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The tract terminations in the temporal lobe: Their location and associated functions

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ABSTRACT

Temporal lobe networks are associated with multiple cognitive domains. Despite an upsurge of interest in connectional neuroanatomy, the terminations of the main fibre tracts in the human brain are yet to be mapped. This information is essential given that neurological, neuroanatomical and computational accounts expect neural functions to be strongly shaped by the pattern of white-matter connections. This paper uses a probabilistic tractography approach to identify the main cortical areas that contribute to the major temporal lobe tracts. In order to associate the tract terminations to known functional domains of the temporal lobe, eight automated meta-analyses were performed using the Neurosynth database. Overlaps between the functional regions highlighted by the meta-analyses and the termination maps were identified in order to investigate the functional importance of the tracts of the temporal lobe. The termination maps are made available in the Supplementary Materials of this article for use by researchers in the field.

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1. Introduction

The temporal lobe has been implicated in a multitude of cognitive domains, including audition (Kaas & Hackett, 1999), vision (Goodale & Milner, 1992; Grill-Spector & Malach, 2004), language (Cloutman, 2013; Price, 2010), memory (Scoville &

Milner, 1957) and semantic processing (Lambon Ralph, 2014). The successful execution of these higher cognitive functions is not carried out by the temporal lobe alone, but requires a complex interaction with other widely distributed brain regions. This interaction is underpinned by the white matter – the brain's information 'super-highway' – which consists of

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bundles of neural axons that carry information over long distances from one area of cortical grey matter to another (Curran, 1909; Martino, Brogna, Robles, Vergani, & Duffau, 2010; Sarubbo, De Benedictis, Maldonado, Basso, & Duffau, 2013). While information processing occurs in the cortical grey matter, the white matter connections govern the nature and flow of information to and from this grey matter. Indeed, neuroanatomical, neurological and computational accounts have all emphasised that the form and pattern of the white matter connectivity will exert a strong influence over the nature of the neural computation in each area (Binney, Embleton, Jefferies, Parker, & Lambon Ralph, 2010; Brodmann, 1909; Mesulam, 1998; Plaut, 2002). These hypotheses have been supported by experimental surgical reorganisation of the major auditory and visual pathways in animals (Roe, Pallas, Kwon, & Sur, 1992; Sharma, Angelucci, & Sur, 2000; Sur, Garraghty, & Roe, 1988). Accordingly, in order to understand the roles played in higher cognition by different cortical regions, it is important to understand its underlying structural connectivity in detail.

Previous work on the connectivity of the temporal lobe has identified six major association fibre tracts [uncinate fasciculus (UF), inferior longitudinal fasciculus (ILF), inferior frontooccipital fasciculus (IFOF), middle longitudinal fasciculus (MdLF), arcuate fasciculus (AF) and cingulum] and two main commissural fibres [the corpus callosum and anterior commissure (AC)] that lie within the temporal lobe (Catani, Jones, Donato, & Ffytche, 2003, Catani, Jones & Ffytche, 2005; Catani & Mesulam, 2008; Curran, 1909; Davis, 1921; Déjerine & Dejerine-Klumpke, 1895; Forkel et al., 2012; Makris et al., 2009; Tusa & Ungerleider, 1985). The extreme capsule (EmC) has also been suggested to constitute an important tract within the ventral language system (Makris & Pandya, 2009; Schmahmann and Pandya, 2007, 2009). However, this is with some controversy, and there is a growing consensus that the capsule represents a region within the brain where several tracts converge, and is not a specific tract itself (Bajada, Lambon Ralph, & Cloutman, 2015; Duffau, Herbet, & Moritz-Gasser, 2013). As such, the temporal connections of the EmC can either be considered to be part of the IFOF (Duffau et al., 2013), part of an adjacent temporo-frontal fasciculus (Petrides, 2013) or part of the UF. Due to dissection, tracer and magnetic resonance imaging (MRI) studies, much is known about the trajectory of these temporal fibre bundles (Martino, Vergani, Robles & Duffau, 2010, Martino, et al., 2011; Menjot de Champfleur et al., 2013), but less is known about where these tracts originate and terminate.

Dissection methods (e.g., Curran, 1909; Maldonado et al., 2013; Martino, Brogna, et al., 2010, Martino, Vergani, et al., 2010; Sarubbo et al., 2013), are generally poorly suited to determining tract terminations for several reasons. First and foremost, the destructive nature of the dissection method poses the greatest challenge in determining the cortical termination points of a given tract: one of the first steps in the process is cortical removal in order to expose the tract under examination, and thus the termination regions of interest are largely destroyed by this method. In addition, in order to perform a dissection, strong prior information regarding tract location is required and many subjective decisions must be made throughout the procedure before reaching the

termination of a tract (Curran, 1909). Additionally, the limited number of samples available for dissection makes it difficult to comment with confidence on the variability of tract termination patterns across a population. Finally, only a small number of tracts can be targeted within a single brain and replication on the same brain is impossible.

Tracer studies, in contrast, are able to provide very precise data regarding the terminations of a given tract. In this method, a visualisable tracer agent (such as horseradish peroxidase) is injected into a cortical region of interest, enabling the afferent and efferent neural pathways connecting this region to other areas of the brain to be delineated (Hackett, Stepniewska, & Kaas, 1998). Like anatomical dissection, however, the results of these studies are guided by strong anatomical priors that dictate where to inject the tracer. Also, as the animal is sacrificed in order to examine the path of the tracer, replication in the same brain is impossible. In addition, the tracer method allows only a limited number of injection sites, meaning that only a proportion of a cortical region of interest can be covered in a single specimen. Most importantly, due to the invasive nature of the technique, all data are from non-human primates and other animals, requiring extrapolation to human anatomy which is not precise.

Diffusion MRI tractography is a method that allows one to examine multiple white matter tracts in the same brain. Since the data are not destroyed in the analysis process, the examination can be replicated within the same brain. In this method, the trajectory of fibre bundles is inferred by the orientational preference of movement of water molecules within the brain (Parker, Haroon, & Wheeler-Kingshott, 2003). Although recent years have seen great technical advancements in the analysis of white matter bundles using diffusion imaging (Basser, 1998; Behrens et al., 2003; Makris et al., 1997; Mangin et al., 2013; Mori, Crain, Chacko, & van Zijl, 1999; Parker et al., 2003), to date, the majority of tractography studies have focused on delineating the course of these white matter pathways and not their specific cortical terminations within the cortex. As such, while much is known regarding the relative trajectories of the fibre bundles within the temporal lobe, precisely where they begin or end remains unclear.

In the current paper, we use probabilistic tractography (Parker et al., 2003) to map the tract terminations of key fibre bundles within the temporal lobe. In order to delineate the cortical terminations of these tracts rather than their trajectories, tractography was first performed from the entire temporal lobe and the resulting output used to identify specific tracts of interest. Regions of the cortex that contributed to the tractographic output for a given tract were then identified, linking the tract to its terminations within the temporal cortex. This approach allowed for the generation of tract termination maps that provide information regarding the probability of a voxel within the temporal lobe having connections via a particular tract of interest. The resultant termination maps are provided in the Supplementary Materials for use by the research community. In addition to delineating the areas of the temporal cortex connected via these key white matter tracts, the potential functional roles of these temporal pathways were also explored. To that end, eight automated meta-analyses (episodic memory, hearing, speech perception, phonological processing, speech

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