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Abbreviated title: Frontotemporal resilience to aging

Robust resilience of the frontotemporal syntax system to aging

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44 Abstract

45

46 Brain function is thought to become less specialized with age. However, this view is largely based on
47 findings of increased activation during tasks which fail to separate task-related processes (e.g.,
48 attention, decision making) from the cognitive process under examination. Here we take a systems-
49 level approach to separate processes specific to language comprehension from those related to
50 general task demands and to examine age differences in functional connectivity both within and
51 between those systems. A large population-based sample (N = 111; 22-87 years) from the Cambridge
52 Centre for Ageing and Neuroscience (Cam-CAN) was scanned using functional MRI (fMRI) during two
53 versions of an experiment: a *natural listening* version in which participants simply listened to spoken
54 sentences and an explicit *task* version in which they rated the acceptability of the same sentences.
55 Independent components analysis (ICA) across the combined data from both versions showed that
56 while task-free language comprehension activates only the auditory and frontotemporal (FTN)
57 syntax networks, performing a simple task with the same sentences recruits several additional
58 networks. Remarkably, functionality of the critical FTN is maintained across age groups, showing no
59 difference in within-network connectivity or responsivity to syntactic processing demands despite
60 grey matter loss and reduced connectivity to task-related networks. We found no evidence for
61 reduced specialization or compensation with age. Overt task performance was maintained across
62 the lifespan and performance in older, but not younger, adults related to crystallized knowledge,
63 suggesting that decreased between-network connectivity may be compensated for by older adults'
64 richer knowledge base.

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66 Keywords: aging, language comprehension, syntax, ICA, functional connectivity, task demands

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Significance Statement

69 Understanding spoken language requires the rapid integration of information at many different
70 levels of analysis. Given the complexity and speed of this process, it is remarkably well-preserved
71 with age. While previous work claims that this preserved functionality is due to compensatory
72 activation of regions outside the frontotemporal language network, we use a novel systems-level
73 approach to show that these 'compensatory' activations simply reflect age differences in response to
74 experimental task demands. Natural, task-free language comprehension solely recruits auditory and
75 frontotemporal networks, the latter of which is similarly responsive to language-processing demands
76 across the lifespan. These findings challenge the conventional approach to neurocognitive aging by
77 showing that the neural underpinnings of a given cognitive function depend on how you test it.

78 Introduction

79 Several cognitive abilities are thought to decline with age, but these abilities are rarely tested in a
80 process-pure manner. Indeed, the nature of most cognitive experiments necessarily requires the
81 recruitment of several domain-general processes which are specific to the task itself (e.g.,
82 maintenance of task instructions, goal switching; Dosenbach et al., 2006). These additional processes
83 not only affect one's ability to isolate and measure a particular cognitive function, but they may also
84 affect the neural mechanisms assigned to that function – for instance, giving the impression that a
85 certain process (e.g., memory binding) relies on a wider set of regions (Buckner et al., 1999) than is
86 known to be the case from patient and animal work (Squire, 1992).

87 This mixing of component processes may be particularly problematic in the study of
88 neurocognitive aging because age differences in the recruitment of domain-general processes may
89 be misattributed to age differences in how the brain carries out a specific cognitive process (Grady,
90 2012; Morcom and Johnson, 2015). For instance, research on syntactic processing with brain-
91 damaged patients emphasizes the dependence of this process on a left-lateralized, frontotemporal
92 system, the computations of which cannot be performed elsewhere in the brain (Caplan et al., 1996;
93 Hagoort et al., 2003). However, several studies of language comprehension and aging show an age-
94 related increase in right frontal activations during syntactic processing (Wingfield and Grossman,
95 2006), leading to the suggestion that these right hemisphere regions are somehow compensating for
96 the core left-lateralized system, allowing for preserved performance (Peelle et al., 2010; Tyler et al.,
97 2010a). An alternative explanation is that the core syntax system is relatively resilient to age and
98 these additional activations reflect domain-general functions associated with the task itself and not a
99 change in how the aging brain carries out syntactic computations. In line with this view, Davis and
100 colleagues (2014) recently showed that natural, task-free language comprehension activates the
101 auditory and left-lateralized frontotemporal networks alone, while performing an explicit task with
102 the same sentences activates several additional networks, and it is these domain-general networks
103 that show increased activation with age.

104 Thus, current models of neurocognitive aging may be wrong in important ways. One cannot
105 claim that a given cognitive function has become “dedifferentiated” or “compensated” for without
106 first separating that function from processes related to the task itself (Shafto and Tyler, 2014). Here,
107 we attempt to redress this issue by taking a systems-level approach: identifying networks uniquely
108 associated with specific cognitive functions and then relating functional connectivity both within and
109 between those networks to age, grey matter, and cognitive performance. A large population-based
110 sample from the Cambridge Centre for Ageing and Neuroscience (Cam-CAN) was scanned using
111 functional magnetic resonance imaging (fMRI) during two versions of an experiment: an explicit *task*
112 *condition* in which participants rated the acceptability of sentences varying in syntactic complexity
113 and a *natural listening condition* in which they simply listened to the same sentences. Data from
114 both experiments were jointly submitted to an independent components analysis (ICA; Calhoun et
115 al., 2008) which allowed us to separate functional networks uniquely involved in syntactic processing
116 from those associated with overt task performance.

117 We expected natural listening to solely recruit the auditory and frontotemporal networks,
118 while active task performance should additionally recruit domain-general networks. We also
119 examined the effects of age and experimental task demands on functional connectivity both within
120 and between the ICA-identified networks. While previous work has primarily focused on age
121 differences in connectivity either at rest (Ferreira and Busatto, 2013) or during multi-componential
122 tasks (Sambataro et al., 2010; Spreng and Schacter, 2012), this is the first study to examine systems-
123 level interactions during a task with such well-defined and separable neural underpinnings (Tyler et
124 al., 2011). Finally, in light of evidence that prior knowledge can compensate for age-related declines
125 in processing efficiency (Salthouse, 1984; Soederberg Miller, 2009), we test whether crystallized
126 intelligence mitigates fluid declines by becoming increasingly related to syntactic performance with
127 age.

128 Materials and Methods

129 *Participants*

130 A population-derived sample (N = 111, 22-87 years old, M = 54.57, SD = 17.84) was recruited
131 as part of the Cam-CAN project (Shafto et al., 2014). Demographic information (including sex) is
132 provided in Table 1. Hearing was assessed using the Siemens HearCheck Screener, which tests
133 participants' ability to detect three sound pressure levels (75 dB SPL, 55 dB SPL, and 35 dB SPL) at
134 two frequencies (1000 Hz and 3000 Hz). Exclusion criteria for the Cam-CAN Stage 2 cohort (who
135 underwent extensive cognitive, MRI and MEG testing) included low performance (< 25) on the mini
136 mental state exam (MMSE; Folstein et al., 1975), poor hearing (failing to hear 35dB at 1000Hz in
137 both ears), poor vision (below 20/50 on the Snellen test; Snellen, 1862), non-native English speaker,
138 self-reported substance abuse, current serious health conditions (e.g., self-reported major
139 psychiatric conditions, current chemo/radiotherapy, or a history of stroke), and contraindications to
140 MRI (for full exclusion criteria, see Shafto et al., 2014). Handedness was assessed using the
141 Edinburgh Handedness Inventory and all but two participants were right-handed (excluding these
142 participants from the analyses did not change the pattern or significance of the results). Informed
143 consent was obtained from all participants and ethical approval for the study was obtained from the
144 Cambridgeshire 2 (now East of England – Cambridge Central) Research Ethics Committee.

145 *Cognitive Tasks*

146 *Language comprehension.* Participants were scanned while listening to spoken sentences
147 that varied in the level of syntactic processing required (Tyler et al., 2011). In both the natural
148 listening and task conditions, sentences either contained a syntactically ambiguous central phrase
149 (e.g., "...cooking apples...") or an unambiguous phrase that was similar in structure (e.g., "...sneering
150 boys"...). Unambiguous sentences (n = 42) had only one possible syntactic interpretation (e.g.,
151 "sneering boys are..."), whereas ambiguous sentences had two possible interpretations: one that is
152 more expected or *dominant* (n = 42) given its higher frequency in the language (e.g., "cooking apples
153 are...") and one that is less expected or *subordinate* (n = 42) given its relative infrequency (e.g.,
154 "cooking apples is..."). This paradigm capitalizes on syntactic ambiguity, a naturally occurring
155 phenomenon in human language, to manipulate the level of syntactic processing required by each

156 sentence. Subordinate sentences require the most processing, as listeners must overturn an
157 automatically activated dominant interpretation (e.g., “cooking apples are inedible without lots of
158 sugar”, where “cooking apples” is a noun phrase) in favor of a less expected subordinate
159 interpretation (e.g., “cooking apples is an easy task”, where “cooking” functions as a gerund).
160 Dominant sentences still contain ambiguity, and thus are more complex than unambiguous
161 sentences, but the resolution of that ambiguity is in line with the listeners’ expectations so no
162 revision is required. Previous work has shown that listeners are sensitive to these varying demands,
163 responding slowest to subordinate sentences, followed by dominant and finally unambiguous
164 sentences (Tyler and Marslen-Wilson, 1977; Tyler et al., 2013).

165 During natural listening, participants were simply asked to listen attentively to the
166 sentences, with their eyes open. Sentence stimuli were pseudorandomly intermixed with non-
167 linguistic baseline items (n = 21), consisting of envelope-shaped ‘musical rain’ which shares the
168 complex auditory properties of speech without any of the linguistic meaning (Uppenkamp et al.,
169 2006). During the task version, participants listened to the same sentence and musical rain stimuli,
170 but were now asked to perform an explicit acceptability judgement task. In this task, participants
171 hear the first part of the sentence spoken in a female voice up until the end of the central phrase
172 (e.g., “The class observed that cooking apples...”), followed by a single word spoken in a male voice
173 (e.g., “are”). Participants’ task was to decide if the final word was an acceptable continuation to the
174 sentence or not. All sentences were grammatically acceptable, but a normal pattern of responding
175 for people without language impairments is to reject more (and respond more slowly to)
176 subordinate sentences than dominant and unambiguous sentences, with little difference between
177 the latter two conditions (Tyler et al., 2011). Thus, we focus primarily on the difference between the
178 subordinate and unambiguous conditions in subsequent behavioral and fMRI analyses reported, as
179 these conditions differ most in syntactic processing demands. One participants’ behavioral
180 responses were lost due to equipment error (N = 110 for all behavioral analyses, including those
181 relating brain to behavior).

182 *Crystallized and fluid intelligence.* In order to examine the potential compensatory role of
183 crystallized knowledge in older adults' maintained performance on the syntax task, we also obtained
184 measures of crystallized and fluid intelligence outside the scanner. Crystallized intelligence was
185 measured using the Spot-the-Word Test (Baddeley et al., 1993), in which participants see word-
186 nonword pairs (e.g., pinnacle-strummage) and decide which is a real word. Fluid intelligence was
187 measured using the Cattell Culture Fair (Cattell and Cattell, 1960), a timed pen-and-paper test in
188 which participants perform a series of nonverbal puzzles. Because fluid and crystallized intelligence
189 tend to be moderately correlated (Cattell, 1963; Baddeley et al., 1993), we wanted to control for
190 fluid intelligence in our analyses to isolate the unique contribution of crystallized knowledge. In
191 order to determine whether crystallized knowledge becomes a stronger predictor of syntax
192 performance with age, we used a moderation model predicting syntax performance from age,
193 crystallized knowledge, and the age x crystallized knowledge interaction (with fluid intelligence
194 included as a covariate).

195 *MRI Acquisition and Preprocessing*

196 Imaging was performed on a 3T Siemens TIM Trio System at the MRC Cognition Brain and
197 Sciences Unit, Cambridge, UK. A 3D-structural MRI was acquired for each subject using T1-weighted
198 sequence (Generalized Autocalibrating Partially Parallel Acquisition (GRAPPA); Repetition Time (TR) =
199 2250ms; Echo Time (TE) = 2.99ms; Inversion Time (TI) = 900ms; flip angle $\alpha = 9^\circ$; matrix size 256mm x
200 240mm x 19 mm; field of view (FOV) = 256mm x 240mm x 192mm; resolution = 1mm isotropic;
201 accelerated factor = 2) with acquisition time of 4 minutes and 32 seconds. For the functional runs,
202 T2*-weighted fMRI data were acquired using a Gradient-Echo Echo-Planar Imaging (EPI) sequence
203 (TR = 1970 milliseconds; TE = 30 milliseconds; flip angle = 78 degrees; 32 axial slices of thickness of
204 3.7mm with an interslice gap of 20%; FOV = 192mm x 192 mm; voxel-size = 3 mm x 3 mm x 4.44
205 mm). The natural listening and task versions were acquired in separate runs, with run times of 15.73
206 minutes (479 volumes) and 16.29 minutes (496 volumes), respectively.

207 Preprocessing was performed using SPM12 (Wellcome Department of Imaging
208 Neuroscience, University College London, London, UK), implemented in the automatic analysis (AA)
209 batching system (<http://imaging.mrc-cbu.cam.ac.uk/imaging/AA>; Cusack et al., 2015). The functional
210 images were motion-corrected and slice-time corrected. The T1-weighted images were coregistered
211 to an MNI template image, bias-corrected, and segmented into various tissue classes using unified
212 segmentation (Ashburner & Friston, 2005). The segmented grey matter images were then used to
213 create a study-specific anatomical template, using the DARTEL procedure to optimize inter-
214 participant alignment (Ashburner, 2007), which was then transformed to MNI space. The EPI images
215 were then coregistered to the T1 image, normalized to MNI space using the DARTEL flowfields, and
216 smoothed using an 8mm FWHM Gaussian kernel. The segmented grey matter images were also
217 smoothed for subsequent structural analyses using a 10mm FWHM Gaussian kernel.

218 *Independent Components Analysis*

219 ICA was used to identify networks that were either commonly activated across the two
220 experimental conditions (natural listening and task) or unique to one particular state. All
221 participants' data from both the natural listening and task conditions were temporally concatenated
222 and submitted to the same ICA analysis, using the Group ICA of fMRI Toolbox
223 (<http://mialab.mrn.org/software/gift/index.html>; Calhoun et al., 2001). This method decomposes
224 the fMRI signal into a set of independent components, each with a set of individual spatial maps and
225 timecourses which were standardized using z-scores. Given recent evidence favoring low model
226 order analyses for the purpose of examining large-scale brain networks (Smith et al., 2009; Laird et
227 al., 2011; Ray et al., 2013), and to allow for continuity of comparison with our previous report using
228 similar methods, we set the number of components to 33 (Davis et al., 2014).

229 Temporal regression was used to select components that related to our four language
230 conditions of interest. We used an event model previously shown to maximize sensitivity to
231 ambiguity by testing only the period immediately following the ambiguous phrase (Tyler et al.,
232 2011). To this end, we defined the onset of each condition separately as the onset of the

233 disambiguating verb following the ambiguous central phrase (or an equivalent point in the
234 unambiguous sentences and musical rain stimuli), with a variable duration equivalent to the
235 remaining length of the phrase (Task: mean duration = 403 ms, SD = 30 ms; Natural Listening: mean
236 duration = 1789 ms, SD = 451 ms). We also included an extra regressor of no interest with onset at
237 the start of each sentence and duration up to the onset of the disambiguating verb (Task and
238 Natural Listening: mean duration = 2185 ms, SD = 317 ms). This “first-half” regressor does not
239 distinguish between conditions (i.e., it is a single regressor which corresponds to the first half of all
240 sentences, or the equivalent time period for musical rain stimuli) and thus, does not correlate with
241 the disambiguating word regressors. This model tests for effects of the second half of the sentence
242 while controlling for those of the first half. These onsets were then used to create stimulus
243 regressors in SPM12 by convolving the stimulus functions with the canonical hemodynamic response
244 function. Four task conditions were modelled in addition to the first-half of the sentences and
245 standard motion regressors (i.e., *x/y/z* translation, pitch, roll, and yaw): 1) *subordinate* or
246 unexpected continuations to ambiguous sentences, 2) *dominant* or highly predicted continuations to
247 ambiguous sentences, 3) matched continuations to syntactically *unambiguous* sentences, and 4) the
248 *acoustic baseline* condition. To determine which components related to our conditions of interest,
249 linear regression was used to predict each participant’s component timecourse from the set of task-
250 related and motion regressors. This analysis yields a set of β parameters (or ‘loading values’) for each
251 participant (for each condition) indicating the extent to which each of their component timecourses
252 relates to each of the task conditions during natural listening and task (similar to standard voxel-wise
253 modelling of the same design matrix, but with far fewer comparisons).

254 In order to identify networks related to our conditions of interest, components were rank-
255 ordered according to their mean loading values (i.e., β parameters) across the language conditions
256 (subordinate, dominant, and unambiguous). The seven strongest components were selected for
257 further analysis, as subsequent components appeared to capture artefact. Conventional significance
258 testing of the β parameters (i.e., against zero; St Jacques et al., 2011) was not appropriate in this

285 *Summary of main findings*

286 In order to guide the reader, we preface our main results here. We find that 1) overt task
 287 performance is preserved with age, in that older adults' RTs vary to the same extent as younger
 288 adults in response to syntactic processing demands; 2) natural listening only recruits AUD and FTN
 289 networks, while performing a task with the same stimuli recruits several additional domain-general
 290 networks; 3) responsivity of these networks to syntactic processing demands did not differ with age
 291 or GMC, but did predict overt task performance, with the MDN as the strongest predictor (an effect
 292 that was not moderated by age); 4) within-network connectivity during the task (not natural
 293 listening) decreased with age/GMC loss in some domain-general networks, but not in the critical
 294 FTN; 5) between-network connectivity declined with age/GMC for several network pairs during the
 295 task, and only connectivity between the critical FTN and other domain-general networks predicted
 296 performance; and finally, 6) crystallized knowledge became increasingly related to performance with
 297 age.

298 *Behavioral data*

299 On the syntax task, our critical measure of interest was the extent to which reaction times
 300 (RTs) varied as a function of syntactic processing demands (Tyler et al., 2013). Anticipatory responses
 301 (< 200 ms) were removed (< 1% of trials) and RT data were inverse transformed (Ratcliff, 1993)
 302 before calculating cell means per condition per subject (means were then reverse-transformed to
 303 standard ms units). Mean RTs were submitted to an ANOVA with condition (subordinate [most
 304 demanding], dominant, and unambiguous [least demanding]; see Methods) as a within-subjects
 305 factor and age as a continuous covariate. There was a main effect of condition, $F(2, 216) = 16.41, p <$
 306 $.001, \eta_p^2 = .13$, with participants responding more slowly to subordinate continuations ($M = 1330$
 307 $ms, SD = 384$) than dominant continuations ($M = 1125 ms, SD = 381; t(109) = 12.14, M_{diff} = 205.76, p$
 308 $< .001, 95\% CI [172.00, 239.53], d = 1.16$), which in turn were slower than unambiguous sentences
 309 ($M = 1056 ms, SD = 390; t(109) = 5.79, M_{diff} = 68.32, p < .001, 95\% CI [44.83, 91.80], d = .55$). There

310 was also a main effect of age $F(1, 108) = 48.73, p < .001, \eta_p^2 = .31$, due to older adults responding
311 more slowly on average (see Figure 1a; note that age is always treated as a continuous variable
312 throughout the analyses, though sometimes shown as a categorical variable for visualization
313 purposes, as in Figure 1a). Importantly, the age x condition interaction was not significant, $F < 1$,
314 confirming that our syntactic manipulation had the same effect on RTs across the lifespan. We also
315 calculated a *syntactic sensitivity* measure as the difference in RTs to subordinate and unambiguous
316 sentences for each subject and correlated this measure with age. As can be seen in Figure 1b,
317 syntactic sensitivity did not differ with age, $r = -.01, p = .88$. These results are in line with previous
318 results showing no effect of age on syntactic processing within this task (Tyler et al., 2010a; Davis et
319 al., 2014).

320 *Independent components analysis*

321 *Effects of task and syntactic processing demands.* In order to separate task-related networks
322 from those specific to language processing, we performed an ICA over the combined data from task
323 and natural listening. This analysis identified seven components that related to language processing
324 (Figure 2). These included 1) a left-lateralized frontotemporal network (FTN) including the left
325 inferior frontal gyrus (BA45 and BA47) and middle temporal gyrus (MTG; BA22) similar to previously
326 reported (Tyler et al., 2011), 2) an extended auditory (AUD) network which included primary
327 auditory cortex, extending into superior temporal gyrus and, to a more limited extent, MTG, 3) a
328 bilateral frontal network highly similar to the previously established multiple demand network
329 (MDN; Duncan, 2010), comprising bilateral middle and inferior frontal gyri, a superior medial frontal
330 region, and (just below threshold, at $Z > 2.3$) the left intraparietal sulcus, 4) an opercular (OPRC)
331 network including anterior cingulate cortex and bilateral anterior insula, 5) a basal ganglia (BG)
332 network, 6) a bilateral motor (MOT) network, and 7) a negatively loading default mode network
333 (DMN).

334 To determine the effect of the experimental manipulations on network activity, we
335 submitted condition-specific loading values (i.e., β parameters) for our seven event-related networks

336 to a 2 x 2 multivariate analysis of variance (MANOVA) with Task (task, natural listening) and
337 Language (subordinate, unambiguous) as within-subject factors. Reporting the results of the
338 omnibus multivariate tests first, overall there were main effects of Task, $T = 7.31$, $F(7, 104) = 108.62$,
339 $p < .001$, $\eta_p^2 = .88$, and Language, $T = 3.26$, $F(7, 104) = 48.39$, $p < .001$, $\eta_p^2 = .77$, and a significant
340 interaction between Task and Language, $T = 1.85$, $F(7, 104) = 27.47$, $p < .001$, $\eta_p^2 = .65$. As Table 2
341 shows, there was a main effect of Task for all seven networks, and a main effect of Language for all
342 networks except the DMN. Further, the Task x Language interaction was significant for all networks,
343 with the largest effect seen for the MDN. Pairwise comparisons revealed that during the task, there
344 was significantly greater activity in response to subordinate than unambiguous sentences in all
345 networks except the DMN (see Table 2). Critically, during natural listening, only the FTN and AUD
346 networks increased activation in response to syntactic processing demands (i.e., subordinate >
347 unambiguous; Table 2). Although 3 other networks showed a significant difference between
348 Language conditions, none of these showed greater activation to the language conditions relative to
349 the musical rain baseline (see Figure 2). Taken together, these results suggest that while natural
350 listening recruits language-specific networks which are sensitive to syntactic processing demands,
351 when listeners hear the same sentences within the context of an explicit task, a dissociable set of
352 domain-general networks are also activated.

353 *Relationship to age and grey matter.* What effect do increasing age and grey matter decline
354 have on the ability of these networks to respond to syntactic processing demands (i.e., subordinate
355 – unambiguous loadings) during natural listening and task conditions? Looking at the effect of age
356 during natural listening, there was no age-related difference in network responsivity during task-free
357 language comprehension (Table 3). In fact, even during the task, network responsivity was not
358 significantly related to age (Table 3; smallest $p = .03$ for the FTN, which does not survive Bonferroni
359 correction). Further, despite the robust decline in mean grey matter concentration (GMC) within
360 each network with age (Table 3), individual differences in network GMC did not relate to network

361 responsivity, either during natural listening (Table 4; smallest $p = .02$ for MDN, which does not
 362 survive correction) or during the task (Table 4; smallest $p = .048$ for the FTN, which does not survive
 363 correction). These findings suggest that syntactic processing, even within the context of an artificial
 364 task, is relatively robust to both age and age-related structural declines.

365 *Relationship to performance.* What is the strongest predictor of overt task performance –
 366 responsivity of the syntax system itself or that of the domain-general networks? Performance was
 367 measured as the difference in RTs to subordinate and unambiguous sentences (i.e., our “syntactic
 368 sensitivity” measure above) and was positively correlated to responsivity of the FTN ($r_{110} = .19, p <$
 369 $.05$), AUD ($r_{110} = .23, p < .05$), MDN ($r_{110} = .38, p < .001$), and BG ($r_{110} = .22, p < .05$) during the task
 370 (only MDN survives Bonferroni correction). If we enter all seven networks into the same regression
 371 predicting task performance, the overall model is significant, $R^2 = .19, F(7, 102) = 3.31, p < .01$, and
 372 only MDN responsivity is a significant predictor ($\beta = .37, t = 3.29, p < .01, 95\% \text{ CI } [.14, .58]$; for this
 373 and all subsequent regression analyses, we report standardized coefficients). Thus, despite the fact
 374 that syntactic processing critically depends on a left-lateralized frontotemporal system (Caplan et al.,
 375 1996; Hagoort et al., 2003; Tyler et al., 2010b), performance on the task was most strongly related to
 376 responsivity of the domain-general MDN. Indeed, MDN responsivity, but not that of the other
 377 networks, also correlated with a measure of fluid intelligence performed outside the scanner ($r =$
 378 $.26, p < .01$, controlling for age; see Methods), further suggesting that the MDN plays a role in
 379 flexible adaptation to experimental demands across a wide range of tasks (Duncan and Owen, 2000).
 380 Nevertheless, in a moderation analysis, MDN responsivity did not interact with age to affect syntax
 381 performance ($t = 1.26, p = .21$), suggesting that recruitment of this domain-general network aids
 382 performance at any age and is not simply a compensatory response amongst older adults.

383 *Within-network connectivity.*

384 *Connectivity during task and natural listening.* The ICA analysis identified a set of networks
 385 that relate to our conditions of interest, but how is the internal coherence of (or functional
 386 connectivity within) those networks affected by task manipulations, age, and grey matter decline? In

387 order to address this question, we first quantified within-network connectivity as the average
 388 correlation between all pairs of voxels within the thresholded component maps (after detrending
 389 and regressing motion parameters from the raw fMRI timecourses; see Methods). Mean
 390 connectivity within each network during task and natural listening is shown in Table 5. To determine
 391 whether task demands affect within-network connectivity, we submitted mean connectivity for each
 392 of our seven networks to a MANOVA with Task (task, natural listening) as a within-subjects factor.
 393 Reporting the results of the omnibus multivariate test first, overall there was a main effect of Task, T
 394 $= 0.39$, $F(7, 104) = 5.80$, $p < .001$, $\eta_p^2 = .28$. Follow-up pairwise comparisons show that connectivity
 395 increased slightly from natural listening to task in the MDN, $t(110) = 3.38$, $M_{diff} = .02$, $p < .01$, 95% CI
 396 $[.01, .03]$, $d = .32$, and MOT network, $t(110) = 2.61$, $M_{diff} = .02$, $p < .05$, 95% CI $[.004, .03]$, $d = .25$,
 397 with no other networks differing between the two states (see Table 5). Thus, connectivity within
 398 most of these networks remains remarkably stable across different experimental states, despite the
 399 increase in loading values (or relationship to task conditions) of many of these networks during the
 400 task. This is in line with previous work showing that the brain's functional architecture during active
 401 task performance is primarily determined by an intrinsic network structure that is also apparent at
 402 rest and across different task states, and to a lesser extent by domain-specific changes linked to a
 403 particular task (Cole et al., 2014; Krienen et al., 2014).

404 *Relationship to age and grey matter.* During both natural listening and the task, connectivity
 405 within the FTN did not differ with age. In fact, only the BG network showed a significant age-related
 406 decline (see Table 3). We also examined the effect of mean GMC within each network on that
 407 network's within-network connectivity strength. Grey matter did not significantly relate to within-
 408 network connectivity during natural listening (Table 4), but it did relate to connectivity within some
 409 of the networks during the task (Table 4), with the MDN, OPRC, and BG surviving correction.
 410 Entering each of these networks into a regression predicting connectivity from age and GMC, as a
 411 means to determine the unique contribution of each factor, we see that connectivity within the
 412 MDN is predicted by GMC ($\beta = .34$, $t = 2.92$, $p < .01$, 95% CI $[.11, .58]$), not age ($\beta = .01$, $t = 0.11$, $p =$

413 .92, 95% CI [-.23, .26]; model $R^2 = .11$, $F(2, 108) = 6.82$, $p < .01$); OPRC by GMC ($\beta = .27$, $t = 2.30$, $p <$
 414 $.05$, 95% CI [.04, .49]), not age ($\beta = -.07$, $t = 0.64$, $p = .53$, 95% CI [-.32, .16]; model $R^2 = .10$, $F(2, 108) =$
 415 5.94 , $p < .01$); and BG by age ($\beta = -.42$, $t = 4.10$, $p < .001$, 95% CI [-.66, -.23]), not GMC ($\beta = .04$, $t =$
 416 0.39 , $p = .70$, 95% CI [-.17, .25]; model $R^2 = .20$, $F(2, 108) = 13.47$, $p < .001$). Thus, connectivity within
 417 the MDN and OPRC networks related to GMC within these networks, irrespective of age, while
 418 connectivity within the BG network showed a steep age-related decline which does not appear to be
 419 due to age-related declines in grey matter within that network.

420 *Relationship to performance.* Within-network connectivity was not significantly related to
 421 task performance for any of the individual networks ($r_{110} = .11, .21, -.00, .08, .09, .05, .01$, for the
 422 FTN, AUD, MDN, OPRC, BG, MOT, and DMN, respectively; smallest $p = .03$ for the AUD, which does
 423 not survive correction).

424 *Between-network connectivity.*

425 *Connectivity during task and natural listening.* We have shown that relative to natural
 426 listening, task-based language comprehension recruits several networks in addition to the critical
 427 frontotemporal syntax system, but do these networks interact with the FTN to affect performance?
 428 To address this question, we calculated between-network connectivity as the correlation between
 429 each pair of network timecourses during the task and natural listening separately (see Methods;
 430 Allen et al., 2011). As shown in Figure 3a, most networks were strongly connected to each other
 431 during the task, but less so during natural listening (Figure 3b). Figure 3c shows the difference in
 432 connectivity between the two experimental states ($p < .05$, Bonferroni corrected). Between-network
 433 connectivity was stronger during the task than natural listening in most cases with the notable
 434 exception of FTN-AUD connectivity, which was stronger during natural listening. This finding fits well
 435 with the observation that only the FTN and AUD networks are active during natural listening,
 436 whereas a host of other networks come online during active task performance. Moreover, these
 437 domain-general networks show significantly greater connectivity to the critical frontotemporal

438 syntax system during the task; this pattern suggests that this integration between networks has
439 implications for task performance (see below).

440 *Relationship to within-network connectivity.* Is stronger between-network connectivity
441 related to weaker within-network connectivity (as suggested by findings of decreased network
442 segregation with age at rest; Chan et al., 2014; Geerligts et al., 2014b)? To address this question, for
443 each pair of networks (separately for task and natural listening), we calculated the correlation
444 between within-network connectivity for each network in the pair and the connectivity between the
445 two networks. As shown in Figure 3d, in general, stronger within network connectivity during the
446 task related to stronger between network connectivity (and this relationship was not moderated by
447 age, t 's < 2, p 's > .10, except for the age x MOT-within interaction predicting MOT-DMN, $t = 2.13$, $p =$
448 .04, and the age x DMN-within interaction predicting DMN-BG, $t = 2.24$, $p = .03$, both of which do not
449 survive correction). Natural listening shows a similar pattern to the task, in that stronger *within*
450 relates to stronger *between*, but with fewer significant correlations (Figure 3e), likely due to weaker
451 connectivity between networks during natural listening (Figure 3c). Focusing on the FTN during the
452 task, we see that stronger connectivity within this network relates to stronger connections to other,
453 domain-general networks (and as mentioned above, this does not differ with age), further
454 reiterating the fact that these between-network connections are likely not compensatory (i.e., in
455 response to decreased WNC; cf. Meunier et al., 2014) but reflect normal systems-level interactions
456 in the service of task goals.

457 *Relationship to age and grey matter.* We were primarily interested in the effect of age and
458 GMC on between-network connectivity during the task, when all seven networks were most strongly
459 activated (however, for the sake of completeness, the same analyses are shown for the Natural
460 Listening condition in Figure 4c-d). Figure 4a shows the relationship between age and between-
461 network connectivity during the task ($p < .05$, Bonferroni corrected). Age was associated with
462 decreased connectivity during the task between the following network pairs: FTN-AUD, FTN-MDN,
463 AUD-MDN, AUD-DMN, BG-OPRC, BG-DMN, and MOT-OPRC. In contrast, connectivity increased with

464 increasing age between the AUD-BG networks, and between the MDN-DMN systems. A similar, but
 465 less robust, pattern of results is seen for GMC (averaged across both networks in the pair; Figure 4b).
 466 More grey matter was associated with stronger connectivity between the FTN-MDN, AUD-MDN, and
 467 BG-OPRC networks; while less grey matter was associated with stronger connectivity between the
 468 MDN-DMN networks.

469 In order to determine whether age and grey matter make independent contributions to
 470 functional connectivity between the FTN-MDN, AUD-MDN, MDN-DMN, and OPRC-BG, we entered
 471 each network pair into a regression predicting between-network connectivity from age and mean
 472 GMC. We found that connectivity between the FTN-MDN is predicted by age ($\beta = -.37, t = 3.50, p <$
 473 $.001, 95\% \text{ CI } [-.61, -.17]$), with a trend for GMC ($\beta = .18, t = 1.72, p = .088, 95\% \text{ CI } [-.03, .40]$); model R^2
 474 $= .26, F(2, 108) = 18.98, p < .001$); AUD-MDN connectivity is predicted by age ($\beta = -.50, t = 5.07, p <$
 475 $.001, 95\% \text{ CI } [-.73, -.32]$), not GMC ($p = .32$; model $R^2 = .32, F(2, 108) = 25.57, p < .001$); MDN-DMN
 476 connectivity is predicted by age ($\beta = .36, t = 3.30, p < .01, 95\% \text{ CI } [.15, .60]$), not GMC ($p = .24$; model
 477 $R^2 = .21, F(2, 108) = 13.88, p < .001$); and OPRC-BG connectivity is predicted by both age ($\beta = -.40, t =$
 478 $4.11, p < .001, 95\% \text{ CI } [-.62, -.22]$) and GMC ($\beta = .26, t = 2.68, p < .01, 95\% \text{ CI } [.07, .45]$); model $R^2 =$
 479 $.36, F(2, 108) = 29.91, p < .001$). Thus, between-network connectivity was most strongly related to
 480 age, with GMC only making an independent contribution to some of the network pairs.

481 *Relationship to task performance.* In line with the critical role of the frontotemporal network
 482 in syntactic processing, performance on the task only related to functional connectivity between the
 483 FTN and other networks (Figure 5a). Specifically, better performance related to stronger connectivity
 484 between the FTN-MDN ($r = .24, p = .01, 95\% \text{ CI } [.05, .40]$) and FTN-OPRC ($r = .25, p = .008, 95\% \text{ CI}$
 485 $[.09, .41]$). Further, between-network connectivity did not interact with age to predict performance
 486 ($t = 1.46, p = .15$, and $t = 0.24, p = .81$, for the interaction between age and the FTN-MDN and FTN-
 487 OPRC, respectively), suggesting that connectivity between the FTN and these domain-general
 488 networks is not a compensatory response, but rather contributes to successful performance across
 489 the lifespan. Moreover, if we enter average connectivity between these networks (FTN-MDN and

490 FTN-OPRC) into a regression model with FTN responsivity to predict performance, the overall model
 491 is significant, $R^2 = .10$, $F(2, 107) = 6.06$, $p < .01$, and we see that between-network connectivity is a
 492 significant predictor ($\beta = .26$, $t = 2.76$, $p < .01$, 95% CI [.07, .43]), while the FTN alone is not ($\beta = .15$, t
 493 $= 1.55$, $p = .13$, 95% CI [-.04, .32]). Taken together, these findings suggest that explicit task
 494 performance is not a straightforward reflection of FTN responsivity, but a mixture of the FTN (doing
 495 syntactic computations) and other, more domain-general networks contributing task-related
 496 processing.

497 *Effect of crystallized knowledge on performance.*

498 If functional connectivity between the FTN and MDN is positively related to performance on
 499 the task, but negatively affected by age and decreasing grey matter, how is it that performance
 500 remains stable across the lifespan? Some work suggests that age differences on tasks which place
 501 heavy demands on domain-general processes (and typically decline with age) are sometimes
 502 minimized when older adults can make use of existing knowledge (Charness, 1981; Castel, 2005;
 503 Soederberg Miller, 2009). Indeed, this may be the case during normal language comprehension,
 504 which depends on well-practiced, largely automatized processes and highly familiar language inputs
 505 (Marslen-Wilson and Tyler, 1975; Zhuang et al., 2014). Thus, we might expect that preserved
 506 performance on this task may become increasingly dependent on crystallized knowledge with age,
 507 potentially compensating for decreased domain-general control. To test this, we entered age,
 508 crystallized knowledge, and the age x crystallized knowledge interaction into a regression model
 509 predicting task performance, controlling for fluid intelligence (which is known to correlate with
 510 crystallized intelligence; Cattell, 1963). The model was significant, $R^2 = .18$, $F(4, 105) = 7.53$, $p < .001$,
 511 and while the main effect of age was not significant ($\beta = .16$, $t = 1.60$, $p = .11$, 95% CI [-.04, .37]),
 512 there were main effects of fluid intelligence ($\beta = .29$, $t = 2.38$, $p < .05$, 95% CI [.05, .52]) and
 513 knowledge ($\beta = .22$, $t = 2.24$, $p < .05$, 95% CI [.03, .42]), and importantly, an age x knowledge
 514 interaction ($\beta = .26$, $t = 2.05$, $p < .05$, 95% CI [.01, .50]). This interaction appears to be due to
 515 crystallized knowledge becoming increasingly related to task performance with age (Figure 5b).

516 Separate regression analyses performed in each age group (group N's provided in Table 1) confirms
517 this, with crystallized intelligence becoming a significant predictor of task performance in the oldest
518 group (young: model $F < 1$, $\beta_{\text{crystallized}} = .09$, $t = .73$, $p = .47$; middle-aged: model $F < 1$, $\beta_{\text{crystallized}} = .11$, t
519 $= .66$, $p = .51$; older: overall model $R^2 = .32$, $F(2, 36) = 8.60$, $p < .001$, $\beta_{\text{crystallized}} = .46$, $t = 3.30$, $p < .01$,
520 95% CI [.20, .83], $\beta_{\text{fluid}} = .26$, $t = 1.85$, $p = .07$, 95% CI [-.04, .80]). Thus, older adults may be able to
521 compensate for age-related declines in domain-general abilities by relying more heavily on an ever-
522 growing body of crystallized knowledge.

523 Discussion

524 We used a systems-level approach to separate processes specific to language
525 comprehension from those related to general task demands and to interrogate age differences in
526 functional connectivity both within and between those systems in the service of syntactic
527 processing. We show that task-free language comprehension solely recruits the auditory and
528 frontotemporal syntax networks, while active task performance calls upon several additional
529 networks which interact with the critical FTN to predict overt task performance. Despite age-related
530 declines in FTN grey matter, functionality of this network remains remarkably intact with age,
531 showing no age-related difference in within-network connectivity or responsiveness to syntactic
532 processing demands. However, in the context of a task, although aging did not affect the expression
533 of individual networks, connectivity between the FTN and MDN decreased with age, suggesting that
534 even if a network remains functionally intact with age, its ability to flexibly interact with other
535 networks in the service of task goals may be affected. However, despite the decline in FTN-MDN
536 connectivity with age, we found that overt task performance was maintained across the lifespan,
537 possibly due to older adults' richer reserve of verbal knowledge which helps to offset fluid declines.

538 The BOLD activity measured with fMRI represents a mix of signals from different sources
539 within the brain. Independent components analysis (ICA) allows for the separation of those signals
540 (Calhoun et al., 2009; Beckmann, 2012) and in this case, enabled us to tease apart those networks
541 which are required for syntactic processing from those required for general task demands. This

542 method, combined with our use of two versions of the same syntactic processing experiment (one
543 which isolated our cognitive process of interest, and another which introduced simple task demands
544 common to many cognitive experiments), allowed us to more accurately characterize the nature of
545 age-related functional differences. Contrary to previous reports of an age-related increase in right-
546 frontal activation during language comprehension (Peelle et al., 2010; Tyler et al., 2010a), we did not
547 find evidence for this “compensatory” response – either during task-free language comprehension
548 or during the active task version. We have argued previously that the topography of the core
549 frontotemporal syntax network changes little with age (Davis et al., 2014; Shafto and Tyler, 2014),
550 and that increased right-frontal activation commonly identified using standard univariate analysis
551 methods may actually be attributable to task-related processes – processes that would fall under the
552 purview of domain-general networks if the covariance between regions was taken into account.

553 In this case, we did not observe an age-related increase in the activation of frontal control
554 networks. Furthermore, increased reactivity of the MDN, as well as greater FTN-MDN connectivity,
555 related to better task performance across the lifespan (i.e., was not moderated by age), suggesting
556 that this was not a compensatory response in older adults, but related to better performance in all
557 participants. These divergent findings may be due to the population-representativeness of our
558 sample. Our recruitment process excluded term-time students (Shafto et al., 2014) and thus, our
559 sample of younger adults was more diverse than those typically used in psychological experiments,
560 which primarily consist of students from (often top-tier) universities. Thus, the task may have been
561 similarly demanding to all of our participants and as a result, we did not observe an age-related
562 increase in frontal control regions that older adults typically show at lower levels of demand (Reuter-
563 Lorenz and Cappell, 2008).

564 Another aim of the study was to examine the effect of age and experimental task demands
565 on functional connectivity both within and between ICA-identified networks. Previous work
566 examining the effect of age on large-scale network organization has primarily focused on the resting
567 state (Ferreira and Busatto, 2013) or age differences in large-scale systems (such as the DMN and

568 FPN, the precise functions of which remain unclear) during attentionally demanding tasks (e.g.,
569 Madden et al., 2010; Clapp et al., 2011; Spreng and Schacter, 2012; Geerligs et al., 2014a), but no
570 study to date has isolated a higher-order network with as clearly defined a function as the FTN (Tyler
571 et al., 2011) and examined how age and task demands affect both its internal functioning and
572 interactivity with other networks. We found that connectivity within this network, as well as other
573 domain-general networks, changed very little moving from natural listening to task (although the
574 MDN and MOT did show a modest increase), suggesting that network architecture remains
575 remarkably stable across varying task states task (Cole et al., 2014; Krienen et al., 2014; Geerligs et
576 al., 2015b). Functional connectivity between networks, on the other hand, increased during active
577 task performance, particularly between networks generally thought to be responsible for attentional
578 control (MDN, OPRC; Dosenbach et al., 2008; Duncan, 2010) and those responsible for
579 sound/language processing (AUD, FTN), likely reflecting the reliance of task-based decisions on
580 auditory and linguistic processing output. While only the BG showed a significant decline in within-
581 network connectivity with age, between-network connectivity decreased with age during the task
582 for several network pairs (although MDN-DMN and AUD-BG connectivity increased). While some
583 work has shown an age-related decline in network segregation during rest (i.e., decreased within-
584 network connectivity coupled with increased between; Chan et al., 2014; Geerligs et al., 2014b), we
585 see little evidence of this during an active language comprehension task. Thus, age differences in
586 functional connectivity observed at rest may not extrapolate to cognitive tasks.

587 One of the most remarkable findings of this study is the maintained functionality of the
588 frontotemporal syntax system, despite age-related declines in grey matter integrity and disrupted
589 connectivity to task-related networks. Unlike the reduced function seen after focal damage to the
590 FTN (Tyler et al., 2010b, 2011), which itself tends to track with the extent of the damage (Wright et
591 al., 2012), the relatively diffuse and gradual reduction in structural integrity associated with normal
592 aging seems to have little effect on FTN function. This may be because syntactic processing is a
593 relatively automatic process (e.g., Marslen-Wilson and Tyler, 1975), involving a set of obligatory

594 computations and relying on a separate pool of “resources” from conscious, control processes
 595 (Waters and Caplan, 1996). Compared to effortful control, automatic processes are thought to be
 596 relatively preserved with age (Hasher & Zacks, 1979). As long as the input is audible (Gordon-Salant
 597 and Fitzgibbons, 1997; Pichora-Fuller, 2003) and not presented too quickly (Wingfield et al., 1999,
 598 2003), both older and younger adults alike obligatorily (and rapidly) integrate the syntactic and
 599 semantic properties of each word into an online sentential representation. However, it remains
 600 unclear, from a neural perspective, *why* automatic processes are preserved while controlled
 601 processes decline. Both cross-sectional and longitudinal work suggests that frontal control regions
 602 tend to be more affected by age than more posterior regions (e.g., Raz et al., 2005, 2010; Peelle et
 603 al., 2012), with the latter more closely tied to obligatory functions (e.g., object recognition [Clarke
 604 and Tyler, 2015]; reading [Gold et al., 2009]; memory binding [Moscovitch, 1992]). Indeed, in our
 605 sample, grey matter within the left inferior frontal cortex (LIFG; BA44, 45, and 47) declined more
 606 with age ($r_{111} = -.68, p < .001, 95\% \text{ CI } [-.77, -.56]$) than that within the MTG (BA 21 and 22; $r_{111} = -.51,$
 607 $p < .001, 95\% \text{ CI } [-.63, -.36]$; Meng’s Z test for dependent correlations sharing a variable: $Z = 3.25, p =$
 608 $.001$), albeit decline within the MTG was clearly substantial. It may be that this relative preservation
 609 of structure in the MTG is sufficient to sustain connectivity with the left inferior frontal cortex and
 610 maintain functionality. A critical question for future research is how much is enough? That is, at
 611 what point do structural declines become so great that automatic processes, such as syntax, start to
 612 break down?

613 Finally, we show that when language comprehension occurs within the context of a task,
 614 even a simple task conducted online, successful performance relates most strongly to the MDN, a
 615 network previously shown to be under-recruited by older adults as attentional demands increase
 616 (Cappell et al., 2010; Nagel et al., 2011; Campbell et al., 2012). Despite the observed age-related
 617 decline in FTN-MDN connectivity during the task, overt performance on the task did not differ.
 618 Older, but not younger, adults with higher crystallized intelligence performed better on the syntax
 619 task, in line with previous work showing that older adults can make up for generalized declines with

620 increased domain-specific knowledge (Charness, 1981; Salthouse, 1984; Soederberg Miller, 2009).
621 Future work, with better temporal resolution (Tyler et al., 2013), is required to determine whether
622 this benefit of verbal knowledge to performance arises from better prediction of upcoming words,
623 faster revision of misinterpreted ambiguities, or post-syntactic decision processes.

624 Our aim was to gain a more accurate picture of neurocognitive aging by separating natural
625 language comprehension from task-based processes which are far from natural. In our view, this
626 separation of domain-specific from domain-general processes is a necessary step in order to move
627 beyond ill-defined terms, such as “dedifferentiation” and “compensation”, to more detailed models
628 of how age affects the instantiation of specific cognitive processes in the brain. A challenge going
629 forward will be to find ways to test other cognitive functions (e.g., memory encoding and retrieval,
630 verbal production) in more naturalistic ways (e.g., Stephens et al., 2010; Hall et al., 2013; Campbell
631 et al., 2015), minimizing task demands. We are ultimately interested in how age affects the brain
632 and cognition, not the task itself.

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805 Figure Legends

806 *Figure 1.* (A) Mean RTs for the subordinate, dominant, and unambiguous conditions (error bars =
807 standard errors). Data are split into 3 age groups detailed in Table 1. (B) Scatterplot showing the
808 relationship between age and syntactic sensitivity (i.e., subordinate – unambiguous RTs).

809 *Figure 2.* Functional networks differentially active during natural listening and task. Left panel shows
810 the group average spatial map for each component rendered on a canonical brain. Right panel
811 shows mean loading values for each network during Natural Listening and Task for the four
812 conditions (acoustic baseline, subordinate, dominant, and unambiguous). Error bars = standard
813 errors.

814 *Figure 3.* Effects of task and within-network connectivity (WNC) on between-network connectivity
815 (BNC). BNC matrices for (A) Task and (B) Natural Listening. Pairwise correlations were computed
816 between subject-specific timecourses for each of the seven networks and then averaged across
817 participants. Color bar indicates the strength of the average correlation (avg corr), with grey squares
818 indicating non-significant correlations ($p > .05$, Bonferroni corrected). (C) Difference in BNC between
819 task and natural listening. (D) and (E) are asymmetrical matrices showing the correlation between
820 WNC in each network and BNC during Task and Natural Listening, respectively. Network labels listed
821 down the left-hand side signify both the WNC value being correlated, as well as one of the networks
822 in each BNC pair (the other is listed along the bottom). FTN = frontotemporal, AUD = auditory, MDN
823 = multiple demand, OPRC = opercular, BG = basal ganglia, MOT = motor, DMN = default mode.

824 *Figure 4.* Relationship of between-network connectivity (BNC) to age and grey matter during the task
825 (A-B) and natural listening (C-D). Background color indicates average BNC strength. Black dots
826 indicate the correlation between BNC and age or grey matter concentration (GMC), with diamonds
827 indicating a negative relationship and circles indicating a positive relationship. The size of the dot
828 indicates the strength of the correlation. Some of the effects seen during the task are also replicated

829 during Natural Listening (e.g., age to AUD-FTN, MDN-DMN, and GMC to MDN-DMN), while other
830 effects are novel.

831 *Figure 5.* Predictors of overt task performance. (A) Background color indicates average BNC strength
832 during the task and black dots indicate a significant correlation ($p < .05$, uncorrected) between
833 connectivity and syntactic sensitivity (i.e., subordinate – unambiguous RTs). (B) Scatterplot showing
834 that crystallized intelligence becomes a stronger predictor of task performance with age.

835

Table 1. Participant demographics and mean cognitive performance

Age group	Young	Middle	Older
<i>N</i>	35	37	39
Age range (years)	22 – 45	46 – 64	65 – 87
Sex (male/female)	17/18	18/19	20/19
Highest Education			
University	30	23	19
A' Levels	4	9	11
GCSE grade	1	5	5
None over 16	0	0	4
Proportion of tones	.99 (.03)	.93 (.11)	.89 (.16)
MMSE	29.34(1.1)	29.08(0.9)	28.08(1.5)
Crystallized intelligence	53.71(3.9)	54.38(4.8)	53.23(5.8)
Fluid intelligence	37.31(4.4)	33.32(4.6)	27.28(5.5)

Note. Values in parentheses are standard deviations. Proportion of tones detected on Siemens HearCheck Screener test; MMSE = mini mental status examination; Crystallized intelligence = Spot-the-Word test; Fluid intelligence = Cattell culture fair test.

Table 2. Main effects and interactions of Task and Language condition in the seven ICA networks related to language processing

Component	ANOVAs									Pairwise Comparisons					
	Task			Language			Task x Language			Sub vs. Unamb during Task			Sub vs. Unamb during Natural Listening		
	<i>F</i>	<i>p</i>	η_p^2	<i>F</i>	<i>p</i>	η_p^2	<i>F</i>	<i>p</i>	η_p^2	<i>M_{diff}</i> [95% CI]	<i>t</i> (108)	<i>p</i>	<i>M_{diff}</i> [95% CI]	<i>t</i> (108)	<i>p</i>
Frontotemporal	108.99	< .001	.49	51.73	< .001	.32	15.11	< .001	.12	1.12 [.73, 1.50]	5.77	< .001	0.36 [.23, .48]	5.87	< .001
Auditory	103.62	< .001	.48	32.46	< .001	.23	7.25	< .01	.06	0.76 [.40, 1.12]	4.20	< .001	0.27 [.17, .38]	4.97	< .001
Multiple demand	375.35	< .001	.77	302.69	< .001	.73	139.29	< .001	.56	3.48 [3.02, 3.94]	15.03	< .001	0.77 [.64, .90]	11.78	< .001
Opercular	215.63	< .001	.66	18.76	< .001	.15	10.27	< .01	.08	0.88 [.42, 1.34]	3.82	< .001	0.13 [-.002, .26]	1.95	.054
Basal ganglia	154.56	< .001	.58	27.57	< .001	.20	47.61	< .001	.30	1.09 [.74, 1.45]	6.09	< .001	-0.11 [-.21, -.03]	2.66	< .01
Motor	164.71	< .001	.60	17.22	< .001	.13	18.95	< .001	.15	0.71 [.38, 1.04]	4.28	< .001	-0.01 [-.11, .08]	-.29	.77
Default mode	99.61	< .001	.47	< 1	.99	.00	7.99	< .01	.07	0.28 [-.12, .67]	1.39	.17	-0.27 [-.37, -.17]	5.21	< .001

Note: Lefthand results are from follow-up ANOVAs testing the main effect of Task (task, natural listening) and Language (subordinate, unambiguous), as well as the Task x Language interaction on the loading values (i.e., β parameters) for each component. Righthand results are from paired samples t-tests testing the difference between subordinate and unambiguous β parameters separately during Task and Natural Listening.

Table 3. Pearson's correlation between age and mean grey matter concentration, responsivity, and within-network connectivity for each component

Component	GMC		Responsivity				WNC			
	<i>r</i> [95% CI]	<i>p</i>	Task		Natural Listening		Task		Natural Listening	
			<i>r</i> [95% CI]	<i>p</i>	<i>r</i> [95% CI]	<i>p</i>	<i>r</i> [95% CI]	<i>p</i>	<i>r</i> [95% CI]	<i>p</i>
Frontotemporal	-.56 [-.67, -.44]	<.001	-.21 [-.37, -.03]	.03	-.08 [-.27, .10]	.39	.03 [-.13, .20]	.73	.14 [-.04, .32]	.14
Auditory	-.49 [-.62, -.36]	<.001	-.16 [-.33, .02]	.09	-.10 [-.25, .08]	.31	-.20 [-.35, -.04]	.04	-.04 [-.23, .15]	.65
Multiple demand	-.64 [-.73, -.52]	<.001	-.15 [-.32, .03]	.11	-.16 [-.33, .02]	.09	-.21 [-.35, -.04]	.03	-.06 [-.25, .13]	.52
Opercular	-.61 [-.71, -.50]	<.001	.03 [-.17, .23]	.78	-.01 [-.18, .16]	.92	-.24 [-.39, -.06]	.01	-.09 [-.28, .12]	.37
Basal ganglia	-.55 [-.67, -.43]	<.001	.07 [-.13, .25]	.49	.06 [-.12, .22]	.56	-.45 [-.56, -.33]	<.001	-.30 [-.45, -.13]	.001
Motor	-.57 [-.69, -.43]	<.001	.15 [-.04, .33]	.13	.14 [-.03, .32]	.15	.14 [-.06, .33]	.15	.21 [.002, .38]	.03
Default mode	-.55 [-.66, -.41]	<.001	-.05 [-.24, .15]	.63	.10 [-.08, .28]	.29	.05 [-.12, .24]	.61	.16 [-.04, .36]	.10

Note: Responsivity (to syntactic processing demands) = subordinate – unambiguous loadings; GMC = grey matter concentration; WNC = within-network connectivity. CI = 95% bootstrap confidence intervals.

Table 4. Pearson's correlation between GMC and network responsivity and WNC

Component	Responsivity				WNC			
	Task		Natural Listening		Task		Natural Listening	
	<i>r</i> [95% CI]	<i>p</i>	<i>r</i> [95% CI]	<i>p</i>	<i>r</i> [95% CI]	<i>p</i>	<i>r</i> [95% CI]	<i>p</i>
Frontotemporal	.19 [.00, .36]	.05	.10 [-.09, .28]	.30	.18 [-.01, .34]	.07	.03 [-.16, .21]	.76
Auditory	.06 [-.11, .23]	.53	-.06 [-.26, .16]	.52	.22 [.04, .38]	.02	.17 [-.004, .34]	.07
Multiple demand	.11 [-.09, .31]	.24	.21 [.07, .35]	.02	.34 [.18, .47]	<.001	.18 [.03, .33]	.06
Opercular	-.07 [-.27, .11]	.44	.03 [-.19, .23]	.79	.31 [.16, .44]	.001	.24 [.09, .39]	.01
Basal ganglia	-.02 [-.18, .13]	.82	-.01 [-.18, .18]	.95	.27 [.12, .42]	.004	.19 [.04, .34]	.04
Motor	.03 [-.18, .22]	.80	-.12 [-.29, .04]	.21	-.14 [-.32, .03]	.14	-.17 [-.33, .02]	.08
Default mode	.07 [-.14, .28]	.50	-.12 [-.31, .08]	.20	.05 [-.13, .23]	.57	-.01 [-.20, .19]	.95

Note: Correlation values for each component are between mean grey matter concentration (GMC) within that component and 1) its responsivity to syntactic processing demands (i.e., subordinate – unambiguous loadings; first two columns) and 2) its mean within-network connectivity (WNC; second two columns). CI = 95% bootstrap confidence intervals.

Table 5. Mean within-network connectivity during task and natural listening

Component	Task	Natural listening	Task vs. Natural Listening		
			M_{diff} [95% CI]	t (110)	P
Frontotemporal	.43 (.08)	.43 (.07)	.007 [-.005, .02]	1.19	.24
Auditory	.48 (.09)	.49 (.08)	-.006 [-.02, .01]	-.97	.34
Multiple demand	.52 (.09)	.50 (.08)	.02 [.01, .03]	3.38	< .01
Opercular	.46 (.09)	.46 (.08)	-.001 [-.01, .01]	-.17	.87
Basal ganglia	.49 (.08)	.48 (.08)	.004 [-.01, .01]	.67	.50
Motor	.57 (.08)	.55 (.08)	.02 [.004, .03]	2.61	< .05
Default mode	.54 (.09)	.54 (.08)	.002 [-.01, .01]	.34	.73

Note: Values in the two left-hand columns reflect mean within-network connectivity across participants during Task and Natural Listening (standard deviations in parentheses). Right-hand columns show results from follow-up paired samples t-tests testing the difference in WNC between Task and Natural Listening.

Figure 1

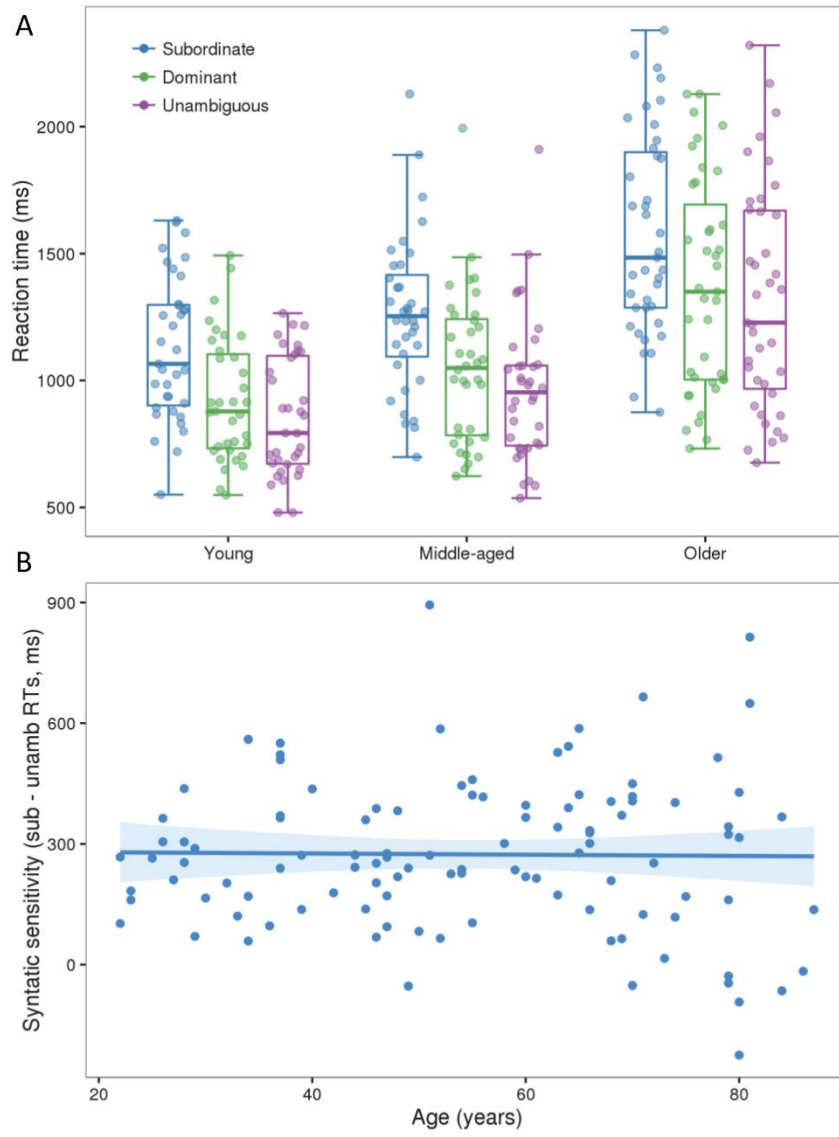


Figure 2

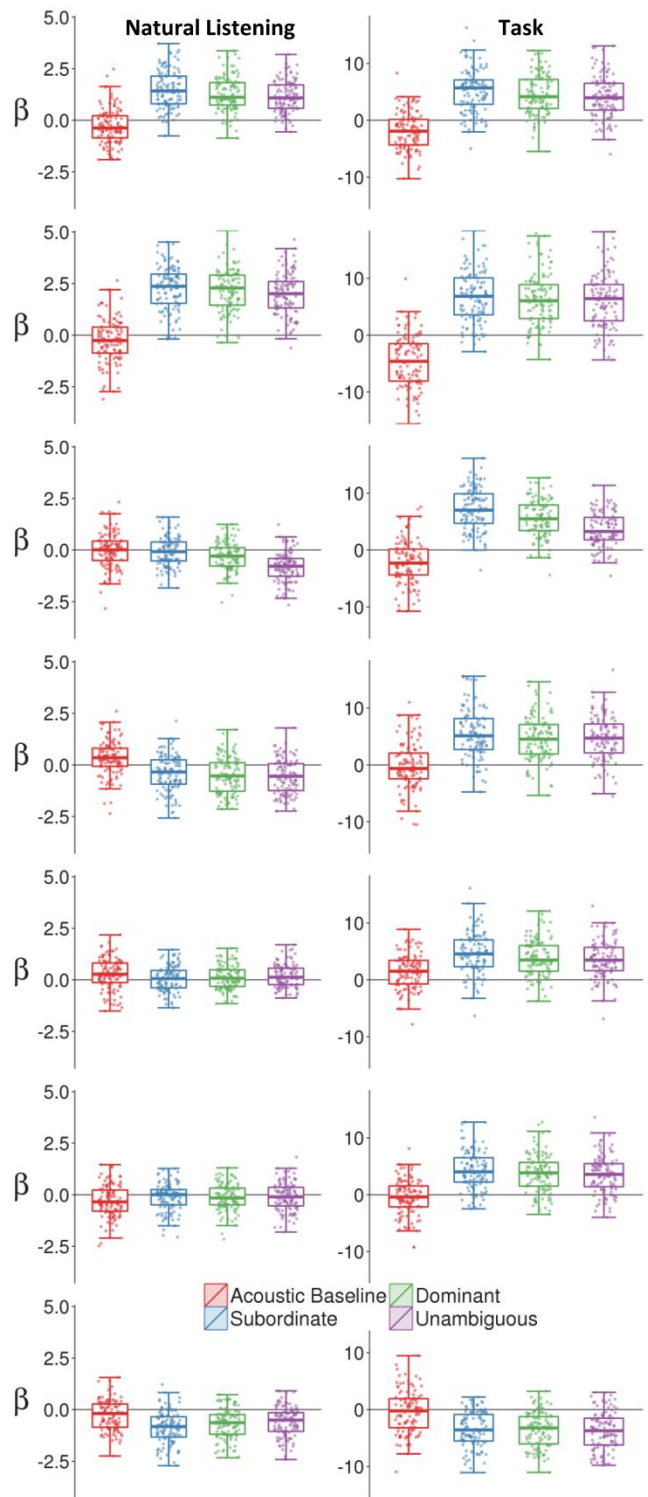
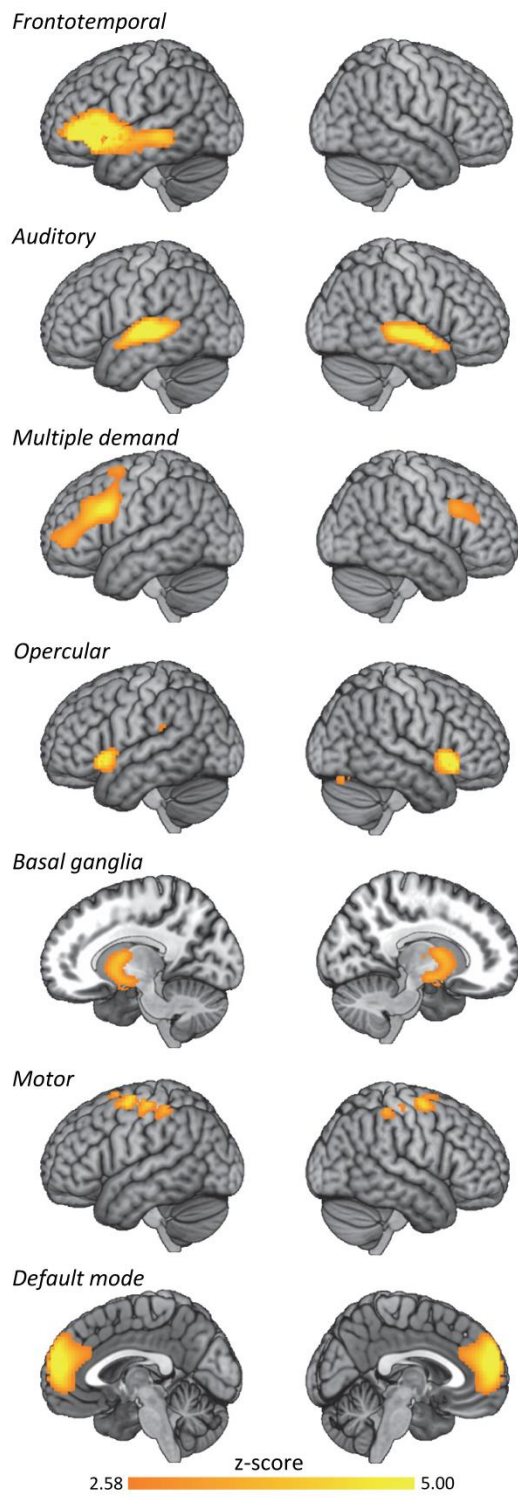


Figure 3

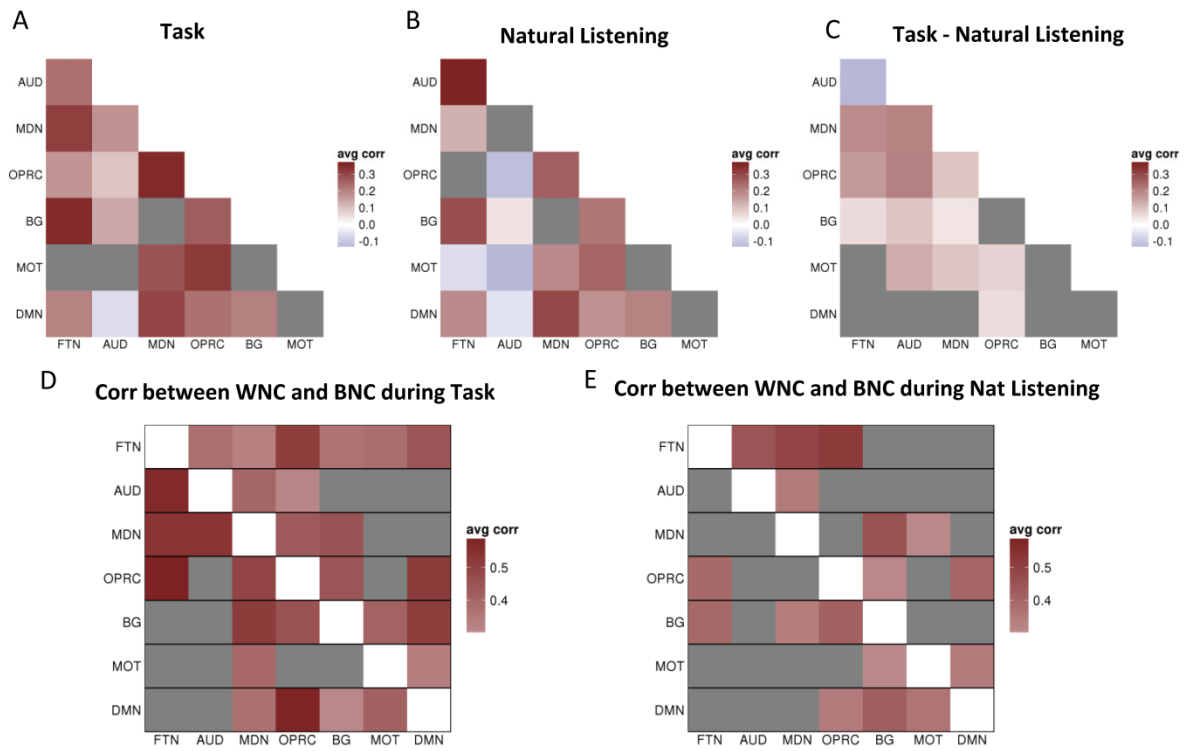


Figure 4

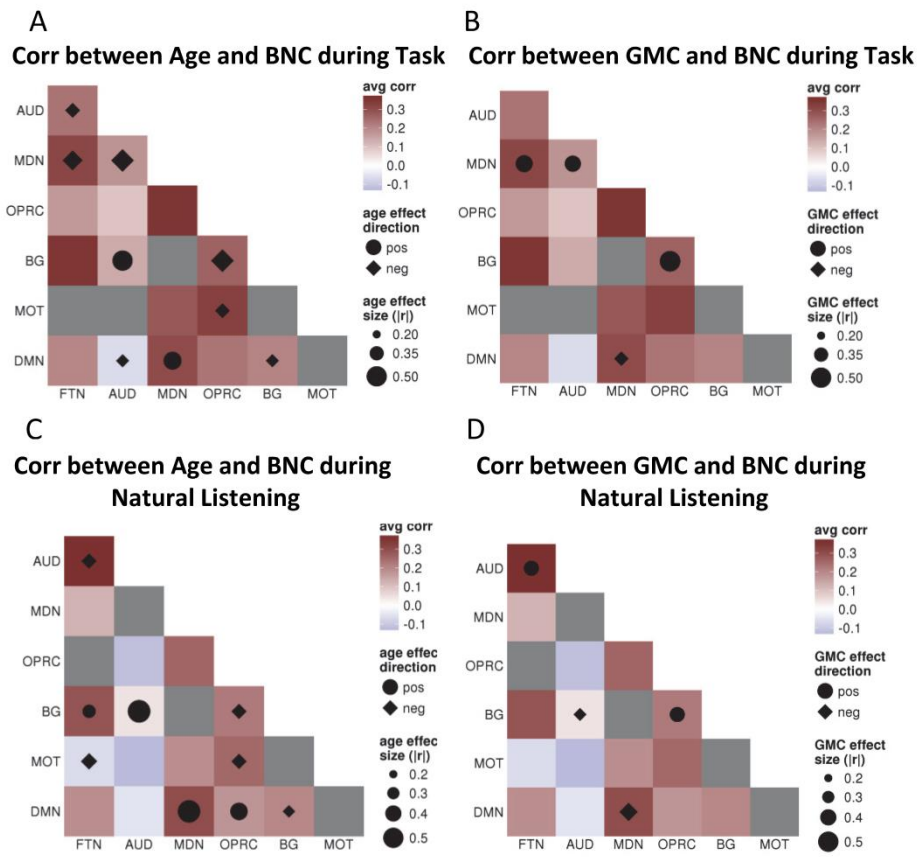


Figure 5

