Inhibitory processes and the control of memory retrieval

Benjamin J. Levy and Michael C. Anderson

People are often confronted with reminders of things they would prefer not to think about. When this happens, they often attempt to put the unwanted memories out of awareness. Recent research shows that the capacity to suppress distracting traces is mediated by executive-control processes that are analogous to those involved in overriding prepotent motor responses, and it is these processes that cause persisting memory failures for the suppressed items. There is evidence that memory retrieval and motor tasks that are likely to demand executive control recruit overlapping neural mechanisms, suggesting that a common process mediates control in these domains. Together, these findings indicate that memory failures often arise from the mechanisms that lie at the heart of our capacity to influence the focus of thought.

Benjamin J. Levy*
Michael C. Anderson
Dept of Psychology, 1227 University of Oregon, Eugene, OR 97403-1227, USA.
*e-mail: blevy@darkwing.uoregon.edu

While calling a friend, you realize that you are dialing their old telephone number by mistake. You push the outdated number out of your mind and, with effort, recall the correct one. As you call the new number more often, eventually the old one will stop intruding; indeed, you might not be able to recall it even if you wanted to, although you may have dialed it hundreds of times. This tendency to be disrupted by distracting memories pervades daily life: we may accidentally walk to yesterday's parking spot instead of today's or believe we took our medicine today when we are remembering taking it yesterday. Sometimes, cues remind us of things we would prefer not to think about. A friend's face might bring to mind a recent argument, despite our attempt to interact constructively with them, or an object, event or location might remind us of a traumatic experience. Confronted with such reminders, we often try to refocus attention and ignore the unwanted memory. These examples illustrate a simple point: having good memory for things that we have learned is not always a virtue, and they highlight the need to control a memory system that is sometimes too efficient, too able to deliver information, even when such remembrances conflict with our current goals. What mechanisms permit people to limit awareness of interfering memories and under what conditions do these mechanisms operate?

In this article, we review research that indicates that our ability to control distracting memories is accomplished, in part, by executive-control mechanisms that are not limited to controlling memory. In particular, we argue that the ability to control memory is a special case of a broad class of situations, termed response-override situations, that are thought to require executive control. In response-override situations (Fig. 1) one must stop a strong habitual response to a stimulus because of situational demands. Overriding the response is thought to be accomplished by inhibitory processes that suppress it and enable a more flexible, context-sensitive control over behavior [1–3]. A core theme advanced here is that the inhibitory mechanisms that control overt behavior are also targeted at declarative memories to control retrieval.

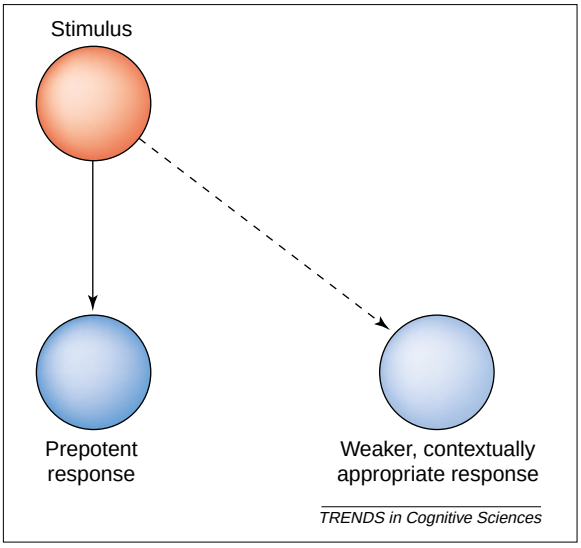

Fig. 1. Typical response-override situations. A stimulus is associated with a strong prepotent response but, depending on the situation, either a weaker, contextually more appropriate response to the stimulus is selected (e.g. Stroop tasks) or the prepotent response is withheld (e.g. Go/No-Go tasks).

In support of this view, we discuss evidence for the involvement of inhibitory processes in two memory situations that are likely to require response override: the need for selection during retrieval and the need to stop retrieval itself. Selection is required during retrieval when the goal is to recall an event or fact from long-term memory in the face of interference from related traces. The need to stop retrieval arises when we confront a cue or reminder and wish to prevent an associated memory from entering awareness. In both selection and stopping situations, attempts to limit the influence of activated and potentially distracting memories impair memory for those traces, which highlights an important connection between our capacity to control retrieval and forgetting. We conclude by reviewing neurobiological evidence indicating that many of the regions involved in response override are also recruited to control memory retrieval.

Inhibitory control in selective memory retrieval

When retrieving specific events or facts, the cues that guide retrieval are typically related to many other traces. Over a century of research indicates that

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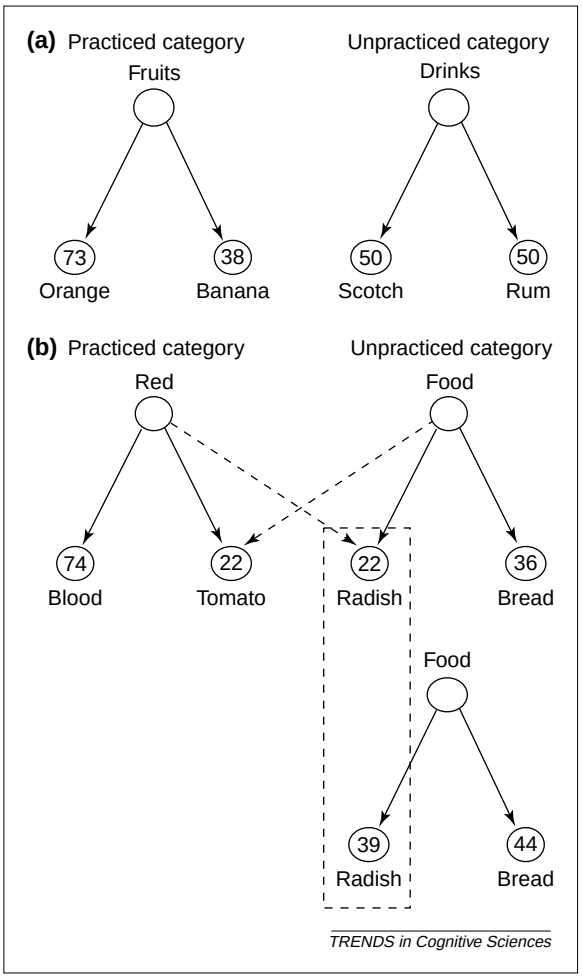

Fig. 2. The retrieval-practice paradigm. The numbers show the percentage of items that were recalled correctly on the final cued-recall test. (a) In the practiced categories, *orange* represents the items that received retrieval practice, and *banana* represents unpracticed items. Other exemplars represent items from categories that were studied initially but not practiced during the retrieval-practice phase. Retrieval-induced forgetting is evident in the reduced recall of unpracticed members of the practiced category (*banana*), relative to performance in baseline categories (*scotch* and *rum*). (b) Cross-category inhibition. Subjects studied categories such as *red* things and *food*. Although each item is only studied under a single category, some items (e.g. *tomato* and *radish*) are also members of the other category (dashed lines). This allows assessment of the impact of retrieval practice of *blood* on the later recall of both *tomato* and *radish*. The lower panel shows performance on the unpracticed category when the related category is not studied (the control against which to measure inhibition on items such as *radish*). Cross-category inhibition of *radish* is apparent following retrieval practice of the related category.

activation of these other traces interferes with retrieval of the desired item, with the amount of interference thought to depend on the number and strength of the competitors [4,5]. Overcoming competition would be hastened, however, and the speed and accuracy of target retrieval increased, if interfering traces could be suppressed, [6–9]. Thus, inhibitory control might be recruited to override competition from prepotent memories so that a target trace can be selectively retrieved.

If inhibitory mechanisms suppress competing traces, the later recall of competing memories should be impaired. We found evidence consistent with this in a procedure called the 'retrieval practice paradigm' [6]. In this paradigm, subjects study lists of category–exemplar pairs (e.g. *fruits–banana*, *drinks–scotch* and *fruits–orange*). They then perform retrieval practice on half of the exemplars from half of the categories by completing cued stem-recall tests (e.g. *fruit–or*____?) three times on each practiced item. After a 20-min delay, subjects are given a final cued recall test for all the exemplars. Performance can be examined for three item types on this test: practiced items (*orange*), unpracticed competitors (*banana*) and baseline items from unpracticed categories (*scotch*). As shown in Fig. 2a, recall of the practiced exemplars was improved relative to recall of baseline exemplars, whereas recall of unpracticed competitors was impaired. This finding – that remembering makes subjects forget related memories – is known as 'retrieval-induced' forgetting (RIF) [6]. Research on RIF has built on classic work on output interference to establish that retrieval-induced memory impairments are long-lasting [10,11]. RIF is consistent with the view that inhibitory control is recruited to overcome interference during retrieval practice, with inhibition manifesting as recall impairment for competitors on later retention tests.

However, the memory impairment observed in the above study can also be explained without inhibition. Several long-standing models of memory [12,13] can explain RIF through changes in the relative strength of practiced and unpracticed exemplars. According to this view, retrieval practice strengthens the practiced items. On the final test, these strengthened items intrude so persistently that subjects abandon efforts to recall unpracticed exemplars. This approach does not require inhibitory processes; rather, practiced items become so strongly activated that they block the retrieval of other exemplars. Other noninhibitory mechanisms might also contribute. For example, retrieval practice may either damage the association that links the category to the affected exemplar or alter the meaning of the practiced category (e.g. by biasing '*fruits*' towards '*citrus fruits*') so that the category label is no longer a functional cue for retrieving unpracticed competitors [14].

According to the preceding theories, retrieval practice does not disrupt the unpracticed competitors themselves. Rather, it (i) strengthens cue–target associations between the practiced items, (ii) weakens cue–target associations of the unpracticed competitors, or (iii) biases the meaning of the category cue. Only the inhibition hypothesis attributes impairment to suppression localized to the memories themselves. This feature makes a distinctive prediction: impaired recall of unpracticed competitors should be 'cue independent'. That is, impairment should generalize to cues other than the one used to guide retrieval practice. To test this prediction, the retrieval practice paradigm has been modified (Fig. 2b) [7]. As in the original experiment, subjects studied categories containing sixÿexemplars each; however, unlike the original study, some items could be classified under more than one category. For example, subjects studied *tomato* as a

Box 1. Generality of retrieval-induced forgetting (RIF)

Exemplars from taxonomic categories
Several studies replicated the basic RIF result using verbal stimuli with categorical relationships [a–h].

Ambiguous words
Subjects studied cue–response word pairs where each cue was a homograph that had two different response words; one related to the dominant meaning and one related to the non-dominant meaning. Retrieval practice on response words related to the non-dominant meaning caused RIF of the 'dominant' response word [i].

Visuo-spatial objects
Location and shape were given as cues to recall the color of some of the studied items. This impaired the retrieval of colors of other objects of the same shape. By varying which dimensions (color, location or shape) were used as the retrieval practice cues, subjects could be induced to forget the color, location or shape of the other items [j].

Propositions
Retrieving some facts about a topic impairs recall for other facts linked to that topic [k–m].

Previous novel actions
Retrieval practice using photographs of novel actions performed two days earlier (e.g. tracing a boomerang), impaired later retrieval of other actions also performed earlier [n].

Mock crime scenes
Interrogating subjects about details of a mock crime scene impairs their memory for other related details that were not discussed during the interrogation [o,p].

Personality traits
Retrieval practice on some personality traits of a person impairs later retrieval of other personality traits for that person [m,q].

Various of these studies replicated other distinctive features of RIF: the cue-independence of the impairment [b,c,i,k,l], and impairment specific to retrieval practice condition [d,e,i,j].

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member of the *red* category, but *tomato* is also a *food*. The key question was whether retrieval practice on items such as *red–blood* would not only impair competitors studied under the same category (e.g. *red–tomato*), but also *red* items that were studied and tested under separate category cues (e.g. *food–radish*).

According to the noninhibitory models, retrieval practice on *red–blood* should not impair recall for *food–radish*. *Radish* should remain unimpaired because it is tested with a different cue, *food*, which should circumvent noninhibitory factors. However, if retrieval practice on *red–blood* initially activates all *red* items, both *tomato* and *radish* should become activated, causing interference that triggers inhibitory control and the resulting suppression should be observed later, even when *radish* is tested with a different cue. Indeed, recall of *food–radish* was impaired (Fig. 2b), indicating that inhibition does occur. Such cue-independent impairment has been described many times with stimuli of varying type and complexity [7,15–18], which indicates that it is a general property of RIF.

Although these results argue that inhibition contributes to RIF, they do not address whether it is linked with selective retrieval. Perhaps strengthening practiced items in any way impairs the cued recall of related memories. For instance, inhibition might occur even if items were strengthened through repeated study exposures. However, many studies report that replacing retrieval practice with extra study exposures eliminates inhibition of competing items, despite strengthening practiced items to a similar degree [19–23]. Furthermore, strengthening items through retrieval practice does not impair unpracticed exemplars when the latter items are unlikely to interfere with retrieval. For example, RIF occurs for high-frequency competitors (e.g. *fruit–orange*), but not low-frequency competitors (e.g. *fruit–kiwi*) because low-frequency items are less likely to intrude during retrieval practice [6,18,24]. This indicates that inhibitory control is recruited specifically to support retrieval in the face of distraction from interfering representations.

If inhibitory control mechanisms resolve interference in memory retrieval generally, we would also expect them to function in semantic retrieval. Consistent with this, Bauml found that episodic memory for several studied exemplars of a category was impaired if subjects generated new exemplars of the same category from semantic memory during the interval between study and test [19]. However, episodic recall was unimpaired when this 'semantic generation practice' was replaced by

Table 1. Boundary conditions for retrieval-induced forgetting

Boundary conditions for RIF	Manipulation	Influence on RIF[a]	Refs
Similarity	Subjects were instructed to find similarities or differences between all exemplars	Similarity increased RIF	[28]
	The similarity between practiced items and competitors was varied	Similarity decreased RIF	[29]
	Subjects were instructed to focus on similarities or differences between practiced item and competitors	Similarity decreased RIF	[16]
	Subjects were instructed to focus on similarities or differences between the competitors	Similarity increased RIF	[16]
Integration	Subjects were instructed to integrate category members together during the initial study phase	Integration decreased RIF	[30]
Duration	24-h delay between retrieval practice and test	No RIF	[64]
	24-h delay between initial study and retrieval practice	Normal RIF	[64]

[a]Abbreviation: RIF, retrieval-induced forgetting.

study exposures using the same novel exemplars, showing that impairment derived specifically from semantic retrieval. In a related study, Blaxton and Neely found that subjects were slower to generate a critical target exemplar (*fruit–a___*?) from semantic memory after generating four other prime exemplars from the same category [20]. By contrast, subjects generated the same target faster when prime items were presented intact to subjects for speeded naming. Research on lexical ambiguity has shown that retrieving one meaning of a homograph impairs later processing of the other meaning [25,26]. Similar findings are observed in episodic memory experiments using homographs, which establish that inhibitory effects are induced specifically by recall [18]. Lastly, research using the rare-word paradigm has found that difficult semantic retrievals impair later retrieval of related competitors [8,27].

Retrieval-induced forgetting has been demonstrated to occur with a broad range of stimuli, not just verbal categories (see Box 1), but there are also conditions under which this impairment is attenuated (Table 1). Inter-item similarity might be one such condition, although the first studies of the effects of this variable on RIF produced conflicting results [28,29]. However, these were later explained by a two-factor theory in which similarity between practiced items and competitors and similarity between the competitors themselves have different effects on RIF [16]. Encouraging subjects to find similarities between targets and competitors during encoding decreases the amount of RIF, whereas finding similarities between the competitors themselves increases RIF. Other studies show that RIF is either greatly reduced or eliminated when subjects are encouraged to integrate the members of studied categories with one another during the study phase [30]. In studies of the fan effect, Radvansky [17] found a similar pattern of reduced inhibition when subjects integrated propositional knowledge into what he called location schemas. By integrating facts into more cohesive representations, subjects experience less interference between related facts and require less inhibitory control (see [31] for a similar integration benefit in fact memory). The timing of these experiments is also important. Whereas standard methodology shows that RIF persists for at least 20 minutes, introducing a delay of 24 hours between the retrieval-practice phase and the test phase was shown to eliminate RIF in one study. However, it is unclear whether this time frame is consistent across different materials and different schedules of retrieval practice.

Some studies have begun to explore the implications of RIF in social psychological phenomena and other practical applications. Taken together, these findings indicate that RIF is not limited to episodic retrieval or taxonomic categories; rather, it is a general consequence that arises when inhibitory control is recruited to guide selection in the face of competition from distracting traces.

Stopping retrieval through inhibitory control

Response-override mechanisms are also recruited when people must stop a prepotent response. Anderson and Green [32] recently addressed the possibility that this also occurs in retrieval by examining how stopping a retrieval attempt affects the to-be-retrieved memories (see also Box 2). To study this, they developed a new procedure, termed the Think/No-Think paradigm, which was modeled after the Go/No-Go task, that has been used to study the ability to stop a prepotent motor response in both humans [33,34] and monkeys [35]. In a typical Go/No-Go task, subjects must provide a motor response (e.g. pressing a button) in response to a variety of stimuli (e.g. letters). However, a specific, infrequently presented stimulus (e.g. the letter X) requires the suppression of that response. Subjects' ability to withhold that response is taken as a metric of effective inhibitory control.

To explore whether people can stop retrieval in Think/No-Think paradigm, subjects studied pairs of weakly related words (e.g. *flag–sword*, *ordeal–roach*) and were then trained to provide the second, response word when they given the first word as a cue. Subjects then entered the Think/No-Think phase, which required them to exert executive control over the retrieval process. For most of the trials in this phase, the task was the same as during training – to recall and say aloud the corresponding word as quickly as possible when the cue word was presented. For some cues, however, subjects were admonished to avoid thinking of the response word. It was emphasized that it was not enough to avoid saying the response word, and that they should prevent the associated memory from entering conscious awareness at all.

Box 2. Biased competition or direct suppression?

The two memory situations, selective retrieval and memory stopping, require inhibitory control. But do they recruit a single underlying mechanism or are the mechanisms functionally separate, despite being conceptually similar? Here we outline two classes of mechanisms that are used to explain response override and show how either could account for both selection and stopping.

Indirect suppression

According to indirect suppression models [a], inhibition arises from lateral inhibitory connections between the representations of competing responses. Focusing attention on one response both facilitates that response and suppresses other, related responses by automatic lateral inhibition. This model accounts for many findings in retrieval-induced forgetting; focusing attention on target items during retrieval practice might cause lateral inhibition of other interlinked exemplars that are in the same category. Using lateral inhibition to account for retrieval stopping situations requires additional assumptions because there are no overt competitors for the memory – one simply wants to stop retrieval of a single target word. However, subjects might stop retrieval by thinking of something else to distract themselves from the response word. If this diversionary thought is also associated to the cue, attending to it might laterally inhibit the unwanted memory (i.e. the response word). One difficulty with this approach, however, is that extra study exposures to practiced items (in studies of retrieval-induced forgetting) should also laterally inhibit competitors, but this is not observed typically.

Direct suppression

According to the direct-suppression model [b–d], inhibition is a separate executive-control process that can be targeted directly at a representation without facilitating a competing item. This approach provides a natural account of the impairment observed in the Think/No-Think task. When subjects are confronted with a cue that activates a prepotent memory, inhibitory processes would act directly on the unwanted trace to suppress it. In selective retrieval tasks, interference from competing memories would trigger their direct suppression, enabling selection of the more contextually appropriate target item. According to this view, the inhibition observed in retrieval-induced forgetting is not tied to selection itself, rather selection sets the occasion for a suppression process that directly targets competing memories to retrieve the desired trace.

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Of course, we cannot measure directly whether subjects stopped the memory from entering their consciousness. However, if inhibitory mechanisms were recruited to override retrieval, later recall of the excluded memory should be impaired. To examine this, subjects were given the cues for all of the pairs immediately after the Think/No-Think phase, but were asked to recall the response for every one. As expected, forgetting occurred: response words that subjects tried to keep out of awareness were impaired compared to baseline pairs they had studied initially but had not seen during the Think/No-Think phase (Fig. 3a,b). Furthermore, the more often subjects tried to stop retrieval, the worse recall became for the excluded memory. Avoided words were harder to recall even though subjects had encountered up to 16 reminders (i.e. cues) during the Think/No-Think phase. Under normal circumstances, reminders would be expected to facilitate the reminded memory, as with the items to which subjects continued to respond (Fig. 3a,b). In addition, impairment is cue independent: forgetting occurred regardless of whether subjects were tested with the originally studied cue word (e.g. *ordeal*) or with a novel cue that had not been studied (e.g. *insect–r____* for *roach*). From this cue-independence, we argue that the forgetting is unlikely to be caused solely by associative interference; rather, impairment reflects suppression of the excluded memory itself.

Anderson and Green also ruled out several alternative explanations to the inhibitory account [32]. They demonstrated that subjects were not confused or purposefully withholding the avoided items during the final test (Fig. 3c–f) and that the results were not caused by suppression of the vocal response (Fig. 3g). These results isolate forgetting in the Think/No-Think paradigm to processes directed at keeping the unwanted declarative memory out of awareness and demonstrate that this cognitive act has persistent consequences for the avoided memories.

The capacity to voluntarily inhibit memories might be adaptive because it allows us to limit the influence of distracting representations [36]. For example, it might regulate the accessibility of unpleasant or intrusive memories, so providing a mechanistic basis for the voluntary form of repression (suppression) proposed by Freud [37]. Thus, studying inhibitory control in memory might have implications for clinical phenomenon that relate to intentional forgetting [38–41].

Neural substrates of inhibitory control

The mechanisms that override prepotent memories may share neural substrates with those involved in perceptual motor response-override tasks. Although suppression of motor responses is traditionally associated with orbital prefrontal regions [42], recent neuroimaging evidence indicates that the dorsolateral prefrontal cortex [DLPFC; Brodmann areas (BAs) 9 and 46] and anterior cingulate cortex (ACC; BAs 24 and 32) are also involved. These regions are coactivated in a variety of cognitive tasks, including the Stroop task, the anti-saccade task, sequence learning, working memory and the perception of degraded visual stimuli [43]. Activation of these regions by such diverse cognitive demands suggests that they have a role in domain-general computations [44–46]. Recent work to isolate these computations suggests that the ACC and DLPFC have distinct roles. According to one view, the ACC detects conflict between competing responses and signals a need for greater control to the DLPFC. The DLPFC, in turn, implements control via top-down modulation of posterior cortical or subcortical regions [47,48], a possibility that is supported by recent neuroimaging studies (see [3,47,49,50] for related ideas).

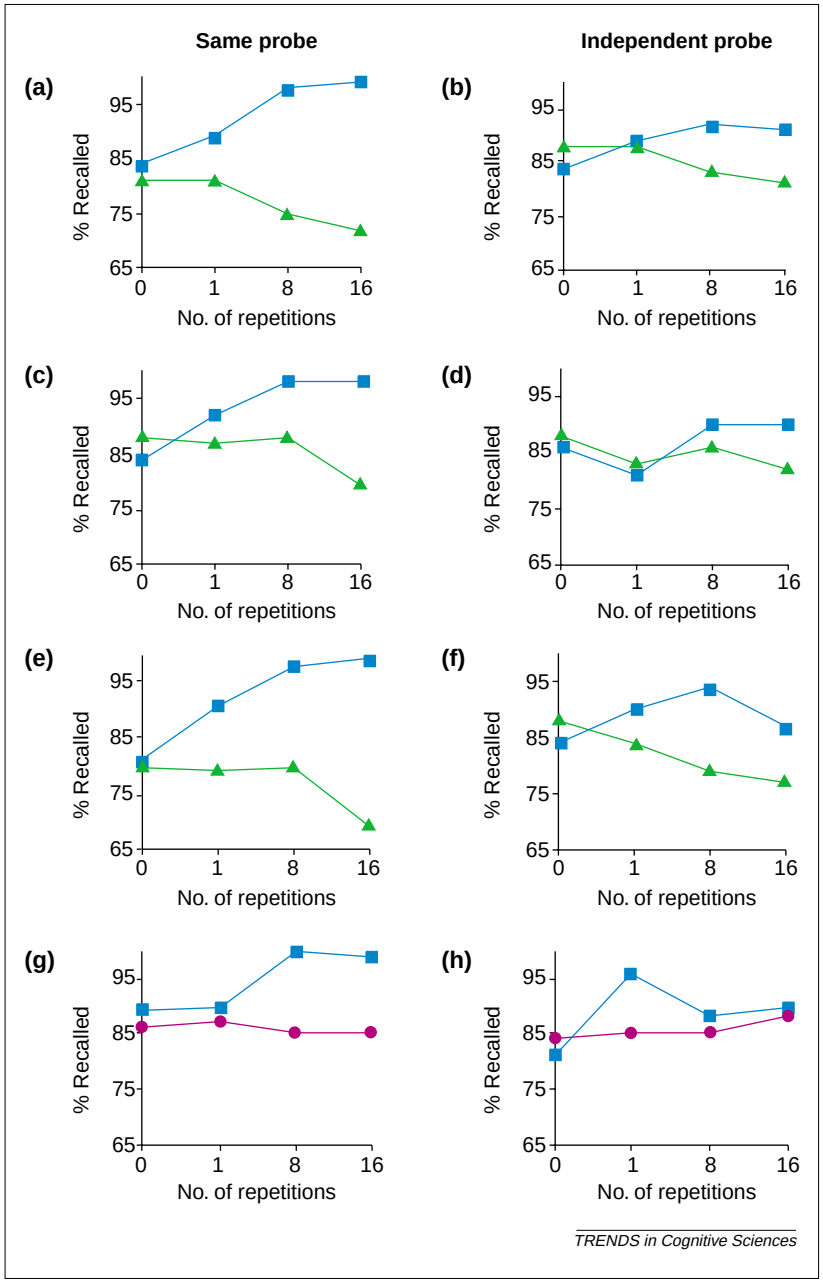

Fig. 3. The effects of preventing a memory from entering awareness. Each graph represents the final recall performance for 'respond items' that subjects were asked to recall (squares) and 'suppress items' that they had to prevent from coming to mind (triangles). Performance is displayed as a function of the number of times the cues were presented during the Think/No-Think phase. The final recall accuracy depends on whether subjects were tested with (a) the original studied cue ('same probe' condition), or (b) an unstudied category and letter-stem retrieval cue ('independent probe contition; e.g. *insect–r___* for *roach*). (c,d) Subjects were encouraged to guess by explicit instructions and paid rewards for all correct answers. (e,f) Subjects' expectations were manipulated by telling them (just before the final recall test) that attempting to avoid thinking about things makes them more accessible. (g,h) A control condition in which subjects did not have to avoid thinking of the response but only had to avoid saying it out loud ('withold' condition, circles). The flat function for the withold items shows that this manipulation does not produce inhibition.

If retrieval requires executive-control processes that are shared with response-override tasks, episodic and semantic retrieval should also recruit the DLPFC and ACC. In support of this, episodic retrieval coactivates the ACC and DLPFC in addition to prefrontal regions not activated in conflict tasks [43,51] (see [52,53] for related findings concerning the regulation of interference in working memory). Indeed, damage to the prefrontal cortex causes substantial deficits on free recall tasks (which requires, among other things, the resolution of interference between competing memories) but has less influence on recognition memory [3]. Patients with lesions of the prefrontal cortex also exhibit heightened susceptibility to interference during episodic [54] and semantic retrieval tasks [55,56]. However, neuroimaging studies indicate that, rather than recruiting the DLPFC, semantic retrieval generally recruits the left inferior prefrontal cortex (BAs 44, 45 and 47) and the ACC [57,58], with a more pronounced involvement when there is a need to select between several responses [59]. Thus, imaging and neuropsychological evidence indicates that circuits involving both prefrontal cortex and ACC are recruited during episodic and semantic retrieval, although inferior frontal regions have a greater role in the latter. If this functional analysis is correct, the activation of the ACC and PFC in retrieval tasks indicates that response-override mechanisms might be recruited to override prepotent memories. If this is the case, the findings reviewed here indicate that prefrontal regions, achieve response override, in part, through active suppression.

Concluding remarks

In this article, we have reviewed evidence that executive control mechanisms that are important for overriding prepotent responses are recruited during memory retrieval in at least two situations – selectively retrieving a memory in the face of interference from competing memories, and terminating retrieval itself. In both situations, research has found that controlling interference from unwanted memories impairs later recall of those traces. The characteristics of this impairment suggest that the memories have been actively inhibited. The parallels between these situations – selection and stopping – and those thought to require executive control more broadly, suggest the existence of a general response-override mechanism recruited for these tasks. Consistent with this, the neural structures activated during the many cognitive and perceptual-motor tasks that demand response override are also activated during memory retrieval tasks, particularly tasks in which interference must be resolved.

The capacity to suppress distracting memories is crucial to our ability to focus cognition in a goal-directed manner. However, as this review indicates, this capacity is not cost free because persistent suppression of distracting memories impairs their recall, even when they are desired. Such impairment has been observed in a variety of situations, with both verbal and visuo-spatial materials, in both episodic and semantic memory, and in situations that range from the recall of the meaning of individual words to eyewitness memories of complex events. The ubiquity of memory retrieval in our daily lives

and the generality of inhibitory effects indicates that many memory lapses – for past experiences, for friends' names or for ideas with which we were once adept – might arise from the effort to control the direction of thought.

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