Auditory-Language Networks involving the Superior Temporal Gyrus: Patterns of Connection and Lateralization

H. A. Haroon[1], M. A. Lambon Ralph[2], Y. Watson[1], O. Ciccarelli[3], C. A. Wheeler-Kingshott[3], D. C. Alexander[4], S. Luzzi[5], G. J. Parker[1]

[1]Imaging Science & Biomedical Engineering, The University of Manchester, Manchester, England, United Kingdom, [2]School of Psychological Sciences, The University of Manchester, Manchester, England, United Kingdom, [3]Department of Headache, Brain Injury and Neurorehabilitation, Institute of Neurology, UCL, London, England, United Kingdom, [4]Department of Computer Science, University College London, London, England, United Kingdom, [5]Department of Neuroscience, University of Ancona, Ancona, Italy

Introduction We present a study of the anatomical connections of the superior temporal gyrus (STG) to major auditory-language centres in both hemispheres. We use probabilistic tractography, incorporating crossing fibre information, in a group of 10 healthy subjects to assess STG connectivity internally to Wernicke's area (WA), and externally to Broca's area (BA) and the thalamus (Th). For the first time in living human beings, we provide evidence for parcellation of the STG into anterior regions connecting largely to BA, posterior regions connecting largely to WA, and two distinct regions connecting largely to Th, and provide evidence for the lateralisation of the BA and WA connections. Our findings are closely consistent with previous invasive studies mapping STG connections in rhesus macaque[1].

Methods MR diffusion weighted data were acquired in 10 right-handed healthy volunteers. Imaging was carried out on a GE Signa 1.5 Tesla scanner with a standard quadrature head coil. Sequence parameters, data acquisition and reconstruction details are as given in [4].

Anatomical images for each individual were transformed into standard space, where volumes of interest (VOI) were defined to delineate the STG, BA (Brodmann area 44), WA (Brodmann area 22) and Th in the both hemispheres[1-5] (with WA forming a sub-volume of the STG, and the homologue of BA being defined in the right hemisphere). VOIs were defined to encompass the grey matter relating to each area and neighboring gyral white matter. All VOIs were transformed back into acquisition space for each individual, where probabilistic fibre tracking was performed from every voxel in the STG VOI using the PICo software package[6,7]. Probability density functions (PDF) of cerebral fibre orientations were estimated for the presence of one or two fibres by modeling water diffusion in a single fibre by a single Gaussian density and in multiple fibres by a mixture of Gaussian densities[7]. The tracking process generated maps of connection probability to every voxel in the brain from each voxel within the STG. The connection probability of each STG voxel map within BA, WA and Th was then used to determine the probability of connection of each STG voxel to either BA, WA or Th[8]. Each individual STG-BA, STG-WA and STG-Th map was then transformed into standard space and combined to allow group analysis.

A range of thresholds in connection probability were applied to the STG-BA, STG-WA and STG-Th maps for both hemispheres to assess the degree of lateralization of connection over the group caused by more or less confidently-identified connected volumes. Lateralization of the connected volume between hemispheres was expressed as a lateralization index (LI) calculated at each threshold [4].

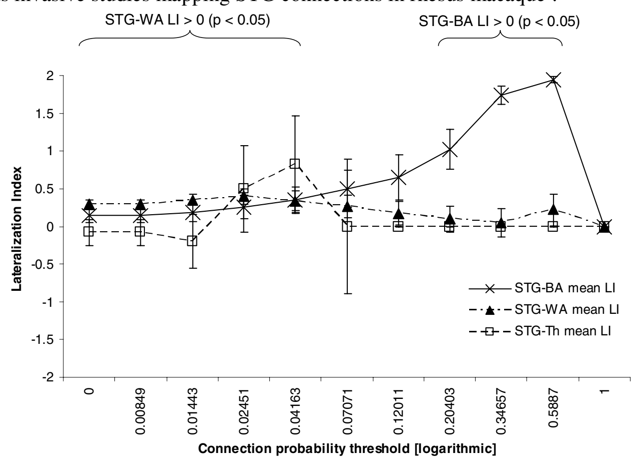

Figure 1. *Plot of mean LI against connection probability threshold. Positive LI indicates left hemisphere dominance. Connection thresholds are shown on a logarithmic scale. Error bars show the standard error in LI across the group. Significant differences from zero in LI across the group indicated at p < 0.05 (one sample t test, 2-tailed).*

Results A plot of the mean LI against connection probability threshold for STG-BA, STG-WA and STG-Th connections is shown in Fig. 1. At all connection threshold values STG-BA and STG-WA connection volumes are lateralized towards the left side, with this being most significant for the STG-WA connections at low connection probability and for the STG-BA connections at high connection probability ($p < 0.05$, 2-tailed, one sample t test against zero lateralization, not corrected for multiple comparisons). There was no evidence that the STG-Th connections were lateralized at any threshold. Figures 2(a,b) show the remaining group-averaged connection volume in the STGs at connection thresholds giving statistically significant positive mean LI values in Fig. 1 for STG-WA and STG-BA, respectively. Fig. 2(a) shows that the lateralization towards the left side of STG-WA connection is due to the fact that a region of relatively low connection probability extends from the left WA to the anterior areas of the left STG, which is less apparent on the right. Otherwise there is little left-right difference between the volume of densest areas of highest connection probability located within WA itself. This suggests that connection from WA towards the anterior region of the STG may be stronger on the left side. Fig. 2(b) shows that STG-BA connection lateralization is due to loss of the dense high probability connection volume to BA in the anterior (although not as anterior as the temporopolar area) region of the right STG when compared with the left STG. Fig. 2(c) shows the distribution of STG-Th connection without any threshold applied. A similar distribution of connection probability is seen along the STG on both sides to the thalami, with the densest high probability connection in the posterior-medial region (mostly primary auditory area) and temporopolar region of the STG. Connection to the thalami in the middle region of the STG (that occupied by the densest STG-BA connecting region) is more sparse and weaker. In general there is little overlap between the regions identified with highest connection probability as connecting Broca's area, Wernicke's area and the thalamus. This indicates a degree of connection target-specific parcellation within the STG. Figure 3 shows a schematic representation of the observed parcellation, which agrees well with the results of a similar experiment in rhesus macaques performed using microelectrode recording with invasive anatomical tract-tracing [1], showing analogous results between the two species.

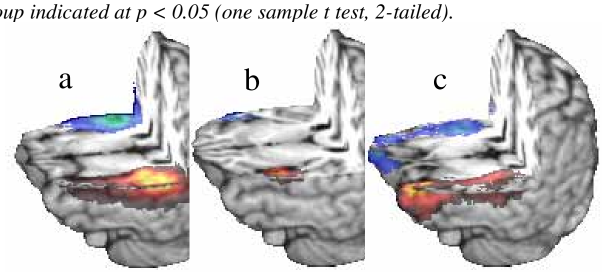

Figure 2. *Distribution of STG connections to WA (a) and BA (b) at threshold values corresponding to statistically significant positive lateralisation indices in Fig. 1 (0.02451 and 0.204, respectively); and similarly to Th (c) with no threshold applied. Distribution of connection probability values are represented by a hot colour scheme overlay for the left STG and a cold colour scheme for the right.*

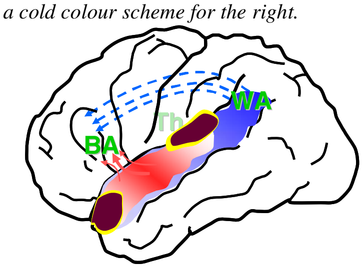

Figure 3. *Schematic of the STG connections from Fig. 2. STG-WA connections represented in blue; STG-BA connections in red; STG-Th connections in brown and yellow (shown as distinct areas for ease of display; Fig. 2 shows this area of connection to be continuous, but with lower connection probability between the two loci illustrated). Less dense colours reflect lower connection probability.*

Conclusion We have applied probabilistic diffusion MRI tractography using crossing fibre information to parcellate the STG according to connection to Broca's area, Wernicke's area, and the thalamus. We have demonstrated a pattern of connection within the STG closely resembling that in non-human primates. We have also shown lateralization of elements of this network, mirroring the known lateralization of language function.

References 1. Romanski, L.M., *et al.*, *Nat. Neurosci.*, 2, 1131, 1999. 2. Kaas, J.H. and Hackett, T.A., *Nat. Neurosci.*, 2, 1045, 1999. 3. Gloor, P., *The temporal lobe and limbic system*. New York: Oxford University Press, 1997. 4. Parker, G.J.M., *et al.*, *NeuroImage*, 24, 656 2005. 5. Parker, G.J.M., *et al.*, *Proc. Int. Soc. Magn. Res. Med.*, 1269, 2004. 6. Parker, G.J.M., *et al.*, *J. Magn. Reson. Imag.*, 18, 242, 2003. 7. Parker, G.J.M. and Alexander, D.C., *Lect. Notes Comput. Sci.*, 2737, 684, 2003. 8. Behrens, T.E.J., *et al.*, *Nat. Neurosci.*, 6, 750, 2003.

Acknowledgements This work was supported by a Pathfinder Award from the UK's Medical Research Council (grant number G0300952).