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Cognition through the lifespan: mechanisms of change

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Cognitive abilities rise steeply from infancy to young adulthood and then are either maintained or decline to old age, depending on the specific ability. This pattern suggests corresponding continuities of mechanism and process, but it is striking that the fields of cognitive development and cognitive aging make little contact with each other's methods and theories. In this review we examine reasons for this cultural separation, and show how recent findings from both areas fit a framework couched in terms of cognitive representation and control. These two broad factors have very different lifespan trajectories; consideration of their relative growth and decline makes it clear that cognitive aging is not simply 'development in reverse'. This framework is offered in light of recent interest in finding greater continuity throughout the lifespan and creating a more comprehensive explanation of cognitive function and cognitive change.

Introduction

There is symmetry to our physical lives: we are independent and robust in youth and middle age, but dependent and frail in infancy and old age. On the surface, cognition appears to follow the same general pattern of building up and wearing down. In the brain, too, the consolidation of networks in infancy and early childhood is mirrored by the reduction of connectivity and structural atrophy in older age (Box 1). In all these cases, there is a vulnerability in youth and old age that is not present in the middle of life. However, the conclusion that cognitive aging is 'development in reverse' is an oversimplification of a dynamic that unfolds over the lifespan, fuelling the changes that are reflected in distinct types of cognitive ability at different times of life. In the brain, for example, similar behaviors in older and younger adults are often mediated by different neural circuits [1,2]. Our purpose in this article is to propose a framework for examining changes in cognition over the lifespan and consider the implications of that framework for conceptions of cognition and the factors responsible for its change.

There are remarkably few integrated accounts of lifelong changes in cognitive ability, making the exceptions particularly noteworthy. For example, in a dynamic view of lifespan development, Baltes and his colleagues [3,4] have stressed that change can occur at any time, that development depends on interactions among genetic, environmental and social factors, that all processes of development entail both gains and losses, and that the relative mixture of biological and social-cultural factors change with age. From a different perspective, Salthouse [5,6] has shown that processing speed increases from infancy to young adulthood and then declines from the twenties to old age; he has argued that this general slowing is the primary cause of age-related declines in cognitive performance. Aside from these exceptions, the fields of cognitive development and cognitive aging have shown little contact.

An integration of the processes of cognitive change in development and aging is essential to the construction of a comprehensive account of the structure of cognition and the factors that influence cognitive performance. The details of cognitive change at each end of the lifespan are now sufficiently known that a broader perspective can be applied. However, a lifespan description of cognitive change requires more than a simple blending of the two fields. Taking language as an example, vocabulary and grammar develop through childhood with only small age-related losses from age 70 on [7]. But aging brings problems of *access* to stored information, even if there is no decrease in knowledge. The most common memory complaint of older adults is their difficulty in recalling names and words that are specific labels [8]. This information has not been lost from memory, as it can be retrieved later either spontaneously or with better cues. Therefore, although knowledge deficiencies are associated with both development and aging, the limitation in children is due to incomplete acquisition whereas the limitation in old age is associated with difficulties of access. Such asymmetries need to be explained.

Representation and control in lifespan cognition

Our proposal for a more comprehensive explanation of cognitive change is that processes concerned with representation, control, and their interaction evolve across the lifespan and determine cognitive ability. *Representations* are the set of crystallized schemas that are the basis for memory and knowledge of the world; *control* is the set of fluid operations that enable intentional processing and adaptive cognitive performance (Box 2). These systems are interactive: representations of the world are not constructed randomly but are selected on

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Box 1. Brain changes in development and aging

Although all 10 billion or so neurons constituting the human brain are present at birth, the brain increases in size and weight between infancy and adulthood by a factor of 4 or 5, owing to the explosive growth of synaptic connections between neurons (gray matter) and to myelination of nerve fibers (white matter). In general, the volume of gray matter in the cortex increases until adolescence, reflecting the growth of synapses but then decreases after adolescence reflecting synaptic pruning. This pruning is largely determined by environmental influences and represents learning. Gray matter volume therefore shows a U-shaped trend developmentally, whose peak age varies across brain regions – about age 12 for frontal and parietal lobes, age 16 for the temporal lobe, and age 20 for the occipital lobe [33]. The rapid rise in gray matter volume is followed by a much slower decline from age 20 to senescence, reflecting further synaptic pruning and neuronal atrophy. Changes in gray matter density also signal learning: Mechelli and colleagues reported a correlation between gray matter density in the left inferior partietal cortex and proficiency in a second language [55]. Whereas gray matter changes are shaped by the environment, white matter changes are largely under genetic control. Myelination starts before birth in the phylogenetically older regions of the brainstem and spinal cord, and proceeds through subcortical to cortical structures. In the parietal cortex, myelination continues through to adolescence, and in the frontal cortex the process is not completed until the thirties. Thereafter, the negative effects of aging work in reverse, with white matter in the frontal lobes most vulnerable to atrophy and to damage from failures of the vascular blood supply.

Efficient cognitive functioning depends on the degree of myelination and integrity of white matter, on the density and richness of synaptic connections, and on the specificity of synaptic pruning caused by fruitful interactions with the external environment. In childhood, regions of the brain mature at different times, culminating in development of the prefrontal and lateral temporal areas responsible for higher associative thought, the last type of cognitive ability to become established [34]. In older age, deterioration of the brain begins primarily with the frontal regions [35,37]. Similarly, cortical activation in young children tends to be bilateral until greater expertise is achieved and the activation becomes more focal and lateralized [56]; older age is again characterized by a more bilateral pattern of activation than that found for younger adults [2]. In neither case is the maturation, deterioration or activation of specific brain regions a sufficient explanatory mechanism for cognitive change. Neither does the trajectory of a single development process adequately account for cognitive change across the lifespan. Dissociations in the development and decline of white matter and gray matter, combined with dissociations in the maturity and functioning of specific brain regions and networks, underlie changes in cognitive performance across the lifespan and obviate the possibility of linking cognitive change to a single function in the developing brain.

the basis of needs and desires. In turn, these representations influence the further selection of schema-relevant information from the outside world, thereby demonstrating control. In this way, control processes determine the construction of representations, and these representations later play a part in further controlled processing. We assume that representational knowledge increases markedly during childhood, continues to accumulate at a slower pace throughout adulthood, but remains relatively stable in old age. This is the pattern depicted for 'crystallized' intelligence or 'cognitive pragmatics' in Figure 1b. By contrast, cognitive control increases in power, speed and complexity from infancy to young adulthood, and declines thereafter, as shown for 'fluid' intelligence or 'cognitive mechanics'. An example of the interaction of representation and control is the suggestion

Box 2. Two general factors in intelligence

There is widespread agreement that two general factors underlie intelligent thought and action – one representing accumulated knowledge of the world and the other representing the ability to use that knowledge flexibly and adaptively. The best known version of this approach is the notion that general intelligence comprises crystallized intelligence and fluid intelligence [57–59]. *Crystallized intelligence* (Gc) depends on learning and cultural influences and reflects experience, breadth of knowledge, comprehension, judgment and wisdom, whereas *fluid intelligence* (Gf) indicates the ability to identify complex relations and to draw inferences on the basis of that comprehension, as measured by cognitive tasks in which general knowledge plays little part. Researchers have noted that these follow different trajectories across the lifespan, with Gf declining from the mid-twenties on, and Gc rising until age 70 or so [60,61]. Similar ideas have been developed by Paul Baltes and his colleagues in their lifespan theory, which distinguishes between neurobiological *mechanics* (genetic inheritance, maturation and decline of neurological processes, etc.) and socio-cultural *pragmatics* [3,4]. These two sets of influences interact in a reciprocal fashion across the lifespan, resulting in a dynamic and adaptive balance at all ages. Unlike traditional theories of cognitive development, there is no stable 'endstate' that the organism aspires to; rather, the continuing dynamics allow the possibility of growth and change at all stages of life, although different factors are dominant at different ages. Declining biological efficiency also limits the effects of socio-cultural influences at older ages, so more social and environmental input is required to maintain stability. A schematic rendering of these ideas, and their relations to the notions of Gf and Gc is shown in Figure 1 in the main text.

by Braver and colleagues [9] that working memory selects aspects of existing representations to act as a kind of internal context to support relevant processing operations. Our suggestion is that control is not a disembodied abstract construct but constrains the particular way in which representations can be used.

Age-related changes in sensory and motor processes contribute a third component to cognitive development and decline. It has been found for example that the efficiency of these processes correlates highly with general cognitive functioning in both childhood and aging [10,11]. Although we will not discuss their contributions in depth, it is important to bear in mind that changes in these elementary 'biological mechanics' are essential precursors of change in both representation and control. In the remainder of this article, we consider changes in representation and control separately, and then explore the consequences of their interaction.

Lifespan changes in representation

It is generally agreed that humans encode and store relevant aspects of the external world and that these internal systems of knowledge representation are organized hierarchically and have evolved phylogenetically, but still permit access to earlier or simpler systems [12,13]. For example, Nelson [14] traces the development from sensori-motor learning in infancy, through social development and the development of systems of symbolic representation, to a representational stage she describes as historical and metacultural – that is, the child learns to adopt an objective, impersonal stance when absorbing

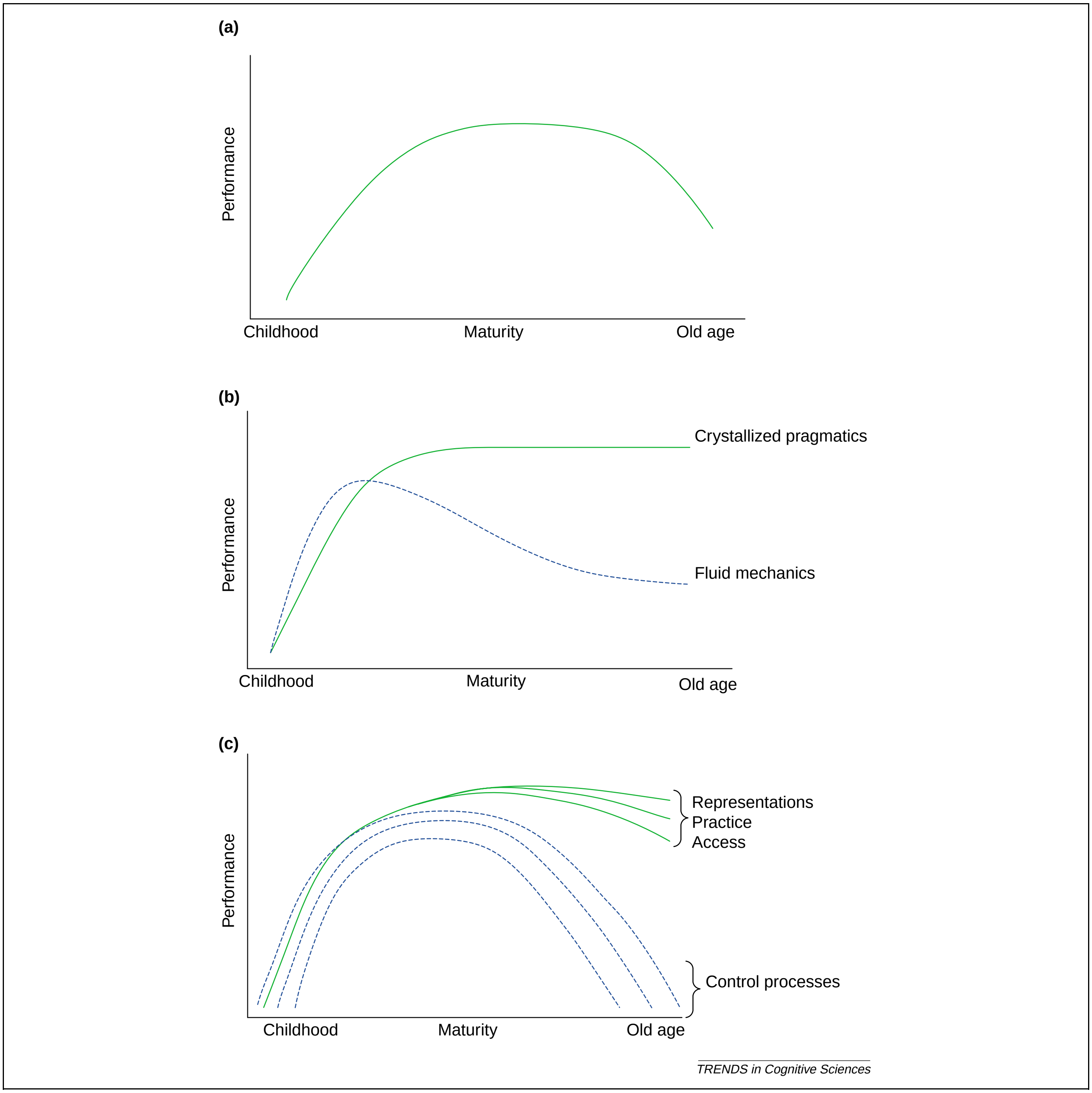

Figure 1. Three speculative models of cognitive change across the lifespan. **(a)** A single 'mirror-image' view; performance rises in childhood, is maintained in middle age and declines in late adulthood. **(b)** The different lifespan trajectories of crystallized intelligence ('cognitive pragmatics') and fluid intelligence ('cognitive mechanics'); the former is well maintained at older ages whereas the latter declines. **(c)** A more realistic version of (b), in that representations are generally well maintained at older ages, but some knowledge is either lost (especially with lack of practice) or becomes inaccessible. Control processes develop at different ages and also decline differentially, depending in part on the brain areas involved.

facts and general world knowledge. These stages emerge successively, but following Donald [12], Nelson stresses that all levels of representation remain available, to be used as the learning context demands. This type of explanation in terms of emerging systems of representation was first proposed by Piaget: Piagetian schemes (which are representations) begin as sensori-motor responses, then organize themselves hierarchically into more complex routines, then become symbolic but remain limited by their need for environmental support, and finally evolve as abstract representations that can be contemplated even in the absence of the relevant contextual reference. Although few researchers agree with the details of Piaget's theory, his emphasis on representational development and its evolution into complex and abstract systems remains a prototype for theories of cognitive development.

The importance of context to support representations changes across the lifespan. As Piaget noted, the external context is a necessary component of early behavior, not only during learning, but also in evoking learned responses. Rovée-Collier's ingenious demonstrations of infant learning [15] fall into this category, as do Bauer's experiments [16] with young children learning event sequences. Reinstatement of context becomes progressively less important as higher-order representational systems are used, but is necessary again in the elderly for successful retrieval of information [17].

Representations change not only in their type and their dependence on environmental support, but also in their specificity or detail. For example, language acquisition begins with lexical items that serve general meanings (e.g. 'doggie' used to refer to all animals) and evolves both in specificity (separate words for 'dog', 'cat' and 'cow') and abstraction ('animals' as a common category for dogs, cats and cows). As well as this linguistic differentiation, the growing child establishes separate domains of knowledge and differentiates the concepts within each domain [18,19]. As Nelson points out, the gradual formation of a schema representing 'the self' is central to the child's perception and understanding of the world and to the development of autobiographical memory – the representational record of personal experiences [14].

The acquisition of language illustrates a representational system that develops rapidly in childhood and is maintained into older adulthood [7,20,21]. Other examples include general knowledge [22], procedural skills such as playing musical instruments [23], and high-level games such as chess and bridge [24]. These representations remain stable throughout life, but with three qualifications. First, although there is good retention of existing representations, the formation of *new* representations becomes problematic for older adults [25]. Second, the maintenance of both declarative knowledge and procedural skills depends on frequency of use and continuing practice, especially for high levels of skill such as those achieved by musicians [23]. Third, representations depend on access to adequate levels of control, a point we elaborate in the section on expertise.

An important premise in this account is that representational systems are hierarchically organized: general, conceptual, context-free knowledge occupies the higher levels, and specific episodic instances [14,17], lexical and phonological information [26], and category exemplars occupy the lower levels. Access to the different levels develops asymmetrically over the lifespan: children have good access to the lower levels and gradually build concepts at the higher levels whereas older adults retain access to these higher conceptual levels but progressively lose access to the lower levels, resulting in failures of name and word finding, and episodic recollection [26–28]. This account is consistent with the notion of 'de-differentiation' proposed by Baltes, Lindenberger and their colleagues [29,30]. Just as knowledge systems differentiate into sub-domains in childhood, the process reverses in the later stages of the lifespan such that use of these sub-domains is impaired and finally lost. Other researchers reject the notion of de-differentiation, simply suggesting instead that some processes remain stable in old age whereas others decline in efficiency [31]. The extent to which these age-related losses reflect changes in *access* or loss of representations themselves is a question for future research.

Lifespan changes in cognitive control

The frontal lobes of the brain play a major role in planning, decision-making, conflict resolution, and executive functions. For example, some patients with extensive frontal lesions show automatic 'utilization' behaviors in which responses are dominated by the current context (e.g. the sight of sewing materials will induce sewing; a plate of food will induce eating) suggesting that control has reverted to the external environment [32]. The frontal lobes are the last cortical areas to mature in children [33,34] and among the first to be impaired in aging [35]; it would therefore be expected that frontally mediated executive functions should show a gradual development in children and a gradual decline in the course of aging, with young children and elderly adults being most influenced by the external environment. The literature generally supports this assumption [36,37]. The essential task of executive functions is to overcome the prepotent 'default mode' of automatic behavior [38] and allow the person to attend selectively, to concentrate on a particular task, to make choices in line with current goals, and to facilitate new learning and adaptive responding. This overriding of predominant response tendencies is typically accompanied by conscious awareness, linking executive functions to the notion of working memory [39,40].

The working memory component of executive functioning is already apparent in the first year of an infant's life. In the 'A-not-B' task, originally documented by Piaget, an interesting object is shown to an infant and hidden repeatedly in one location (A), from which the child successfully retrieves the toy. On the test trial, the infant watches as the object is hidden in a new location (B), but infants of up to 8–12 months still reach out to location A to retrieve it. One account of how success is achieved is that the child becomes able to hold the new location in working memory [36]; in another account, the learned response of reaching to A is highly accessible and so dominates responding until the controlled process of recollection develops to override the 'accessibility bias' of previous trials [28]. In both cases, the developing child gradually gains cognitive flexibility and independence from the here-and-now, in part through a growing ability to overcome 'attentional inertia'. In general, the stronger the pull of the current situation, the later the age at which the appropriate control develops. Thus the ability to overcome the natural tendency to move the eyes towards a visual target appearing briefly in peripheral vision, and instead move the eyes rapidly *away* from it, does not develop until the age of 6 or 7 years [41]. The developments responsible for these improvements in control include the increasing ability to inhibit attention to irrelevant stimuli, to maintain task set and select choices in line with current goals, to hold information in working memory, and to reflect on integrated higher-order rules [42]. These allow the older child to act flexibly and adaptively and override the prepotent influences of environmental tendencies. Just as representations differentiate into progressively more specific subdomains,

Box 3. Influence of bilingualism on cognitive control

The efficiency with which cognitive control can direct performance in executive function tasks has been shown to respond to practice, improving children's ability to direct attention after training [62]. Naturally occurring experience can have the same effect: video game players have demonstrated better cognitive control than non-game players on a series of visual attention tasks [63,64]. For bilinguals, the need to monitor attention to two competing but active language systems [65] provides the stimulus for the constant practice of attentional control. If the mechanisms used by bilinguals to control attention to their two language systems recruit the same control processes as those needed to solve nonverbal tasks of executive control, then the experience of constant use should make bilinguals more efficient than monolinguals when these processes are required in a variety of tasks and situations.

A growing body of research supports this claim. For children between the ages of about 4 and 8 years, bilinguals are more advanced than monolinguals of comparable intelligence in solving problems of attentional control, especially when the problem includes misleading or conflicting perceptual cues [66,67]. The bilingual children generally perform at the level of monolingual children who are approximately one year older. Moreover, these advantages have been shown to extend throughout life; in older age, the decline of these processes is less severe for bilinguals, producing an increasing gap between the performance of bilinguals and monolinguals in these situations [68,69].

control first emerges as the simple ability to override the perceptual present but then differentiates into more complex higher-level abilities [41].

Cognitive control peaks in the late teens and early twenties and declines with aging, although this decline is modulated by various factors – genetic endowment, health, fitness, and exposure to trauma being obvious examples. A further factor is bilingualism; recent research has shown that bilingualism enhances cognitive control in children and retards its rate of loss in older adults (see Box 3). One demonstration of lifelong changes in cognitive control comes from studies of task switching in which participants respond to stimuli on the basis of one of two rules, such as 'respond to color/shape', or 'respond on the target side/non-target side of the display'. The rule is either maintained for a complete block of trials or switched from trial to trial within a block, and there are various effects associated with switching. *Specific switch cost* is the difference in response speed between successive trials that require a switch to the other rule; *general switch cost*, or 'mixing' cost, is the difference in response speed between trials presented in a mixed block containing two rules and single blocks containing only one. Most studies have shown that general switch costs increase from younger to older adults but specific switch costs show no age-related trend when age-related slowing is factored out, especially if the switches are predictable rather than random [43–45]. Recently, Reimers and Maylor demonstrated these different age-related trajectories for general and specific switch costs in a sample of over 5000 individuals (Figure 2). One suggestion for why a U-shaped trajectory is found only for general switch costs is that these require the individual to maintain two opposing task sets in working memory simultaneously, and working memory is at optimal efficiency in young adulthood [41]. An alternative view is that in mixed blocks each stimulus evokes two competing response tendencies, requiring good control mechanisms to ensure correct response selection [43,46].

Other studies have replicated the pattern of decline in executive processing over the adult years using such paradigms as the Wisconsin Card Sorting Task [47], task coordination [48] and inhibitory control [49]. There are further demonstrations of inverted-U control functions co-existing with age-invariant measures of automatic

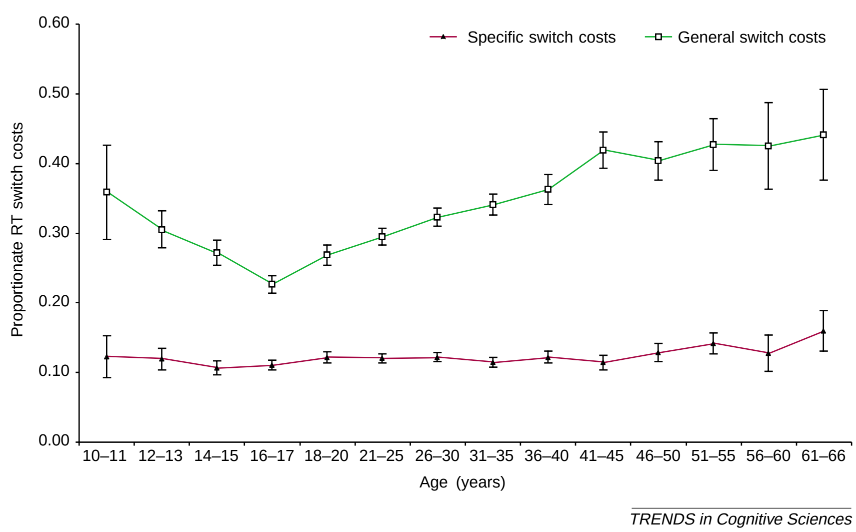

Figure 2. Over 5000 participants whose ages ranged from 10 to 66 years performed a task-switching experiment on the Internet. On each trial, one of 4 faces was displayed on the computer screen; a happy female, a sad female, a happy male or a sad male. The participant's task was to classify each face as quickly as possible by either gender or emotion. Blocks of trials contained either a constant single instruction (e.g. all were gender) or alternated between instructions in a repeated AABB design. Two measures of executive control were calculated: General switch costs (sometimes called 'mixing costs') reflect the difference in classification times between trials in the switching block and trials in the single task blocks; specific switch costs reflect the difference between switch (AB or BA) and non-switch (AA or BB) trials in the switching block. The values shown in the figure are proportionate costs; that is, response reaction times (RTs) were divided by baseline RTs. The baseline for general switch costs was non-switch block RT, and the baseline for specific switch costs was RT for non-switch trials in a switching block. Error bars are standard errors of the mean. The data show very little change in specific switch costs across the age range studied, but a strong quadratic trend relating age to general switch costs. Reproduced with permission from [44].

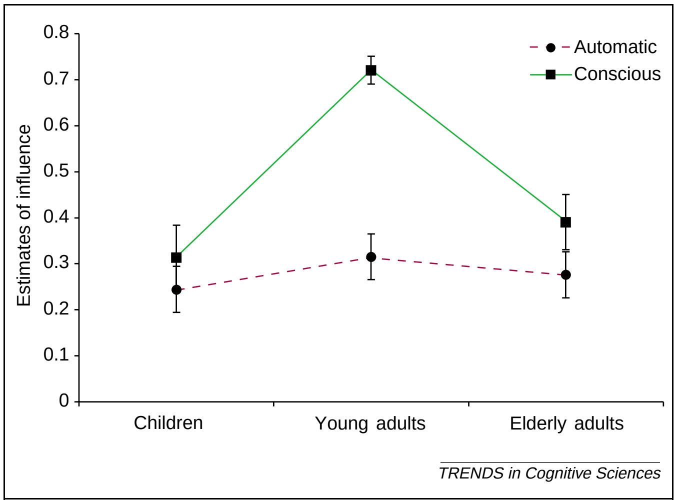

Figure 3. Estimates (and standard errors) of automatic and consciously controlled influences in a word-stem completion task as a function of age group. The mean ages of the groups were: children =8.8 years, young adults =22.3 years, elderly adults =71.1 years. Participants attempted to complete three-letter word stems (e.g. CHA-, GRA-) either with words from previously studied auditory and visual lists (Inclusion) or with words from the auditory list only, excluding words from the visual list (Exclusion). The difference between completing stems of words from visual lists in the Inclusion condition (in line with instructions) and the Exclusion condition (against instructions) provides a measure of conscious recollection of presentation modality. An estimate of automatic processing is given by the probability of Exclusion divided by (1−probability of conscious recollection) [28]. The figure shows that consciously controlled recollection has a strong quadratic relation to age, whereas the measure of automatic processing does not change significantly from age 9 years to the early seventies. Reproduced with permission from [50].

processing in the same participants, as was the case for specific and general switch costs. For example, Zelazo and colleagues used Jacoby's 'process dissociation' procedure to analyze performance on a word-stem completion task [50]. This procedure yields independent estimates of bias and conscious recollection [28]; the results showed a quadratic trend across the lifespan for the controlled process of recollection but no age difference for the automatic measure of bias (Figure 3).

Expertise: interactions of representation and control

Representation and control are separate entities in that they refer to different aspects of processing, develop in response to different contingencies, and probably reside in different parts of the brain. Nonetheless, there are extensive interactions between them, which are central in explaining significant aspects of cognitive performance and cognitive development. These interactions define what we might call 'expertise'. For example, specific practical pursuits lead to the development of highly specialized representational systems. Polk and Farah [51] have shown that Canadian postal workers who constantly process mixed sequences of digits and letters (e.g. M6A 2E1) show less representational segregation of letters and numbers at the neurological level. Similarly, Scribner demonstrated that individuals working in the same dairy plant developed different computational skills depending on the practical tasks carried out in their jobs [52]. In Scribner's terms, the 'problem-solving process is restructured by the knowledge and strategy repertoire available.'

There are also dissociations between levels of expertise in complex skills and basic abilities defined by levels of representation or control on their own. Salthouse and Mitchell [53] have shown that scores on psychometric tests of visuo-spatial ability differentiated young architects from non-architects, but that this relationship did not hold for older adults. A similar result was found in a study of 200 bank managers [54]. Increased age was associated with lower scores on tests of reasoning, but the tests did not predict managerial ability. These results suggest that although individual differences in specific abilities might lead young people into particular professional fields, differences in expertise after many years depend more on experience and practice in a particular domain.

Integrating descriptions of cognitive change across the lifespan

We have suggested that lifespan cognitive development can be understood in terms of the growth and stability of representational systems and the growth and decline of control processes acting on these systems. Thus, the notion that cognitive aging is simply 'development in reverse' is too simple, even though some crucial aspects of cognitive change do follow the symmetrical pattern of rising and falling over the lifespan. One example is the role of environmental support in the construction of representations and in the execution of controlled processes on those representations. In childhood and older age, much of cognitive performance is initiated in response to environmental contingencies; only in young adulthood and middle age is behavior truly under the control of internal mental states.

Our proposal provides a means for understanding why the fields of cognitive development and cognitive aging have evolved independently despite being concerned with problems that are fundamentally similar. Because cognitive change at each end of the lifespan appears to be strikingly different, theoreticians working in each field have concentrated on different aspects of performance and focused on different theoretical premises. Factors such as maturation, environmental influence, and individual differences such as speed, processing efficiency and learning experience have different relative impacts on individuals at different times of life. In development, the primary emphasis is on the changes in representations as the child constructs a coherent interpretative basis for understanding the world; in cognitive aging, the primary emphasis is on the decline in control processes as they produce impairments of access to existing knowledge, integration of new and existing information, and translation of knowledge into timely and adaptive action. This difference in emphasis is reflected in the dominant theoretical approach to each field and is clearly a factor in their mutual neglect. The representation and control framework provides a means of recombining these factors into a coherent lifespan description and offers a means of testing the model by positing different relations between representation and control at different stages in life.

Our goal is to create a framework for integrating the complexities of cognitive change at different times into a unified description that highlights the continuity of these processes across the lifespan. We believe that basing this

Box 4. Questions for future research

- How do frontal regions or circuits relate to specific control processes, and how do these relationships change across the lifespan?
- Do control processes 'differentiate' and 'de-differentiate' in the same way as representations appear to?
- Is cognitive decline in old age associated with a reversion to a smaller number of general abilities (de-differentiation), or is the decline better described as reflecting loss of specific abilities?
- Do other long-lasting training experiences act like bilingualism to enhance the efficiency of control processes over a range of tasks?
- How do knowledge representations and control processes interact to guide behavior?
- What is the role of the external environment in regulating behavior, and how does it change over the lifespan?
- What are the neural correlates of representational change across the lifespan as knowledge and abilities differentiate and de-differentiate?

exercise on the distinction between representation and control contributes to that enterprise and provides a means of exploring these connections in greater detail (see Box 4) in the search for a more complete account of the cognitive functioning of the human mind.

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