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Inhibitory Deficit Theory: Recent Developments in a "New View"

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A major view in cognitive psychology presumes the existence of limits on mental capacity, limits that vary with circumstances and task demands and that largely determine the performance of individuals (see, e.g., Kahneman, 1973). The Daneman and Carpenter (1980) measure of working memory (and its many variants; see, e.g., Engle, Cantor, & Carulo, 1992; Friedman & Miyake, 2004) is thought to give a snapshot of capacity by assessing an individual's ability to actively maintain important information while also engaging in some form of ongoing processing. From a capacity viewpoint, the bigger the mental desk space, the better performance should be on a wide range of tasks, including reading comprehension and reasoning. On the assumption that older adults have reduced working memory capacity, age differences might be explained.

However, a study on reading comprehension and memory had findings that were uninterpretable from this perspective (Hamm & Hasher, 1992). Older adults showed comprehension of stories that equaled that of young adults but did so by keeping more, not less, information in mind as they read. These capacity-challenging findings were critical to the development of an alternative view of cognition and of age (and individual) differences in cognition (Hasher & Zacks, 1988). Two simple hypotheses were advanced: (a) that activation in response to familiar cues and thoughts is largely automatic, as is its spread through a network, and (b) that activation requires down-regulation for goals to be accomplished. Activation was presumed to be equivalent across people and circumstances. Down-regulation was presumed to require inhibition and also to differ among individuals and across groups and circumstances so as to account for performance in a wide range of tasks.

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The Functions of Inhibition

The inhibitory framework suggests that an efficient (i.e., fast and accurate) mental life requires the ability to limit activation to information most relevant to one's goals. Inhibition is likely to be inefficient in older adults; in very young children; and for people operating under conditions of fatigue, reduced motivation, or emotional stress or at a nonoptimal point in their circadian arousal cycle (Hasher, Zacks, & May, 1999). Three functions of inhibition were proposed: (a) controlling access to attention's focus, (b) deleting irrelevant information from attention and working memory, and (c) suppressing or restraining strong but inappropriate responses. In this section, we review and provide some evidence on each of the proposed functions of inhibition.

Access

Early in the processing stream, inhibition functions to prevent irrelevant information from gaining access to the focus of attention. Deficits in access control enable distraction to influence the processing of target stimuli, sometimes by disrupting and at other times by facilitating performance, depending on the relation between the distractors and the targets. For example, older adults are differentially slowed in reading aloud when distraction is inserted in unpredictable locations in text (e.g., Carlson, Hasher, Connelly, & Zacks, 1995). The reduced ability to ignore distraction may also partially account for widely reported age differences in speed of processing. Several of the tests commonly used to assess speed (e.g., letter comparison) present a cluttered display with many items on each page. If older adults have difficulties preventing irrelevant information from gaining access to the focus of attention, this cluttered, distracting display might slow them down. Consistent with this hypothesis, reducing the clutter (by presenting the items one at a time) speeded older adults' performance by over 15% on computerized versions of several such tests (Lustig, Hasher, & Tonev, 2006; see Figure 8.1) but had no impact on the performance of younger adults.

Deficits in control over access can also improve performance. For example, May (1999) presented young and old adults with a problem-solving task in which target words were presented either alone or in the presence of distraction. When the distraction led toward a solution, older adults showed greater benefits than younger adults. More recent evidence suggests that older adults' greater tacit knowledge of distraction can actually improve their performance on subsequent tasks. For example, older adults showed priming for irrelevant words that were superimposed on pictures in the context of a picture identification task, whereas younger adults showed no priming for those same words (Rowe, Valderrama, Hasher, & Lenartowicz, 2006; see also Kim, Hasher, & Zacks, in press).

A frequent concern about inhibitory explanations is the degree to which the results reflect a deficit in inhibition of distraction as opposed to a failure to increase activation of relevant information. A number of findings suggest that activation processes are largely preserved, at least with age. For example,

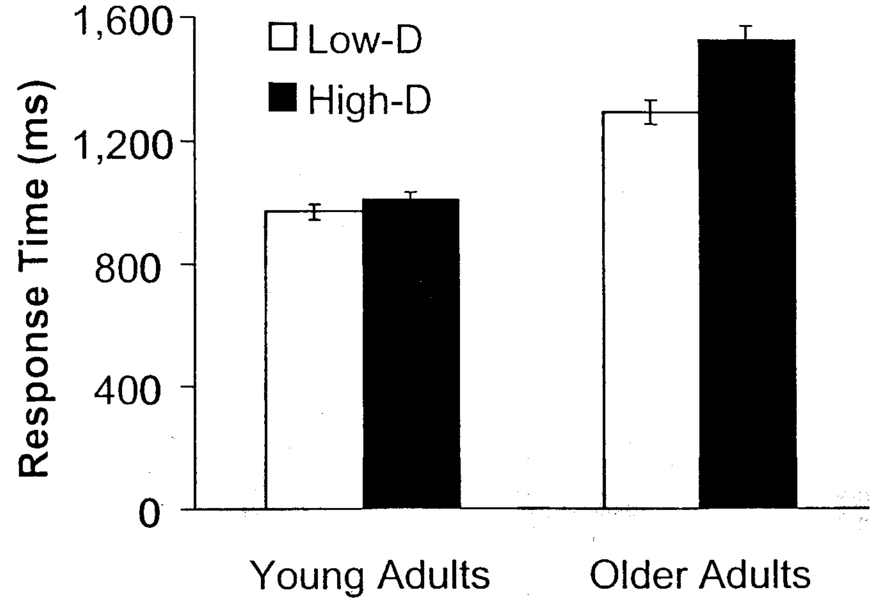

Figure 8.1. Effects of distraction on digit symbol performance. Data are from a computerized version of the digit symbol substitution test, part of the Wechsler battery (Wechsler, 1981) and a common measure of fluid intelligence. Young adults showed little or no effect of the distraction manipulation, whereas older adults were much faster in the reduced distraction (Low-D) condition. Error bars indicate standard error of the mean. Adapted from "Distraction as a Determinant of Processing Speed," by C. Lustig, L. Hasher, and S. T. Tonev, 2006, *Psychonomic Bulletin & Review, 13,* p. 621. Copyright 2006 by the Psychonomic Society.

older and younger adults do not differ on a variety of tasks entailing activation but little or no inhibition (e.g., categorization decisions, most repetition and semantic priming tasks; see Hasher et al., 1999).

Recent neuroimaging results using functional magnetic resonance imaging also support the idea of preserved activation and specific deficits in inhibition for older adults. Gazzaley, Cooney, Rissman, and D'Esposito (2005) asked participants to view alternating photographs of scenes and faces under conditions in which they were instructed to either (a) remember one category (e.g., scenes) and ignore the other (e.g., faces) and vice versa or (b) passively view faces and scenes. Under instruction to remember scenes, both younger and older adults showed at least equivalent activation, relative to the passive-viewing baseline, in the area selective for scene processing (the left parahippocampal/lingual gyrus). In contrast, although young adults showed substantially less activation during the ignore condition than during the passive-viewing condition, older adults showed equivalent activation across the ignore and passive conditions. The groups were equally able to increase activation to the scene information when it was relevant, but older adults showed a specific deficit in preventing the irrelevant scene information from gaining access to the stage of processing when it was irrelevant. Furthermore, only the degree of reduced activation under the ignore instruction predicted memory for scenes; heightened activation under the attend instruction did not do so, providing further evidence of the importance of age and individual differences in down-regulation.

Deletion

Inhibition also functions to delete irrelevant information from the focus of attention. Irrelevant information may be information that eluded the access function but was subsequently recognized as irrelevant, or information that relevant in a previous situation but that is not relevant in the current one. Both explicit and implicit directed forgetting procedures require participants to forget some information, sometimes in the service of better memory for relevant, to-be-remembered information. Older adults often produce more of the irrelevant information, especially relative to their production of relevant, to-be-remembered information (e.g., May, Zacks, Hasher, & Multhaup, 1999; Zacks, Radvansky, & Hasher, 1996), suggesting a reduced ability to down-regulate no-longer-relevant information.

The deletion function also appears to play an important role in estimates of working memory capacity. Such tasks typically present lists in an increasing order of length from shortest to longest (e.g., Daneman & Carpenter, 1980) or in a random order (e.g., Engle et al., 1992), setting the stage for recall of the longest lists to be vulnerable to disruption from any nonsuppressed material from earlier lists. When the longest sets are given first to younger and older adults, age differences in span are reduced and can even be eliminated (see Lustig, May, & Hasher, 2001; May, Hasher, & Kane, 1999; Rowe, Hasher, & Turcotte, 2006). In addition, scores derived from the reversed sequence procedure do not predict performance on a standard outcome measure (prose recall in Lustig et al., 2001). The typical age differences seen on working memory span tasks thus seem to be the product of a reduced ability to delete or suppress no-longer-relevant material rather than of age differences in mental work space (see also Bunting, 2006; Friedman & Miyake, 2004; Hedden & Park, 2003). That is, age differences in span may not reflect age differences in the size of the mental workspace per se as much as they reflect age differences in the ability to keep it free of irrelevant information and therefore use it effectively. Indeed, a recent study suggested that all of the age-related variance in standard working memory scores was accounted for by measures of the ability to regulate distraction (Hambrick, Helder, Hasher, Zacks, & Swensen, 2005).

Restraint

Perhaps the most-studied function of inhibition is to suppress or restrain strong responses that are inappropriate for the current situation. Go/no-go and stop-signal tasks are often used to study this function across different populations (children, young adults, old adults, people with brain damage or mental disorders) and are also popular in neuroimaging research. These tasks typically require participants to respond rapidly to all stimuli except a specific (no-go) stimulus, to which they are to withhold responding, or to respond rapidly to stimuli unless a signal (e.g., a tone) is presented that indicates no response should be made (Logan, 1994). These tasks seem to be strongly dependent on the dorsolateral prefrontal cortex regions that show pronounced changes with age (e.g., Raz, 2005). Parallel to the development of these structures, performance on stop-signal and go/no-go tasks improves from childhood through early adulthood and then declines (e.g., Bedard et al., 2002; Kramer, Humphrey, Larish, Logan, & Strayer, 1994). Age differences in the inhibitory component of these tasks appear to have a different developmental trajectory than do changes in overall response speed (Bedard et al., 2002).

Likewise, age differences in the ability to inhibit a strong but incorrect response are separable from the ability to activate and produce the appropriate response. May and Hasher (1998) asked participants to perform a category verification task (e.g., *furniture–chair*, with the correct response of yes; *furniture–hamburger*, with the correct response of no) as quickly as possible but to withhold responding on trials in which a tone was sounded after the category–item pair was presented. Although older adults were generally slower, their accuracy in making the category judgments was the same as that of the young adults. In contrast, older adults' ability to withhold a response on stop trials was significantly impaired. Furthermore, for older adults, deficits in restraint on the stop-signal task were correlated with deficits in restraint on two standard neuropsychological tasks (Stroop [Stroop, 1935] and Trails [Reitan & Wolfson, 1995]).

Age differences in restraint are evident on both low-level and high-level tasks. For example, the antisaccade task requires participants to look away from a cue that automatically attracts attention. Butler, Zacks, and Henderson (1999) found that older adults were more likely than younger adults to make errors by looking toward the attention-attracting stimulus rather than away from it. Restraint may also play a role in language processing if the context leads toward a strong but incorrect inference (see Yoon, May, & Hasher, 2000).

Inhibitory Failures: Not Just for Older Adults

Inhibitory deficit theory provides a theoretical framework for understanding which aspects of cognitive functioning change with age and which remain relatively stable. The theory is a general one, intended to cover a broad array of phenomena and people. Breakdowns due to aging or other disorders were proposed as extreme cases that would provide insights into inhibition's role in normal cognitive function, just as the performance of patients with amnesia provides important insights into memory.

Individual and group differences in inhibitory function may underlie many individual and group differences in cognition. Patient populations with inhibitory deficits provide even more extreme cases than those with normal aging (see chaps. 11, 12, and 13, this volume). Normal variation in academic achievement and intelligence scores is influenced by inhibitory abilities. This variation includes differences between individuals and between different developmental stages, as well as between those with specific reading and language difficulties (e.g., Chiappe, Hasher, & Siegel, 2000; Dempster & Corkill, 1999; Gernsbacher, 1997; Kail, 2002). To the degree that inhibitory abilities play a role in working memory span measures (see the preceding discussion), much of the work on high-span versus low-span college students can also be understood from the perspective of group differences in inhibitory function.

Circadian Influences

Inhibitory function may differ not only among individuals, but also within the same individual over different mental or physiological states. In particular, the circadian cycle is a significant source of intraindividual variation in inhibitory function. A wide variety of biological functions show regular circadian cycles, including those that are likely to affect the brain. These include the actions of cholinergic and catecholamine neurotransmitters that are likely to be especially related to attention and inhibitory function (Arnsten, 1988; Aston-Jones, Chen, Zhu, & Oshinsky, 2001). The functions of these systems also vary with age (Sarter & Bruno, 2004; Volkow et al., 1998). Further, there are age differences in the circadian function of these neurotransmitters, with older individuals frequently showing shorter, flatter, and often more irregular cycles (Edgar, 1994; Monk & Kupfer, 2000).

Circadian fluctuations in biological processes correlate well with responses on the Horne and Ostberg (1976) Morningness–Eveningness Questionnaire. This questionnaire classifies individuals on a continuum from *definitely evening* to *definitely morning* types. Membership in these categories appears to have a genetic basis and is associated with fluctuations in many physiological processes (e.g., Hur, Bouchard, & Lykken, 1998). In keeping with age differences in the circadian fluctuations of many physiological measures, distributions of scores change across adulthood: Most young adults identify as evening or neutral types, whereas the vast majority of older adults identify as morning types (e.g., Yoon et al., 2000).

Age–circadian interactions have been reported for all three functions of inhibition we described earlier in this chapter (Hasher et al., 1999). With respect to the access function, there is evidence that both the costs and benefits of distraction are greater at off-peak than at peak times of day (May, 1999; Rowe, Hasher, & Turcotte, 2006).

The deletion function also varies across the day, with greater effectiveness at peak than at off-peak times. For example, both young and older adults showed large effects of testing time in a sentence-based version of a directed forgetting task (May & Hasher, 1998). Participants first generated the likely ending to a sentence (e.g., "Before you go to bed, remember to turn out the _____"; with the correct response of *lights*) and were then told to remember a new, experimenter-provided ending instead (e.g., *stove*). During a subsequent implicit test, participants completed sentences that had a medium-range probability of being completed by either the self-generated, no-longer-relevant ending (e.g., "The baby was fascinated by the bright _____; correct response *lights*) or the experimenter-generated, to-be-remembered ending (e.g., "She remodeled her kitchen and replaced the old _____"; correct response *stove*).

Performance on the critical test varied with testing time and age. For participants tested in the afternoon (young adults' optimal time, older adults' nonoptimal time), young adults produced even fewer of the no-longer-relevant items than would be predicted by normative completion probabilities, whereas older adults produced a relatively large proportion of such items. For participants tested in the morning (young adults' nonoptimal time, older adults' optimal time), there were no age differences in the production of to-be-deleted items. Both groups produced more no-longer-relevant items at their nonoptimal time of day, indicating that this inhibitory function varies across the day.

The restraint function also shows strong circadian influences. Strong motor responses are less controllable at nonoptimal times, with more slips of action than at other times (e.g., Manly, Lewis, Robertson, Watson, & Datta, 2002). In the stop-signal task (May & Hasher, 1998), the usual age differences in stopping probability and efficiency were found for participants tested in the afternoon. However, there were no age differences for participants tested in the morning. These findings reflected a crossover interaction: Young adults showed their worst performance in the morning and best performance at the later testing time. In contrast, older adults showed their best performance in the morning and their worst performance in the late afternoon. Again, these patterns were limited to the aspects of the task that depended on inhibitory restraint. For the go trials, which did not make inhibitory demands, older adults were slower overall, but neither response time nor accuracy varied with time of day or interacted with age. Roughly comparable findings have been reported for old rats at the end of their activity cycle (Winocur & Hasher, 2004).

Time of day may also have a strong influence on social judgments and decision making. At nonoptimal times of day, people are more likely to be distracted by the peripheral aspects of a persuasive text, such as the status of the source or heuristics such as "the majority is always right," as opposed to processing the central meaning (Martin & Marrington, 2005). The tendency to judge people on the basis of stereotypes is also stronger at nonoptimal times (Bodenhausen, 1990). These effects might respectively be seen as reflecting failures in the access and restraint functions of inhibition.

Time of day effects seem to be strongest for inhibitory functions. Tasks that simply require activation do not show much variation with circadian phase. For example, completing sentences with high-probability endings did not change over the course of the day for either young or older adults, nor did response time in go trials of the go/no-go task (May & Hasher, 1998). Many other relatively simple speeded tasks also do not show circadian variation per se, although they do vary with related factors such as sleepiness (e.g., Graw, Krauchi, Knoblauch, Wirz-Justice, & Cajochen, 2004; Song & Stough, 2000). Even challenging tasks that require only activation, not inhibition (e.g., a difficult vocabulary test), do not vary over the day (e.g., May & Hasher, 1998). There is some suggestion that expertise in a domain (e.g., reading) may spare performance even when inhibition is required (Li, Hasher, Jonas, Rahhal, & May, 1998). These patterns fit well with a theoretical framework suggesting that inhibition, not activation, is a major source of variation in cognitive performance (Hasher et al., 1999).

Questions and New Directions

Inhibitory deficit theory provides a powerful framework for understanding variation in performance in healthy young adults, as well as more extreme examples due to developmental changes or disease. However, the development of this theory has not been without challenges. The following sections describe how the theory has evolved in response to critiques and new data while remaining true to its central tenets: Inhibitory processes are the major source of performance differences, whereas automatic activation processes are largely constant across individuals, groups, and situations. Inhibition serves goals by reducing the activation of one or more competitors for thought or action, enabling the selection of those consistent with objectives.

Defining Inhibition

Questions have been asked about what type of theory inhibition theory is (e.g., Burke, 1997). Zacks and Hasher (1997) borrowed the term *pragmatic* from Baddeley (1992) to describe their approach to theory building. This approach emphasizes general principles, nonreductionist reasoning, and verbal theory statements. The alternative, a formal computational modeling approach, has significant strengths, especially its precision in assumptions and predictions (see chaps. 5 and 9, this volume). The strength of the more informal, verbally based approach stems from its applicability across a wide variety of tasks that are sometimes seen as issues in themselves.

The term *inhibition* (like many other terms) is used differently across literatures and investigators, and this variation can result in misunderstandings and misattributions. Many researchers do not include the access and deletion functions of inhibition, reserving the term *inhibition* for the restraint-related functions involved in tasks such as the stop-signal procedure (e.g., Friedman & Miyake, 2004). Others collapse across the three processes we suggest, although the interdependence (or not) of these processes remains to be empirically determined. Ideas about potentially separable processes of inhibition are a relatively new research focus and are likely to undergo further development as more evidence (including that from neuroimaging and circadian dissociations) becomes available. At its core, inhibitory deficit theory is largely concerned with inhibition as an active, goal-directed process that acts in conjunction with automatic activation processes to control the contents of consciousness (Hasher & Zacks, 1988; Hasher et al., 1999; Zacks & Hasher, 1997).

Measuring Inhibition: Are Its Functions Related?

Concerns have also been raised over the attempt to find agreed-on, stable measures of inhibitory function (e.g., McDowd, 1997). For a time, negative-priming tasks were seen as promising candidates to measure inhibition, but they were quickly found to be quite complex, vulnerable to several influences (e.g., May, Kane, & Hasher, 1995; see also chap. 4, this volume), and not consistently reliable as an index of inhibition. A lack of stable, canonical measures has been especially troublesome for large-scale, individual-differences studies that attempted to statistically derive factors on the basis of shared variance among multiple tests that putatively converge onto a hypothesized construct (e.g., Salthouse, Atkinson, & Berish, 2003).

At least three factors may contribute to the difficulty of finding inhibitory measures with good psychometric properties (for a similar list, see Friedman & Miyake, 2004). First, inhibitory deficits by their nature lead to performance that changes across trials. Furthermore, the degree of change varies according to the severity of an individual's inhibitory deficit. Such cross-trial variation may be an especially important factor for the deletion function. Failures to delete irrelevant information from prior trials lead to greater and greater buildup of proactive interference across trials, with a steeper slope of decline for individuals who are poor at deletion. Furthermore, failures in deletion can also lead to cross-task contamination (Lustig & Hasher, 2002), especially if the tasks use similar materials. The opposite problem may also come into play, especially for the other functions of inhibition: As participants become practiced at the task, they may become more skilled in exercising inhibition, or they may find alternative, idiosyncratic strategies to solve the task without using inhibition (Davidson, Zacks, & Williams, 2003).

Second, tasks are not process pure (Jacoby, 1991), and individuals may differ in which functions they emphasize or at which stages of processing. For example, in the Stroop task, the word information is irrelevant and is to —be inhibited, whereas the ink color information is relevant. Participants may both try to prevent the word information from gaining access to consciousness and, to the degree that access control fails, may have to restrain themselves from responding on the basis of word information as opposed to ink color.

Third, until recently, many studies did not recognize the different functions of inhibition, reducing the chances of finding shared variance. One task that loads highly on deletion and one that emphasizes restraint might well be expected to share less variance than two tasks that both make high demands on the restraint function. In earlier studies, all of these tasks would be considered to measure a single construct, inhibition, although many authors have proposed multiple mechanisms (e.g., Dempster, 1993; Nigg, 2000; see also chap. 13, this volume).

More recently, there have been attempts to assess the different components of inhibition (e.g., Friedman & Miyake, 2004) using multiple measures of each component process to create latent variables, followed by structural equation modeling. The Friedman and Miyake components do not entirely agree with the Hasher and Zacks functions discussed in this chapter. For example, resistance to proactive interference was used as a measure of inhibition, but from the present framework, it is an outcome (of reduced control over access and deletion). The latent variable approach is extremely valuable for assessing the existence of separate inhibitory functions, their interrelations across adulthood, and their impact on various outcomes.

The idea of related, but separable, inhibitory functions is an important theoretical and methodological development. However, it is also relatively recent, and many questions remain. How many functions of inhibition are there? Are they related, and if so, how? Do the functions of inhibition map directly onto specific mechanisms? What are the biological bases of the shared and distinct aspects of inhibitory function?

Preliminary answers to these questions may be emerging. For example, there is evidence that populations with deficits in one inhibitory function also tend to have deficits in others, although the degree to which different functions are impaired may vary (e.g., Barkley, 1997; Chiappe et al., 2000; Faust & Balota, 1997; Spieler, Balota, & Faust, 1996; Stuss et al., 1999). Studies of healthy college students indicate related but separable constructs (e.g., Friedman & Miyake, 2004), as do studies of circadian variations in both young and old adults (Hasher et al., 1999; West, Murphy, Armilio, Craik, & Stuss, 2002). Data from recent neuroimaging studies also support the idea of a small number of inhibitory functions that are related but distinct.

A growing body of evidence suggests that different inhibitory functions tap a common network that includes anterior cingulate cortex, dorsolateral prefrontal cortex, inferior frontal gyrus, posterior parietal cortex, and anterior insula (Nee, Wager, & Jonides, 2005; Nelson, Reuter-Lorenz, Sylvester, Jonides, & Smith, 2003; Sylvester et al., 2003; Wager et al., 2005).[1] These regions are found in common both in single studies that test the same participants on multiple tasks (Sylvester et al., 2003; Wager et al., 2005) and in meta-analyses that compare across experiments (Nee et al., 2005).

Different functions of inhibition also show distinct regions of activation. For example, Sylvester et al. (2003) compared task-switching activations (possibly requiring the deletion of one task set to focus on another) with activations associated with response inhibition or restraint (responding in the opposite direction of a given cue). In addition to the common network, the deletion task also activated the left prefrontal and left parietal cortex; the restraint-related task showed preferential activation for more medial, subcortical regions and the frontal polar cortex (for similar results using different tasks, see Nelson et al., 2003).

In summary, a common network of regions is shared across tasks that differentially emphasize the different functions of inhibition. There is at least heuristic similarity across experiments in the distinct regions activated for different functions of inhibition, with some variation that may be due to specific task demands, materials, and baseline conditions. A meta-analysis that included restraint-related tasks such as go/no-go, Stroop, and response-compatibility tasks reached similar conclusions, with medial regions largely in common and some variation in lateral regions across different types of task (Nee et al., 2005). Attempts to understand the shared and independent aspects of different inhibitory functions hold a great deal of promise for future research.

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[1] These authors used the theoretically neutral term *interference resolution* in describing their data. Our use of terms related to different inhibitory functions (*access*, *deletion*, *suppression*) is a reinterpretation of the data in light of the current discussion of inhibitory deficit theory. However, it is interesting that these studies often subtract out activation from conditions that presumably require intentional, goal-oriented processing but do not make strong demands on inhibition (e.g., positive trials in Nelson et al., 2003).

Activation, Goals, and Compensation

Critiques of the inhibitory view often question the degree to which performance differences can be ascribed to inhibition as opposed to a failure to activate relevant information. Hasher et al. (1999) pointed out that failures to activate information are unlikely to be the sole cause of age differences in performance: Across several different tasks (directed forgetting, repetition priming, garden path sentences, garden path paragraphs), older adults showed, if anything, greater activation of information than did young adults (Hamm & Hasher, 1992; May, Zacks, et al., 1999; Zacks et al., 1996). The neuroimaging data of Gazzaley et al. (2005) are also consistent with this view. When told to remember scenes, older adults showed activity at least as strong as that of young adults in brain regions involved with scene processing. However, although young adults reduced activation in these regions when told to ignore scenes, suggesting that they were suppressing the processing of scene information, older adults did not. Further, as expected from inhibition theory, individual differences in suppression, not activation, predicted memory performance.

By now, greater or more distributed activation by older than by younger adults is a common neuroimaging finding in both frontal and posterior regions (for a recent review, see Reuter-Lorenz & Lustig, 2005). Additional activations are often interpreted as reflecting compensation, but there are several examples of greater activation being associated with poorer performance, either between young and old adults or within a sample of older adults (e.g., Madden et al., 1999). Whether greater activation reflects compensation or inappropriate processing likely differs by task and region (for a review of these interactions, see Rajah & D'Esposito, 2005).

New data on task-related deactivations and "default-mode" processing also suggest a specific inhibitory deficit in older adults. A network of regions, including the posterior cingulate and medial frontal cortex, are more active during unconstrained, no-task conditions than during cognitive tasks (Shulman et al., 1997). These regions show below-baseline activation (deactivation) during active, cognitively demanding tasks and are inversely correlated with positive activations in prefrontal regions involved in task performance (Fox et al., 2005). The deactivation of these regions during active tasks is thought to reflect a switch from unconstrained, largely self-directed thinking (e.g., thinking about one's day, monitoring one's comfort and internal state) to a focus on the task (Raichle et al., 2001). Young adults deactivate these regions more as tasks become more difficult, and greater deactivation has been associated with better performance (Daselaar, Prince, & Cabeza, 2004; McKiernan, Kaufman, Kucera-Thompson, & Binder, 2003).

Older adults show impaired deactivation of these regions, even in situations in which they show frontal activations as great as or greater than those of young adults (Lustig et al., 2003; Persson, Lustig, & Reuter-Lorenz, 2005). Age differences in deactivation are apparent even by middle age and increase across the life span (Grady, Springer, Hongwanishul, McIntosh, & Winocur, 2006). For example, Lustig et al. (2003) found that older adults activated the left frontal cortex to an even greater degree than did young adults during a semantic decision task. However, in regions that show deactivation in young adults, older adults showed little or no modulation. Time courses of activation (see Figure 8.2) showed that young adults quickly suppressed activation in these regions, whereas in older adults, activation was roughly constant during both task and baseline (fixation) conditions. Persson et al. (2005) found that failures to deactivate correlated with interference effects on a verb-generation task. Although other interpretations are possible (baseline differences, compensation), these data are consistent with the idea that older adults have difficulty inhibiting default-mode processing—despite an apparently spared ability to activate regions associated with task performance.

Questions have been raised about the degree to which performance on different tasks reflects inhibition as opposed to other processes, such as goal maintenance (e.g., Braver et al., 2001; see chaps. 1 and 7, this volume). Older adults can fail to deactivate task-irrelevant regions, even when regions related to the task are robustly activated (Lustig et al., 2003, Persson et al., 2005). This pattern seems inconsistent with the idea that older adults are not able to successfully activate and maintain goal-directed behavior. Likewise, older adults may maintain task-irrelevant information even when they show task-relevant performance (requiring goal maintenance) similar to that of young adults (e.g., Hamm & Hasher, 1992). Furthermore, individual differences analyses from the Gazzaley et al. face–scene suppression task indicate that suppression, not activation, is related to measures of working memory capacity for both young and old adults (Gazzaley, Cooney, Rissman, et al., 2005; Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005).

It has been suggested that working memory capacity is intrinsically linked to goal maintenance and that goal maintenance in turn is the determining factor in inhibitory performance (see chap. 7, this volume). However, Hester, Murphy, and Garavan (2004) identified several brain regions that were sensitive to both working memory load and inhibition demands, but they also identified regions uniquely associated with inhibition. Data from the think/no-think procedure (see chap. 5, this volume) also seem incongruent with the idea that inhibition is isomorphic with goal maintenance. In this procedure, participants first learn arbitrary paired-associate pairs (e.g., *ordeal–roach*). During each test trial, they are presented with a cue word and asked either to retrieve its paired associate from memory or to avoid thinking of the associate during the trial. Presumably, both of these conditions require effortful processing and attention to the goal. Indeed, on an a priori basis, one might predict that the retrieval (think) condition should be the one more dependent on effortful, goal-directed processing. However, Anderson et al. (2004) identified several prefrontal and hippocampal regions that were more active during the no-think condition, which required inhibition of the associate. Furthermore, activation in these regions was correlated with subsequent forgetting, as revealed on a later memory test. These patterns support the idea of active, effortful inhibition over and above the goal maintenance required in the think condition.

This is not to say that goals are unimportant. Indeed, inhibitory deficit theory proposed that inhibition operates in the service of goals, that these goals might differ between individuals and groups, and that these differences might have consequences for behavior (Hasher et al., 1999; Hasher & Zacks, 1988). Hasher and Zacks (1988) proposed that older adults may emphasize

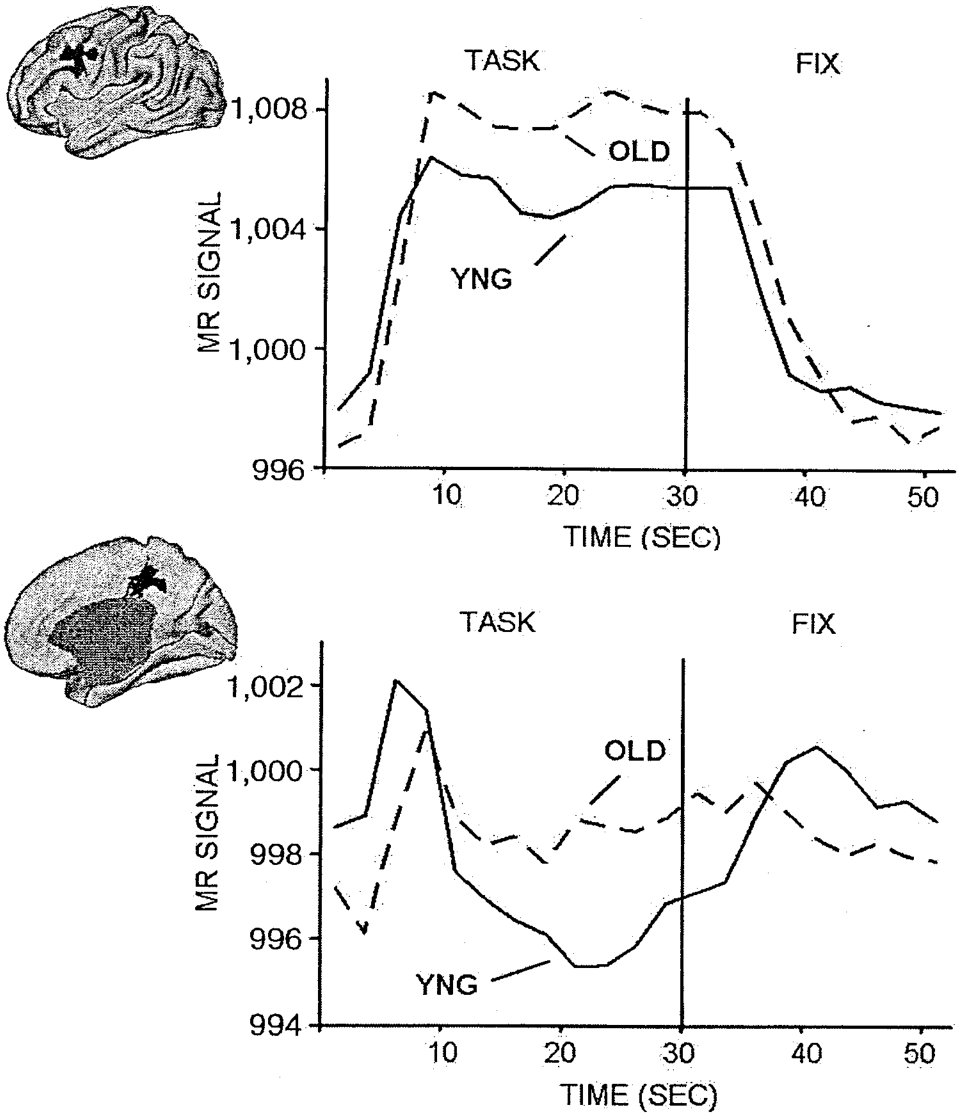

Figure 8.2. Time course of brain activation during a block design study in which people alternated between an active task (semantic decision) and staring at a fixation. Older adults showed successful frontal activation that was, if anything, greater than that of young adults (top panel). Young adults showed the typical pattern of deactivation (suppression during the task as compared with the baseline [fixation] condition) in a posterior cingulate region (bottom panel). Deactivation magnitude was reduced in older adults. MR = magnetic resonance; OLD = older adults; YNG = young adults; SEC = seconds. Adapted from "Functional Deactivations: Change With Age and Dementia of the Alzheimer Type," by C. Lustig, A. Z. Snyder, M. Bhakta, K. C. O'Brien, M. McAvoy, M. E. Raichle, et al., 2003, *Proceedings of the National Academy of Sciences, USA, 100,* p. 14506. Copyright 2003 by the National Academy of Sciences, USA.

personal values and relationships over objective task performance. As a result, they may integrate this information into their processing or perform better on tasks that make use of such processing. Recent work on socioemotional selectivity theories of aging is highly congruent with this idea (e.g., Carstensen & Mikels, 2005).

Older adults often perform as well as or even better than young adults if tasks are presented in ways that are consistent with their goals and personal experience (e.g., Kim & Hasher, 2005; May, Rahhal, Berry, & Leighton, 2005). Inhibitory deficits may also lead to changes in goals and strategies. For example, if retrieval of specific, task-relevant information is impaired because the cue for that information is also associated with irrelevant, interfering information, individuals may increasingly rely on immediate cues in the environment to control their response. Such a strategy shift should lead to more gist-based processing and intrusions of related but incorrect information—performance patterns that are typical of older adults and others thought to have poor inhibitory function (Hasher & Zacks, 1988).

Conclusion

Hasher and Zacks (1988) made a simple, if controversial, proposal: Inhibition of information irrelevant to one's goals is a major contributor to performance and to differences among individuals and groups. As our overview in this chapter suggests, there is strong evidence for this view from a variety of behavioral tasks as well as from emerging evidence in the neuroimaging literature. New applications of statistical methods and neuroimaging techniques may help resolve some of the difficulties caused by different uses of the term *inhibition* across investigators and the fact that tasks are not process pure. Of course, such issues are not exclusive to the idea of inhibition but rather apply to nearly all putative mechanisms, particularly those that are general or high level in nature. Challenges for the future include a more precise definition of inhibitory functions and their relations and further integration with neuroimaging findings and research on goals. Our reading of the current evidence, including evidence offered in this book by us and other authors, is that inhibition—from the Hasher and Zacks perspective as it has developed over the years—is alive and well and extremely useful.

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