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Age-related sensitivity to task-related modulation of language-processing networks

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ABSTRACT

It is widely assumed that cognitive functions decline with age and that these decrements are associated with age-related changes in patterns of functional activity. However, these functional changes may be due to age-related increased responsiveness to task demands and not to other cognitive processes on which neural and behavioural responses rely, since many ageing studies use task paradigms that may not be orthogonal to the cognitive function being investigated. Here we test this hypothesis in adults aged 20–86 years by combining measures of language comprehension, functional connectivity and neural integrity to identify functional networks activated in two language experiments with varying task demands. In one, participants listened to spoken sentences without performing an overt task (the natural listening condition) while in the other they performed a task in response to the same sentences. Using task-based ICA of fMRI, we identified a left-lateralised frontotemporal network associated with syntactic analysis, which remained consistently activated regardless of task demands. In contrast, in the task condition only a separate set of components showed task-specific activity in Opercular, Frontoparietal, and bilateral PFC. Only the PFC showed age-related increases in activation which, furthermore, was strongly mediated by grey matter health. These results suggest that, contrary to prevailing views, age-related changes in cognitive activation may be due in part to differential responses to task-related processes.

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1. Introduction

Ageing brains exhibit many changes in task-induced brain activity across the lifespan, most of which cannot be explained by physiological factors alone (D'Esposito, Zarahn, Aguirre, & Rypma, 1999; Kannurpatti, Motes, Rypma, & Biswal, 2010). A central challenge in the study of healthy ageing is to understand how these neural changes relate to cognitive processes. One of the most common patterns associated with increasing age – increased bilateral prefrontal cortex (PFC) activity – has been observed across a wide range of tasks involving many cognitive functions (Dennis & Cabeza, 2008; Eyler, Sherzai, Kaup, & Jeste, 2011). The functional relevance of this effect remains controversial (Grady, 2012), with some claiming that it may reflect either non-selective recruitment associated with decreased specialisation (Logan, Sanders, Snyder, Morris, & Buckner, 2002), or proactive cognitive control strategies formed in response to structural changes (Nyberg et al., 2010; Persson et al., 2011; Velanova, Lustig, Jacoby, & Buckner, 2007). Support for both viewpoints has relied on the relationship between changing patterns of PFC activity and behavioural performance (Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008; Persson et al., 2006).

These findings raise a fundamental question: how do task requirements impact cognitive functions as we age? Previous studies have shown that task-related components generate additional functional activity in young participants over and above that involved in domain-specific processes (Cabeza et al. 2004; Meyer, Friederici, & von Cramon, 2000; Wright, Randall, Marslen-Wilson, & Tyler, 2011). Here we ask whether the relationship between task-related and domain-specific processes during language comprehension changes with age. We define here a *task effect* as the set of operations intrinsic to maintaining performance in the context of the experimental situation (Orne, 1962). Maintaining attention, storing arbitrary task heuristics, and manipulating information over short periods of time are demands ubiquitous in most studies of the ageing brain, yet form only a part of everyday life. Many everyday activities are highly practised and automatic, minimising the contribution of the kinds of task variables typically tested in studies of age-related changes in cognition. A growing number of studies have endeavoured to address this problem by using more realistic stimuli in fMRI studies. These novel paradigms include movie watching (Hasson, Furman, Clark, Dudai, & Davachi, 2008), story listening (Lerner, Honey, Silbert, & Hasson, 2011), and free recall of previously encoded personal events (St Jacques, Conway, Lowder, & Cabeza, 2011).

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The focus on task effects poses particular problems for understanding the nature of the age-related changes in higher cognitive functions, since it is well-established that older adults show impairments in many of the mental operations intrinsic to performing experimental tasks. For example, older adults show performance deficits in disengaging with irrelevant stimuli (Hasher, Lustig, & Zacks, 2007; Healey, Campbell, & Hasher, 2008; Madden, Spaniol, Bucur, & Whiting, 2007), switching between cognitive tasks (Jimura & Braver, 2010), and re-engaging after task interruption (Clapp, Rubens, Sabharwal, & Gazzaley, 2011), all of which have been associated with changes in bilateral PFC function. Previous ageing studies have addressed this problem by using a task-general approach to compare activation *across* different tasks in either empirical (Cabeza et al., 2004; Davis et al., 2008) or meta-analytic approaches (Spreng, Wojtowicz, & Grady, 2010); however, these strategies do not eliminate the problem since similar operations may be associated with many tasks.

In contrast to age-related decrements in such task-related cognitions, some cognitive functions are relatively preserved across the lifespan, especially when tested in more naturalistic contexts: implicit memory (Jennings & Jacoby, 1993), general knowledge (Hedden, Lautenschlager, & Park, 2005) and language comprehension (Radvansky & Copeland, 2001) each tap elements of everyday language function, and all show minimal effects of age when task demands are low and ecological validity is high. For example, Hedden et al. (2005) found that decrements in free recall performance are attenuated by general knowledge, suggesting that age-related increases in knowledge may compensate for age-related declines in performing a memory task. Similarly, Radvansky and Copeland (2001) showed that in contrast to more task-oriented memory for propositional information (which shows reliable age-related declines), both younger and older adults are similarly able to update event representations during natural story comprehension. These functions therefore represent ideal models in which to evaluate age-related effects of an experimental task on cognitive functions that, in their natural contexts, are highly automatised, but which in more experimental conditions show stronger age-related decrements.

In this study we investigated the effects of tasks on cognitive functions in ageing by focussing on a core component of human language—syntax. Much experimental research over the past 30 years has shown that syntactic analysis is highly automatised (Marslen-Wilson, 1975, 1987; Marslen-Wilson & Tyler, 1980) involving the rapid and obligatory mapping from speech sounds to lexical representations and the construction of syntactically structured sentential representations. These automatic processes are revealed in neural responses to spoken sentences even when participants are merely listening to the sentences without performing an explicit task (Crinion, Lambon-Ralph, Warburton, Howard, & Wise, 2003; Tyler et al., 2010). Furthermore, syntactic comprehension remains preserved across the lifespan and involves a reliable left-lateralised frontotemporal network (Dapretto & Bookheimer, 1999; Tyler et al. 2011), comprising a consistent set of regions including the left inferior gyrus (including Brodmann area 45) and the middle temporal gyrus (MTG), which can be characterised in young adults either with (Meyer et al., 2000) or without (Tyler et al., 2011) the involvement of an explicit task. Although considerable evidence suggests that this left frontotemporal network is engaged in the young in response to syntactic manipulations (Rodd, Longe, Randall, & Tyler, 2010; Turken & Dronkers, 2011; Tyler, Cheung, Devereux, & Clarke, 2013; Tyler et al. 2010), there is some evidence that bilateral frontal regions are activated in older adults. However, these increases in right PFC activity are not typically correlated with better syntactic performance (Antonenko et al. 2013; Tyler et al., 2010), raising the issue of what its functional role is. Thus, while a number of neuroimaging studies in older adults have reported bilateral PFC patterns of activation during language function, the relationship between the left frontotemporal language network and other task-related networks across the adult lifespan is unclear. One possibility – explored in the current paper – is that the additional right PFC activity in older people is related to the increased contribution of other task-related networks; our study therefore seeks to explicitly address under which conditions the bilateral frontal PFC network and the left frontotemporal language network are relevant to normal language function.

Independent component analysis (ICA) has proven to be very effective in isolating independent but overlapping functional networks present in a given fMRI dataset and provides information that augments the classical univariate approach (Beckmann & Smith, 2004; Calhoun, Adali, Pearlson, & Pekar, 2001). These advantages are particularly useful for cognitive neuroscience investigations of ageing, as differences in response time (Salthouse, 1996) and hemodynamic responsivity (Huettel, Singerman, & McCarthy, 2001; Velanova et al. 2003) may complicate and confound the interpretation of significant differences between age groups based on standard univariate approaches. In the current study we carried out an ICA-based functional connectivity analysis of fMRI data, combining information from two language studies: one in which participants performed an explicit task in response to sentential stimuli [*task condition*] and one in which they simply listened to the same sentences [*natural listening condition*]. This analysis allowed us to separate the neurocognitive networks that were stable between the two scanning studies, from networks that come online in response to performing an experimental task. This, in turn, allowed us to characterise the age-related changes in functional network activity occurring during the task in relation to those occurring during natural listening.

2. Material and methods

2.1. Participants

The participants consisted of 50 healthy, native British English speakers across a broad range of ages (20–86 years). Participants were tested in two scanning experiments – *task* and *natural listening* – and were evenly divided between the two experiments (task: 12 females; natural listening: 13 females), with equivalent distributions of subjects across the lifespan in each experiment (Mann–Whitney $U=284.0$, $p=0.58$). There was no overlap in the participant pools between the *task* and *natural listening* experiments. They were all right-handed with no history of neurological illness or head injury and free of psychiatric illness or psychoactive medication for at least 6 months prior to scanning. No participant had audiometer measurements that indicated severe hearing impairment (hearing threshold for all subjects >70 dB based on guidelines published by the British Society of Audiology) or were cognitively impaired (25 or higher on MMSE and/or 26 or higher on Ravens Coloured Progressive Matrices).

2.2. Ethics statement

The study was approved by the Cambridge Psychology Research Ethics Committee. All participants gave written informed consent prior to participation, and were compensated for their participation according to the time they spent on the study.

2.3. Stimuli

fMRI scanning occurred while subjects were listening to spoken sentences described previously (see Tyler et al. (2011) for further details). The test stimuli in both the *task* and *natural listening* fMRI

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