Language in the Aging Brain: the Network Dynamics of cognitive Decline and Preservation

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**Abstract:** Language is a crucial and complex lifelong faculty, underpinned by dynamic interactions within and between specialized brain networks. While 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 lifespan, and that both younger and older adults depend on dynamic neural responses to linguistic demands. While some aspects of network dynamics change with age there is no robust evidence that core language processes are underpinned by different neural networks in younger and older adults.

**One sentence summary:** Despite age-related changes to brain structure and function, neurocognitive systems underpinning language functions remain largely stable across the lifespan.

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 lifespan, 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 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 while aspects of production decline. These variable age effects make language an ideal model system for investigating the relationship 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 neurobiological models of the language system, two key examples of age-related language preservation and loss: syntactic processing during comprehension which is preserved with age, and phonological access during production which shows age-related impairments. We highlight the challenges in determining whether age-related neural changes signify deterioration of specialized sub-components 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 grey and white matter brain changes (*6*) which show considerable regional variation  across the brain in the earliness 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, suggesting 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*), suggesting that prefrontal cortex may be a general neural "resource" which flexibly supports performance (*5*).  However, many experimental tasks involve executive or attentional processes which also rely on frontal function, raising 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 due to its involvement in a wide range of functional networks underpinning different cognitive processes (e.g., *11, 12-14*).  Networks are formed from multiple co-activating brain regions, and are thought to be functionally specialized by virtue of their inter-regional 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 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, reducing integration within networks and increasing 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 which are both typically preserved and 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 lifespan: 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, 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, requiring the listener to keep pace with the speaker in order to interpret the input effectively and avoid an overload of uninterpreted auditory input. This system has been termed optimally efficient since listeners process the speech input at around 200 milisecond delay, constructing high-level representations millisecond-by-millisecond (*16*).

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, while 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 underway by 200 milliseconds

after viewing an object, phonological retrieval occurs at around 300 milliseconds, and articulation between 400 - 600 milliseconds (*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 suggest 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, and since 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*) while 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 Figure 1A; *40*). The precise subregions of frontal and temporal cortices vary across studies (*41*), but data from brain damaged patients shows that BA 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 (*46*). 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 (*46*).

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 (See Figure 1B and 1C; *14*). This increased interhemispheric connectivity in older adults is consistent with age-related dedifferentiation in that it is associated with decreased grey matter (15; see Figure 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 following structural decline in

the left hemisphere syntax network, diffuse activity as a result of reduced efficiency, or attempted but unsuccessful compensatory activity (*47*).

Under some circumstances, increased bilateral activity may reflect task demands. As discussed earlier, experimental tasks often engage executive or attentional processes. A recent 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, while 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, 48*). 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 (*49*). The degree to which patients' syntactic processing abilities were intact correlated only with the residue of the left hemisphere fronto-temporal 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*). While 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*) while accessing phonological representations involves primarily left-lateralized posterior superior temporal and left inferior frontal cortices (see Figure 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 (*50*). As with comprehension, these processes occur rapidly, with phonological access during picture naming typically underway within 600 milliseconds 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, leading to dyfluencies 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 (*51*) 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  (see Figure 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 (*52-53*), 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 which supports recovery: In younger adults, picture naming errors and TOTs elicit activity in a bilateral regions associated with cognitive control, including anterior insula, middle and inferior frontal and anterior cingulate cortices (see Figure 1E; *54, 55-56*). Similar activity is not found in TOT tasks when participants simply don't know the correct name, indicating that partial phonological activation is necessary to trigger support from this cognitive control system (*56*). 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 milliseconds post-stimulus), TOTs elicit a weaker response compared to successful naming in left inferior frontal and temporal regions (*57*). It is only at later time points, after 700 milliseconds, that TOTs generate a stronger response compared to 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 (*58*). Older adults' activity during successful object naming is similar to that of younger adults during TOTs, suggesting 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. While better-performing older adults have TOT-related activity

similar to younger adults, older adults on average do not reliably show TOT-related recruitment (*56*). Consistent with this, during TOTs younger adults often report partial phonological information (like the first sound or letter of a word), while 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 (*59*).

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 (*58*), 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 processes 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 sub-networks 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 amongst 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 relationships 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.

## References

1.  T. R. La Tourette, s. Meeks, *Journal of Language and Social Psychology* **19**, 463 (2000).

2.  P. Verhaeghen, *Psychol. Aging* **18**, 332 (2003).

3.  D. M. Burke, M. A. Shafto, in *The Handbook of Aging and Cognition,* F. I. M. Craik, T. A. Salthouse, Eds. (Psychology Press, New York & Hove, 2008), pp. 373-443.

4.  D. M. Burke, D. G. MacKay, L. E. James, in *Models of cognitive aging,* T. J. Perfect, E. A. Maylor, Eds. (Oxford University Press, Oxford, England, 2000), pp. 204-237.

5.  D. C. Park, P. A. Reuter-Lorenz, *Annu. Rev. Psychol.* **60**, 173 (2009).

6.  C. D. Good *et al.*, *Neuroimage* **14**, 21 (2001).

7.  N. Raz, K. M. Rodrigue, *Neurosci. Biobehav. Rev.* **30**, 730 (2006).

8.  R. Cabeza, *Psychol. Aging* **17**, 85 (2002).

9.  C. Davis *et al.*, *Brain Lang.* **105**, 50 (Apr, 2008).

10. S. W. Davis, J. Zhuang, P. Wright, L. K. Tyler, *Neuropsychologia*, (2014).

11. L. Geerligs, R. J. Renken, E. Saliasi, N. M. Maurits, M. M. Lorist, *Cereb. Cortex*, (Feb 13, 2014).

12. L. Geerligs, N. M. Maurits, R. J. Renken, M. M. Lorist, *Hum. Brain Mapp.* **35**, 319 (Jan, 2014).

13. D. Meunier, S. Achard, A. Morcom, E. Bullmore, *Neuroimage* **44**, 715 (2009).

14. D. Meunier, E. A. Stamatakis, L. K. Tyler, *Neurobiol. Aging* **35**, 42 (2014).

15. P. B. Baltes, U. Lindenberger, *Psychol. Aging* **12**, 12 (1997).

16. W. D. Marslen-Wilson, *Nature* **244**, 522 (1973).

17. R. Thornton, L. L. Light, in *Handbook of the Psychology of Aging,* J. E. Birren, K. W. Schaie, Eds. (Elsevier, San Diego, CA, 2006).

18. P. A. Tun, *Psychol. Aging* **13**, 424 (1998).

19. G. DeDe, D. Caplan, K. Kemtes, G. Waters, *Psychol. Aging* **19**, 601 (2004).

20. G. S. Waters, D. Caplan, *Psychol. Aging* **16**, 128 (Mar, 2001).

21.     L. K. Tyler, *Spoken language comprehension: An experimental approach to disordered and normal processing*.  (MIT Press, Cambridge, MA, 1992), pp. 308.

22.     J. E. Peelle, V. Troiani, A. Wingfield, M. Grossman, *Cereb. Cortex* **20**, 773 (2010).

23.     L. K. Tyler, P. Wright, B. Randall, W. D. Marslen-Wilson, E. A. Stamatakis, *Brain* **133**, 3396 (Nov 2010, 2010).

24.     K. D. Federmeier, C. Van Petten, T. J. Schwartz, M. Kutas, *Psychol. Aging* **18**, 858 (2003).

25.     D. Foygel, G. S. Dell, *Journal of Memory and Language* **43**, 182 (2000).

26.     P. Indefrey, W. J. M. Levelt, *Cognition* **92**, 101 (May-Jun, 2004).

27.     W. J. M. Levelt, P. Praamstra, A. S. Meyer, P. I. Helenius, R. Salmelin, *J. Cogn. Neurosci.* **10**, 553 (Sep, 1998).

28.     S. Kemper, A. Sumner, *Psychol. Aging* **16**, 312 (Jun, 2001).

29.     H. Bortfeld, S. D. Leon, J. E. Bloom, M. F. Schober, S. E. Brennan, *Lang. Speech* **44**, 123 (2001).

30.     Y. Neumann, L. K. Obler, H. Gomes, V. Shafer, *Aphasiology* **23**, 1028 (2009).

31.     D. M. Burke, D. G. MacKay, J. S. Worthley, E. Wade, *Journal of Memory and Language* **30**, 542 (1991).

32.     E. A. Lovelace, P. T. Twohig, *B Psychonomic Soc* **28**, 115 (1990).

33.     E. S. Cross, D. M. Burke, *Brain Lang.* **89**, 174 (2004).

34.     L. E. James, D. M. Burke, *Journal of Experimental Psychology: Learning, Memory, and Cognition* **26**, 1378 (2000).

35.     M. Bozic, L. K. Tyler, D. T. Ives, B. Randall, W. D. Marslen-Wilson, *Proc. Natl. Acad. Sci. U. S. A.* **107**, 17439 (Oct 5, 2010).

36.     P. Wright, B. Randall, W. D. Marslen-Wilson, L. K. Tyler, *J. Cogn. Neurosci.* **23**, 404 (4th March 2010, 2011).

37.     S. K. Scott, R. J. S. Wise, *Cognition* **92**, 13 (2004).

38.     G. Hickok, D. Poeppel, *Nature Reviews: Neuroscience* **8**, 393 (2007).

39.     J. R. Binder, R. H. Desai, W. W. Graves, L. L. Conant, *Cereb. Cortex*,  (2009).

40.     T. Rolheiser, E. A. Stamatakis, L. K. Tyler, *J. Neurosci.* **31**, 16949 (2011).

41.     A. D. Friederici, S.-A. Rueschemeyer, A. Hahne, C. J. Fiebach, *Cereb. Cortex* **13**, 170 (2003).

42.     L. K. Tyler *et al.*, *Brain* **134**, 415 (2011).

43.     L. K. Tyler, T. P. L. Cheung, B. J. Devereux, A. Clarke, *Frontiers in Language Sciences* **4**, 271 (May 2013, 2013).

44.     J. Zhuang, L. K. Tyler, B. Randall, E. A. Stamatakis, W. D. Marslen-Wilson, *Cereb. Cortex* **24**, 908 (2014).

45.     P. Hagoort, *Neuroimage* **20**, S18 (2003).

46.     L. K. Tyler *et al.*, *Cereb. Cortex* **20**, 352 (2010).

47.     R. Cabeza, N. A. Dennis, *Principles of frontal lobe function*, (2012).

48.     M. Grossman *et al.*, *Neuroimage* **15**, 302 (2002).

49.     P. Wright, E. A. Stamatakis, L. K. Tyler, *J. Neurosci.* **32**, 8149 (2012).

50.     G. Hickok, *Phys Life Rev* **6**, 121 (Sep, 2009).

51.     J. K. Taylor, D. M. Burke, *Psychol. Aging* **17**, 662 (2002).

52.     M. A. Shafto, D. M. Burke, E. A. Stamatakis, P. P. Tam, L. K. Tyler, *J. Cogn. Neurosci.* **19**, 2060 (Dec, 2007).

53.     E. A. Stamatakis, M. A. Shafto, G. Williams, P. Tam, L. K. Tyler, *PLoS ONE* **6**, e14496 (2011).

54.     S. Abel *et al.*, *Neuroimage* **44**, 1113 (2009).

55.     A. Maril, A. D. Wagner, D. L. Schacter, *Neuron* **31**, 653 (2001).

56.     M. A. Shafto, E. A. Stamatakis, P. P. Tam, L. K. Tyler, *Journal of Cognitive Neuroscience* **22**, 1530 (2010).

57.     M. Lindín, F. Díaz, A. Capilla, T. Ortiz, F. Maestú, *Neuropsychologia* **48**, 1757 (2010).

58.     C. E. Wierenga *et al.*, *Neurobiol. Aging* **29**, 436 (2008).

59.     K. A. Cappell, L. Gmeindl, P. A. Reuter-Lorenz, *Cortex* **46**, 462 (Apr, 2010).

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**Fig 1.** Age-related changes in behavioral and neural measures during syntactic comprehension and word production. **(A)** Comprehension and production systems (blue) with (i) left hemisphere syntactic processing network (red), including key white matter pathways (white arrows); and (ii) 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 towards a *dominant* interpretation and a weak bias towards 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 to dominant resolutions, and this difference reflects syntactic sensitivity. **(C)** Changes to functional connectivity in relation to grey 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 grey matter integrity. (c) Blue lines show cross-hemisphere functional connectivity that increases with decreasing grey 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 (*52*). (ii) TOT rates increase with age across the lifespan (*52*) . **(E)** Neural activity and performance in response to TOTs (*56*), where (i) TOTs boosts 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 (*56*). 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 have lower TOT rates.

**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 lifespan

**D** Tip of the tongue task

(i) Know  Don't Know  TOT

(ii) TOTs increase across the lifespan

**C** Functional connectivity and syntactic processing

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

*a* Left hemisphere syntax system, grey matter decreases with age

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

*b* Grey matter decrease, decreased syntax connectivity

(ii) Syntactic performance and cross-hemisphere functional connectivity

IFGoperc.L
IFGoperc.R
IFGtriang.L
IFGtriang.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

**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