On the Tip of the Tongue: An Event-Related fMRI Study of Semantic Retrieval Failure and Cognitive Conflict

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Summary

The tip of the tongue (TOT) state refers to a temporary inaccessibility of information that one is sure exists in long-term memory and is on the verge of recovering. Using event-related fMRI, we assessed the neural correlates of this semantic retrieval failure to determine whether the anterior cingulate-lateral prefrontal neural circuit posited to mediate conflict resolution is engaged during metacognitive conflicts that arise during the TOT. Results revealed that, relative to successful retrieval or unsuccessful retrieval not accompanied by a TOT, retrieval failures accompanied by TOTs elicited a selective response in anterior cingulate-prefrontal cortices. During a TOT, cognitive control mechanisms may be recruited in attempts to resolve the conflict and retrieval failure that characterize this state.

Introduction

Memory is prone to various kinds of forgetting and distortion. One common type of memory failure is known as blocking (Schacter, 1999, 2001): a temporary inability to gain access to information that is stored in memory and that can be retrieved at a later time. Perhaps the most extensively studied form of retrieval blocking is the "tip of the tongue" (TOT) state (Brown and McNeill, 1966). In a TOT state, people are unable to retrieve a particular bit of information, but at the same time have a strong subjective conviction that they know the item and are on the verge of producing it. The great psychologist William James (1893, p. 251) provided an eloquent characterization of the TOT state:

"Suppose we try to recall a forgotten name. The state of our consciousness is peculiar. There is a gap therein; but no mere gap. It is a gap that is intensely active. A sort of wraith of the name is in it, beckoning us in a given direction, making us at moments tingle with the sense of our closeness and then letting us sink back without the longed-for term. If wrong names are proposed to us, this singularly definite gap acts immediately as to negate them. They do not fit into its mold."

In a classic early study, Brown and McNeill (1966) induced TOT states by providing subjects with definitions of rare words (e.g., *zither*), and instructing them that "If you are unable to think of the word but feel sure that you know it and that you feel that it is on the verge of coming back to you then you are in a TOT state (p. 327)". They found that subjects reported TOT states for approximately 13% of the rare word definitions.

Numerous subsequent behavioral studies have replicated, extended, and refined Brown and McNeill's (1966) classic results (for review, see Brown, 1991; Schwartz, 1999). These studies have revealed that during TOT states, subjects have access to a variety of different kinds of information about items they cannot retrieve, including initial and later letters of the word (Koriat and Leiblich, 1977), number of syllables and syllabic stress (Rubin, 1975), syntactic properties of a word (Miozzo and Caramazza, 1997; Vigliocco et al., 1997), and similar words that are related in sound or meaning (Cohen and Faulkner, 1986; Reason and Lucas, 1984).

Although a good deal is known about the cognitive properties of TOT states, the neural systems underlying TOT remain unexplored. In the context of semantic retrieval, information obtained about brain activation during TOT, compared with successful retrieval or unsuccessful retrieval that is not accompanied by TOT, would indicate what brain regions are involved in this unique metacognitive state, above and beyond those that are typically observed during semantic retrieval tasks (e.g., Poldrack et al., 1999; Fiez, 1997; Petersen et al., 1988; Price et al., 1997).

Equally important, the TOT state is of theoretical interest because it provides a window on issues related to studying cognitive control and conflict. Cognitive conflict occurs in a variety of situations. For example, when writing checks in January, many people write the previous year as the date, even though if explicitly asked, they would state the correct year. Writing the correct year may require mechanisms that permit the detection and override of prepotent habitual responses; processes that also may be required in the extensively studied Stroop experimental paradigm (Stroop, 1935). In this paradigm, subjects are shown color words such as "red" printed in a conflicting color (e.g., blue) and are asked to name the color of the word. In order to respond correctly, they have to overcome the prepotent tendency to name the word. Another instance of conflict arises when attempting to understand sentences that present semantic conflict, such as Groucho Marx's "time flies like an arrow but fruit flies like a banana." That is, the same ambiguous words are used in both parts of the sentence (flies, like), but having initially established one meaning, it must be overcome in order to assign the alternative, correct meaning during the latter occurrences of the words. In each of these examples, a conflict is created by the existence of competing responses—a correct response and an incorrect but prepotent and more readily accessible response.

Resolving cognitive conflict requires a system that can detect the conflict and manage it for the purpose of executing an eventual response that accords with

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one's intentions. During the past decade, considerable effort has been invested in attempting to identify the neural systems and computations responsible for detection and resolution of conflict. These efforts have primarily explored conflict within the context of the Stroop paradigm (e.g., Pardo et al., 1990; MacDonald et al., 2000; Bush et al., 1998) or of experimentally manipulated situations that yield increased response competition (e.g., Corbetta et al., 1991; Carter et al., 1998; Barch et al., 2000). Such studies have provided evidence for the involvement of anterior cingulate and lateral prefrontal cortices in the detection and monitoring of cognitive conflict and in implementation of cognitive control (e.g., MacDonald et al., 2000).

In the present study, we exploited the naturally occurring conflict that accompanies the unique TOT state during retrieval failure from semantic memory in order to examine two central questions regarding the nature of conflict detection and memory monitoring.

First, the TOT represents a conflict between the metacognitive level—a person's confidence in the existence of knowledge—and the cognitive level—his or her actual inability to retrieve the target knowledge. Do the mechanisms supported by anterior cingulate cortex (ACC) that participate in conflict detection mediate monitoring of the metacognitive conflict that characterizes the TOT state?

Second, the behavioral manifestations of TOT described earlier suggest that this retrieval state might be expected to engage the left inferior prefrontal cortex, a common component of the circuitry supporting semantic retrieval (e.g., Petersen et al., 1988; Gabrieli et al., 1996; Wagner et al., 1997; Poldrack et al., 1999). In addition, the TOT state should also engage the right dorsolateral prefrontal region—a common component of the circuitry supporting retrieval monitoring (e.g., Henson et al., 1999a, 1999b). In light of the wealth of partial information that is retrieved during a TOT state, subjects must actively monitor the status of this information or similar targets for relevance and correctness. Moreover, subjects must also assess whether such information is leading to target retrieval, or whether it is an "interloper" or "blocker" that is interfering with target recovery (Reason and Lucas, 1984; Jones and Langford, 1987), which creates further conflict. Evaluation of these conflicting possibilities is predicted to engage the right dorsolateral prefrontal cortex.

Note, however, that engagement of right dorsolateral prefrontal retrieval monitoring processes has been observed during attempts to retrieve from episodic memory (e.g., Tulving et al., 1994; Rugg et al., 1996; Schacter et al., 1997; Wagner et al., 1998; Henson et al., 2000; I.G. Dobbins et al., submitted) but not during attempts to retrieve from semantic memory (e.g., Petersen et al., 1988; Kapur et al., 1994; Fiez, 1997; Wagner, 1999; Thompson-Schill et al., 1997). Thus, a further question can be addressed by using fMRI to study the TOT: are right dorsolateral prefrontal monitoring processes restricted to the monitoring of episodic knowledge, or do these processes reflect more general evaluative mechanisms that monitor the goal relevance of recovered knowledge irrespective of whether this knowledge is episodic or semantic? The TOT state permits consideration of this question because the evidence suggests

that monitoring processes that are associated with the right dorsolateral prefrontal region, at least within the context of episodic retrieval, are more likely to be engaged during unsuccessful compared with successful retrieval (e.g., Henson et al., 1999a, 2000).

In the present experiment, we used event-related fMRI to examine which brain regions are involved in the detection and management of the conflict associated with TOT during attempts to retrieve from semantic memory. In particular, such TOT conflicts were compared with relatively conflict-free retrieval states, such as when a person successfully retrieves knowledge from semantic memory or simply does not know the relevant information probed during retrieval. We developed a behavioral paradigm that elicits TOT states with a frequency comparable to that reported in previous literature. Subjects were presented with pairs of semantic cues (e.g., Chinatown + director; Iraq + capital) that converged on a target (e.g., Roman Polanski; Baghdad). Most of the target items were proper names (people or places), because proper names are frequently associated with TOT states (Brown, 1991). During scanning, subjects were given four seconds to indicate whether they knew the target, did not know the target, or experienced a TOT. We then conducted event-related fMRI analyses to examine neural activity during the TOT state compared to the "know" and "don't know" conditions. To the extent that retrieval failures accompanied by TOTs entail conflict and retrieval monitoring that are mediated by general mechanisms, we anticipated that the neural signature of the TOT would include increased activation in ACC and right dorsolateral prefrontal regions associated with cognitive and mnemonic control (Cohen et al., 2000; MacDonald et al., 2000).

Results

Subjects were scanned while responding to each of 414 general knowledge questions. Depending on each subject's responses, trials were sorted into three response-based bins: know (K), don't know (DK), and tip of the tongue (TOT). The mean percent (SEM percent) of K trials was 39.9% (0.08%); of DK trials, 51.6% (0.10%); and of TOT trials, 9.25% (0.02%). On a postscanning verification test (see Experimental Procedures), 93% of all responses were verified. Mean (SEM) median reaction times differed across conditions [K, 1835 (66); DK, 2159 (124); TOT, 2942 (127) ms, $F_{(2,39)} = 38.2, p < 0.0001$]. Planned contrasts revealed that while the response time (RT) difference between K and DK trials was significant [$F_{(1,13)} = 6.2, p = 0.02$], this difference was relatively modest compared with the marked RT difference between these trials and TOT trials [DK, $F_{(1,13)} = 36.2, p < 0.0001$; K, $F_{(1,13)} = 72.4, p < 0.0001$].

The fMRI data were analyzed to assess activation associated with performance of the semantic retrieval task, as well as to assess how this activation differed depending on the outcome of the retrieval attempt (K, DK, and TOT). Performance of the semantic retrieval task, as reflected in the comparison of all retrieval conditions to baseline, elicited activation in numerous brain regions, including regions in left prefrontal, left parietal, and bilateral occipital cortices. These regions generally
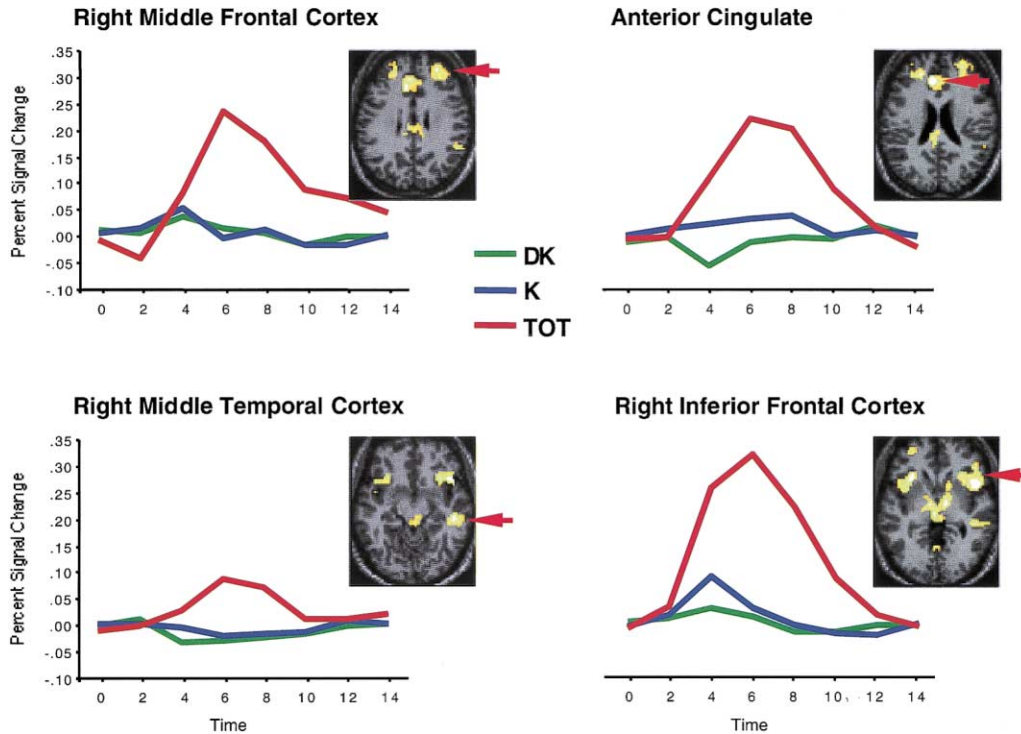
Figure 1. Four Regions Demonstrated a TOT-Selective Response

Displayed are axial sections through each region that demonstrated a TOT-selective response and averaged event-related responses associated with each retrieval outcome. Activation was significantly above baseline only during the TOT state in right middle frontal cortex (BA 9; 30, 51, 27), anterior cingulate cortex (BA 32/24; −6, 39, 21), right middle temporal cortex (BA 21; 51, −24, −12), and right inferior frontal cortex (BA 44/45; 51, 15, −3). DK, don't know; K, know; TOT, tip of the tongue.

converge with prior neuroimaging studies of semantic retrieval (e.g., Petersen et al., 1988; Gabrieli et al., 1996; Wagner et al., 1998).

Direct contrasts between K, DK, and TOT retrieval outcomes revealed regions that were differentially engaged depending on the subject's retrieval state. In particular, and consistent with our hypotheses, TOT trials were accompanied by a significantly greater activation in right middle frontal (Brodmann's area [BA] 9) and anterior cingulate (BA 32/24) cortices (Figure 1). Both voxel-based and ROI analyses revealed that activation in each of these regions was significantly greater during TOT trials relative to the K and the DK trials. In contrast, there was no difference between the magnitude of activation during K and DK trials, and neither of these trial types elicited above-baseline activation. A similar pattern of activation was also observed in two additional regions, the right inferior frontal (BA 44/45), and the right middle temporal (BA 21).

One interpretation of the response in these TOT-selective regions is that it marks the recruitment of processes that are specifically demanded when retrieval elicits a TOT state. However, given that the response latencies were longer during TOT trials, an alternative interpretation is that these regions mediate more general retrieval processes that are differentially recruited depending on the degree of effort expended during a retrieval attempt, as indicated by time-on-task. The observation that activation in these regions was not above baseline during the K and DK trials would appear to argue against a

general effort interpretation. However, to further examine the possibility that the activation observed in these TOT-selective regions merely reflects time-on-task, K, DK, and TOT trials were median-split into long and short K, DK, and TOT trials. This analysis allowed us to compare response latencies for TOT trials with the upper RT range of both K and DK trials; it also allowed us to compare latencies for long versus short K trials and for long versus short DK trials.

The first median-split analysis revealed the same TOT-selective pattern in all four regions, specifically, long K and long DK trials activated each region to a significantly lesser extent than did TOT trials (Figure 2). Moreover, TOT-related activation was even observed when we performed a median split on TOT trials, and compared the short TOT trials with long K and DK trials. This analysis yielded TOT-specific effects in the anterior cingulate and right middle frontal cortices (as well as in the right inferior frontal region), but it did not yield significant effects in the right middle temporal region. This latter finding raises the possibility that the right middle temporal activation is associated with general retrieval effort, rather than with processes specific to the TOT; hence, we must view this activation with caution.

Although the magnitude of activation in the TOT-selective regions did not track retrieval effort (as reflected by RT), the median split analysis permitted assessment of whether other regions were sensitive to retrieval effort. Activation in two of the regions that were engaged during performance of the semantic retrieval
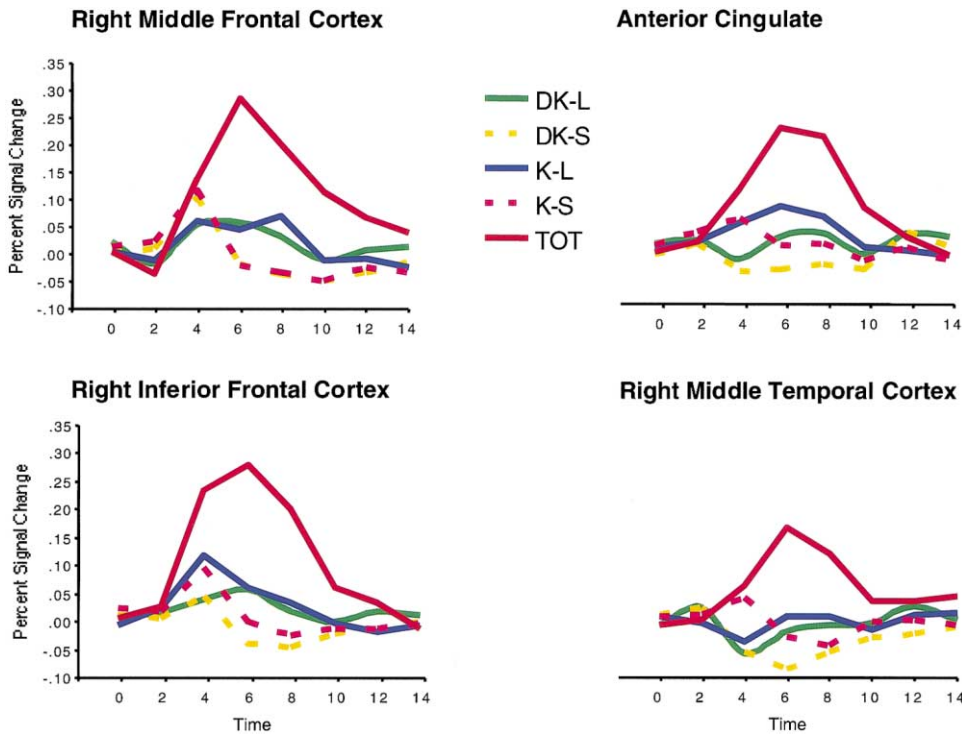
Right Middle Frontal Cortex

Anterior Cingulate

Right Inferior Frontal Cortex

Right Middle Temporal Cortex

Figure 2. Averaged Event-Related Responses in TOT-Selective Regions, with Know and Don't Know Trials Median Split by RT

For all regions, a greater response was observed during TOT trials relative to the long and the short response latency know and don't know trials. DK-L, long don't know; DK-S, short don't know; K-L, long know; K-S, short know; TOT, tip of the tongue.

task—left middle (BA 46/9) and left inferior (BA 44/45) prefrontal cortices—was modulated by retrieval effort (Figure 3). Left inferior prefrontal cortices have been previously implicated in performance of semantic processing tasks (Fiez, 1997; Poldrack et al., 1999). Although prior evidence indicates that activation in left inferior prefrontal cortices does not simply track with task difficulty (Demb et al., 1995), recent findings indicate that these regions mediate controlled semantic retrieval processes (Wagner et al., 2001). The present finding that activation in these regions covaries with increased effort suggests that demands on such controlled retrieval processes increased from the DK to the K to the TOT trials.

Finally, a success-related pattern—greater activation during both long and short K trials compared to DK and TOT trials—was observed in the inferior occipito-temporal cortex (BA 37/19) (Figure 3).

Discussion

The objective of the present study was to investigate the brain regions recruited for conflict detection and retrieval monitoring by examining the unique retrieval failure accompanied by a TOT state. Consistent with our predictions, the TOT state was associated with selective activation in anterior cingulate and right middle frontal regions. These activations did not appear to reflect increasing retrieval effort because they did not track across-condition differences in retrieval times. Rather, TOT-related activation in these regions suggests that

these structures mediate retrieval processes that are recruited when retrieval fails but is associated with a sense of impending success. While retrieval failures accompanied by TOT likely involve a number of processes, our discussion will focus on the predicted role of the anterior cingulate and lateral prefrontal cortices in this retrieval state.

Anterior Cingulate and Right Middle Frontal Cortices

The anterior cingulate cortex (ACC) and prefrontal cortex (PFC) have been posited as two components of a cognitive control system (Cohen et al., 2000; MacDonald et al., 2000). It has been hypothesized that the ACC contributes to cognitive control through conflict monitoring and subsequent facilitation of PFC function (Cohen et al., 2000; MacDonald et al., 2000). Consistent with this hypothesis, a recent fMRI study revealed increased ACC activation during error trials (compared to correct trials), and during correct trials that were accompanied by high levels of response competition (Carter et al., 1998). This latter outcome suggests that ACC does not mediate error detection per se. Rather, ACC appears to detect processing situations that include response or representational conflict. Further support for this framework is found within the context of the verb-generation paradigm, where subjects generate a verb in response to a given noun (Petersen et al., 1988). Notably, when generating a verb for a noun that has many associated verbs—an increased competition condition—ACC activation increases relative to generating a verb for a noun
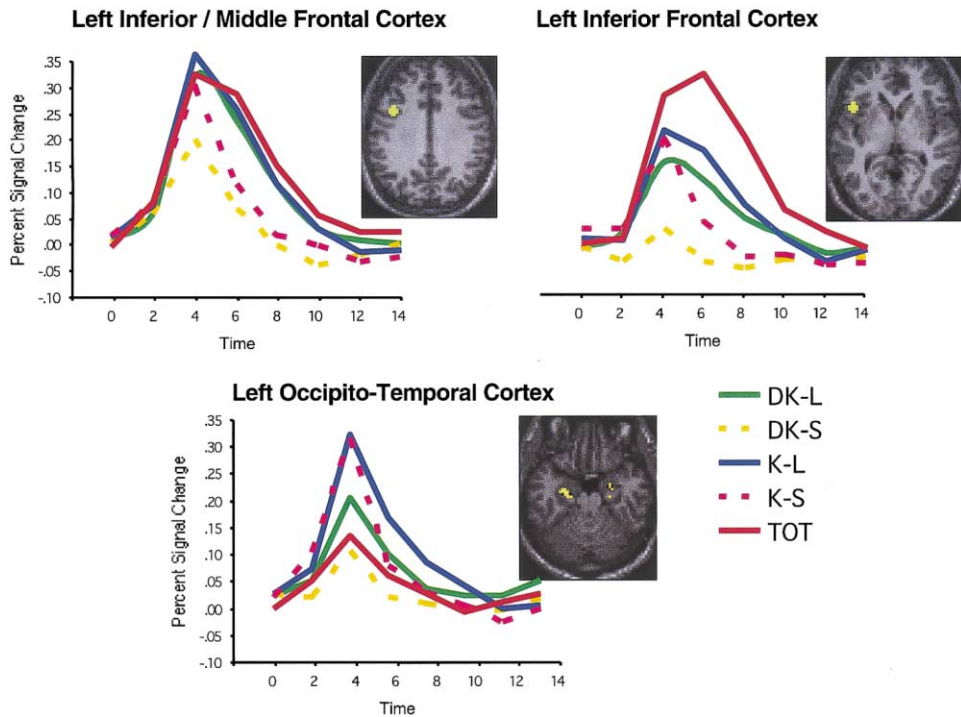
Left Inferior / Middle Frontal Cortex

Left Inferior Frontal Cortex

Left Occipito-Temporal Cortex

DK-L
DK-S
K-L
K-S
TOT

Figure 3. Effects of Retrieval Effort and Retrieval Success Were Observed in Frontal and Inferior Temporal Cortices

Displayed are functionally defined ROIs and the resultant averaged event-related responses. The extent of activation in left inferior/middle frontal (BA 46/9; −42, 12, 31) and left inferior frontal (BA 44/45; −48, 18, 0) cortices covaried with retrieval effort, as indexed by RT. In contrast, left occipito-temporal cortex (BA 37/19; −51, −51, −24) demonstrated greater activation during trials accompanied by successful knowledge recovery.

that has a single dominant verb (Barch et al., 2000). ACC activity may reflect the engagement of a conflict monitoring process elicited when multiple responses are activated during retrieval.

A possible concern in this study is that the ACC activation associated with TOT trials may reflect the difficulty of the response decision rather than the experience of TOT, because the TOT decision is presumably less unequivocal than K and DK decisions. It is inherently difficult to distinguish between making a response and the experience that precipitated it in event-related fMRI studies such as the present experiment, where trials are sorted based on subjects' responses. However, while the decision for K trials is guided by successfully retrieved information and, thus, is probably less difficult than the TOT decision, decisions for long DK trials may be more similar to decisions for TOT trials. In both TOT and long DK trials, retrieval is unsuccessful, subjects are nonetheless motivated to continue with an extended search, and the search concludes without an unequivocal answer. Despite these similarities, we observed greater ACC and right prefrontal activation during TOT than in long DK trials. These considerations do not definitely rule out the possibility that the TOT decision is more difficult or equivocal than the long DK decision. However, they also do not encourage the idea that the distinctive neural correlates of TOT in our study simply reflect the greater difficulty of the TOT decision.

Right dorsolateral PFC activation has been previously observed in studies of episodic retrieval (e.g., Schacter

et al., 1997; McIntosh et al., 1997; Wagner et al., 1998). Recent fMRI data suggest that activation in this region is modulated by demands on postretrieval monitoring operations (Henson et al., 1999a, 1999b), consistent with prior suggestions (Schacter et al., 1997; Rugg et al., 1996). In one study, fMRI conducted during an episodic recognition test revealed that memory based on familiarity without recollection of specific episodic details ("knowing") was associated with increased activation in right dorsolateral PFC compared to memory based on recollection of specific details ("remembering") and "miss" trials (Henson et al., 1999a). A subsequent study of the effects of retrieval confidence provided further evidence for the centrality of right PFC in the "working with" or monitoring of retrieval products (Henson et al., 2000). In that study, greater right dorsolateral PFC activation was observed during recognition judgments accompanied by low confidence compared to those accompanied by high confidence; this effect of confidence was observed for both hits and correct rejections. Thus, increased activation in right dorsolateral PFC may reflect a higher demand on retrieval monitoring operations when retrieval results in a sense of familiarity in the absence of full recovery of target information.

Other fMRI and electrophysiological data suggest that the two components of the ACC-PFC cognitive control circuit interact during, and make unique contributions to, control. For example, within the context of a modified Stroop paradigm, dorsolateral PFC—but not ACC—activation was associated with delay period activity,

suggesting that dorsolateral PFC represents the target goal or context state (MacDonald et al., 2000). In contrast, ACC—but not PFC—activation was greater during Stroop incongruent (conflict) trials relative to congruent trials (MacDonald et al., 2000; Pardo et al., 1990). These data suggest that dorsolateral PFC and ACC are complementary components of a cognitive control network. Moreover, electrophysiological data suggest that the intact functioning of this network depends on interactions between the two components. For example, patients with PFC lesions failed to demonstrate the standard error-related negativity (ERN) that is thought to derive from the ACC (Gehring and Knight, 2000). The diminished ERN following frontal insult suggests that PFC and ACC may interact when cognitive control requires conflict detection.

The present finding of selectively increased activation in ACC and right PFC during TOT trials is consistent with the hypothesized ACC-PFC cognitive control circuit, indicating that engagement of this circuit occurs during attempts to resolve conflict within semantic memory. Moreover, these data provide the first window on the neuroanatomical correlates of the TOT retrieval state. Extensive behavioral research has shown that TOT states are marked by recovery of partial information from long-term memory (Brown and McNeill, 1966; Schwartz, 1999). This recovery may lead to a strong sense of familiarity about a nonretrieved target. At the same time, however, the partially retrieved knowledge often does not give rise to a coherent body of information converging on the sought after target, thus resulting in retrieval failure. It has been hypothesized that some of the recovered partial information may be related to the target in ways that are even detrimental to the attempt to recover target knowledge, such as competing items that resemble the target phonologically or semantically (Reason and Lucas, 1984; Jones and Langford, 1987). Thus, the recovered partial information may not be sufficiently specific to permit recovery of the sought after target from long-term memory, and could give rise to conflict or competition during attempts to resolve the TOT.

For example, given the cue "Aida + Composer," subjects may recover the first letter of the last name, V, as well as the semantic knowledge that the composer is Italian. These recovered items, however, may not be specific enough to enable the recovery of Verdi and may bring to mind another conflicting answer that is consistent with both—for example, Vivaldi. Not every TOT trial necessarily produces a full competing alternative. Sounds, such as /v/, the feeling that the name is short and ends with an /i/ sound, or the high level of familiarity produced by retrieval of partial knowledge all constitute products that a control system could work with by evaluating accuracy and relevance, suppressing items identified as hindering search, and using those identified as relevant to guide further retrieval attempts. Our data indicate that the ACC-PFC control network postulated above is likely to be involved in guiding these processes. Although speculative, differential activation of these regions may be associated with differential probabilities of resolving the TOT state; future research could explore this possibility.

Our results may also have implications for understanding the nature of age-related differences in the TOT state (Cohen and Faulkner, 1986; Burke et al., 1991). While the TOT state in younger adults is typically accompanied by activation of partial information in the process of searching for the inaccessible target, as stated earlier, older adults more often describe their TOT state as "drawing a blank" (Burke et al., 1991; Cohen and Faulkner, 1986), that is, they portray a retrieval state that is not typically accompanied by the recovery of partial information. Thus, the TOT state in older adults might not engage the processes recruited for conflict detection and retrieval monitoring, or at least not to the same extent that younger adults do. Based on our results, we would expect that during TOT states older adults, when compared to younger adults, will show less evidence of activation in the ACC and right PFC regions.

Right Inferior Frontal Cortex

TOT-selective activation in the right inferior frontal region raises the possibility that when trying to resolve TOTs, subjects adopt a strategy that relies heavily on visuo-spatial information (see Awh and Jonides, 1998, and Wagner, 1999, for discussion of evidence relating memory for visuo-spatial information to right inferior frontal activation). Though we did not systematically collect data regarding the strategy used by subjects when in a TOT state, informal observations suggest that, when confronted with a TOT, subjects may rely on visual imagery in attempts to recover the target knowledge. For example, some subjects noted that they tried to "keep looking" at the face of the person whose name escaped them, or that they attempted to "read" the name of an author from an imagined book cover. To the extent that the subjects in our fMRI study used a visual imagery strategy when in a TOT condition, the activation observed in right inferior PFC could constitute the neural correlates of these efforts to resolve these retrieval failures.

In summary, although the TOT state has been characterized behaviorally in numerous studies, our results provide evidence of neural computations that are specifically associated with the occurrence of a TOT. Increased activation in ACC and PFC associated with TOT trials fits well with prior behavioral studies of the TOT state, which suggest that subjects need to actively monitor many different kinds of information that come to mind during a TOT, including conflicting knowledge. The engagement of the ACC-PFC control circuit may represent, at the neural level, evidence of the cognitive struggle that accompanies the "intensely active gap" that William James (1890) described over a century ago.

Experimental Procedures

Subjects
Participants were 14 right-handed, native speakers of English (nine men, ages 19–27 years), with normal or corrected-to-normal vision. Participants received $50 for participation. Data from four additional participants were excluded due to poor task performance. Informed consent was obtained in a manner approved by the Human Studies Committee of the Massachusetts General Hospital.

Stimuli and Behavioral Task
Across six scans, 414 two-part general knowledge questions cued retrieval. Each question was presented for 3 s, followed by 1 s of visual fixation. Additional periods of baseline fixation lasting be-

tween 2 and 8 s were interspersed between the experimental trials to optimize the efficiency of the design matrix (Dale, 1999). For experimental trials, subjects responded to each trial by pressing one of three response keys to indicate their retrieval outcome—successful retrieval ("know"), unsuccessful retrieval not accompanied by a TOT ("don't know"), or unsuccessful retrieval accompanied by a TOT ("TOT"). Prior to the experiment, detailed instructions aimed to clarify what constitutes a TOT state. Subjects were instructed to avoid responding TOT in cases in which they felt they *should* know the answer but were unable to retrieve it. In addition, they were asked not to be misled by the familiarity of the questions and to indicate a TOT only when they were absolutely sure that they knew the specific answer and felt that they were on the verge of recovering this knowledge. Moreover, they were instructed not to respond TOT for cases in which they think they knew the answer, but were unsure it was the correct one.

To verify (albeit indirectly) the responses that subjects provided during scanning, all questions were subsequently re-presented outside of the scanner. During this verification test, subjects provided a written answer to each item, responding "don't know" or "TOT" if that was still applicable, or providing the answer if they knew it.

Functional Imaging

A 1.5 T Siemens Sonata system was used to acquire high-resolution T1-weighted anatomical images (MP-RAGE), and T2*-weighted gradient-echo echo-planar functional images (TR = 2000 ms, TE = 40 ms, 21 axial slices aligned parallel to the AC-PC plane, 5 mm thickness, 1 mm interslice skip, 200 mm FOV, 64 × 64 matrix, 198 volume acquisitions per run). Four additional volumes were collected and discarded at the beginning of each run to allow for T1 equilibration. A bite bar was used to minimize head motion.

Data Analysis

Data were preprocessed using SPM99 (Wellcome Department of Cognitive Neurology, London). Images were first corrected for differences in slice acquisition timing by resampling all slices in time to match the first slice, followed by motion correction across all six runs (using sinc interpolation). Data were then spatially normalized to an EPI template based upon the MNI305 stereotactic space (Cocosco et al., 1997). Images were resampled into 3 mm cubic voxels and then spatially smoothed with an 8 mm FWHM isotropic Gaussian kernel.

Statistical analysis was performed using the general linear model in SPM99. K, DK, and TOT trials were modeled using a canonical hemodynamic response. These effects were estimated using a subject-specific fixed-effects model, with session-specific effects and low-frequency signal components treated as confounds. Linear contrasts were used to obtain subject-specific estimates for each of the effects of interest. These estimates were entered into a second-level analysis treating subjects as a random effect, using a one-sample Student's t test against a contrast value of zero at each voxel. Statistical parametric maps were created for each contrast of interest, and were subsequently characterized using the theory of Gaussian random fields in order to obtain corrected p values for the entire imaged volume (p < 0.05, clusters of at least 5 voxels). To further explore the nature of activation associated with each retrieval outcome, regions of interest (ROIs) were identified from clusters that survived the thresholding criteria. The hemodynamic responses were extracted from each ROI on a subject-by-subject basis and were subjected to subsequent repeated measures analyses that included factors for condition (K, DK, and TOT; or long K, long DK, short K, short DK, and TOT) and peristimulus time (0–14 s).

Acknowledgments

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