Neuroscience and Biobehavioral Reviews 84 (2018) 134–150

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Age-related changes in the neural networks supporting semantic cognition: A meta-analysis of 47 functional neuroimaging studies

Paul Hoffman*, Alexa M. Morcom

Centre for Cognitive Ageing and Cognitive Epidemiology (CCACE) & Department of Psychology, University of Edinburgh, UK

ARTICLE INFO

Keywords:
Semantic memory
fMRI
Multiple demand network
Default mode network

ABSTRACT

Semantic cognition is central to understanding of language and the world and, unlike many cognitive domains, is thought to show little age-related decline. We investigated age-related differences in the neural basis of this critical cognitive domain by performing an activation likelihood estimation (ALE) meta-analysis of functional neuroimaging studies comparing young and older people. On average, young people outperformed their older counterparts during semantic tasks. Overall, both age groups activated similar left-lateralised regions. However, older adults displayed less activation than young people in some elements of the typical left-hemisphere semantic network, including inferior prefrontal, posterior temporal and inferior parietal cortex. They also showed greater activation in right frontal and parietal regions, particularly those held to be involved in domain-general controlled processing, and principally when they performed more poorly than the young. Thus, semantic processing in later life is associated with a shift from semantic-specific to domain-general neural resources, consistent with the theory of neural dedifferentiation, and a performance-related reduction in prefrontal lateralisation, which may reflect a response to increased task demands.

1. Introduction

Semantic knowledge, of the meanings of words and properties of objects, shapes our understanding of the world and guides our behaviour. Most of our interactions with the environment, linguistic and non-linguistic, require us to harness this knowledge in some way. This use of semantic knowledge is often termed semantic cognition (Rogers and McClelland, 2004). Unsurprisingly, given its central role in higher cognitive function, semantic cognition activates a complex set of brain regions which overlap with other neural systems such as the multiple demand network (Duncan, 2010) and the default mode network (Buckner et al., 2008). In this meta-analysis, we investigated age-related differences in the functional neuroanatomy of semantic cognition. While formal meta-analysis techniques have been used to investigate functional brain activation in a number of domains (Li et al., 2015; Maillet and Rajah, 2014; Spreng et al., 2010), this is the first to focus on semantic cognition specifically. This is important because most aspects of semantic processing are thought to remain stable into older age, in stark contrast to the declines in function observed in many other cognitive domains (Nilsson, 2003; Nyberg et al., 1996; Park et al., 2002; Rönnlund et al., 2005; Salthouse, 2004; Verhaeghen, 2003). Important insights into the nature of successful cognitive ageing can be gained through better understanding of the changes in neural activity that underlie this maintenance of function. In what follows, we first provide an overview of the neural correlates of semantic cognition, as revealed by studies of young people. We then consider the predictions made by current theories of neurocognitive ageing for age-related differences in the networks engaged by semantic cognition in younger and older adults, before testing these predictions in a formal meta-analysis of 47 neuroimaging studies.

1.1. The neural basis of semantic cognition

Semantic cognition activates a distributed neural network in young adults, including frontal, temporal and parietal regions (Binder et al., 2009; Noonan et al., 2013). Key regions are illustrated in blue in Fig. 1 (alongside other networks to be described later). It is important to note at the outset that the semantic network is somewhat left-lateralised, although, as we discuss later, the degree of lateralisation can vary dependent on stimulus, brain region and task difficulty. The ventral anterior temporal lobe (vATL) is thought to be involved in the storage of multi-modal semantic representations (Lambon Ralph et al., 2017). This is based on the strong association between damage to this region and the clinical syndrome of semantic dementia, which involves a profound and selective loss of semantic knowledge (Patterson et al., 2007). fMRI studies often overlook vATL, in part because of well-known

* Corresponding author at: Centre for Cognitive Ageing and Cognitive Epidemiology, Department of Psychology, University of Edinburgh, 7 George Square, Edinburgh, EH8 9JZ, UK.
E-mail address: p.hoffman@ed.ac.uk (P. Hoffman).

https://doi.org/10.1016/j.neubiorev.2017.11.010
Received 21 July 2017; Received in revised form 10 November 2017; Accepted 17 November 2017
Available online 26 November 2017

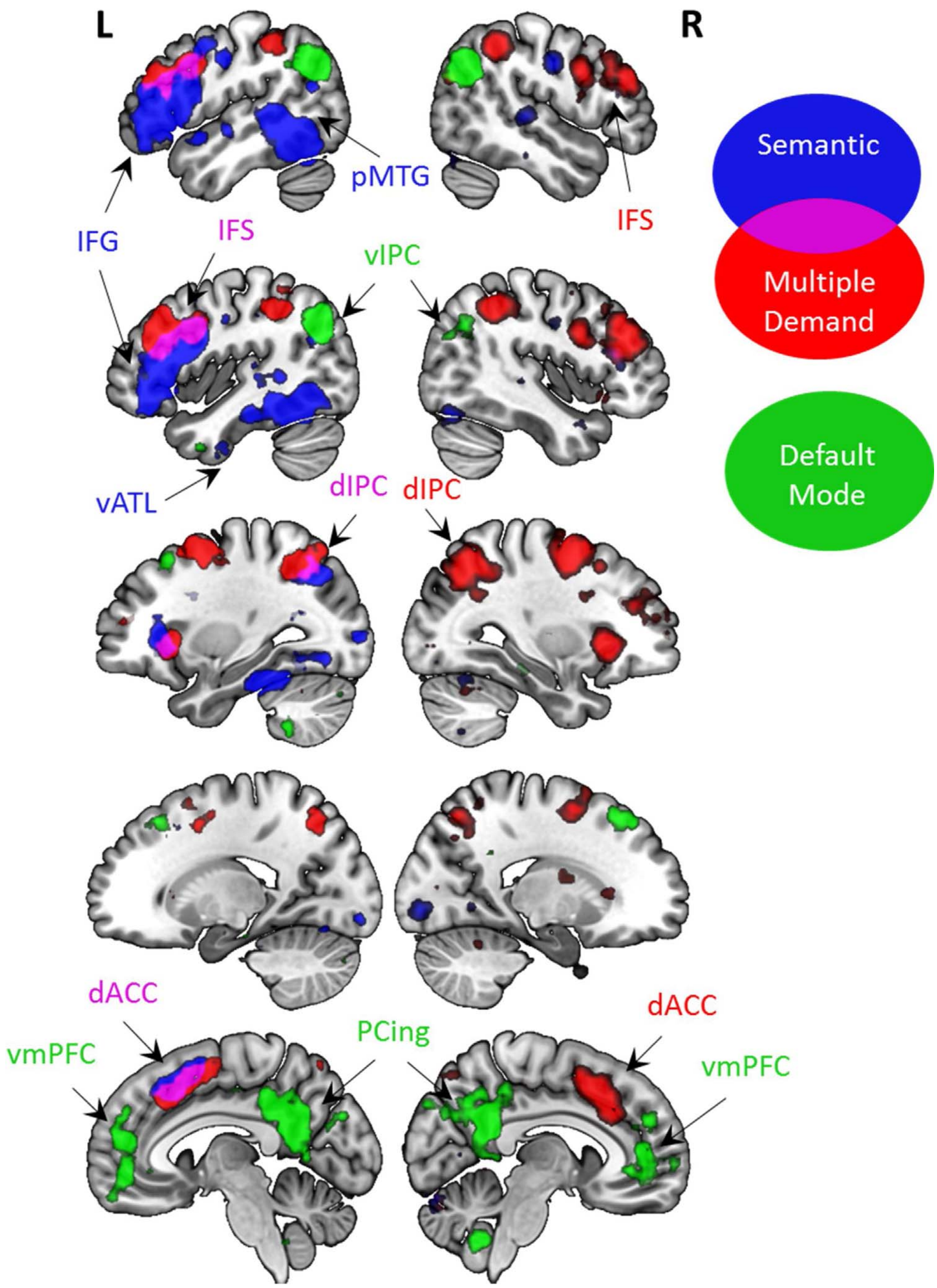

Fig. 1. Regions typically associated with semantic processing and with the multiple demand and default mode networks. Figure show areas of activation associated with particular topics in the Neurosynth database of over 10,000 neuroimaging studies (Yarkoni et al., 2011). Topics were extracted using automated analysis of terms used in the target articles (Poldrack et al., 2012). The semantic topic included the keywords [semantic; words; meaning; picture; conceptual; association; knowledge]. The multiple demand topic included [task; performance; control; executive; difficulty; demands; goal]. The default mode topic included [network; resting; default; intrinsic; spontaneous]. The database does not discriminate between young and older participants; however; since the vast majority of neuroimaging participants are young; these networks predominately reflect activation patterns in young adults. IFG = inferior frontal gyrus; pMTG = posterior middle temporal gyrus; IFS = inferior frontal sulcus; vIPC = ventral inferior parietal cortex; vATL = ventral anterior temporal lobe; dIPC = dorsal inferior parietal cortex; dACC = dorsal anterior cingulate cortex; PCing = posterior cingulate cortex; vmPFC = ventromedial prefrontal cortex.

technical difficulties in acquiring signal from the ventral temporal cortices, due to the proximity of air-filled sinuses (Devlin et al., 2000). However, recent studies using methods that combat these issues have reliably identified activity in the left vATL during semantic processing (e.g., Halai et al., 2015; Hoffman et al., 2015; Humphreys et al., 2015). vATL activation is greater in the left hemisphere during written word semantic processing and speech production, but displays a more bilateral distribution during other forms of semantic processing (Rice et al., 2015a).

Other regions are involved in the executive regulation of semantic knowledge, ensuring that task and context-appropriate information is activated (Jefferies, 2013). This is critical because we store a wide range of knowledge about any concept and different aspects of this information are important in different situations. For example, the relevant semantic features of *pianos* change depending on whether one is asked to play a piano or to move one across the room (Saffran, 2000). This element of semantic processing, often termed semantic control, has chiefly been associated with activity in the left inferior frontal gyrus (IFG) (Badre and Wagner, 2002; Hoffman et al., 2010; Thompson-Schill et al., 1997). More recently, it has become clear that left posterior middle temporal gyrus (pMTG) is also activated by manipulations of semantic control (Noonan et al., 2013; Whitney et al., 2011). The two regions also display strong structural and functional interconnectivity (Turken and Dronkers, 2011). Current theories hold that both IFG and pMTG serve to regulate performance in semantic tasks by exerting top-down control over the activation of semantic representations in the vATL (Lambon Ralph et al., 2017).

Semantic tasks also activate some areas within the "multiple demand" network (MDN) (Duncan, 2010; Fedorenko et al., 2013). This network comprises a set of brain regions that respond to increasing task demands across many cognitive domains and are thought to be involved in the planning and regulation of goal-directed cognition and behaviour