (*in press*) proposed a distinction between proactive and reactive control to account for their effects. When high gF individuals expect interference to occur, they prepare for it and engage in some processing of the target-set during the retention interval to prepare for the interference that may come with the probe. What this

processing is remains to be discussed below. When interference cannot be predicted, both groups of subjects simply react to the interference that is elicited by presentation of the probe. In both cases, though, the critical site of activation, whether engaged proactively or reactively, is left inferior frontal cortex. This result echoes and expands on observations by Mecklinger et al. (2003) of enhanced performance by high working memory capacity individuals in the recent-negatives task.

Other proactive interference effects

Of course, the Recent-Probes task is not the only way of tapping into processes of proactive interference-resolution in working memory. Although the behavioral literature includes many other tasks (e.g. Wickens et al., 1963), there have not been investigations of most of these tasks using the tools of cognitive neuroscience. An exception is tasks that engage directed-forgetting operations. In such tasks, a subject is provided some material to hold in memory, after which a cue is presented directing the subject to forget a subset of the material currently in mind. A probe is then presented to test memory for the to-be-remembered information. In this task, proactive interference can be assessed by examining whether the to-be-forgotten information intrudes at the time of retrieval.

This procedure has been successfully used to study working memory by Zhang et al. (2003). On each trial, they had subjects study six letters, three on each side of center. Following a short delay, either the left or the right three of these letters were re-presented with the instruction to forget these letters and retain just the remaining three. Then a probe appeared to test retrieval. The probe could demand a positive or a negative response depending on whether it did or did not match one of the remaining three letters. When it did not match, it might have been a letter not presented in the original display (a “low familiar” negative probe) or it might have been a letter that was one of the three to be forgotten on that trial (a “high-familiar” negative probe). The design of this task makes it similar to the recent-negatives task in that the items to be forgotten are re-presented as the forgetting cue, and so they have a recent status in their presentation history as do the recent-negatives in the Recent-Probes task. And, as in the Recent-Probes task, performance on the probes that were to be forgotten was worse (by 136 ms and 2.6% in accuracy) than on control probes. Zhang et al. (2003) went on to compare activations due to the two types of negative probes in the left inferior frontal region identified by Jonides et al. (1998) for the Recent-Probes task, and they discovered reliably higher activation for probes that were to be forgotten. In addition to this region, there was only one other region that showed reliable activation for this contrast, and that was Brodmann’s region 32 in anterior cingulate cortex (ACC). We shall return to this cingulate activation below. (We note that Leung and Zhang (2004) have re-done this study using spatial locations as memoranda, but their behavioral effects and imaging effects were only marginally reliable, so it is difficult to draw conclusions from this study.)

A second task relevant to proactive interference effects is the *n*-back task as investigated by Gray et al. (2003). They had subjects perform the 3-back task. In their version, subjects saw a series of single words, and the subjects had to decide for each one whether it matched the word presented three earlier in the sequence. Proactive interference was varied by contrasting two types of trials that differed when the target words did not match the word presented three earlier. Interference was introduced by having lures that matched the item 2-, 4-, or 5-back in the series. So, when a word was presented, if it did not match the one presented three earlier, it might match one of the words in neighboring temporal positions. In this way, an item’s familiarity would lead to a tendency to call it a match even if it was not presented in the imperative 3-back position. The control trials had no such lures and thus no competing familiarity signal for each word. Lures clearly made performance worse, both in time and accuracy. The authors did not report simple activations as a function of whether trials contained lures or not, but they did report whether gF, as measured by the Raven’s test, predicted activation on lure trials. There were many such regions, including several in left lateral prefrontal cortex, consistent with the role of this region in resolving the conflict between the familiarity of an item and that item’s ordinal position in the sequence. Similarly, Derrfuss et al. (2004) have also found activation in left inferior frontal cortex in response to a 2-back task that had lures compared with a 0-back control.

Beyond the directed-forgetting and *n*-back tasks, there are yet other data implicating left inferior frontal cortex in the resolution of proactive interference. Postle and Brush (2004) examined proactive interference in the classic sense identified by Underwood (1957). Keppel and Underwood (1962) had shown that the mere occurrence of previous trials in a sequence of trials was sufficient to induce proactive interference on the current trial regardless of the particular items that had been presented on those trials. Note that studies of the Recent-Probes task, of directed forgetting tasks, and of the *n*-back task lodge PI in the particular items that are present on each trial. So, for example, it is the presence of the particular probe-item on the previous trial that causes the interference on the present trial in the Recent-Probes task. Postle and Brush (2004) examined the effect of previous trials on the accumulation of proactive interference regardless of the particular items that had been presented. They conducted a sort of meta-analysis of seven previous studies of working memory, analyzing brain activations as a function of the position of each trial in a series. Their goal was to determine whether the accumulation of previous trials would have a systematic effect on activations in various regions of frontal cortex independent of whatever independent variables had been manipulated in the original studies. Importantly, they isolated the left IFG region as one of their targets of study, recognizing its central role in the Recent-Probes task and in other tasks that are affected by proactive interference. Their analysis revealed that there was a behavioral effect of increasing accumulation of trials such

that response time gradually increased within blocks of trials as more trials accumulated. Analysis of the fMRI data from these studies revealed that activations in frontal cortex generally decreased with trial position except for the left inferior frontal region. Its activation did not change, thereby singling it and a neighboring region in the middle frontal gyrus as behaving differently. In an experimental follow-up to this work, Postle et al. (2004) simultaneously examined the effect of trial-position and the effect of recent-negative probes to determine whether activations due to these two effects overlapped. Indeed, they did, and the overlap was in the left inferior frontal gyrus region. Furthermore, temporally the effect of proactive interference from previous trials was lodged at the time a probe was presented in the various tasks they examined, similar to the effect for the Recent-Probes task.

What emerges from the study of other tests of proactive interference is similar to what emerges from the study of the Recent-Probes task. There appears to be an important role played by the left inferior frontal gyrus in resolving interference in all these situations. What might this role be? Let us consider some alternative accounts of the computations that might be served by this region.

Mechanisms of proactive interference resolution

Let us begin our discussion of mechanisms by summarizing some facts that have been documented about the Recent-Probes task.

1. Recent-negative probes yield longer response times and often worse accuracy than non-recent negative probes (Monsell, 1978; Jonides et al., 1998; Postle et al., 2004; Badre and Wagner, in press; Mecklinger et al., 2003).
2. Recent-positive probes often, but not always, yield shorter response times and better accuracy than non-recent positive probes (Badre and Wagner, in press, but Jonides et al., 1998).
3. Recent-negative and recent-positive probes result in activation in left inferior frontal gyrus compared with their respective non-recent probes although the activation in this region due to recent-positives is less than due to recent-negatives (Badre and Wagner, in press).
4. The activation due to recent-negatives and recent-positives appears at the time of presentation of the probe in the item-recognition task, not earlier in the trial epoch (D'Esposito et al., 1999; Badre and Wagner, in press; Braver et al., in press).
5. Activation in left inferior frontal cortex is present in other tasks in which proactive interference plays a role (Postle and Brush, 2004; Postle et al., 2004; Gray et al., 2003; Zhang et al., 2003).
6. Additional regions of activation that may accompany the comparison of recent to non-recent probes include anterior frontal cortex, right inferior frontal gyrus, and intraparietal sulcus (Badre and Wagner, in press; Mecklinger et al., 2003).
7. The effects cited here may be independent of the type of stimulus material (Brandon et al., 2004; Postle et al., 2004; Badre and Wagner, in press) although the evi-

dence on this issue is controversial (Mecklinger et al., 2003).

8. Participants who score high on working-memory span or on a measure of gF are less subject to the negative-recency effect than those who score low on these measures (Braver et al., in press; Mecklinger et al., 2003).

9. Activation due to conflicting negative items in a working-memory version of the directed-forgetting task also results in activation in left inferior frontal cortex (Zhang et al., 2003).

We ask now what accounts there might be of these facts, and we consider six possibilities.

1. Time on task. First, we let us consider and dismiss an account that attributes the increased activation to time spent on the item-recognition task. It is possible that the increased activation that accompanies recent negatives is simply a function of the fact that responses to recent negatives take longer than those to their non-recent counterparts. This possibility seems unlikely to us for three reasons: First, if time-on-task were to account for the activation effects, we would expect the activations to appear in the standard places in which one finds activations in working memory tasks in general. Bunge et al. (2001) have, in fact, documented overlap in the activations due to interference and those due to working memory load. However, they also found that different constellations of these regions correlated with interference versus working memory. Interference effects behaviorally correlated with activation in left inferior and right middle frontal gyrus, but activations in these regions did not correlate with working memory load. So, it appears unlikely that there is indistinguishable overlap between activations due to working memory and those due to interference. A second fact that argues against a time-on-task account is that to the extent that they have been documented, activations due to recent-positive probes overlap those due to recent-negative probes, yet recent positives yield responses that are either equal in latency to non-recent positives or faster (Badre and Wagner, in press). Finally, Mecklinger et al. (2003) have found an effect of whether the stimuli in the recent negatives task are letters or objects on activation in IFG and MFG despite the fact that the behavioral interference effects for the two types of tasks were very similar in magnitude. Time-on-task obviously cannot account for these various facts.

2. Effective memory load. Bunge et al. (2001) proposed the possibility that the increased activation accompanying recent-negatives may be the result of an effectively larger memory load on recent-negative trials. That is, memory of previous target-sets may intrude on the current one, making the effective memory load on the current trial larger than the nominal load. In support of this possibility, they found overlap in the activations due to recent-negatives versus explicit variation of memory load. This possibility seems unlikely to us for two reasons, however. First, as we mentioned above, Bunge et al. (2001) themselves found that although there was overlap in activations, different portions of the overlapping regions correlated with

behavioral measures of interference versus memory load. For example, activation in inferior frontal gyrus correlated with the interference effect, not with load. Second, [Postle et al. \(2001\)](#) explicitly varied proactive interference and task-load via trial-length within a trial in a working memory task. They found that proactive interference activated left inferior frontal cortex whereas memory load (implemented as trial-length) activated dorsolateral prefrontal cortex, establishing a neural double dissociation. These two lines of argument suggest that whatever mediates the resolution of proactive interference is different from the mechanisms that are affected by working memory load.

Now, let us consider some alternative possible mechanisms that may be involved in the recent-negatives task, but first let us review the task and its requirements. The item-recognition task can be solved by attending to and using two sorts of evidence about the probe. One is its relative familiarity in that probes that are relatively familiar are likely to have been members of the current target-set. The other is a contextual code that identifies the probe as member of the set to which the other target-set characters belong ([Monsell, 1978](#)). This contextual tag may include associations with other items of the target-set, a temporal code that identifies the item as having been presented in the recent past, and so on. On non-recent trials, positive probes will have both high familiarity because they were presented as part of the current target-set and current contextual tags because they are identified as members of the current set. By contrast, non-recent negative probes will have low familiarity and no contextual tags linking them to the current target-set. So, a discrimination between positive and negative status for these two types of probes will be relatively quick and not encumbered by interference between the two types of information. Also, positive probes that appeared in both the current trial and the previous one (recent-positives) should yield responses at least as fast as positive probes that appeared only on the current trial because their familiarity will be even higher, and both familiarity and contextual relevance point to a positive response.

It is the recent negative probes that present a conflict. They have a high familiarity code relative to non-recent probes because of their presentation on the previous trial, but this higher familiarity conflicts with their not having contextual tags that are appropriate to a positive response on the current trial. At what stage of processing is this conflict resolved and how is that resolution accomplished?

3. Encoding effects. [Jonides et al. \(2000\)](#) raised the possibility that older adults may fare worse at the recent-negatives task because they have poorer contextual encoding of the target-sets. Hence, when a recent-negative probe is presented, its higher familiarity cannot be discounted as readily by its association with the context for the wrong trial. We know that older adults show less activation on recent-negative trials in left IFG than younger adults, and this view would attribute the lower activation to worse encoding processes in the older adults. The basis for this model was a positron emission tomography exper-

iment that blocked the presentation of recent- and non-recent negatives and that did not allow access to the encoding, maintenance, and probe phases of each trial. Functional MRI experiments using an event-related procedure have revealed that the temporal locus of activation in left inferior frontal gyrus is the presentation of the probe, not the encoding of target-sets ([D'Esposito et al., 1999](#); [Badre and Wagner, in press](#)). So ostensibly, it appears that interference does not arise during the encoding epoch. However, we cannot rule out this account just yet. One model that we will discuss below attributes left inferior frontal gyrus activation to the selection of appropriate contextual information ([Badre and Wagner, in press](#)). If older adults fail to encode contextual information as well as younger adults, then selection of a classification of the probe based on contextual information will be compromised. Perhaps it is this failure to use contextual information that produces increased interference effects in older adults. However, even under this model, the *resolution* of conflict appears to occur during probe presentation.

The temporal locus of the conflict-resolution aside, there is an aspect to an encoding-based account of the recent-negatives effect that may be apt. [Braver et al. \(in press\)](#) reported an experiment in which they had blocks of trials with 80% recent-negatives versus blocks with just 20% recent-negatives. This variation was reflected in varying levels of activation in left inferior frontal cortex for subjects who scored well on the Raven's Advanced Progressive Matrices test, identifying them as high in gF. Interestingly, this increased activation was tracked to the retention phase of the experiment, not the probe phase. What it may indicate is that for the blocks with high numbers of recent-negatives, the high gF subjects did additional encoding and consolidation of the target-set during the retention interval to solidify the contextual tags for the items in preparation for a probe that might be a recent-negative. So, it may well be that processes involved in resolving interference, when interference can be expected, can operate during encoding, as [Jonides et al. \(2000\)](#) proposed might be the case for young versus elderly subjects.

4. Response-selection. It has been suggested that conflict in the recent-negatives task remains in the processing system until a response is selected (see [Mecklinger et al., 2003](#), for a similar idea). That is, there is information about recent-negatives that leads to the selection of a positive response and information about them that leads to a negative response. Put another way, when a probe demands a negative response, but on the previous trial that probe was associated with a positive response, the response on the current trial to that item has to be re-selected. One region that has often been implicated in response-selection conflict is the anterior cingulate ([Botvinick et al., 2001](#)). Indeed, in addition to left inferior frontal gyrus activation, [Mecklinger et al. \(2003\)](#) observed activation in the ACC. However, this study compared only recent-negatives which had been responded to positively on the previous trial with non-recent negatives. What is

unclear from this study is whether the ACC is involved in the resolution of proactive interference, or whether it is solely involved in the resolution of response conflict.

A recent experiment by Nelson et al. (2003) explored just this question. To do so, Nelson et al. (2003) performed two separate contrasts: one comparing recent-negatives that had been the probes on the previous trial (thereby yielding a positive response and inducing response conflict), with recent-negatives that were not previously probes (so there was no response conflict). They also compared recent-negatives that did not include response conflict with non-recent negatives. The former resulted in activation in ACC, but the latter did not. Yet, the latter did yield activation in left inferior frontal gyrus. Fig. 3 taken from Nelson et al. (2003) shows this dissociation clearly, and the figure reveals that conflict due to response-selection is resolved differently than conflict due to internal inconsistency in attribute codes for memorized items.

The results of this experiment are consistent with other analyses of the role of ACC in the Recent-Probes task (Jonides et al., 2002). Although there has been a report of some ACC activation in this task (Bunge et al., 2001), the activation in this region did not correlate with the size of the interference effect even though it did correlate with difficulty in the working memory task overall. Other reports of activations in the Recent-Probes task have not included ACC (Jonides et al., 2002). Overall, then, it seems fair to conclude that participation of the anterior cingulate is not critical to resolving interference in the Recent-Probes task if the conflict in this task is due only to interference among different codes assigned to an item (familiarity versus other contextual codes). However, if there is response-conflict associated with the task, as in the work by Nelson et al. (2003), then the anterior cingulate is recruited in response to that conflict. Others have also come to associate ACC

activation with response-based interference effects (e.g. Milham et al., 2001). A second interesting possibility is that the ACC comes online only when conflict is conscious (Bunge et al., 2001), but this claim needs further testing.

Finally, other authors have claimed that the ACC does not respond to conflict per se, but rather computes the likelihood of committing an error on a given trial (Brown and Braver, 2005). By this account, trials that have been associated with greater error-likelihood will elicit increased ACC activation. It is unclear whether this account necessitates that subjects are aware of the increased likelihood of an error. If not, the results of Nelson et al. (2003) do not support the account. Trials that included response-conflict did not differ in error rates from trials that did not include response-conflict, yet ACC activation dissociated response-conflict from non-response-conflict trials. However, if the increased error-likelihood needs to be conscious to take effect, then the present data cannot speak to the model and again, further testing is needed.

5. Episodic-retrieval. Badre and Wagner (in press) have proposed an account in which interference-resolution is accomplished via episodic retrieval. These authors claim that left inferior frontal gyrus is important in selecting relevant contextual features. By their account, the familiarity of recent-negatives induces activation of the previous trial's context which interferes with retrieval of the current context. This increases selection demands which are the domain of left inferior frontal gyrus, and it increases demands to monitor and evaluate the appropriate context, processes associated with frontopolar cortex. Like recent-negatives, recent-positives also induce the retrieval of a previous trial's context, requiring selection via left inferior frontal gyrus. However, recent-positives are also members of the current contextual setting. These authors argue that selec-

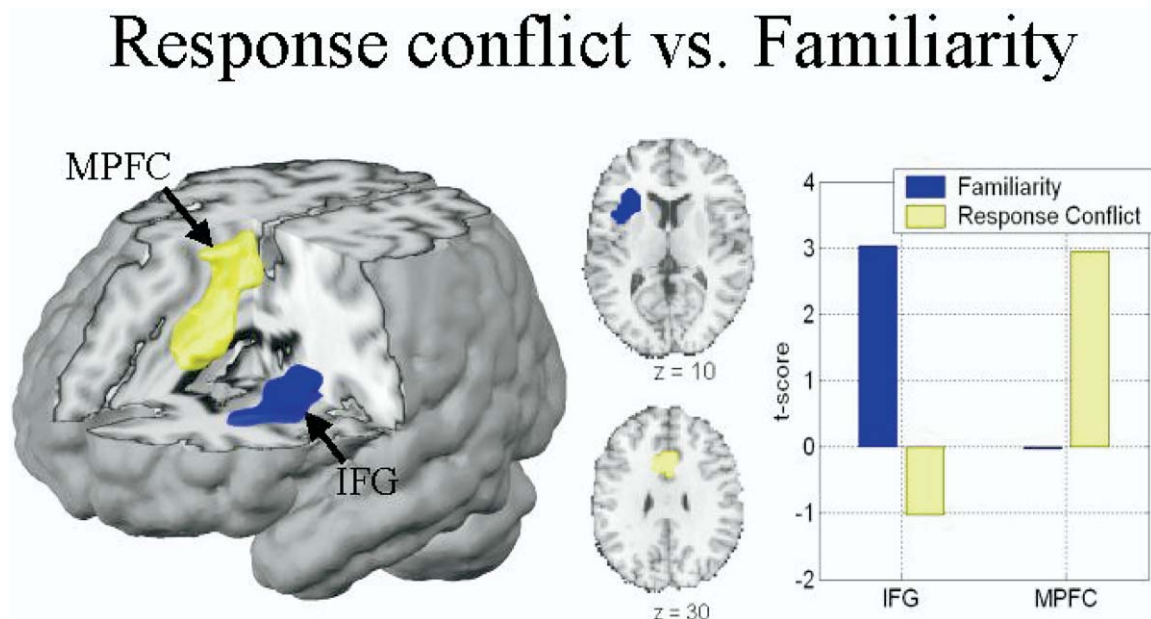


Fig. 3. Taken from Nelson et al. (2003), this figure shows a double dissociation between interference-resolution for response competition (revealed in medial prefrontal cortex versus interference among internal codes for a memorandum (revealed in inferior frontal cortex).

tion of the current contextual setting may be pre-potent, thereby decreasing selection demands. So, both recent-negatives and recent-positives can produce activation in left inferior frontal gyrus, but there will be more activation for recent-negatives. Interestingly, neuroimaging results from the Stroop task also implicate left inferior frontal gyrus when selecting among congruent representations, similar to selection for recent-positives (Milham et al., 2001, 2002). Furthermore, episodic-retrieval accounts have been used to explain interference-resolution in the Stroop task, as well (MacLeod et al., 2004). In support of this account, Badre and Wagner (in press) also found activation in the Recent-Probes task in left frontopolar cortex, a region that has often been associated with episodic-retrieval.

A problem with this approach, however, is that it does not provide for an easy account of the behavioral facilitation for recent-positive probes. If context-selection occurs for recent-positives and not non-recent positives, and context-selection increases reaction time for recent-negatives, how can it facilitate reaction time for recent-positives? What is needed is some account of how the left inferior frontal gyrus is simultaneously responsible for facilitation of responses to recent-positives and slowing of responses to recent-negatives. We turn to an account of this phenomenon next.

6. Biased competition among internal representations.

What has been established by the work of Nelson et al. (2003) is that the left IFG is involved in resolving interference when that interference cashes out as conflict among properties of an internal representation in working memory. Those properties are attributes of that representation that specify its familiarity, its temporal context, its associations with other items, and so forth. How might this conflict present itself in such a way that the left IFG is useful as a resolution tool? The work of Thompson-Schill et al. (1997) and Kan and Thompson-Schill (2004) offers an interesting hypothesis. These authors have argued that one of the functions of left IFG is to select among multiple representations in the service of some task. The hallmark work that supports this argument comes from several tasks, among them the Verb-Generate task. In this task, participants must generate a verb in response to a noun presented on each trial. Thompson-Schill et al. (1997) varied the selection of nouns such that some of the nouns had many possible verbs that might be generated to them (e.g. ball) whereas others had relatively few (e.g. scissors). They found that when contrasting the trials on which many possible verbs could be generated to those on which few verbs could be generated, there was activation in left IFG. They attributed this activation to a selection process among semantic alternatives. The more selection that is required among alternatives, the more mechanisms of IFG are recruited to engage in this selection.

Recently, Kan and Thompson-Schill (2004) have cast this selective mechanism in terms of the Biased-Competition model of Desimone and Duncan (1995), and it is this casting that may be relevant to the Recent-Probes task. According to the Biased-Competition model, selection is

mediated by an attentional template that consists of properties relevant to the goal of some task. In the case of the item-recognition task, the template might be the context of the current trial. What are the properties of this context? They might include other items in the target-set (in this case, making this model a list-search model in the sense of Sternberg, 1966), the temporal epoch in which the items occurred, spatial position of the items, semantic representations of the items if they have semantic content, a certain level of familiarity, or some combination of these properties. Whatever the properties, however, the template represents the context of the current trial. When a probe is presented, it is compared with this template. The greater the similarity between the probe's attributes and the template, the greater the bias to classify the probe as a member of the target-set. The competition, then, is between classification as a target or a non-target, and similarity between the probe and template causes bias to classify as a target. This, in turn, causes weight to be placed on this classification and inhibits the classification as a non-target. When the difference in weight between these two classifications reaches some threshold, an explicit response can be selected and emitted.

Let us apply this model first to the presentation of a recent-negative probe. It will elicit activation of attributes associated with it, which will include some familiarity value due to its recent appearance, some association with the previous trial's context, but no association with the present trial's context. While the lack of association with the present context will lead to bias toward a negative classification of the target, the presence of familiarity will compete with this classification if familiarity is one of the attributes on which the classification is based. Eventually, the target may be properly classified because it does not match the template, but the bias toward this correct classification will have competition from the wrong classification caused by the higher familiarity value of this probe compared with a non-recent negative. This competition will result in a longer time for the weight in favor of the negative classification to build up, leading to a longer response than a non-recent negative.

This model also correctly predicts that responses to non-recent positive probes should be faster than responses to non-recent negative probes (e.g. Jonides et al., 1998). This is because positive probes will match the template and lead to faster biasing of a classification than negative probes. What of recent-positive probes? If one of the attributes in the template is a certain level of familiarity, recent-positive probes will have a higher familiarity value than non-recent positive probes, so they will pass this criterion faster. Thus, bias toward a classification as a member of the target-set will happen faster, leading to a faster positive response, which is often found in this paradigm (e.g. Monsell, 1978). (Note also that this model may account for the well-documented effects of serial position on response time in the item-recognition task which show a pronounced recency effect (Monsell, 1978; McElree and Doshier, 1989).) Badre and Wagner (in press) have further shown that recent-positive probes elicit brain activation in

left inferior frontal gyrus. This may be an indication that even though there is no conflict associated with recent positives, they nonetheless require the engagement of the process that assigns bias to one classification or another. So, it may be this biasing process that is the province of the left inferior frontal gyrus.

According to this model, then, the function of the left inferior frontal cortical region that has been documented in the Recent-Probes task is to assign bias to a representation that matches the attentional template and cause this representation to achieve sufficiently high weight to result in a response while at the same time inhibiting other representations that are inappropriate. This sort of biasing mechanism, as Kan and Thompson-Schill (2004) reviewed, was originally proposed to account for attention to perceptual stimuli. We know that attention to the external world is modulated by mechanisms in parietal lobe, especially intraparietal sulcus and superior parietal lobule. So, the fact that activation in this area has been reported for the Recent-Probes task (Mecklinger et al., 2003) is consistent with the application of the Biased-Competition model to working memory representations as well. Moreover, this is consistent with models that assume that biasing signals involve a network of cortical interactions (Hamker, 2005).

This model accounts as well for other facts that we know about the Recent-Probes task, as reviewed above. For example, the fact that the activation in this task appears at the time of presentation of the probe is consistent with the activation of a mechanism that resolves competition between classifications of the probe. Also this biasing mechanism can be extended to any task in which a prior representation competes with the representation needed to make a current response, such as the directed-forgetting task.

What is especially appealing about this Biased-Competition proposal for proactive interference effects is that it applies a model that has proven valuable for perceptual phenomena to memory phenomena. As Kan and Thompson-Schill (2004) realized, the economy in theory that is achieved by using the same model to account for selection in the perceptual and conceptual worlds is valuable. Extending this same model to account for resolution of proactive interference makes it yet more valuable. Of course, in order for the case to be made that the same mechanism is involved in tasks as different as the Verb-Generate task and the Recent-Probes task, one needs to do a fine examination of brain activations in these different task to see whether they truly overlap. Nelson et al. (unpublished observations) have reported one such test. They had the very same participants engage in the Verb-Generate and Recent-Probes tasks, and they examined regions of activation that overlapped for the two. The comparison for the Verb-Generate task was between nouns for which there were relatively many verbs that could be generated and nouns for which there were relatively few verbs. For the Recent-Probes task, the comparison was the standard one: between recent and non-recent negatives. There was overlap in activations between these two tasks in left infe-

rior frontal gyrus, lending credence to the model we have reviewed here.

This model leaves questions unanswered, however. One has to do with activation in left inferior frontal gyrus and response time to recent probes. Recall that the model assigns to left inferior frontal gyrus the task of biasing a probe-classification when a probe matches the attentional template. This should occur for both recent-positives and recent-negatives. Under the assumptions of the model, greater bias should be assigned to recent-positives relative to recent-negatives because the former match the template not only in familiarity but also in contextual information, while the latter match only in familiarity. The prediction might be, then, that activation in left IFG should be larger for recent-positives because of the greater bias assigned. However, Badre and Wagner (in press) have shown that there is greater left inferior frontal gyrus activation for recent-negatives than recent-positives. Possibly this can be resolved if we assume that the greater bias for recent-positives is achieved faster by parallel buildup of information coming from familiarity and contextual sources. This is speculation at this point and warrants further study.

Another critical question left unanswered has to do the precise computations performed by each of the regions that has been associated with interference-resolution in the Recent-Probes task. Take the left inferior frontal gyrus region first. Badre and Wagner (in press) described evidence showing that within the spatial resolution of fMRI, this same region appears to be activated in both the Recent-Probes task and episodic retrieval tasks, and so they sensibly assigned it a role in retrieving episodic context. Nelson et al. (unpublished observations) found that this same region is activated in the Recent-Probes and Verb-Generate tasks, and so they assigned it a role in selection processes. Assuming that both analyses are correct, and we are talking about the same region of cortex, can these two roles be reconciled? Perhaps so. Suppose that the assignment of bias toward a positive or negative classification of the probe in the Recent-Probes task is based largely on establishing a match between the probe and the context of the current trial in the face of competing information from other contexts and from a possibly misleading familiarity value for the probe. Establishing this match would require retrieving features of the context that might be associated with the probe, and this sort of retrieval may be just the same sort recruited in episodic retrieval tasks, as per the analysis of Badre and Wagner (in press). Once again, though, further investigation is needed.

What of activations in other regions that have been documented for interference-resolution in the Recent-Probes task? Three are prominent. One is parietal cortex in the region of the intraparietal sulcus (e.g. Mecklinger et al., 2003). Another is frontopolar cortex (e.g. Badre and Wagner, in press). A third is middle frontal gyrus in the right hemisphere (e.g. Mecklinger et al., 2003). The fact that there are these other regions in play certainly leads to the view that left inferior frontal cortex is not acting alone to resolve interference in this task, but how is the network best characterized? We know something about the func-

tions of these regions in other tasks that may provide clues to their function in this task. Intraparietal sulcus has been suggested as a source of modulation of attention; frontopolar cortex has been suggested as a site of monitoring and goal-evaluation processes; and middle frontal gyrus has been suggested as a site of processes involved in response-selection. All of these processes may be involved in the Recent-Probes task. Attentional modulation signals may be the trigger that activates biasing processes; monitoring of the success of a classification of a probe is needed until a response-decision can be reached; and selection of a response once a classification has been achieved is the end-product of processing. Whether these roles are played out in this task as indicated again requires further study.

Even in the face of these unanswered questions, there does appear to be some movement in understanding the resolution of proactive interference in this task and, by extension, in others as well. We motivated this review with an introduction that stressed the importance of understanding the factors that control the capacity of working memory, and we argued that proactive interference is a powerful such factor. The canonical task used to measure working memory capacity is the working memory span task, in its several variants, and it has been shown that working memory span is importantly influenced by proactive interference. What ties this behavioral research on memory span to the research on brain mechanisms of proactive interference that we have reviewed here is a finding by [Smith et al. \(2001\)](#). They investigated processes of dual-task coordination in the working memory span test. In their experiment, subjects performed operation-span trials that interleaved arithmetic operations with memory for words, a standard implementation of working memory span. Also, these subjects performed the arithmetic task and the word-memory task individually. [Smith et al. \(2001\)](#) compared brain activations due to the operation-span task with each of the component tasks alone. One very prominent site of activations for the dual versus single-task contrast was in left lateral frontal cortex, including the very same inferior frontal region on which we have concentrated our review. Since performance in the operation-span task requires the resolution of interference from competing tasks, the left inferior frontal gyrus may be resolving interference in the operation-span task. Therefore, the work of [Smith et al. \(2001\)](#) shows us that there may be a tight tie between measured capacity and resolution of proactive interference.

How might capacity and proactive interference be related? One proposal is that what appears to be reduced working memory capacity actually results from proactive interference due to retrieval competition ([Anderson and Neely, 1996](#)). In other words, measured capacity depends on how many items can be retrieved, and proactive interference affects measured capacity by making retrieval more difficult. Indeed, the model we have favored directly embodies this claim: Left inferior frontal gyrus activation mediates context-retrieval which is used in an attempt to overcome increased retrieval competition. Given the dem-

onstrated centrality of working memory capacity as a predictor of other cognitive skills, it therefore appears worth the effort to continue to understand the mechanisms involved in the resolution of proactive interference.

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