Language in the aging brain: The network dynamics of cognitive decline and preservation

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Language is a crucial and complex lifelong faculty, underpinned by dynamic interactions within and between specialized brain networks. Whereas normal aging impairs specific aspects of language production, most core language processes are robust to brain aging. We review recent behavioral and neuroimaging evidence showing that language systems remain largely stable across the life span and that both younger and older adults depend on dynamic neural responses to linguistic demands. Although some aspects of network dynamics change with age, there is no consistent evidence that core language processes are underpinned by different neural networks in younger and older adults.

Understanding and producing language are crucial and complex human behaviors, essential for effective communication, that underpin almost all our social interactions. They are so important for daily life that real or perceived communication problems are assumed to reflect lower intelligence or pathological conditions like dementia (1).

Although aging is associated with specific impairments in language production, most comprehension abilities remain stable as we age, and word knowledge even improves across much of the adult life span, declining only in very old age [(2), see (3) for review]. This pattern of impaired and spared language functions challenges models that propose age-related reductions in general cognitive resources and predict universal cognitive declines, including those in language functions (4). Moreover, the widespread changes in brain structure associated with aging raise the question of why much of language comprehension is preserved as we age, whereas aspects of production decline. These variable age effects make language an ideal model system for investigating the relation between age-related structural and functional brain changes and their behavioral consequences.

As a background to discussing research on the neurobiology of language and aging, we begin this review by highlighting the importance of moving away from a focus on the functional role of individual brain regions to understanding the network dynamics that characterize the effects of aging on cognition. In particular, we discuss claims that age-related neural decline leads to compensatory neural recruitment to support good performance and consider different uses of the term "compensation" (5). We then selectively review how age affects language performance. In the final section we describe, in the context of neuro-

biological models of the language system, two key examples of age-related language preservation and loss: (i) syntactic processing during comprehension, which is preserved with age, and (ii) phonological access during production, which shows age-related impairments. We highlight the challenges in determining whether age-related neural changes signify deterioration of specialized subcomponents of the language system, reorganization of language processes, or changing dynamics between language and other cognitive domains.

The aging brain: Structure, function, and performance

Typical aging is associated with widespread gray- and white-matter brain changes (6), which show considerable regional variation across the brain in the timing and rate of declines. However, there is no simple correspondence between the degree of neural change and cognitive performance (7), perhaps partly because of age-related compensatory neural recruitment: Older adults with relatively preserved performance in cognitive domains that typically decline with age (e.g., episodic or working memory) show increases in neural activity, particularly in prefrontal regions (8). This recruitment often involves bilateral activation in conditions where younger adults only activate the right hemisphere, which suggests functional reorganization, wherein recruited left-hemisphere regions take on right hemisphere processing functions. However, there has been little systematic effort to test whether contralateral regions perform the same functions as the original system. Moreover, increased frontal activity is often accompanied by decreased activity in more posterior regions such as occipitotemporal cortex (9), which suggests that prefrontal cortex may be a general neural "resource" that flexibly supports performance (5). However, many experimental tasks involve executive or attentional processes that also rely on frontal function, which raises the issue of whether recruitment reflects age-related increases in the effect of task

demands rather than changes in cognitive functions per se (10).

Recent studies focusing on age-related changes in network dynamics rather than individual brain regions suggest that prefrontal cortex may be important for compensation in a variety of cognitive contexts because of its involvement in a wide range of functional networks underpinning different cognitive processes [e.g., (11, 12–14)]. Networks are formed from multiple coactivating brain regions and are thought to be functionally specialized by virtue of their interregional connectivity. Each region may be involved in multiple networks, as seems to be the case for frontal cortex. Functional networks have largely been identified in resting-state data by using independent components analysis (ICA), seed-based connectivity, and graph theory methods, where synchronized activity across different regions is thought to reflect intrinsic connectivity. In younger adults, brain-wide networks have an optimized modular organization, with highly integrated local networks and weak connectivity between networks (13). Data from resting state and task-based studies (11–13) suggest that aging disrupts this organization, reduces integration within networks, and increases connectivity between them. Age-related reduced neural specificity, or "dedifferentiation," resulting from biological brain aging (15) may lead to age-related declines in the modularity of brain-wide network organization, an example of regional dedifferentiation in association with dedifferentiation at a network level (11). Given the evidence for compensatory bilateral recruitment (8), increased between-network connectivity may reflect attempts to compensate for within-network disruption, and this compensation may not always be successful (14). In the following sections, we describe core language processes that are typically either preserved or impaired with age and consider whether there is evidence that older adults' performance is underpinned by age-related changes in network dynamics.

Language functions across the adult life span: Evidence from behavioral studies

Spoken language comprehension involves a variety of processes operating in parallel over different time scales that transform the speech input into intermediate levels of representation, including speech sounds (acoustic-phonetic and phonology) and words (lexical semantic and syntactic properties), in the online development of a syntactically coherent and meaningful utterance. A key constraint in understanding this complex set of processes and their interactions is that they must occur very rapidly, as speech consists of a fast-fading input, which requires the listener to keep pace with the speaker in order to interpret the input effectively and to avoid an overload of uninterpreted auditory input. This system has been termed optimally efficient, because listeners process the speech input at around 200 ms delay, constructing high-level representations millisecond-by-millisecond (16).

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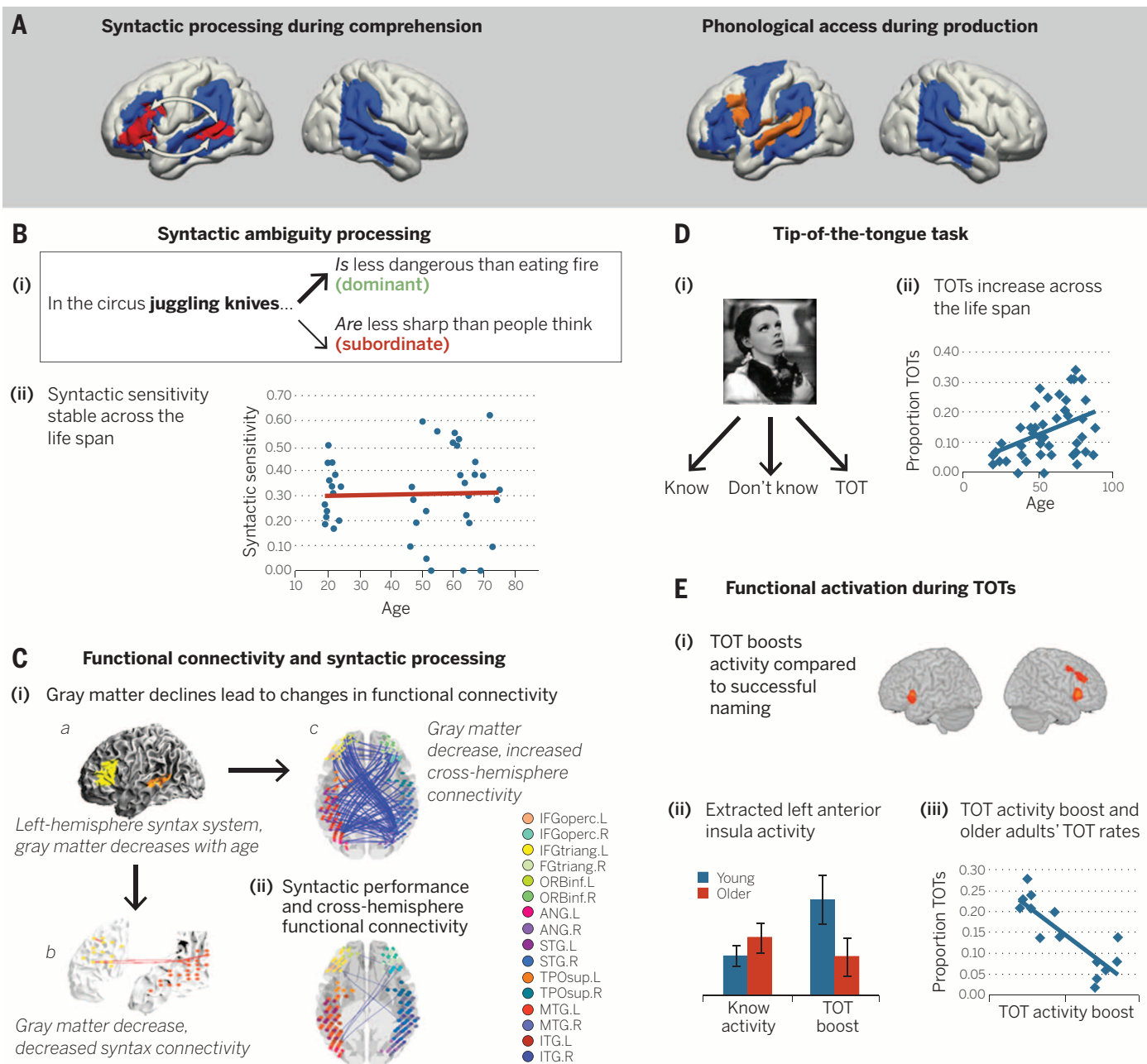*Corresponding author. E-mail: mshafto@csl.psychol.cam.ac.uk

A   **Syntactic processing during comprehension**   **Phonological access during production**

B   **Syntactic ambiguity processing**

(i)   In the circus **juggling knives**…

Is less dangerous than eating fire **(dominant)**

Are less sharp than people think **(subordinate)**

(ii) Syntactic sensitivity stable across the life span

C   **Functional connectivity and syntactic processing**

(i)   Gray matter declines lead to changes in functional connectivity

a

Left-hemisphere syntax system, gray matter decreases with age

c   *Gray matter decrease, increased cross-hemisphere connectivity*

(ii) Syntactic performance and cross-hemisphere functional connectivity

b

Gray matter decrease, decreased syntax connectivity

IFGoperc.L
IFGoperc.R
IFGtriang.L
FGtriang.R
ORBinf.L
ORBinf.R
ANG.L
ANG.R
STG.L
STG.R
TPOsup.L
TPOsup.R
MTG.L
MTG.R
ITG.L
ITG.R

D   **Tip-of-the-tongue task**

(i)

Know   Don't know   TOT

(ii) TOTs increase across the life span

E   **Functional activation during TOTs**

(i) TOT boosts activity compared to successful naming

(ii) Extracted left anterior insula activity

■ Young
■ Older

Know activity   TOT boost

(iii) TOT activity boost and older adults' TOT rates

TOT activity boost

Fig. 1. Age-related changes in behavioral and neural measures during syntactic comprehension and word production. (**A**) Comprehension and production systems (blue) with (left) left hemisphere syntactic processing network (red), including key white matter pathways (white arrows); and (right) left hemisphere regions associated with phonological access and encoding during word production (orange). (**B**) Syntactic processing paradigm (*14*), where (i) participants in an fMRI scanner naturally listen to sentences containing syntactically ambiguous phrases (e.g., "…juggling knives…") with a strong bias toward a dominant interpretation and a weak bias toward a subordinate interpretation. (ii) Age does not affect sensitivity to syntactic ambiguity as measured in a task performed outside the scanner. Participants hear sentences up to the disambiguating word ("is" or "are") and indicate whether the sentence is acceptable. They more often reject subordinate compared with dominant resolutions, and this difference reflects syntactic sensitivity. (**C**) Changes to functional connectivity in relation to gray matter and performance. Graph theory measures of functional connectivity during sentence comprehension were calculated using the weighted correlation method. (i) (a) Within the key regions of the left hemisphere syntax system represented here, (b) red lines show decreasing functional connectivity accompanying decreasing gray matter integrity. (c) Blue lines show cross-hemisphere functional connectivity that increases with decreasing gray matter integrity. Finally, (ii) blue lines show cross-hemisphere functional connectivity that increases with decreasing syntactic sensitivity. (**D**) Example of a TOT-inducing paradigm where (i) participants see pictures of public figures and indicate whether they Know, Don't Know, or are having a TOT for the name (*51*). (ii) TOT rates increase with age across the life span (*51*). (**E**) Neural activity and performance in response to TOTs (*55*), where (i) TOTs boost activity relative to successful naming in bilateral regions, including inferior frontal, left anterior insula, right middle frontal, and anterior cingulate cortices. (ii) Within regions of TOT-related activity, representative activity extracted from left anterior insula is similar for younger and older adults for successful naming, but the boost of activity during a TOT is weaker for older adults (*55*). In whole-brain contrasts, older adults did not reliably activate any of the regions that younger adults engaged in response to TOTs. However, TOT-related activity was relevant for older adults' performance as (iii) older adults with more TOT-related activity have lower TOT rates.

Despite the multiple rapid computations required, core aspects of speech comprehension are well-preserved across the life span, including the automatic access of lexical representations and the online construction of syntactic and semantic representations (3, 17). Older adults perform worse than younger adults when speech occurs rapidly or in noisy environments (18), although age differences are smaller when words occur in context (17, 18). It remains unclear whether sensory deficits affect language comprehension directly or indirectly by taxing central cognitive processes.

Age-related changes in language comprehension are also affected by the experimental tasks used to assess performance. For example, when tasks tap real-time processing, increased syntactic complexity does not differentially affect older adults' comprehension (19–21). In contrast, age-related differences for syntactically complex sentences emerge when tasks probe later, more explicit processes requiring overt responses, such as plausibility or gender judgments, which may involve domain-general processes over and above core language processes (22). Similarly, older adults retain their ability to use online sentential context to support word recognition (23), despite some evidence for age-related delays in processing sentential context using off line comprehension judgments (24).

In sum, although debate continues about which measures of language comprehension decline with age, the weight of behavioral evidence suggest that real-time sentential processing is preserved in older adults (23). We consider in the next section whether neural data provides any evidence that preserved online syntactic processing is supported by compensatory recruitment.

Producing language begins with the speaker's intention to construct a meaningful utterance. Similar to comprehension, this generates a set of rapid, overlapping representations at semantic, syntactic, lexical, phonological, and articulatory levels (25), which are used in constructing structured sequences according to the rules of the language (26). These processes occur rapidly in time: in picture-naming tasks, semantic access is under way by 200 ms after viewing an object, phonological retrieval occurs at around 300 ms, and articulation between 400 and 600 ms (26, 27).

In contrast to many comprehension processes, language production shows reliable age-related declines. Older adults produce propositionally and syntactically simpler speech than younger adults in natural contexts (28), use more vague terms, have more frequent and more empty pauses (29), and are slower to access phonological information in experimental contexts (30). This is consistent with findings that older adults have more difficulty with word finding both during naturalistic speech (28) and in experimental tasks focusing on single-word production. Normal aging leads to slower and less accurate picture naming and increases in "tip of the tongue states" (TOTs), where the meaning of a word is available, but the form is frustratingly out of reach (3, 31). Older adults worry that TOTs

indicate serious memory problems (32), but research suggests they are not caused by difficulties in accessing meanings, but by selective deficits in accessing phonological representations (33, 34).

The network dynamics of language and aging

Syntactic processing: A case of age-related preservation

Language comprehension involves bilateral frontal, temporal, and parietal cortices (35). Functional activity within this extensive system is modulated by different aspects of language processing (phonological, semantic, and syntactic) instantiated in overlapping networks, although the specific details of the regions involved in these networks continue to be debated. As discussed above in the context of behavioral findings, this may be because tasks vary widely in their relevance to natural language processing; because task-related and language-related activations are not always differentiated, task-related activations may be included in models of language functions (10, 36). These caveats notwithstanding, there is broad agreement that auditory processing typically involves a swathe of bilateral superior temporal activity (37, 38), whereas the processes involved in constructing sentential semantic representations involve a bilateral network including superior and middle temporal gyri, as well as angular gyri (39). Syntactic processing, in contrast, involves a strongly left-lateralized network of inferior frontal and middle temporal regions, directly connected by the arcuate fasciculus and extreme capsule fiber pathways (see Fig. 1A) (40). The precise subregions of frontal and temporal cortices vary across studies (41), but data from brain-damaged patients shows that Broca's areas (BAs) 45 and 44 in inferior frontal cortex and left posterior middle temporal gyrus are the essential regions involved in syntactic processing (42). Within this network, during spoken language processing, syntactic information initially flows from left middle temporal to left inferior frontal cortex (43). The frontal cortices per se are not functionally specific, but rather engage in multiple functions including competition, selection (44), or integration (45) during speech processing, depending on the inputs they receive.

The integrity of the left fronto temporal syntax network declines with age, and these changes may be associated with increased right hemisphere frontal activity, even in paradigms with low tasks demands (23). This right hemisphere involvement does not seem to reflect compensatory reorganization to a bilateral system, as, even when performance is preserved in older adults, it is not related to the degree of right hemisphere activity (23). Graph theory analyses of functional networks support a similar conclusion: Age-related declines in the integrity of the left hemisphere syntax network are associated with decreased connectivity within that network and widespread interhemispheric connectivity (Fig. 1, B and C) (14). This increased interhemispheric connectivity in older adults is consistent with age-related dedif-

ferentiation in that it is associated with decreased gray matter (15) (Fig. 1C), poorer performance, and reduced network efficiency, as determined by graph theory measures. However, there is no evidence that the syntax system suffers from dedifferentiation in the sense of becoming less functionally specialized. The function of increased right hemisphere activation remains unclear. It may reflect cross-hemisphere disinhibition after structural decline in the left hemisphere syntax network, diffuse activity as a result of reduced efficiency, or attempted but unsuccessful compensatory activity (46).

Under some circumstances, increased bilateral activity may reflect task demands. As discussed earlier, experimental tasks often engage executive or attentional processes. A recent functional magnetic resonance imaging (fMRI) study shows that, during syntactic processing, age-related increases in prefrontal recruitment only occur when participants perform a task, not during task-free natural listening (10). The potential contribution of task demands is in keeping with findings that, although activity outside the left hemisphere syntax network does not support online syntactic processes during natural listening (14, 23), compensatory recruitment supports older adults' performance on offline comprehension tasks. For example, older adults with better performance on offline tasks generate increased activity in bilateral regions associated with working memory when processing complex syntax (22, 47). Thus, as with behavioral studies, domain-general cognitive processes appear to support offline performance measures rather than online syntactic processing.

If recruitment outside the left hemisphere language network does not support online syntactic processing, how do older adults largely retain the ability to carry out syntactic computations? A recent study of patients with left hemisphere brain damage showed that even when the left hemisphere syntax system was damaged, there were no regions in either hemisphere that compensated by performing the same syntactic computations as those carried out by the left hemisphere system (48). The degree to which patients' syntactic processing abilities were intact correlated only with the residue of the left hemisphere frontotemporal network. A similar explanation may hold for older adults, given that age-related declines in the structural integrity of the left hemisphere syntax system are a matter of degree, not absolute. Therefore, like patients with left hemisphere damage, older adults' syntactic processing may rely solely on the residue of the normal syntax network in normal conversational settings.

In sum, the online syntactic processing during natural language comprehension does not conform to frameworks of aging where preserved cognitive performance is underpinned by compensatory functional reorganization (5). Although functional connectivity analyses suggest that age affects the organization of functional networks underpinning syntactic processing (14), the residue of the left hemisphere syntax system may normally be sufficient to enable syntactic

computations when sentences occur in typical, contextually rich environments.

Word production: A case of age-related impairment

Most neural models of language production focus on single-word production. Accessing word meaning engages bilateral middle temporal cortex (*38*), whereas accessing phonological representations involves primarily left-lateralized posterior superior temporal and left inferior frontal cortices (see Fig. 1A) (*26*). Generating overt speech involves interactions between left-lateralized posterior temporal and parietal regions and more anterior regions, including inferior frontal, anterior insula, and motor cortex involved in word planning and articulation (*49*). As with comprehension, these processes occur rapidly, with phonological access during picture naming typically under way within 600 ms of seeing an object (*26*).

Word production is often examined using picture-naming or TOT-inducing tasks, and in these paradigms, both younger and older adults experience occasional problems accessing phonological representations, which leads to dysfluencies and errors, slower naming, or TOTs (*3*). Normal aging weakens phonological access, making problems more frequent or more severe for older adults. Aging has only limited effects on successful phonological retrieval, for example, reducing phonological facilitation during picture naming (*50*) or delaying phonological access when making judgments about picture names (*30*). However, weaker phonological activation also leads to more retrieval failures for older adults, including higher TOT rates and decreased picture naming accuracy (Fig. 1D) (*31*).

Neural models of language and aging do not yet provide a mechanism for why phonological access is more vulnerable to aging than other language processes [but see (*3*, *4*) for discussion of cognitive accounts]. However, age-related increases in TOTs are associated with reduced integrity in left anterior insula and left arcuate fasciculus (*51*, *52*), which are involved in language production. Despite age-related structural declines, older and younger adults' functional responses are similar in response to incomplete phonological retrieval, engaging a domain-general cognitive control system that supports recovery: In younger adults, picture-naming errors and TOTs elicit activity in bilateral regions associated with cognitive control, including anterior insula, middle and inferior frontal and anterior cingulate cortices (Fig. 1E) (*53*–*55*). Similar activity is not found in TOT tasks when participants simply don't know the correct name, which indicates that partial phonological activation is necessary to trigger support from this cognitive control system (*55*). A recent MEG study of TOTs likewise suggests that cognitive control is recruited in response to weak phonological retrieval: During the time frame of phonological access (around 300 ms post stimulus), TOTs elicit a weaker response compared to successful naming in left inferior frontal and temporal regions (*56*). It is only at later time points, after 700 ms, that TOTs gen-erate a stronger response compared with successful naming in regions associated with cognitive control, including left middle and right inferior frontal cortex.

Like younger adults, older adults respond to production problems by activating regions involved in cognitive control, but their weaker phonological activation appears to affect both when this recruitment is necessary and when it is possible. During successful picture naming, better-performing older adults show greater activation compared to younger adults, both within occipital, temporal, and frontal regions typically active during object naming, and within regions associated with cognitive control, including anterior cingulate, bilateral inferior frontal, and insular cortices (*57*). Older adults' activity during successful object naming is similar to that of younger adults during TOTs, which suggests that older adults need to use cognitive control to overcome reduced phonological activation and maintain performance. However, during retrieval failures like TOTs, older adults' phonological activation is often too weak to trigger cognitive control support. Although better-performing older adults have TOT-related activity similar to younger adults, older adults on average do not reliably show TOT-related recruitment (*55*). Consistent with this, during TOTs younger adults often report partial phonological information (like the first sound or letter of a word), although older adults more often cannot, reporting instead that their mind just "goes blank" (*31*). Thus, the current evidence suggests that weaker phonological activation initially leads to increased recruitment of cognitive control in older adults but will lead to less recruitment relative to younger adults when phonological activation is very weak. This pattern is consistent with the suggestion from other cognitive domains that with increasing task difficulty older adults initially "over-recruit" relative to younger adults but then "under-recruit" when they reach the limits of declining neural systems (*58*).

In summary, as with syntactic processing, current findings from word production suggest that although older adults "over-recruit" regions associated with cognitive control to maintain good performance in challenging situation (*57*), the network dynamics underpinning good performance do not fundamentally change with age: Both younger and older adults experience phonological retrieval problems and, provided sufficient partial activation, they both recruit cognitive control to support recovery.

Outlook

Our brief review of language in the aging brain underlines a key theme in the cognitive neuroscience of aging: Understanding the neural mechanisms of cognitive aging requires grappling with the dynamic interactions within and between the neural networks underlying cognition. Although aging affects network dynamics during language production and comprehension, these changes do not provide robust evidence for age-related reorganization of core language pro-cesses or fundamental changes in how language and domain-general processes interact. Well-preserved abilities like syntactic processing are enabled by the residue of highly connected specialized subnetworks and not by widespread neural compensation. Even in the case of production failures there is little evidence that recruitment reflects age-specific reorganization, as both younger and older adults recruit similar systems in response to naming difficulty. Furthering our current understanding of how aging affects language networks and their interactions with other neural networks requires future research to overcome a number of challenges. Chief among these is disentangling the overlapping and interacting networks involved in complex language processing and characterizing the contribution of networks outside the core language system.

Conclusion

The message from current research on language and aging is that, despite brain-wide changes in structure, older adults' brains remain responsive and capable of flexible network interactions. Moreover, the evidence suggests that good language performance is largely underpinned by the same processes across the adult life span. However, further research is needed to understand the complex relations between changes in network organization and performance and to determine whether the language functions discussed in this review extend more widely to other components of the language system.

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REVIEW

Economic and social implications of aging societies

Sarah Harper

The challenge of global population aging has been brought into sharper focus by the financial crisis of 2008. In particular, growing national debt has drawn government attention to two apparently conflicting priorities: the need to sustain public spending on pensions and health care versus the need to reduce budget deficits. A number of countries are consequently reconsidering their pension and health care provisions, which account for up to 40% of all government spending in advanced economies. Yet population aging is a global phenomenon that will continue to affect all regions of the world. By 2050 there will be the same number of old as young in the world, with 2 billion people aged 60 or over and another 2 billion under age 15, each group accounting for 21% of the world's population.

By the end of the 21st century, demographic trends will converge with declining births, stabilization in population size, and aging populations across the globe (*1*). The age composition of the world's population will alter as median ages rise and a proportionate shift from younger to older people continues. At the turn of the millennium, there were more people over 60 than under 15 in Europe. North America will follow by 2030, Latin America and Asia by 2040. In terms of absolute numbers, the Asian/Pacific region is already the oldest, and by the middle of the century will hold two-thirds of the world's then 2 billion elders (aged 60 years or over). The worldwide numbers of those aged 80 and above will show an even greater rate of increase, rising from 69 million to 379 million by 2050, when nearly 10% of the developed world will be over 80 (*1*) (Fig. 1).

Europe's demographic structure in particular is predicted to age substantially. By 2060, those under 15 in the EU27 countries (European Union members, 2007–2013) will be around 14%. There will be nearly twice that proportion over 65, as this age group will increase from 87.5 million in 2010 to 152.6 million by 2060. Perhaps most striking of all, those aged 80 and over will constitute around 12% of the European population; this group is expected to almost triple in size, from 23.7 million in 2010 to 62.4 million in 2060. The demographic outlier is Africa, which will continue to grow and remain young, with one-third of its population still under 15 by the middle of the century (*1*).

Drivers

The conventional belief is that population aging is driven by falling mortality rates and increasing longevity. Although this is an important component of the process, it is widely accepted that the major driver is falling fertility, which fundamentally alters the subsequent age structure of a population and, if sustained, leads to increasing median ages and demographic aging (*2*).

Falling fertility or childbearing

Two-thirds of the world's countries now have childbearing rates or total fertility rates (*3*) near

or below replacement level, crudely defined as 2.1. These are diverse and drawn from most world regions, including Asia (for example, Hong Kong,
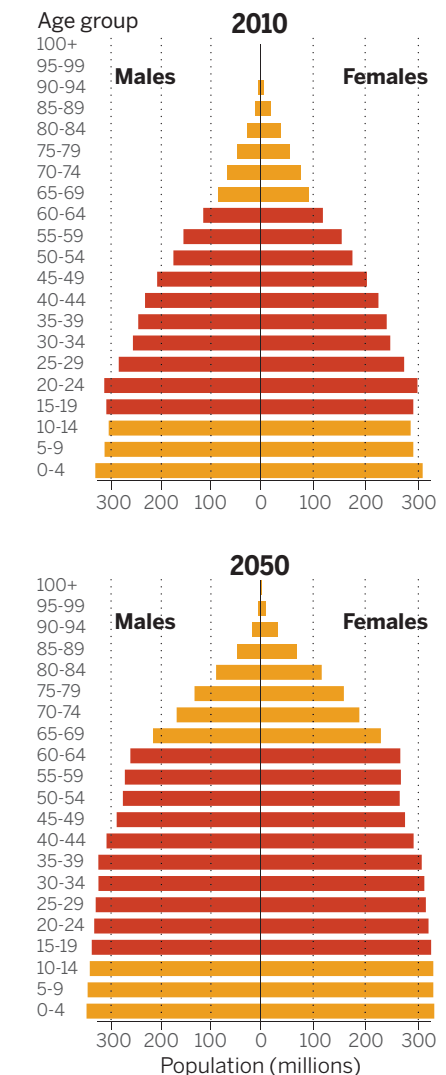

Fig. 1. World population pyramids. Population age structure for 2010 and projections for 2050 are shown. The working-age proportion is shown in red. Source: (*1*).

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Language in the aging brain: The network dynamics of cognitive decline and preservation

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