ESSAYS ON THE CONCEPT OF INHIBITION

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Many of the concepts discussed in this volume are concerned with mechanisms that enable or enhance memory. To see memory only through the lens of facilitatory mechanisms however, is to miss a class of processes vital to its proper functioning: inhibition. Inhibition refers to a mechanism that acts upon a memory trace to induce a potentially reversible and graded change in its state, making the trace less accessible. At first blush, the idea of a process that impairs memory might seem odd, because forgetting is considered undesirable by most people. More often than people realize, however, having good memory for a prior experience is not what we want. We are frequently confronted with intrusive remindings that undermine performance on some task or that otherwise distract us. Sometimes, these remindings are unpleasant—memories of trauma or loss, or of events that make us sad, anxious, or embarrassed. Other times, our motives for controlling unwanted memories may be utilitarian, as when we simply need to ensure that only the most current knowledge is accessed (e.g., today's parking spot, and not yesterday's). When unwanted memories intrude into mind, some means of reducing their accessibility becomes desirable (Anderson, 2003; Bjork, 1989).

In this chapter, I discuss the idea that inhibition functions to regulate the accessibility of unwanted traces in memory. The first section reviews key theoretical attributes of inhibition, and the functions that it serves. I then illustrate these attributes and functions with examples from research on the role of inhibitory control in forgetting.

The Concept of Inhibition

The previous definition points to four important attributes of inhibition. First, the term inhibition implies a mechanism external to a memory trace that acts upon it. The term does not refer to just any process that changes a memory; it excludes, for example, changes in the structural integrity of a memory that were not induced by an external process (e.g., memory decay). Second, inhibition modifies the state of a trace. This claim implies (a) that independent of its associative connections to other traces, a memory has a state of excitation that influences its accessibility, and (b) that that state can be altered by inhibition in graded fashion. Third, the reduction in activity renders the trace less accessible, impairing recall. Finally, the change in a memory's activation state is often thought to be reversible, so that a memory can regain some of its accessibility. This reversibility contrasts with permanent changes (e.g., unlearning) that might affect the structural integrity of the memory.

Most inhibition theorists also believe that inhibition achieves at least one of two computational functions: resolving competition between representations or processing structures, or stopping a process. Thus, when multiple responses are activated by a cue, or a process needs to be disengaged, inhibition limits the influence of undesired representations. These ideas are clearly reflected in work on memory control, to which I turn next.

The Role of Inhibition in Memory Control

The foregoing properties and functions of inhibition are well illustrated through work on how people control unwanted memories. In my work, for example, I have argued that people control unwanted memories by recruiting inhibitory mechanisms similar to those used to control overt action (*Anderson, 2003*). By this view, memory control is an instance of response override, in which one must stop a strong habitual response to a stimulus due to situational demands. For example, each of us has reflexively tried to catch a falling object. If the object is a cactus, however, this reflex needs to be stopped to prevent a painful outcome. The ability to override habitual responses is thought to be supported by inhibition. If inhibition is central to stopping action, might it also be engaged to control internal "actions," like retrieval?

We have examined inhibition in two memory situations likely to require response override: the need for selection during retrieval and the need to stop retrieval itself. In both cases, overriding unwanted memories appears to impair memory in a manner consistent with inhibition. I discuss these two situations in turn.

Inhibition in Selective Retrieval. The role of inhibition in selective retrieval can be illustrated through the phenomenon of retrieval-induced forgetting. A central problem during retrieval is how we access a target trace when the cues guiding retrieval are related to many memories. A century of research shows that storing similar competing traces in memory impedes retrieval, and increases the chances of a retrieval error (see Anderson & Neely, 1996, for a review of this literature). While calling a friend, you may dial their old telephone number by mistake, or while leaving work, you may accidentally walk to yesterday's parking spot. Such intrusions are at best distracting, and at worst, dangerous. According to the response override view, memory intrusions trigger control mechanisms that inhibit the unwanted trace. If inhibition persists, it may be detected by examining later recall of the distracting trace. Thus, this view makes a counter-intuitive prediction: the very act of remembering should cause forgetting. This predicted effect has been referred to as *retrieval-induced forgetting (Anderson, Bjork, & Bjork, 1994).* Retrieval-induced forgetting has been found in a broad range of circumstances, including the retrieval of facts, semantic memories, word meanings, autobiographical memories, and eyewitness memory (see Levy & Anderson, 2002; Anderson, 2003 for reviews).

The impaired recall of unpracticed items implies an active process that increases forgetting for competing items, beyond what would be expected by the passage of time. However, the enhanced forgetting does not by itself imply that inhibition was at work because there are many ways that recall can be impaired without inhibition (Anderson & Bjork, 1994). The claim that inhibition underlies retrieval-induced forgetting amounts to the specific claim that the memory traces of the affected items have been reduced in their activation by an activation-reducing process that functions to overcome interference, and that memory impairment derives from this change in state.

Several properties of retrieval-induced forgetting specifically favor inhibition, however, and illustrate the concept outlined at the outset of this chapter. For example, retrieval-induced forgetting exhibits (a) *interference dependence*--- retrieval only impairs related traces if they interfere with retrieval, consistent with the idea that inhibition resolves competition (*Anderson et al. 1994*); (b) *retrieval-specificity*—other forms of practice that do not require recall (e.g., extra study) do not impair competitors, showing that inhibition only occurs when intrusive memories need to be overridden (*Anderson,* *Bjork, & Bjork, 2000*); and (c) *cue-independence*---impairment generalizes to novel final test cues unrelated to those used for retrieval practice (e.g., *Anderson & Spellman, 1995*). Retrieval-induced forgetting also occurs on tests of item accessibility, including item recognition and lexical decision (Veling & van Knippenberg, 2004), confirming that impairment reflects a change in the state of the affected item. And finally, retrieval-induced forgetting has been found to recover after 24 hours (MacLeod & Macrae, 2001), suggesting that in at least some cases, impairment reflects a reversible change in state (however, see Anderson, 2003, Anderson & Spellman, 1995, for an alternative perspective on why inhibition may not recover with time). Together, these findings show that retrieval engages inhibition to overcome interference from competing memories, rendering them less accessible generally (see Anderson, 2003 for a review), illustrating the core concept of inhibition.

Inhibition in Memory Stopping. A second situation likely to engage response override is the need to stop retrieval. So, for instance, upon confronting a reminder to an unpleasant memory, we may engage inhibition to stop retrieval, preventing the reminder from eliciting the memory. Can the mechanisms that stop reflexive responses be engaged to override retrieval? To study this, we put people in a situation in which they repeatedly confronted a reminder to a recently encoded memory, and asked them to attend to the reminder while willfully excluding the associated memory from consciousness. Afterwards, we asked subjects to recall the memories that they had previously kept out of awareness. Interestingly, the repeated presentations of reminders during the prior no-think phase not only failed to improve people's later retention of the associated memory—as one might ordinarily expect reminders to do---it impaired performance compared to performance on baseline items that were learned initially, but for which no reminders were presented in the interim. Thus, excluding an unwanted memory from awareness leads to a memory deficit for the avoided trace, and the properties of this deficit are consistent with inhibition (Anderson & Green, 2001).

Recent findings confirm that the brain mechanisms underlying this type of memory inhibition are related to the ability to override reflexive responses. Suppressing unwanted memories recruits the dorsolateral prefrontal cortex, a brain region associated with inhibiting prepotent responses; this suppression reduces activation in the hippocampus, a structure associated with declarative memory (Anderson et al., 2004). Importantly, the engagement of frontal cortex and the modulation of hippocampal activation predict the amount of memory impairment for suppressed items. Whether the forgetting produced by suppression reflects the direct or indirect consequences of neuronal inhibition remains to be established, although the impairment is clearly related to modulation of brain activity at the systemic level. The capacity to inhibit unwanted memories may help people regulate consciousness of unpleasant or intrusive memories.

Concluding Remarks

Taken together, the findings on memory inhibition suggest that many of our experiences of forgetting are produced by an inhibition process that regulates the accessibility of memory traces. When a memory interferes with retrieval or is otherwise unwanted, inhibition can be engaged to alter that memory's state of activation, rendering it less accessible when later desired. Although we have discussed inhibition in memory retrieval and retrieval stopping, many other phenomena may also be produced in whole or in part by inhibition, including the classic concept of retroactive interference (see Anderson & Neely, 1996, for a review), part-set cuing inhibition, and output interference (see Bauml, 1996, 1998, and Bauml & Aslan, 2004, for evidence concerning the role of inhibition in these phenomena). If correct, this view suggests a new perspective on forgetting that contrasts with the passive view that has prevailed in psychology for much of its history—a new perspective that emphasizes the role of control processes in regulating the accessibility of our knowledge and of experience to accommodate the need for focused, goal-directed cognitive activity.

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Diversity of cortical functions is secured by inhibitory mechanisms

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Homeostatic dynamics in the brain can only be maintained if the excitatory forces are balanced by equally effective inhibitory forces. The required inhibition in the cerebral cortex is provided by specialized classes of inhibitory neurons. If only excitatory cells were present in the brain, neurons could not create form or order or secure some autonomy for themselves. Principal cells can do only one thing: excite each other, resulting in an avalanche of excitation involving the whole population.

Inhibitory networks generate non-linear effects

The most basic functions accomplished by neuronal networks are pattern completion and pattern separation, functions related to *integration and differentiation*. Separation of inputs in a network with only excitatory connections is not possible. However, with inhibitory connections, the competing cell assemblies and even neighboring excitatory neurons can be functionally isolated, and excitatory paths re-routed by the traffic-controlling ability of coordinated interneuron groups. The specific firing patterns of principal cells in a network thus depend on the temporal and spatial distribution of inhibition. As a result, in response to the same input, the same network can produce a different output pattern at different times, depending on the state of inhibition. The coordinated inhibition ensures that excitatory activity *recruits the right number of neurons in the right temporal window* and that excitation spreads in the *right direction*. None of these important features can be achieved by principal cells alone. The balanced partnership between excitatory and inhibitory neurons ensures an overall homeostatic regulation of global firing rates of neurons over extended territories of the cortex. At the same time, this balance allows for dramatic increases of local excitability in short time windows, which is necessary for sending messages and modifying network connections. Balance and feedback control are also essential principles for oscillations, and interneuron networks are the backbone of many brain oscillators (Buzsaki and Chrobak, 1995).

Interneurons multiply the computational ability of principal cells

Brain systems with “simple” computational demands evolved only a few neurons types. For example, the thalamus, basal ganglia or the cerebellum, systems that can support only non-conscious memories, possess a low degree of variability in their neuron types. In contrast, cortical structures have evolved not only five principal cell types but numerous classes of GABAergic inhibitory interneurons as well (Freund and Buzsaki, 1996). Every surface domain of cortical principal cells is under the specific control of a unique interneuron class. This is a clever way of multiplying the functional repertoire of principal cells, using mostly local interneuron wiring. Adding more interneurons of the same type linearly increases the network’s combinatorial properties. Adding novel interneuron types to the old network, even if in very small numbers, offers a non-linear expansion of qualitatively different possibilities.

The extensive computational capacity of a single principal cell is seldom utilized at once. Furthermore, principal cells with a large or small dendritic arbor, or neurons with similar geometry but different distribution of ion channels, generate a different output in response to the same input. Dividing the full computational power of principal cells into numerous subroutines that can be flexibly used according to momentary needs is an enormous advantage; this important service is provided with ease by the interneuron system. Interneurons can functionally "eliminate" a dendritic segment or a whole dendrite, selectively inactivate Ca^{2+} channels, or segregate dendrites from the soma or the soma from the axon. In effect, such actions of interneurons are *functionally equivalent to replacing a principal cell with a morphologically different type*. The division of labor and, consequently, the multiplexed output of principal cells are brought about by a diverse group of interneurons (Freund and Buzsaki, 1996; Somogyi et al., 1998).

In their relation to the principal cells, three major interneuron families are recognized. The first and largest family of interneurons, basket cells and chandelier cells, controls the spiking output of principal cells by providing perisomatic inhibition. Interneurons of the second family target specific dendritic domains of principal cells. Every known excitatory pathway in the cortex has a matching family of interneurons. Several additional subclasses seek out two or more overlapping or non-overlapping dendritic regions, and yet other subclasses innervate the somata and nearby dendrites with similar probability. Because the different domains of principal cells have different functional dynamics, interneurons innervating those specific domains adapted their kinetic properties to match their targets. Not surprisingly, members of the dendrite-targeting interneuron family display the largest variability.

In addition to affecting the activity of principal cells, interneurons also innervate each other by an elaborate scheme and affect each other's biophysical properties. An important subgroup with at least some overlap with the dendrite-targeting family contains a special set of interneurons whose axon trees span two or more anatomical regions and some axon collaterals cross the hemispheric midline and/or innervate subcortical structures, hence the term "long-range" interneuron. Such widely projecting, long-range neurons are rare but, in light of the functional importance of small-world graphs, their role must be absolutely critical. They provide the *necessary conduit for synchronizing distantly operating oscillators* and allow for *coherent timing* of a large number of neurons that are not connected directly with each other. The third distinct family of interneurons has the distinguishing characteristics that their axons completely avoid principal cells and contact exclusively other interneurons. With perhaps 20 or more distinguished interneuron types in the cerebral cortex, the complexity of their wiring must be enormous, although the critical details are not yet known (Somogyi et al. 1998).

The advantage of varying the surface domain innervation of the principal cells by the different interneuron classes becomes especially clear when temporal dynamics are also included. For example, basket cells respond with decreasing efficacy when stimulated by high frequency inputs because of their "depressing" input synapses. In contrast, several types of dendrite-targeting interneurons fail to generate spike output when driven at low frequency and require several pulses before they begin to discharge because their input synapses are of the facilitatory type. The consequence of such dynamics is easy to visualize. When a pyramidal neuron discharges at a low rate, it activates almost exclusively its perisomatic interneurons. On the other hand, at a higher discharge rate the somatic inhibition decreases and inhibition is shifted to the dendritic domain. Time *is thus transformed into subcellular space,* due to the frequency filtering behavior of synapses.

The interneuron system as a distributed clock

Despite its multifarious wiring, the *principal cell system alone cannot carry out any useful computation*. It is the inhibitory neuronal network, when coupled to the principal cells that provides the flexibility needed for the complex operations of the brain. *Balance of opposing forces,* such as excitation and inhibition, often *gives rise to rhythmic behavior*. Providing rhythm-based timing to the principal cells at multiple time scales is one of the most important roles of interneurons. Once a collective oscillatory pattern arises, it constrains *the timing freedom of its members* and decreases the windows of opportunity for the principal cells to discharge: principal cells, therefore, get synchronized. Synchronization by oscillation occurs at multiple time scales, according to the large numbers of oscillators at various frequencies, covering time epochs from tens of seconds to milliseconds. The duration of the oscillation, in turn, regulates the length of messages that can be transmitted as well as the spatial extent of neuronal pools involved. The oscillations, the interneuron system allows multiple temporal and spatial organizations of principal cells in the cerebral cortex (Buzsaki and Draguhn, 2004). The essence of cortical function is that the result of local computation is transmitted to distant groups. Conversely, large-scale cortical activity constrains local computation. This bidirectionality is a fundamental aspect of global cortical computation. Only systems with such regenerative and self-organized (spontaneous) activity can give rise to conscious behaviors.

Summary

In addition to principal cells, the cortex contains diverse classes of interneurons that selectively and discriminately innervate various parts of principal cells and each other. The hypothesized “goal” of the daunting connectionist schemes of interneurons is to provide maximum functional complexity. Interneurons provide *autonomy and independence to neighboring principal cells* but at the same time also offer useful *temporal coordination*. The functional diversity of principal cells is enhanced by the domain-specific actions of GABAergic interneurons, which can dynamically alter the qualities of the principal cells. The balance between excitation and inhibition is often accomplished by *oscillations*. Thus, the cerebral cortex is not only a complex system with complicated interactions among identical constituents but it has developed a diverse system of components as well.

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Inhibition: An Attentional Control Mechanism

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The term "inhibition" has played a role in psychology and physiology since at least the mid 19th century (Smith, 1992). Then, as now, some used the term loosely, others tied it to operations, or to physiology (or both). Indeed, many saw inhibition as an essential process for education, mental health and moral behavior (Smith, 1992, Chapter 7). Many of the great names (e.g., Morgan, Freud, Ribot, James, and Wundt) associated with the origins of psychology commented on, relied on and/or criticized notions of inhibition (see Diamond, Balvin, & Diamond, 1963, Ch 8). In today's light, some of the early meanings attributed to inhibition are insulting (e.g., to women) and wrong headed, others however (e.g., Morgan, 1891, pp 459-461) are congruent with the concept of inhibition proposed by Hasher and Zacks in 1988 (see also, Hasher, Zacks & May, 1999; Hasher, Lustig & Zacks, in press).

In the Hasher & Zacks view, a fundamental assumption is that familiar stimuli activate their representations automatically – with or without awareness – and that this massive activation (and its spread to associated representations) can and must be down regulated in order for organized behavior to achieve an individual's long and short-term goals. This down regulation is accomplished by *inhibitory* mechanisms that operate in the service of goals.

Familiar stimuli are present in both the immediate environment and in the world of thought. Individuals are presumed, in this framework, to differ minimally in activation processes, but to differ greatly in the efficiency of inhibition - or in the ability to down regulate activation. People with generally poor inhibitory abilities will have difficulty ignoring concurrent distraction, as well as difficulty in stopping thoughts and actions that were recently relevant, but that no longer are. As well, they may have difficulty stopping thoughts tied to anticipation of events in the near future. That is, individuals (and groups of individuals) with poor or inefficient inhibitory mechanisms will have particular difficulty living in the moment and satisfying immediate goals because their thoughts and actions are rather more under the control of the excitation triggered by environmental stimuli and recent and future thoughts and events than under the control of their own goals.

Lapses in inhibitory regulation have a number of consequences. For one, they create high levels of distractibility, resulting in slowed and error-prone behavior. Lapses enable the production of strong but momentarily incorrect responses, as well as poor retrieval of specific events. Poor retrieval of details is the consequence of *two* inhibitory-based problems. The first occurs at encoding when poor inhibitory regulation creates memory representations (or bundles) that are cluttered with irrelevant along with relevant information. The problem created for retrieval is that searching through a cluttered memory trace results in slower and less accurate performance than does searching though an uncluttered trace. Inhibition plays a second role at retrieval. Because any cue can retrieve more than one memory representation, inhibition must suppress any non relevant representations that come to mind in order to conduct a search through the relevant memory bundle. That is, the down regulation enabled by inhibition is required for choice in memory retrieval (as it is in any other situation with competing options). Poor suppression at retrieval thus slows choice between activated sets of representations and, should that process be successful, poor suppression will also slow search within a selected memory bundle that contains non relevant representations.

On these bases, one might think that people with poor inhibitory abilities should have a great deal of difficulty achieving their goals and coping with the intellectual and social demands of their world - and some may indeed have such problems. However, it is also possible that the absence of strong inhibition can set the stage for aspects of preserved and possibly even superior cognition. For example, people who don't filter out irrelevant information during encoding will learn about that 'irrelevant' information tacitly and may be able to use that knowledge subsequently (e.g., Rowe, Valderrama, Hasher & Lenartowicz, 2006). As well, greater creativity may be in part a result of reduced inhibitory regulation.

This viewpoint predicts (or postdicts) a number of reliable findings in the aging literature, including slowing, reduced working memory performance, differences in patterns of comprehension, reduced access to details about the past, poor control over strong responses, among others (see Winocur & Hasher, 2002, for similarities and differences in inhibition between older humans and nonhuman animals). It is important to note with respect to human aging that not all differences between normal younger and healthy older adults (or any other groups with reduced inhibitory efficiency) should be attributed to inhibition because at least some differences may well be tied to differences in individuals' or groups' goals and values (e.g., May, Rahhal, Berry & Leighton, in press).

Healthy older adults are not the only individuals with reduced inhibitory regulation; those with mild cognitive impairment may show even greater problems, as may those with dementia. Depressed individuals and perhaps individuals with schizophrenia, with attention deficit disorder, and those operating under high levels of stress may also have inhibitory deficits. Of course, there will be individual differences in the 'normal' young adult population as well. Recent neuroimaging studies with both younger and older adults have shown a relationship between the ability to suppress activation to irrelevant stimuli and the ability to actually remember the targets (Gazzaley, Cooney, Rissman & D'Esposito, 2005).

Some have suggested that the gold standard for demonstrating inhibition is evidence of below baseline activation (where baselines vary with tasks). Such findings have been reported in both neuroimaging and behavioral studies (Gazzaley et al., 2005; May & Hasher, 1998). It is worth noting however, that to be effective, inhibition need not reduce activated representations to such a level, it merely needs to dampen the activation accorded to familiar or recent representations. It is this dampening that likely permits the selection of a goal-related representation in thought (or a product amidst competitors), changes in the current contents of consciousness, the creation of boundaries between events and ultimately, goal driven behavior.

At a conceptual level, it is unclear whether or not there is one type of inhibition, or multiple types, each with different underlying determinants and with different age and individual difference trajectories. For example, the ability to regulate strong responses (termed *restraint* control by Hasher & Zacks , often referred to simply as 'inhibition' by others) may or may not be mediated by the same factors that underlie the ability to ignore concurrent distraction (termed *access* control) and both of these may or may not be different from the inhibition required to stop processing one topic (or to create an event boundary) and so to start another (termed *deletion* control; all terms from Hasher et al., 1998). All of these may or may not be different from the inhibition entailed in paradigms used by Anderson and Bjork (e.g., 1994). The three mechanisms proposed by Hasher et al. are conceptually useful but may or may not prove to be separable at either a behavioral or a neural level.

With respect to the issue of tying behavior to underlying physiology, those connections are highly desirable now, as they were in the last century (Dodge, 1926), and perhaps the goal is more attainable, as well (Gazzaley et al., 2005). In addition to neuroimaging and animal model studies, another approach to understanding the underlying physiology is to explore performance on tasks requiring inhibitory control at peak versus off peak times of day, on the assumption that excitatory processes are invariant across waking hours but inhibitory processes are not (Hasher, Goldstein & May, 2005). What the underlying physiology might be is currently unclear, but some evidence suggests a focus on frontal function and on neurotransmitters that are particularly critical for frontal function and likely pathways from frontal to other regions in the brain.

No good (or bad) concept is without its critics and in this, the concept of inhibition is in excellent company, for example with such concepts as automaticity and capacity. Included among both contemporary - and 19th and 20th century - criticisms of the construct of inhibition are issues such as whether or not a particular task necessitates inhibition as an explanation and the lack of a direct connection from behavior to underlying physiology.

At a purely conceptual level, inhibition is a mechanism that stops ongoing activity or that reduces the activation of one or more competitors for thought and action thereby enabling the selection of those consistent with goals. Like many of our forebears (see Smith, 1992), we view inhibition as a general attentional mechanism impacting on intellectual life broadly, ranging from memory, to choice and decision making, to language comprehension, and to creativity and problem solving. In this conception, inhibition is a seen as a cognitive primitive that underlies individual, age and other group differences in the more commonly studied mechanisms of working memory and speed (see Hasher et al., in press). As such, it may prove to be the (or a) key mechanism underlying general intelligence. When behavior is driven by excitation unmodulated by inhibitory control, people are likely to rely on implicitly acquired and expressed knowledge or on well practiced behavior patterns and highly accessible constructs. Inhibition sets the stage for coherent behavior that is largely under the control of goals, rather than behavior that is under the control of passing stimuli and thoughts.

Author's Note

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Cognitive Inhibition: Elusive or Illusion?

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> *"the arrest of the function of a structure or organ, by the action upon it of another, while the power to execute those functions is still retained, and can be manifested as soon as the restraining power is lifted"* (Brunton, 1883)

What do we mean by "inhibition" in the year 2006? Quite possibly, we mean very much what Brunton meant 123 years ago. When we discover that history already contains the current view, it is quite common to express disappointment that there has been no progress, but this is not at all a necessary conclusion. In fact, our understanding of the concept of inhibition has grown very considerably over the past century and a quarter, particularly in the realm of neuroscience but also in the study of cognition. The interested reader should consult two excellent books on the history of the concept—Diamond, Balvin, and Diamond (1963) and Smith (1992).

Start Vectors

This brief chapter considers several issues critically connected to the concept of inhibition. To begin, however, it is important to indicate two "start vectors." First, this chapter takes as absolute fact that there is inhibition at the level of the brain and nervous system, based on the vast neuroscientific literature that has developed since Sherrington (1906). It is also accepted that we can stop motor actions (see, e.g., Logan & Cowan, 1984), a phenomenon widely called inhibition, although the term has a different meaning there than its neuroscientific cognate, and a more neutral term such as "restraint" or "(executive) control" might be preferable. So the questions considered here relate to the concept of inhibition as invoked to explain memory at the psychological, cognitive, or behavioral level—inhibition at the level of thought, not action (cf. Breese, 1899).

A second start vector is also important to identify explicitly. No matter what one's position on the utility of the concept of inhibition in understanding cognition, it does not strengthen the argument to invoke the concept of neural inhibition. The two operate at fundamentally different levels of analysis. Nor is either a unitary entity: Cohen (1993), for example, identified four distinct subtypes of neural inhibition, each involving a variety of neural components; Buzsaki's (this volume) contribution adds to the list of types of neural inhibition. Certainly different ideas are conveyed by different uses of the term in the study of cognition. True, neural and behavioral inhibition both refer to a suppressed event, but that is where the analogy ends, and any kind of direct mapping seems very unlikely. Indeed, reserving "inhibition" for the neural event and another term such as "suppression" for the cognitive event, if it can be shown to occur, would be preferable. Put simply, a "domain general" central concept does not seem plausible.

What Might Cognitive Inhibition Mean?

According to the *Oxford English Dictionary*, there are four senses of *inhibition*. Two relate to societal or legal prohibition. Interestingly, the other two relate *separately* to the physiological and psychological senses of the term, consistent with the present claim that these two senses are distinct. The defining elements of cognitive inhibition appear to be two—mental withholding and reduced performance. The latter is directly measurable as reduced response likelihood or lengthened response latency, given a suitable neutral baseline or control condition against which to make the comparison. But the former is an inference from performance. Inhibition is not an outcome; it is a theory about the cause of that outcome. Note that Brunton's emphasis on the function returning to "full strength" once inhibition is lifted is only sometimes woven into the definition.

As argued elsewhere (MacLeod, Dodd, Sheard, Wilson, & Bibi, 2003), even the measurement of reduced performance is not without considerable challenges. The choice of a neutral baseline is rarely straightforward nor unanimously agreed upon. And great care must be taken not to reflexively equate reduced performance with inhibition: Inhibition is only one possible mechanism that might contribute to or cause that reduction. The crucial questions then become: How are we to determine whether inhibition was involved? What are the defining features of cognitive inhibition?

Defining Criteria for Cognitive Inhibition

Unfortunately, no "litmus test" exists or is likely to appear, so we must rely on multiple co-occurring symptoms to support a diagnosis of cognitive inhibition. There are only two that have been proposed as specifically filling this role. The first has been used in attention research but not yet in memory research. This is a kind of dissociation criterion wherein a pattern reverses from a benefit to a cost. [The cost/benefit terminology is borrowed (e.g., Jonides & Mack, 1984) and is recommended as admirably agnostic with respect to process or mechanism.] Thus, in the phenomenon of inhibition of return, a cue appears at one of two spatial locations where a soon-to-follow target could appear. Although over trials the cue is not actually predictive of the location of the subsequent target, if the time between cue and target is brief, the cue provides a benefit in response time to a target at the same location. But that benefit switches to a cost if the time between cue and target is lengthened. The received view is that when the delay is longer we inhibit the cued location, thereby slowing detection of the target should it appear there. The experimental conditions are unchanged except for the cue-target lag, so this reversal could serve as a marker for inhibition, although other explanations exist.

The second criterion, in contrast, is unique to the memory literature, and has been championed by Anderson and Green (2001). The logic is that if a memory is truly inhibited by some operation on a representation, then other operations on that same representation should also reveal evidence of that inhibition. Anderson and Green had people try not to think of a previously studied word when provided with a cue that had been studied with that word. They found that this led to poorer recall of the target word than was the case without having tried not to recall it. This outcome could be seen as suggesting inhibition—but in fact does not rule out simple interference. However, the target word was also harder to recall to a (related) cue that had not been studied, suggesting that the target word itself, not just the particular studied association, was suppressed by the act of not thinking about it. Anderson and colleagues have cited this pattern as strong evidence for inhibition in memory (although its replicability has been questioned, see Bulevich, Roediger, Balota, & Butler, in press).

These two are worthy efforts in terms of trying to diagnose true instances of inhibition, but more criteria are needed. [Of course, inhibition is not alone in this predicament; other cognitive mechanisms certainly warrant greater definition.] To differentiate inhibition-based from non-inhibition based memory situations will require considerably more work and ingenuity. In so doing, the hope must be that the coherence of the concept will be considered as well, given that at present inhibition can mean quite different things to different memory researchers.

Plausible Alternatives to Inhibition

What process(es) might cause a cognitive task to slow down or to become more error prone? Inhibition of a component of the response, such as the representation upon which it relies, is certainly a candidate. But discriminating inhibition from interference will continue to be a most difficult problem. So interference—being drawn to another alternative than the nominally correct alternative—is also a candidate. The term "interference" is also problematic, though, sometimes being used to refer to an observed phenomenon and sometimes to a possible explanation of the phenomenon. The crux of the problem was well laid out by Klein and Taylor (1994, p. 146) who said:

> Unlike in the neural sciences, however, where inhibitory mechanisms can be observed in the hardware, in cognitive models inhibition must be inferred on the basis of overt behavior. As such, there is a danger of circularity whereby investigators attribute interference effects to inhibition and subsequently define inhibition on the basis of behavioral interference. For this reason, the terms inhibition and interference are often confused."

In any given situation where inhibition is proposed as a possible account, other possible accounts are certainly available. These other possibilities vary, so a proponent of the idea of cognitive inhibition might argue that one of its virtues is its breadth or parsimony. But a critic could just as readily maintain that because inhibition means quite different things to different researchers, the apparent "value added" of breadth is illusory and actually has considerable potential to create confusion. If those favoring inhibition accounts had to divide inhibition into subtypes, it might actually be better to abandon the umbrella term altogether, focusing instead on these subtypes as distinct processes.

MacLeod et al. (2003) argued, following several other investigators, that a viable alternative account to widespread inhibition in cognition could actually be more directly memory based. Under this account, it is routine, even automatic, to continuously retrieve from memory information relevant to the present situation. Ordinarily, such retrieval is advantageous—a benefit—helping to narrow options and speed the decision regarding what to do. But sometimes, retrieved information will conflict with the present situation, slowing processing and producing a cost. Although such costs could be seen as inhibition, they need not be: They are instead the joint product of automatic memory retrieval and consequent conflict resolution. Such an account works well in many situations that otherwise might seem to demand an inhibitory explanation.

Conclusion

The position put forth here is that we do not have strong evidence of inhibition in memory. There may be inhibitory processes in memory, but we simply do not know yet, and better indices are required. The existence of neural inhibition is seen as a different phenomenon. In the nervous system, it is the balance of excitation and inhibition that determines neural computation and ultimately behavior. It is therefore most likely that even if we can identify true cognitive inhibition, such inhibition will also rely on the balance of neural inhibition and excitation, and will not be uniquely related to neural inhibition. Under this view, the existence of inhibition in the nervous system in no way speaks to the likelihood or character of inhibition in behavior, any more than the existence of neural excitation necessitates a counterpart in cognition.

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Inhibition as an Essential and Contentious Concept in Memory

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In a 1989 essay on "Retrieval inhibition as an adaptive mechanism in human memory," written for a volume honoring Endel Tulving, I argued that inhibitory processes played little or no role in then-current theories of human memory (Bjork, 1989). I viewed that fact as puzzling—given that inhibitory processes had long been acknowledged by brain and behavioral scientists to be critical at the neural, sensory, attentional, and motor levels, and in the ontogeny of brain development. Towards explaining *why* inhibition seemed out of favor as an explanatory concept, I suggested that two aspects of the prevailing research zeitgeist played a role:

> *"First, notions of inhibition or suppression in human memory have an unappealing association to certain poorly understood clinical phenomena, such as repression. Second, the information-processing approach, grounded as it is in the computer metaphor, leads us to think in term of processes like storing, scanning, grouping, erasing, and so forth. Notions like inhibition, suppression, unlearning, and spontaneous recovery are not easily compatible with the computer metaphor. (p. 310)*

My own history of research on directed forgetting, tracing back to my graduate-school days, illustrates the influence of such factors. I spent the first 15-20 years saying and writing that research on directed forgetting was important *not* because it had anything to do with clinical phenomena, such as repression, but because it could shed light on how our memories are kept current, how rehearsal and encoding resources are allocated, and how competing items are segregated and differentiated in memory. In papers I authored or co-authored during what Colin MacLeod (1998), in a remarkable review of the literature, referred to as the "golden age" of research on directed forgetting (1968-74), which began with a paper by Bjork, LaBerge, and Legrand (1968), and through much of what he refers to as the "silver age" (1975-85), I attempted to explain directed-forgetting findings via non-inhibitory processes such as selective rehearsal and set differentiation. It took an accumulation of directed-forgetting findings that proved hard to interpret without reference to inhibition, especially those reported by Geiselman, Bjork, and Fishman (1983), to convince me that retrieval inhibition played a key role in directed forgetting.

Historical Perspective on the Reluctance to Postulate Inhibition

Taking a broader historical view, however, the hesitancy to postulate inhibitory mechanisms in learning and memory theories clearly pre-dates the emergence of computer metaphor and the information-processing approach. In fact, concerns about the necessity of assuming inhibitory processes go back to the early decades of controlled research on human and animal learning and memory. In the experimental and theoretical analysis of extinction phenomena, for example, questions and debates arose that are very reminiscent of present-day issues that have emerged in the context of blocking-versus-suppression accounts of retrieval-induced forgetting phenomena (cf. the Anderson's and

MacLeod's essays in this volume). In research on conditioning, for example, explanations of extinction in terms of inhibitory processes (e.g., Pavlov, 1927, and Hull, 1951) did battle with interference explanations (e.g., Guthrie, 1935) that asserted, in essence, that extinction is merely the learning of a new response to the old conditional stimulus.

Aside from the whether inhibition or interference accounts of extinction could provide a better account of extinction phenomena, such as "disinhibition" effects, or that massing of extinction trials often resulted in more effective extinction than did spacing those trials, whereas the opposite was true for acquisition—both of which posed difficulties for interference/new-learning accounts—reviews from that period clearly reflect the hesitancy to postulate inhibitory processes. In referring to Pavlov's appeal to inhibitory mechanisms in accounting for extinction effects, for example, Woodworth and Schlosberg's (1954) say "Pavlov's rather speculative ideas of what goes on in the brain may be of little importance. Some psychologists go so far as to reject the concept of inhibition, although it seems to be a necessary—and respectable—concept in physiology" (p. 559). And they later, in discussing the reaction of the field to Pavlov's interpretation of disinhibition, comment that "It is not surprising that psychologists who disliked inhibition regarded this suggestion as adding insult to injury" (p. 561). It became common, in fact, and for mostly good reasons, to avoid using the term *inhibition* in labeling empirical effects, but that convention may have been spurred on, in part, by the desire to avoid the concept altogether. In his experimental psychology book, for example, Osgood (1953), for example, in a preamble to his discussion of transfer and retroaction in his experimental psychology book, provides the following caution:

> *"Although the term "retroactive facilitation is commonly and acceptably used for positive retroaction, the term 'retroactive inhibition' has unfortunately been applied when negative retroaction is found. What is referred to here is simply an observed decrement in performance, not a process—the decrement may or may not be due to some inhibitory process—so henceforth we shall use the more neutral term, retroactive interference. (p. 520)*

Roots of the Reluctance.

Why, historically, has there been a reluctance to postulate inhibitory mechanisms? Beyond any unsavory association to poorly understood clinical dynamics, or any effect of the computer metaphor, I think two other factors may play a role. One is a kind of parsimony consideration: If effects can be explained in terms of cognitive processes that are better understood, such as selective rehearsal and interference/blocking dynamics, then why appeal to inhibitory mechanisms, which are more poorly understood? A second and related consideration has to do with our subjective experience. We all have the conscious experience of selecting some items to rehearse or encode or retrieve—and the experience of some items in memory interfering or blocking our access to other items in memory—but inhibitory processes are not accompanied by the same volitional and conscious experience. Even in cases where inhibitory effects are powerful and undeniable, such as in dichotic listening, when attending to one ear is accompanied by a gating out of input from the other ear, what is available to consciousness is the decision to allocate attention to a given ear coupled with the processing of input from that ear, not the inhibitory operations that suppress input from the other ear.

Inhibition in the Current Research Zeitgeist

At the end of my 1989 essay, I predicted that in the "near future" there would be consensus that inhibitory processes play a critical role in the overall functioning of human memory. I made that prediction, in part, because I thought the combination of two developments—the emergence of new techniques to examine neural and structure dynamics in the human brain, and the emergence of neural/connectionist modeling of human memory processes—would lead researchers towards, rather than away from, theories that incorporated inhibitory processes. That proved to be a good prediction—at least as indexed by books devoted to the role of inhibition that appeared shortly thereafter (e.g., Dagenbach & Carr, 1994; Dempster and Brainerd, 1995; Smith, 1992), by the subsequent proliferation of the word "inhibition" in the titles of articles, and by the keen interest in experimental tasks thought to instigate inhibitory processes, such as the retrieval-induced forgetting, think/no-think, and directed-forgetting tasks—but concerns about the necessity of assuming inhibitory processes have been resurrected, too, as exemplified by Colin MacLeod's essay in this volume.

Comments and Perspective on the Present Essays

In the sections that follow, I comment—in the context of the splendid essays by Michael Anderson, György Buzáski, Lynn Hasher and Colin MacLeod—on the definition of inhibition; the adaptive nature of inhibitory mechanisms; and what a see as the remaining key issues and points of contention.

Defining Inhibition

Colin MacLeod cites Brunton's (1983) definition of inhibition, repeated below, and Michael Anderson provides a useful and detailed characterization of the attributes of inhibition that goes beyond, but is consistent with, Brunton's definition:

> *"the arrest of the function of a structure or organ, by the action upon it of another, while the power to execute those functions is still retained, and can be manifested as soon as the restraining power is lifted" (Brunton, 1883)*

I endorse that definition, but with respect to *retrieval* inhibition in particular, I have tended to adopt an empirical, rather than conceptual, definition—one that focuses on the impairment of the *recall* of inhibited memory representations. One result that implicates retrieval inhibition is a violation of what might be called the "law of forgetting"; that is, when something that is not recallable after a shorter delay becomes recallable at a longer delay. An example of such an effect is when the earlier learned of two competing memory representations becomes more recallable, in absolute terms, as time passes. Such "regression" effects (Bjork, 1978) are common in both motor and verbal learning, they occur on time scales ranging from seconds to months and years, and they occur across species (for a review, see Bjork, 2001). A second result that implicates retrieval inhibition is when something becomes non-recallable, but remains at full strength by other measures. An example is when an instruction to forget impairs subsequent recall of the to-be-forgotten materials, but not the subsequent recognition or relearning of those materials, or the effects of those materials on indirect measures of retention, such as priming (see, e.g., Bjork & Bjork, 2003). Again, such effects are very general and appear in research on animal learning as well as human learning. As Bouton (e.g., 1994) and Rescorla (e.g., 2001) have emphasized, based on research with animals, new associations do not over-write or destroy old associations and post-treatment “return of fear,” which is common in the clinical treatment of phobias (see Lang, Bjork, & Craske, 1999), is an especially salient example that the same is true for humans as well.

Inhibition as an Adaptive Mechanism

A thread that runs through the essays by Anderson, Buzsaki, and Hasher is that inhibitory processes play a key and adaptive role in how our brains function and in how we contend with the learning, memory, decision, and emotional challenges that are part of living, learning, and managing ourselves. Gyorgy Buzsake, in remarkably few words, provides a clear and compelling description of how inhibitory networks and inhibitory interneurons multiply and refine the computational power of principal cells. That “brain systems with ‘simple’ computational demands,” such as the basal ganglia, thalamus, or cerebellum, are characterized by only a few neuron types, whereas systems that support conscious memory functioning are characterized not only by five principal cell types, but also by “numerous classes” of inhibitory neurons, is an interesting and provocative aspect of the brain’s structure. Speculatively—perhaps *too* speculatively on my part—that property of the brain’s neural organization seems to link to Hasher’s argument that familiar stimuli “activate their representations automatically” and that in many circumstances “this activation (and its spread to associated representations) can and must be down regulated in order for organized behavior to achieve an individual’s long and short-term goals.” The basic idea is that such down regulation is accomplished by “inhibitory mechanisms that operate in the service of goals.”

The emphasis, in Hasher’s treatment, is on attentional control and the ability to have one’s thoughts and actions be guided by goals and plans, not by the activation triggered by environmental and other stimuli. Individuals, in her view, who have poor inhibitory abilities will also have difficulty “in stopping thoughts and actions that were recently relevant, but no longer are.” Such a stopping function maps to one of the two adaptive functions Michael Anderson attributes to inhibition, the other being to resolve competition in the use of our memories, but the emphasis is a bit different in Anderson’s and Hasher’s frameworks. Anderson’s emphasis is on “memory stopping”—that is, on stopping the retrieval of information that is stored in memory, but, when recalled, is a source of emotional discomfort or “undermine performance on some task”—whereas Hasher’s emphasis is on inhibiting activations that are stimulus driven, automatic, and perhaps unaccompanied by awareness.

With respect to resolving competition among items in memory, Anderson argues that selective retrieval—that is, selecting a target item from memory from among all the items in memory that might be associated to a given retrieval cue or cues—engages an inhibitory mechanism that suppresses the non-target/competing items and, thereby, enhances access to the target representation. This suppression, though, can persist and result in *retrieval-induced forgetting* of non-target items (Anderson, Bjork, & Bjork, 1994)—at least for some time—should the recall of those items be required. Anderson and Spellman (1995) have argued that selective retrieval has properties that are parallel to selective attention; in both cases inhibitory mechanisms act to enhance access to the external or internal target by suppressing competition from unattended external or internal non-targets. Bjork, Bjork, and Anderson (1998) have pushed that argument further by suggesting that such a selection-plus-suppression mechanism may be "*the* primary solution in the functional architecture of the human as an information-processing device to the problem of avoiding interference and competition at various levels of cognitive processing … in a broad range of motor and cognitive activities, *selecting* appears to involve *inhibiting*." (p. 133)

In my own case, I have argued that retrieval inhibition is a uniquely human and adaptive solution to the problem of keeping one's memory current. In contrast to man-made memory devices, in which—without special precautions—the storage of new information replaces or erases old, out-of-date, information, learning and using new information (such as a new home phone number) does not destroy the representation of the information it replaces, but, rather, renders it non-recallable overtime. The old phone number (or street address, software procedure, maiden name, locker number, etc.) remains in memory, can often be recognized, and—should it again become relevant—can be relearned with great rapidity and savings.

Remaining Issues and Points of Contention

In his current essay, and in earlier review (MacLeod, Dodd, Sheard, Wilson & Bibi, 2003), Colin MacLeod provides a broad critique of the readiness of today's researchers to attribute various empirical findings to inhibitory mechanisms. The central arguments reiterate, update, and embellish the arguments that emerged decades ago in accounting for phenomena such as extinction, as alluded to above, and retroactive interference. With respect to his two "start vectors, " that there is (a) no denying that there is inhibition at the neural/brain level, but that (b) the evidence of such inhibition cannot, by itself, be offered as evidence of inhibition at the cognitive/memory level, I believe there can be no serious disagreement. Nor should there be any disagreement with his reiteration of the time-honored caution in discussions of interference versus interference: "inhibition is not an outcome; it is a theory about the cause of the outcome" (p. XXX).

At the risk of over-simplifying MacLeod's arguments, I interpret his critique as saying, first, that to attribute some empirical effect to inhibition, versus some alternative process, requires meeting rigorous criteria and, second, that alternative interference-based explanations must be ruled out before inhibition is inferred. With respect to the first point, he suggests that we need evidence of dissociations analogous to those that have implicated inhibition in research on attention, such as the effect, in research on inhibition of return, of a pre-cue changing from a benefit to a cost with cue-target delay. I believe that results of that kind, if not exactly of that kind, already exist. In A-B, A-D paired-associate list-learning experiments, for example, one type of evidence supporting response-set-suppression hypothesis (Postman, Stark, & Fraser, 1968) is that the retroactive effects of list-two on list one are greater than the proactive effects of list one on list two, given a short retention interval, but the converse is true at a long delay—consistent with the proposal that B responses are suppressed during A-D learning, but then recover.

A recent finding from research on retrieval-induced forgetting can also, in my view, be seen as a kind of dissociation that implicates inhibition. Items that are most recallable if tested—by virtue, for example, of being the strongest associates to a category cue (Anderson et al., 1994), or by virtue of their valence (Storm, Bjork, & Bjork, 2005)—turn out to be the most, not least, subject to retrieval-induced forgetting. This result, one of the three properties of retrieval-induced forgetting Anderson cites as favoring inhibition, is especially difficult to accommodate from within an interference/blocking interpretation. Another recent finding—that retrieval success is not necessary for retrieval-induced forgetting to happen (Storm, Bjork, Bjork, & Nestojko, 2006)—also poses a major problem for interference/blocking theories, given that no competitor is strengthened when retrieval practice fails, but is readily interpretable in terms of a suppression mechanism.

There is, I think, an implicit—and subtle—assumption in MacLeod’s analysis, one that is widely shared, even by those of us who are convinced that inhibitory processes play a key role in human memory. The assumption is that a kind of theoretical pecking order is justified: non-inhibitory ideas are to be preferred, unless totally untenable, and the burden of proof is on inhibition theorists. Before an inhibition interpretation is to be believed, interference mechanisms must be refuted, whereas the converse requirement does not seem, typically, to be placed in interference interpretations. This subtle assumption, which might even be justified via a kind of Bayesian prior-odds reasoning, constitutes, I think, another reflection of the reluctance to assume inhibitory processes.

Finally, even if the evidence of inhibition is considered convincing, a key question remains: Is inhibition a by-product of other activities, such as selective retrieval, selective attention, or self distraction, or does what might be termed “pure” inhibition also characterize human memory and cognition? Stated in the context of Anderson and Green’s () think/no-think paradigm, can we respond to instruction not to think of a target item in a direct, unmediated, way that inhibits subsequent access to the target, or can such suppression only be achieved via, say, self distraction or active retrieval of arbitrary non-target items? In the context of research on directed forgetting, research by Gelfand and Bjork (1985; described in Bjork, 1989) suggests that the subsequent inhibited access to to-be-forgotten items is a by-product of new learning coupled with the mental set to replace to-be-forgotten items with upcoming to-be-remembered items, but the question remains, as do many other questions about exactly how and if inhibition is involved in human cognition.

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