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Semantic Retrieval, Mnemonic Control, and Prefrontal Cortex

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Accessing stored knowledge is a fundamental function of the cognitive and neural architectures of memory. Here, the authors review evidence from cognitive-behavioral paradigms, neuropsychological studies of patients with focal neural insult, and functional brain imaging concerning the mechanisms underlying retrieval of semantic knowledge and their association with prefrontal cortex. First, the authors examine behavioral and neuropsychological evidence distinguishing between controlled and automatic semantic retrieval. Then the authors review the subregions of prefrontal cortex that functional neuroimaging has associated with semantic retrieval across a range of memory demanding tasks. Finally, two hypotheses concerning the nature of processing in these brain regions—the controlled semantic retrieval and selection hypotheses—are critically examined, and a possible synthesis is proposed.

Key Words: semantic memory, controlled retrieval, cognitive control, executive function, frontal cortex, PFC

Recovering meaning about the world in a context-relevant manner is critical to cognition. It allows us to flexibly access information about concepts and objects to comprehend inputs and generate responses. Consider, for example, that you want to pound in a nail without the benefit of a hammer. You might have other objects at your disposal, such as a hardback book. Information strongly associated with the concept of *book*, such as how books can be used as a reference, would probably not help in the current context. However, we are capable of accessing other features of a book when context demands, such as that it is heavy, fairly wieldy, and rather suitable as a hammer. The ability to comprehend stimuli requires a system that can guide access to relevant knowledge in cases when strongly associated semantic infor-

mation is insufficient or is not present to meet task demands. Hence, a mechanism is required that can represent the task context or goal and can enact strategic, controlled semantic retrieval.

Prefrontal cortex (PFC) is a critical component of the neural architecture underlying cognitive control (Miller & Cohen, 2001; Stuss & Benson, 1986), including the control of memory (Fuster, 1997; Goldman-Rakic, 1987; Shimamura, 1995; Wagner, 2002). Models of cognitive and mnemonic control conceptualize PFC functions as top-down bias mechanisms that facilitate the processing of task-relevant representations that do not readily come to mind, thereby favoring relevant representations even in the presence of prepotent, irrelevant codes (Cohen & Servan-Schreiber, 1992; Dehaene & Changeux, 1992; Desimone & Duncan, 1995; Miller & Cohen, 2001). Extant data indicate that the representation of task context and biasing of goal-relevant information from semantic memory partially depends on left ventrolateral PFC. However, at present, there is little agreement about the nature of this semantic control process, its configuration in PFC, or the parameters that govern its operation.

In this review, the processes guiding semantic retrieval and their neural underpinnings in PFC are considered. First, we review the cognitive behavioral literature distinguishing between two routes by which meaning can be recovered: (a) automatic semantic retrieval

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and (b) controlled semantic retrieval. Then, we briefly consider neuropsychological evidence regarding controlled and automatic semantic retrieval in the brain. Subsequently, we review neuroimaging evidence implicating left ventrolateral PFC in tasks involving semantic processing and further discuss evidence for functional segregation within this broader neural region. Finally, having established some of the operating principles of semantic retrieval and their basic association with ventrolateral PFC, we critically examine two theoretical perspectives on the type of control operations subserved by ventrolateral PFC—controlled semantic retrieval and selection—and advance a possible synthesis of apparently conflicting results.

ROUTES TO RECOVERING MEANING

Throughout a lifetime, humans encode and retain a tremendous amount of general knowledge about the world. This general knowledge—*semantic memory*—includes long-term memory for facts, concepts, and information about objects, as well as knowledge of words and their meanings (Tulving, 1972). Semantic memory is a form of declarative or explicit memory, as we are consciously aware of and can declare this knowledge. In contrast to episodic memory—another form of declarative memory that supports the conscious remembrance of our personal everyday experiences—semantic memory is detached from a specific learning context (Gabrieli, 1998; Schacter, Wagner, & Buckner, 2000; Squire, 1987). To be useful, semantic knowledge must be readily accessible and sufficiently abstracted such that it can be flexibly retrieved in a variety of contexts.

A discussion of the neurocognitive structure of semantic knowledge is beyond the scope of this review (for discussion, see Damasio, 1990; Martin & Chao, 2001), and we will remain relatively theory-neutral regarding its specifics. However, there are a few characteristics of semantic representations that bear on the processes that access those representations. First, semantic knowledge is stored in a distributed, associative network that links conceptual representations and components of representations. Second, the associations between representations have variable strengths depending on their frequency of prior co-occurrence, their overlap in features, and/or their categorical relationship. Third, multiple representations can compete for processing through mutually inhibitory interactions.

As the context demands, relevant knowledge must be retrieved from this associative semantic structure. The processes guiding retrieval can take two basic forms that reflect the extremes of a continuum. *Automatic semantic retrieval* occurs when the associations between the

retrieval cues and relevant knowledge are strong enough that bottom-up activation of the target representations is sufficient to result in recovery of the relevant knowledge. Hence, when a cue is presented and its representation in long-term memory is activated, other associated representations may become active, either due to the strength of prior pairing with the cue or due to the degree of overlap between the features in the two representations. Such spreading activation occurs relatively automatically and outside of volitional control. Hence, automatic semantic retrieval (a) occurs rapidly, (b) is obligatory and impervious to conscious control, and (c) is context independent, thus yielding retrieval of associated knowledge irrespective of whether it is task-relevant or irrelevant (Carr, 1992; Neely, 1991).

By contrast, *controlled semantic retrieval* occurs when representations brought online through automatic means are insufficient to meet task demands or when some prior expectancy biases activation of certain conceptual representations. Hence, controlled semantic retrieval may depend on a top-down bias mechanism that has a representation of the task context, either in the form of a task goal or some expectancy and that facilitates processing of task-relevant information when that information is not available through more automatic means (Neely, 1991). Relative to automatic semantic retrieval, controlled semantic retrieval (a) is slower and more effortful, (b) can bias retrieval of task-relevant information even in the face of stronger, prepotent task-irrelevant representations, and (c) can either directly or indirectly inhibit the retrieval of prepotent, task-irrelevant information.

Automatic Semantic Retrieval

Behavioral evidence for cue-driven automatic activation of semantic representations has been obtained from a number of paradigms, including the lexical decision task (LDT) (Meyer & Schvaneveldt, 1971; Neely, 1991). In the normative variant of the LDT, an initial prime word is presented and is followed by a target word to which the participant makes a word/nonword decision. Typically, the response time (RT) to verify the target as a word is shorter when the target is semantically related to the prime than when it is unrelated (Neely, 1991). This semantic priming effect presumably emerges because the related prime activates the associated target representation in memory, thus facilitating its recovery. This facilitated access could be due to a close semantic relationship within conceptual space or strong lexeme-to-lexeme associations.

The strength of association between two representations in semantic memory affects the degree of automatic semantic retrieval as evidenced by the magnitude

of semantic priming. The strength of association between two concepts is often determined by free association norms. Estimates of associative strength derived from free association norms are a better predictor of the time to verify the conceptual accuracy of a sentence (e.g., “a robin is a bird”) than are other estimates such as hierarchic organization (Conrad, 1972). With respect to semantic priming on the LDT, the stronger the association between prime and target, the greater the magnitude of priming (McNamara, 1992; Moss, Ostrin, Tyler, & Marslen-Wilson, 1995).

Automatic retrieval emerges outside of conscious control, as evidenced by its being impervious to context manipulations that influence expectancy and thus controlled processing. For example, in an LDT manipulation (Favreau & Segalowitz, 1983; Neely, 1977), participants were instructed that some category primes (e.g., BIRD) were “category nonshift primes” in that the target following that prime (e.g., “robin”) would come from the same category as the prime. By contrast, other primes (e.g., BODY) were “category shift primes” in that the target that would follow these primes (e.g., “house”) would come from a predictable other category (e.g., BUILDING). Given this structure, the expectancy when primed with a category shift prime would be the predictable other category; this expectancy could elicit context-aware control processes that favor task-relevant representations associated with the predictable category rather than the potentiated, but task-irrelevant, representations associated with the presented category. However, when a target was presented shortly after the prime, comparable facilitation on the LDT was observed for prime-related targets in the shift- and nonshift conditions. Furthermore, targets unrelated to the prime were not facilitated, even if the target was from the task-relevant shift category. Hence, with a short interval between prime and target, expectancies that emerge from the context have little effect on what is automatically accessed.

The rapid nature of cue-driven automatic activation was further demonstrated in the shift/nonshift paradigm when the prime-target interval—the stimulus onset asynchrony (SOA)—was varied (Favreau & Segalowitz, 1983; Neely, 1977). As just described, at a short SOA (e.g., < 400ms), rapid automatic retrieval processes yield priming for related targets regardless of the expectancy. However, at longer SOAs, the category expectancy determines the priming effect such that shift-category primes have a facilitative effect on targets from the shift category, whereas nonshift category primes only facilitate related targets. Hence, manipulation of SOA modulates the degree of controlled and automatic semantic processing occurring during these semantic tasks; only automatic retrieval is evident at

shorter SOAs, indicating its more rapid, nonvolitional operation.

Controlled Semantic Retrieval

Given their differing temporal dynamics, SOA manipulation within the context of related LDT paradigms has been adopted to further assess automatic and controlled retrieval. As with the above expectancy paradigm, context effects are consistently apparent only with long SOAs. For example, as the proportion of related to unrelated trials increases, so does semantic priming in the LDT, with this *relatedness proportion effect* being absent at shorter SOAs (den Heyer, 1985; Neely, 1977). An increase in the proportion of related trials is thought to yield a greater expectancy that the prime will be followed by a related target. This expectancy fosters controlled biasing of related target representations when there is sufficient time to recruit or implement this control mechanism. Similarly, nonword interference effects—that is, the finding that the time to reject a nonword is longer when the prime is related to the word from which the nonword was derived—are sensitive to the nonword/word ratio and the SOA. At longer SOAs, the larger the ratio, the weaker the behavioral interference (Neely, Keefe, & Ross, 1989), suggesting that this context effect also requires cognitive control.

Changes in control requirements during semantic retrieval also have been explored within the context of semantic classification tasks, using long-term repetition priming paradigms (Thompson-Schill & Gabrieli, 1999; Vaidya et al., 1997; Vriezen, Moscovitch, & Bellos, 1995). In such experiments, a semantic decision (e.g., classifying a word as abstract or concrete) must be made each time a stimulus is presented. Consistently, RTs to repeated (primed) stimuli are faster than RTs to novel stimuli, with these long-term repetition priming effects appearing to differ from the short-term semantic priming phenomena indexed on the LDT as they survive intervening trials and persist across long delays (Roediger & McDermott, 1993; Wiggs & Martin, 1998). Moreover, long-term conceptual repetition priming is sensitive to the overlap between initially and subsequently accessed features: Priming is robust when the same semantic features that were initially retrieved are required for the subsequent decision and declines when different semantic representations from those initially retrieved are subsequently required (Thompson-Schill & Gabrieli, 1999; Thompson-Schill et al., 1998; Vriezen et al., 1995). Critically, these priming effects are thought to emerge due to facilitated access to previously retrieved information, perhaps reflecting a transition from a greater to a lesser dependence on mnemonic control (Raichle et al., 1994) (see Figure 1A and 1B).

Further evidence for the controlled nature of some instances of semantic retrieval derives from dual-task interference studies. Under situations in which attention is divided, the capacity for controlled access to semantic stores should be compromised as such control is presumed to be resource demanding. Consistent with this prediction, semantic priming in the LDT during conditions that typically encourage engagement of controlled retrieval is reduced when LDT is accompanied by dual-task interference (Becker & Killion, 1977; Herdman, 1992). By contrast, LDT facilitation that arises from more automatic retrieval mechanisms is unaffected by divided attention manipulations (McCann, Remington, & Van Selst, 2000). Similarly, long-term conceptual repetition priming during subsequent semantic processing is reduced when attention is divided during initial semantic processing of a stimulus (Mulligan, 1997), underscoring the importance of mnemonic control for these semantic facilitation effects.

This brief review of the cognitive behavioral literature indicates that semantic knowledge can be accessed in a controlled or an automatic manner. Automatic access may emerge through cue-driven, bottom-up activation of related representations, with the degree of activation depending on associative strength. By contrast, in some contexts, retrieval may be guided by a control mechanism that favors relevant or expected representations when they are not available through automatic retrieval routes. In the following section, we consider neuropsychological evidence for a distinction between controlled and automatic semantic retrieval.

DISTINGUISHING CONTROLLED AND AUTOMATIC SEMANTIC RETRIEVAL IN THE BRAIN

Patients who incur damage to regions of ventrolateral PFC often suffer from Broca's aphasia. This language deficit may be more akin to a production deficit than a semantic deficit, *per se*, as these patients are often able to nonverbally identify the uses of various objects and do not usually suffer from verbal comprehension deficits. However, left PFC lesions do have some adverse effects on semantic performance (Metzler, 2001; Swick & Knight, 1996; Thompson-Schill et al., 1998) and also can cause deficits in translating orthographic information into phonological codes (Fiez & Petersen, 1998). Thus, instances of intact semantic processing in the face of left PFC lesions may reflect (a) lesions to left PFC subregions that do not subserve semantic retrieval and the sparing of subregions important for this cognitive function, and/or (b) the effectiveness of automatic retrieval processes that may be mediated by posterior neural structures and that support recovery of strongly associated knowledge without PFC input.

Initial data indicate that patients with left frontal lesions may be particularly impaired on semantic tasks that require some form of cognitive control during semantic or lexical access (Metzler, 2001; Thompson-Schill et al., 1998). Such impairments appear to be associated with lesions to ventrolateral, rather than dorsolateral, PFC (Thompson-Schill et al., 1998). For example, patients with Broca's aphasia demonstrate intact semantic priming on the LDT when there is a strong association between the prime and target (Blumstein, Milberg, & Shrier, 1982). Moreover, when prime-target SOA is varied, priming is not extinguished at a shorter SOA, suggesting that Broca's aphasics can access semantic knowledge using a rapid automatic retrieval system (Hagoort, 1997). By contrast, Broca's aphasics fail to show typical priming magnitudes when the cue-target associative strength is weak (Milberg, Blumstein, & Dworetzky, 1987), an instance in which greater control may be necessary to access relevant semantic knowledge. Similarly, patients with lesions in left ventrolateral PFC show intact semantic priming under conditions in which the relationship between the prime and target is unambiguous, but fail to show intact priming when the relationship between the prime and the target is ambiguous (Metzler, 2001).

If damage to left PFC disrupts controlled semantic access, patients with such lesions should not benefit from expectancy in the same manner as healthy controls. Indeed, comparison of the relatedness proportion effect in Broca's aphasics and healthy controls reveals a differential pattern of priming (Milberg, Blumstein, Katz, Gershberg, & Brown, 1995). Neurally intact (and younger) participants demonstrated an interaction such that when the relatedness proportion was high, there was greater facilitation on related trials and a trend for greater inhibition on unrelated trials. By contrast, Broca's aphasics failed to show this pattern. Rather, they were slower to respond on all trial types when there was a high-relatedness proportion. These patients appear capable of detecting the greater relatedness proportion, but the influence of their expectancy fails to appropriately modulate semantic retrieval. Such outcomes indicate that insult to left ventrolateral PFC may hinder the mechanism through which context comes to guide access to semantic knowledge, suggesting that ventral PFC structures may be necessary for controlled semantic retrieval.

Just as PFC-lesioned patients exhibit deficits when controlled access to semantic knowledge is necessary, other patient populations exhibit deficits in automatic semantic retrieval. For example, patients with Alzheimer's disease sometimes fail to show semantic priming effects on the LDT at short SOAs (Bell, Chenery, & Ingram, 2001). Whether this disruption of automatic

processes arises due to a degraded semantic store or possibly a problem in automatic lexical access remains to be clarified. Either way, this impairment (a) suggests that automatic retrieval may emerge through bottom-up dynamics within long-term representational space and (b) further illustrates that automatic and controlled retrieval mechanisms depend on partially separable neural systems.

INDEXING SEMANTIC RETRIEVAL IN THE HEALTHY BRAIN

Functional neuroimaging methods that offer high spatial resolution—positron emission tomography (PET) and functional magnetic resonance imaging (fMRI)—provide a means to more precisely fractionate ventrolateral PFC along functional lines. The past decade has witnessed evidence that (a) indicates that specific ventrolateral PFC subregions are associated with semantic and phonological computations and (b) begins to adjudicate between alternative hypotheses regarding the nature of PFC-mediated control processes. Here, we briefly review neuroimaging evidence associating left inferior prefrontal cortex (LIPC) with semantic processing, as well as consider evidence for functional subdivisions within LIPC (also see Buckner, 1996; Fiez, 1997; Poldrack et al., 1999; Wagner, 1999).

PET and fMRI studies have consistently revealed increased activity in LIPC during the performance of tasks that demand access to semantic knowledge (Poldrack et al., 1999). Few efforts have explored the neural correlates of semantic priming in the LDT (but see Mummery, Shallice, & Price, 1999). Rather, the vast majority of work has used semantic generation and paradigms to examine the neural bases of semantic computations. For example, in Petersen, Fox, Posner, Mintun, and Raichle's (1988) landmark study of single-word processing, greater LIPC activation was observed when participants retrieved semantic knowledge associated with a word cue (by generating a verb associated with a noun) than when participants simply read the word. Subsequent investigations similarly implicated LIPC in semantic computations, showing greater activation in this region when participants made semantic relative to nonsemantic classifications of words or pictures (e.g., abstract/concrete vs. orthographic decisions) (Demb et al., 1995; Gabrieli et al., 1996; Kapur, Rose, et al., 1994; Price, Moore, Humphreys, & Wise, 1997; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996; Wagner et al., 1998). Differential LIPC responses during semantic versus nonsemantic classification were observed even when task difficulty or duty-cycle was greater during the nonsemantic condition (Demb et al., 1995; Poldrack et al., 1999), indicating that LIPC activa-

tion is modulated by the type of representation attended rather than more global demands on attentional resources. Based on these observations, LIPC has been posited to subserve the top-down control of semantic information stored in posterior neocortices.

Functional Segregation Within LIPC

Moving beyond a general association of controlled semantic processing with LIPC, other neuroimaging evidence points to a functional distinction within LIPC along semantic and phonologic dimensions (see Figure 1C) (Buckner, Raichle, & Petersen, 1995; Poldrack et al., 1999; Wagner, Maril, Bjork, & Schacter, 2001). Specifically, at least two functional subregions within LIPC have been identified: (a) the posterior and dorsal extent of LIPC (pLIPC; approximately Brodmann's [BA] area 44 extending into premotor, BA 6) and (b) the anterior and ventral extent of LIPC (aLIPC; ~BA 47/45).

Studies of verbal working memory (Jonides et al., 1997; Paulesu, Frith, & Frackowiak, 1993) have implicated pLIPC in the maintenance of phonological codes that may be represented or stored in posterior cortices (Awh et al., 1996; Davachi, Maril, & Wagner, 2001; Paulesu et al., 1993). In addition, pLIPC activation frequently has been observed during phonemic classification and simple word reading (Poldrack et al., 1999). By contrast, in addition to modulating pLIPC, semantic generation and semantic classification tasks also consistently elicit activation in aLIPC (Fiez, 1997; Gabrieli, Poldrack, & Desmond, 1998; Poldrack et al., 1999; Wagner, 1999). Differential functional connectivity has also been observed between aLIPC and pLIPC with posterior neocortical structures (Bodke, Tagamets, Friedman, & Horwitz, 2001). Critically, direct comparisons of semantic and phonological classification indicate that aLIPC is differentially sensitive to semantic processing demands, whereas pLIPC is particularly sensitive to phonological demands (Kirchhoff, Wagner, Maril, & Stern, 2000; Otten & Rugg, 2001; Poldrack et al., 1999; Price et al., 1997; Roskies, Fiez, Balota, Raichle, & Petersen, 2001; Wagner, Maril, et al., 2001). Hence, the nature of the stimulus features being processed affects the specific LIPC mechanisms invoked.

Although neuroimaging has revealed clear dissociations, the differential necessity of anterior and posterior LIPC for semantic and phonological control remains largely unknown due to ambiguities in extant lesion data. Consistent with this putative dissociation, intraoperative stimulation of anterior LIPC can disrupt semantic classification but not word reading (Klein et al., 1997), underscoring the importance of this region for semantic rather than orthographic or phonological processing. Moreover, posterior LIPC lesions can disrupt lexical-decision judgments (Swick, 1998), possibly

reflecting a lexical-semantic or phonological access deficit. Divergent data include the previously discussed observation that Broca's aphasics demonstrate diminished controlled semantic priming, and that lesion to posterior LIPC can yield impairments when semantic retrieval requires cognitive control. Whether these effects reflect disruption of posterior LIPC computations or a disconnection of anterior LIPC is unclear. Finally, further complicating matters are two observations of apparently intact semantic processing following anterior LIPC lesion (Price, Mummery, Moore, Frakowiak, & Friston, 1999; Thompson-Schill et al., 1998). These results, however, are also ambiguous because the lesion site in one patient appeared to fall rostral to the anterior LIPC region typically associated with semantic processing, and the behavioral results from the other patient suggested an impairment.

THEORIES OF CONTROL IN LIPC

Although delineation of the differential necessity of anterior and posterior LIPC for semantic control awaits further targeted investigation, it is clear that LIPC is involved in the controlled processing of semantic information. The precise nature of LIPC contributions to semantic control remains controversial. From one perspective, the controlled semantic retrieval hypothesis, LIPC subserves goal-directed controlled retrieval through representing the task context and biasing retrieval of task-relevant information when that information is not available by more automatic means. By contrast, the selection hypothesis posits that LIPC does not guide semantic retrieval *per se*, as retrieval is thought to be supported by posterior neocortical circuits. Rather, once representations have been retrieved, LIPC is critically involved in selecting task-relevant representations from amidst competing, irrelevant knowledge.

LIPC and the Controlled Semantic Retrieval Hypothesis

Under the controlled semantic retrieval hypothesis, demands on LIPC vary inversely with the extent to which task-relevant semantic knowledge can be accessed through bottom-up cue-driven retrieval. When automatic access is insufficient due to weak cue-target associations or the presence of prepotent, competing representations, LIPC control processes play a central role in guiding the recovery of context-relevant meaning (Gabrieli et al., 1996; Raichle et al., 1994; Wagner, Paré-Blagoev, Clark, & Poldrack, 2001). Mechanistically, the nature of this control may be analogous to other posited PFC bias signals that provide a top-down influence on representational space (Miller & Cohen, 2001; Norman & Shallice, 1986), although from the present perspec-

tive, interference from prepotent competitors is not required for its instantiation (Wagner, Paré-Blagoev, et al., 2001).

More specifically, models of retrieval and selective attention hypothesize that multiple representations often compete for processing and recovery (Anderson & Spellman, 1995; Desimone & Duncan, 1995). In certain situations, some representations have a stronger association with the retrieval cue or task context than others and thus have a competitive advantage. When such prepotent responses are present, they will tend to win out over less dominant responses and will tend to be retrieved through more automatic routes. However, in other situations, a less dominant response or representation may be task-relevant and thus must be retrieved to satisfy the current goal. In such situations, a mechanism is required to favor the task-relevant representation over the prepotent, task-irrelevant response. Such goal-directed bias is thought to occur via the top-down allocation of attention, with multiple lines of evidence implicating PFC as a component of the neural substrate of such control (Braver, Cohen, & Servan-Schreiber, 1995; Miller & Cohen, 2001). Thus, with respect to LIPC and semantic retrieval, when prepotent semantic associations interfere with retrieval of target knowledge, LIPC processes may serve to bias the less dominant knowledge, thus contributing to its successful recovery. Importantly, from the controlled retrieval perspective, this LIPC bias mechanism may also guide recovery when cue-target associative strength is weak even if prepotent, task-irrelevant competitors are absent (Wagner, Paré-Blagoev, et al., 2001). When cue-target associations are weak, automatic retrieval may fail simply due to insufficient bottom-up activation and under these circumstances a top-down signal may be required for successful retrieval.

Initial neuroimaging support for the controlled semantic retrieval hypothesis comes from several sources. First, as previously discussed, LIPC is differentially active during semantic versus nonsemantic classification (see Figure 1C), with the former presumably requiring goal-directed retrieval of task-relevant knowledge that does not automatically come to mind on stimulus presentation. Second, studies of semantic (or conceptual) repetition priming reveal that prior access to semantic knowledge, which renders the knowledge more accessible in the future, results in decreased LIPC activation when subsequently reaccessing that knowledge (see Figure 1D) (Schacter & Buckner, 1998). These neural correlates of conceptual repetition priming have at least five important characteristics. First, reduced LIPC activation is thought to reflect decreased cognitive control demands due to the increased availability of the target knowledge (see Figure 1A and B) (Demb et al.,

1995; Wagner, Desmond, Demb, Glover, & Gabrieli, 1997). Second, these effects are thought to reflect the benefits of implicit or nondeclarative memory, as even patients suffering from global amnesia demonstrate reduced LIPC activation during repeated semantic processing of stimuli (Buckner & Koutstaal, 1998; Gabrieli et al., 1998). Third, reduced LIPC activation results from long-term representational changes—changes that are likely instantiated in posterior neocortices—as they are reproducible over long delays (Wagner, Maril, & Schacter, 2000). Fourth, these LIPC priming effects are specific to the particular semantic features retrieved during initial stimulus processing and do not generalize to future attempts to retrieve other semantic features associated with the stimulus (Thompson-Schill et al., 1999). And last, priming in aLIPC emerges when subsequent semantic processing was preceded by prior semantic processing but not by prior nonsemantic processing. In contrast, priming in pLIPC emerges when subsequent semantic processes are preceded by either semantic or nonsemantic processing (Wagner, Koutstaal, Maril, Schacter, & Buckner, 2000). Collectively, the imaging literature on conceptual repetition priming suggests that as the need for controlled processing declines, due to increased accessibility of target representations and/or the strengthening of cue-target associations, so do demands on LIPC (especially aLIPC). This decline may emerge due to the “tuning” or “sculpting” of semantic space that follows initial stimulus processing (Fletcher, Shallice, & Dolan, 2000; Wiggs & Martin, 1998); subsequent retrieval attempts, therefore, are relatively more automatic and require less guidance from LIPC to recover the relevant knowledge from semantic memory.

LIPC and the Selection Hypothesis

An alternative conceptualization of LIPC control, the selection hypothesis, also has received support from neuroimaging and neuropsychological investigations (Barch, Braver, Sabb, & Noll, 2000; Thompson-Schill, D’Esposito, Aguirre, & Farah, 1997; Thompson-Schill et al., 1998, 1999). Rather than operating in the general service of controlled semantic retrieval, under the selection hypothesis, LIPC has a more restricted role. In this view, retrieval is subserved by temporal neocortices such that cue-associated knowledge is accessed through dynamics in long-term semantic space (Thompson-Schill et al., 1999). Hence, LIPC does not subservise retrieval per se. Rather, LIPC contributes to task performance only when a subset of the retrieved semantic knowledge is required for performance. LIPC bias mechanisms effectively select those task-relevant representations from amidst the competing, task-irrelevant representations.

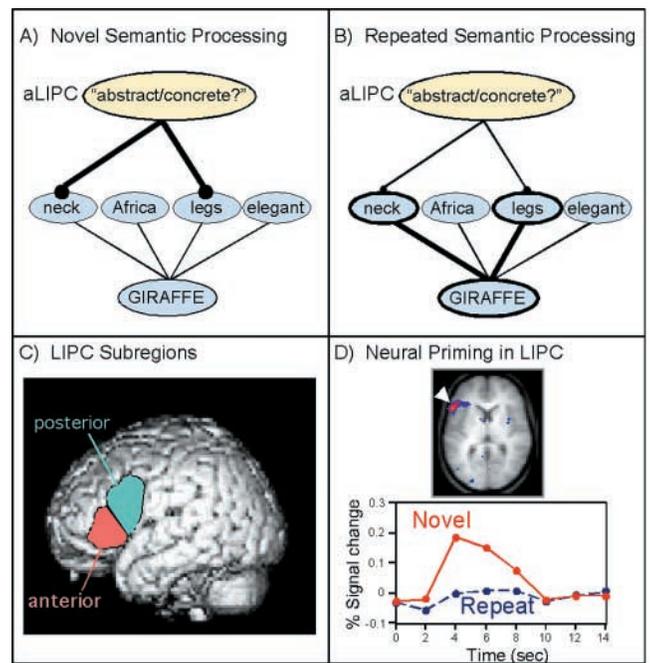


Figure 1: Characterization of Controlled Processing in Left Inferior Prefrontal Cortex (LIPC) Including Schematic Representation of Reduced Demands on Cognitive Control with Repeated Semantic Access, Functional Subdivisions Within LIPC, and Magnitude Changes in LIPC Activation With Reduced Control Demands.

NOTE: A and B are a schematic representation of reduced demands on cognitive control with repeated semantic access. During initial semantic classification (section A), a control component representing the task goal (e.g., “abstract/concrete”) directs access to relevant semantic features (e.g., neck and legs) associated with a cue (e.g., “GIRAFFE”) when those features are not available through automatic routes. During repeated semantic retrieval (section B), less mnemonic control is required because the initial retrieval rendered relevant features more accessible (indicated by the thicker lines). In section C, functional subdivisions have been observed within LIPC. The anterior LIPC (red) has been associated with semantic processing demands, whereas the posterior LIPC (blue) is modulated by phonological processing. In section D, the magnitude of LIPC activation declines during repeated semantic retrieval (data are from Wagner, Koutstaal, Maril, Schacter, and Buckner, 2000). The statistical map renders an aLIPC region that demonstrated greater activation during novel than repeated semantic processing (indicated by the arrow). The percent signal change from this region is plotted below.

The selection account makes two predictions that differ from those of the controlled retrieval hypothesis. First, under the selection hypothesis, demands on LIPC computations should not be modulated by the amount of semantic information to be retrieved because retrieval engages only posterior regions and selection occurs postretrieval. Second, when all knowledge is task relevant, no knowledge must be selected against in the course of task performance. This suggests that, under such circumstances, the degree to which representations come to mind through more automatic or more controlled retrieval processes should not affect LIPC

engagement. Rather, the selection perspective posits that the presence of competitors and the degree of competition from those competitors are the principal influences on LIPC demands. Hence, this view can account for data showing that patients with lesions to PFC demonstrate impairments in semantic tasks that involve resolving ambiguity or selecting relevant representations from amidst competitors (Metzler, 2001; Randolph, Braun, Goldberg, & Chase, 1993; Robinson, Blair, & Ciolotti, 1998; Swaab, Brown, & Hagoort, 1998). Moreover, this account can accommodate LIPC neural priming effects to the extent that these effects emerge from decreased competition (and, thus, selection demands) due to increased dominance of the recently accessed relevant representations (Thompson-Schill et al., 1999).

Support for the selection account comes from a series of fMRI studies that putatively varied both selection and retrieval demands (Thompson-Schill et al., 1997). In one representative experiment, participants made decisions about which of a set of target words (e.g., FLEA and WELL) was similar to a cue word (e.g., TICK). Decisions were based on either global semantics (low selection) or on a specific semantic feature (e.g., color; high selection). When a decision must be made about a specific feature, all other semantic characteristics are irrelevant to the task and so must be selected against in favor of the relevant feature. By contrast, when computing global similarity, Thompson-Schill and colleagues (1997) posited that all features of a concept are task-relevant and so selection demands are low or nonexistent. In this study, trials also varied in terms of the number of possible targets to consider (either two or four). This manipulation putatively varied the amount of semantic retrieval required, presumably being greater when there were more targets. Critically, the fMRI results showed clear pLIPC activation associated with increases in selection demands (i.e., feature > global similarity). However, increased semantic retrieval demands did not yield a significant change in LIPC activation (i.e., four targets \approx two targets). These results were interpreted as indicating that LIPC specifically subserves selection of task-relevant information from amidst competitors and does not mediate semantic retrieval.

Support for the hypothesis that semantic retrieval emerges from posterior neocortical, rather than LIPC, computations comes from a subsequent fMRI study of feature-specific repetition priming (Thompson-Schill et al., 1999). When participants repeated generation of the same feature (i.e., color \rightarrow color repetition) associated with a stimulus, activation in LIPC and ventral temporal cortex decreased relative to novel generation. Importantly, for repeated words in which a different feature was initially retrieved (i.e., action \rightarrow color), LIPC

activation increased relative to the novel condition, whereas temporal cortical activation again demonstrated a decrease. Thus, temporal cortex was interpreted as subserving retrieval of semantic features, irrespective of which are task relevant, such that subsequent retrieval is facilitated due to prior retrieval. By contrast, LIPC may specifically mediate selection: Selection demands may decrease when a specific feature is more readily available due to its prior selection and may increase when a prior selection favored what is subsequently a task-irrelevant feature.

Potentially supportive data also include the observation that left ventral PFC activation increased during intentional episodic encoding of paired-associates in the face of proactive interference (Dolan & Fletcher, 1997; Fletcher et al., 2000). Here, greater LIPC activation during the processing of recombined as opposed to novel word pairs could reflect increased selection demands. Moreover, neuropsychological data indicate that patients with LIPC lesions (especially in pLIPC; BA 44) demonstrate impairments when selection demands are high relative to when they are low (Thompson-Schill et al., 1998).

Selection in Terms of Controlled Semantic Retrieval

The controlled retrieval and selection hypotheses are mechanistically similar with the exception of whether the posited LIPC bias mechanism occurs postretrieval, only selecting from already accessed representations, or subserves both controlled access and selection of target representations when necessary at retrieval. The most influential observation in support of the selection hypothesis, and against the semantic retrieval account, is the simultaneous demonstration that LIPC is sensitive to selection demands (feature > global) but insensitive to the degree of semantic retrieval (four target \approx two target) (Thompson-Schill et al., 1997). However, a closer look at the design of this study reveals a possible reconciliation. As has been discussed, there are generally two routes to the recovery of semantic knowledge, automatic and controlled retrieval. Under the controlled retrieval hypothesis, LIPC computations will be necessary for semantic retrieval only when automatic retrieval fails. Consequently, simply varying the number of possible targets need not invoke greater controlled retrieval processes if the relevant knowledge can be accessed through automatic retrieval routes. Critically, in the "low selection" (global similarity) condition of the Thompson-Schill et al. (1997) study, the correct target was a strong associate of the cue word and the distractor targets were unrelated to the cue. Thus, task performance may have been based solely on automatic retrieval processes. To the extent that this is the case, then the resultant null

would be an insufficient test of the controlled retrieval account.

A recent study tested the critical prediction of the controlled retrieval hypothesis that increased LIPC activity should be observed when the cue-target associative strength is weak even when using a global semantic comparison task that presumably does not require selection (Wagner, Paré-Blagoev, et al., 2001). To manipulate controlled retrieval demands, the pre-experimental associative strength between the cue and the correct target was varied (see Figure 2A). To manipulate the extent of semantic retrieval, the number of targets was varied in an analogous manner to that of Thompson-Schill and colleagues (1997). Critically, the fMRI results provided strong support for the controlled retrieval hypothesis and diverged from the predictions of the selection account. That is, even though selection demands were held constant and to a minimum, LIPC activation increased with the number of targets even when cue-target associative strength was strong (see Figure 2B). Furthermore, the cue-target associative strength manipulation also modulated activation in LIPC, with there being greater LIPC activity during trials with weak cue-target associative strength (see Figure 2C). Conceptually similar effects of associative strength also have been reported by Roskies and colleagues (Roskies et al., 2001; but see Barch et al., 2000), as greater aLIPC activation was observed during categorical decisions about less prototypical exemplars (e.g., BIRD-OSTRICH) than about more prototypical exemplars (e.g., BIRD-ROBIN). Although this latter study may have simultaneously varied selection demands, taken together with the results of Wagner, Paré-Blagoev, et al. (2001)—in which selection demands were presumably minimized and held constant—these data indicate that LIPC is engaged during semantic retrieval when that retrieval requires cognitive control.

Likewise, the controlled retrieval hypothesis may be able to account for many of the neuroimaging and neuropsychological findings that have been argued to support the selection perspective. This is because in the vast majority of the studies that varied selection demands, cue-target associative strength covaried (e.g., Barch et al., 2000; Thompson-Schill et al., 1997, 1998). Perhaps most challenging for this perspective are the observed feature-specific repetition priming effects, where LIPC activation was observed to increase during repeated semantic processing of a stimulus when the target features differed from those that were initially task relevant (Thompson-Schill et al., 1999). Although these data may support the selection hypothesis, four factors warrant further consideration. First, the locus of priming in LIPC, as with previous selection data, fell posterior

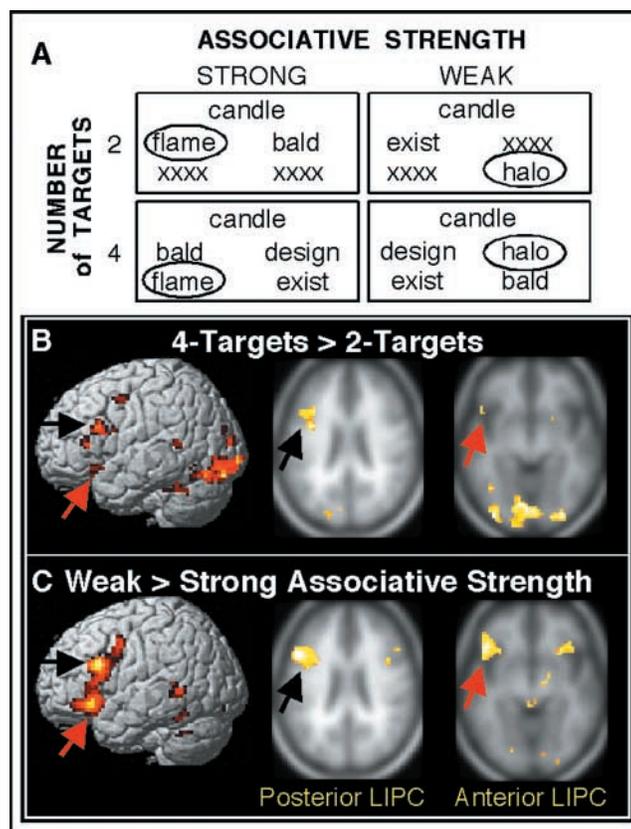


Figure 2: Task Design and Neuroimaging Results From fMRI Study of Controlled Semantic Retrieval.

NOTE: In section A, the experimental tasks that were used in Wagner, Paré-Blagoev, Clark, and Poldrack (2001). Trials consisted of a cue and two or four targets. Participants were required to determine which of the targets was most globally related to the cue. The correct response (circled) was either strongly or weakly associated with the cue, based on normative data. The factors of number of targets and cue-target associative strength were crossed. In section B, activation maps revealed a main effect of the number of targets (four targets > two targets) in both anterior (red arrow; ~BA 47/45) and posterior (black arrow; ~BA 44/6) LIPC. In section C, activation maps revealed a main effect of cue-target associative (weak > strong) in both anterior and posterior LIPC.

to the aLIPC region sensitive to controlled retrieval demands. Second, the increase in pLIPC activation could reflect increased phonological demands, or perhaps semantic retrieval, due to recapitulation of the previously retrieved and now prepotent but irrelevant knowledge. Third, alternatively, the increase in LIPC activation could reflect increased controlled retrieval demands due to retrieval-induced suppression of the now relevant representations during initial retrieval of the now irrelevant representations (Anderson, Bjork, & Bjork, 1994; Anderson & Spellman, 1995). Finally, the observed decreased activation in temporal cortex could reflect cue-based lexical priming rather than a decline in semantic retrieval demands. Given these ambiguities, it

remains unclear whether the observed pattern of PFC and temporal activations in this priming study point to a PFC role in postretrieval selection. Importantly, this discussion suggests that controlled retrieval demands will typically increase as selection demands increase: When competing task-irrelevant information is present, the degree to which task-relevant information will automatically come to mind is likely to be attenuated and thus controlled retrieval becomes necessary.

Although it is possible to account for the principal data in support of the selection hypothesis from a controlled retrieval perspective, not all data in support of the controlled retrieval hypothesis can be accommodated by the selection hypothesis. Consequently, one might ascribe a singular controlled retrieval function to LIPC. However, such a synthesis becomes complicated if one considers the relation between the anatomic correlates observed in studies supporting selection and controlled retrieval. Specifically, the anatomic correlate of semantic selection (Thompson-Schill et al., 1997, 1998), as well as of selection in nonsemantic paradigms that require delineation of relevant from irrelevant phonological or lexical information (Bunge, Matsumoto, Desmond, Glover, & Gabrieli, 2001; D'Esposito, Postle, Jonides, & Smith, 1999; Jonides, Smith, Marshuetz, Koeppe, & Reuter-Lorenz, 1998), appears situated in pLIPC (~BA 44/45). By contrast, direct manipulations of controlled semantic retrieval demands have consistently implicated aLIPC (~BA 47/45). For example, in the study by Wagner, Paré-Blagoev, et al. (2001), aLIPC was observed to be more sensitive to cue-target associative strength than was pLIPC (also see Roskies et al., 2001).

A possible resolution of these functional neuroanatomic differences awaits data from studies that directly cross controlled retrieval and selection demands. Initial results from a recent fMRI study conducted in our lab (O'Kane, Badre, Paré-Blagoev, Poldrack, & Wagner, 2001) suggest that aLIPC may prove sensitive to both selection demands (e.g., feature vs. global similarity decisions) and control demands (e.g., weak vs. strong cue-target associative strength). Results such as this would be consistent with our proposal that resolution of the selection/controlled retrieval debate likely will reside in the operation of a singular top-down bias mechanism.

CONCLUSIONS

Humans are capable of retrieving semantic information in a flexible manner to meet task demands. In this review, we aimed to consider evidence that there are two basic routes to retrieving relevant knowledge from

semantic memory (automatic and controlled). At the neural level, evidence suggests that ventrolateral PFC, or aLIPC more specifically, is a primary substrate of semantic control. This PFC subregion is consistently associated with tasks that demand semantic processing and, furthermore, is sensitive to manipulations that directly modulate the need for cognitive control during semantic access. Selection between competing semantic representations may emerge during retrieval and may rely on the same top-down bias mechanism responsible for the controlled recovery of meaning.

Although considerable progress has been made, questions remain regarding how this controlled semantic retrieval perspective fits with broader conceptualizations of ventrolateral PFC function. Moreover, the domain of semantic representations on which aLIPC operates demands further specification. For example, a view of controlled semantic retrieval that restricts its operational domain uniquely to abstract semantics and not lexical semantics is not consistent with recent results suggesting that aLIPC may also be sensitive to lexical retrieval demands (Tagamets, Novick, Chalmers, & Freidman, 2000; Clark & Wagner, in press; Gold & Buckner, in press). Finally, the task contexts in which controlled semantic retrieval is recruited and is necessary remain underspecified. Neuroimaging data suggest that LIPC computations also contribute to episodic encoding and to source monitoring during episodic retrieval (Dobbins, Foley, Schacter, & Wagner, in press; Kapur, Craik, et al., 1994; Kapur, Tulving, Cabeza, McIntosh, Houle, & Craik, 1996; Wagner et al., 1998). These findings raise the possibility that controlled semantic retrieval is elicited in a broad array of contexts when semantic access is important for task performance. Future investigations that bridge cognitive domains may well demonstrate that the controlled recovery of meaning is central to multiple forms of cognition.

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