



Growth of language-related brain areas after foreign language learning

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ABSTRACT

The influence of adult foreign-language acquisition on human brain organization is poorly understood. We studied cortical thickness and hippocampal volumes of conscript interpreters before and after three months of intense language studies. Results revealed increases in hippocampus volume and in cortical thickness of the left middle frontal gyrus, inferior frontal gyrus, and superior temporal gyrus for interpreters relative to controls. The right hippocampus and the left superior temporal gyrus were structurally more malleable in interpreters acquiring higher proficiency in the foreign language. Interpreters struggling relatively more to master the language displayed larger gray matter increases in the middle frontal gyrus. These findings confirm structural changes in brain regions known to serve language functions during foreign-language acquisition.

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Introduction

Globally, many individuals acquire a foreign language in young adulthood. How learning a foreign language affects the brain, however, remains fairly unexplored. This contrasts with the well-charted neurophysiology of native language (Demonet et al., 2005; Hickok and Poeppel, 2007; Price, 2010), pointing to key roles of the left inferior frontal gyrus (IFG), the left middle frontal gyrus (MFG), and the superior temporal gyri (STG) in the sensorimotor aspects of language. Specifically, the left IFG and left MFG are key regions in the articulatory network and the STG are involved in acoustic-phonetic processes such as spectrotemporal analysis (Davis and Gaskell, 2009; Demonet et al., 2005; Hickok and Poeppel, 2007; Price, 2010). The hippocampus may be critically involved in the memory processes that bind conceptual meaning to particular sounds or signs during vocabulary acquisition (Breitenstein et al., 2005; Davis and Gaskell, 2009).

Acquiring sensorimotor skills (Draganski et al., 2004) and conceptual knowledge (Draganski et al., 2006) in adulthood alters the human brain's gray matter structure in task-relevant areas, suggesting that adult foreign-language learning may be accompanied by increases of gray matter volume in brain regions involved in first-language

acquisition. Support for this prediction comes from comparisons of bilinguals and monolinguals, suggesting that gray matter density in the left inferior parietal lobe maps on to number of words learned, native as well as foreign (Lee et al., 2007; Mechelli et al., 2004). The left inferior parietal lobe has fast corticocortical connections to the STG and slower connections to the hippocampus, and may be involved in the phonological aspect of lexical items (Davis and Gaskell, 2009; Gaskell and Marslen-Wilson, 1997). Additional correlational support also comes from a study of English-speaking exchange students learning German in Switzerland (Stein et al., 2010). In this group of individuals, improvements in foreign-language proficiency were correlated with changes in gray matter density of the left IFG. This correlation was however to a large extent driven by an atypical subject whose gray matter density decreased. Moreover, it is unclear from the report whether the increase in regional brain volume over time was significant. Therefore, further studies including direct comparisons of brain anatomy before and after foreign-language acquisition are needed to establish a causal role of language acquisition on neural changes. Such an approach faces the practical obstacle of identifying individuals who initially have no knowledge of the foreign language but can learn to master a language within a restricted time period. Here we examined conscripts in the interpreter academy of the Swedish military. These individuals study a foreign language at an intensity that is unmatched in the Swedish educational system. Starting from scratch, the interpreters learn a new language to fluency within 10 months. The languages studied (Dari, Russian, or Egyptian Arabic) are very different from the conscripts' native Swedish tongue. The extreme learning rate requires the acquisition of 300 to 500 new words each week. An average weekday

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at the academy includes classes and individual language studies interleaved with soldier training from 08.00 until bedtime. Weekends are at least as demanding, with individual studies throughout the day.

To investigate whether intense language training would lead to changes in cortical thickness and hippocampal volumes, we acquired magnetic resonance images (MRI) immediately before and after the interpreters' first three months of language studies. As a complement to the structural measures we collected behavioral measures of language proficiency and teacher ratings of the amount of effort needed to achieve the goals of the academy. We predicted that intense language studies would lead to increases in hippocampal volume as well as cortical thickness in language-related areas. We also hypothesized that these changes would relate to acquired language proficiency.

Materials and methods

Participants

We recruited volunteers among right handed, and otherwise MRI eligible interpreters and controls. The interpreter group consisted of six women and eight men ($n = 14$) studying at the Swedish Armed Forces Intelligence and Security Centre. Interpreter conscripts are selected based on school achievements, study skills, intelligence, and emotional stability from volunteers among all Swedish 18 year-old men, and among women who choose to undergo military training. Four of the interpreters studied Arabic, eight studied Dari, and two studied Russian. None of the interpreters had any knowledge of these languages prior to the entry to the academy.

Controls were medical and cognitive-science students at Umeå University, Sweden. Ten controls were women and seven were men ($n = 17$). The control group was recruited to be comparable on the dimensions of age, years of education, intelligence, and emotional stability. The controls were measured before and three months after the start of their semester, which matched closely in time with the interpreter studies and the measurements of the interpreters.

The groups of interpreters and controls did not significantly differ on chronological age (interpreters, $M = 19.9$ ($SD = 1.8$); controls, $M = 20.6$, ($SD = 1.0$), $t(28) = -1.34$, $p = .19$) and years of education (interpreters, $M = 12.9$ ($SD = 1.6$); controls, $M = 13.3$ ($SD = .9$), $t(28) = -.93$, $p = .36$). The two groups were also comparable on intelligence (Ravens advanced progressive matrices: interpreters, $M = 10.8$ ($SD = 2.9$); controls, $M = 11.0$ ($SD = 4.4$), $t(29) = -.16$, $p = .88$) and emotional stability (anxiety ratings: interpreters, $M = 38$ ($SD = 5.9$); controls, $M = 34.8$ (6.6), $t(28) = 1.38$, $p = .18$). For details of the measures, see [behavioral measures](#) section.

Behavioral measures

Raven's advanced progressive matrices

The 18 odd-numbered items from set II of this test (Raven, 2000) were presented for both groups at pretest. 10 min in total was allotted to complete the task, and the dependent variable was the number of correctly selected patterns.

Anxiety ratings

A translated (to Swedish) and modified version of the STAI Y-2 (Spielberger et al., 1970) form was used (Filaire et al., 2001). The participants rated anxiety experienced the past month. The questionnaire was administered at pretest.

Proficiency

Our proficiency measure consisted of grades on the mid-year exam at the interpreter academy, performed a few weeks after posttest. This exam is especially important because those that fail are forced to leave the academy (none of our participants had to leave,

indicating that they studied hard). The exam itself consists of two tests, one written and one oral. The written language test includes translating full sentences and texts and the oral tests include non-simultaneous interpreting. Both tests are developed to measure the ability of actual language use in the demanding circumstances a military interpreter might find herself in and as such measure a broad spectrum of language abilities. The exam grades (1–10) represent the mean of the oral and written exam. Each week during the stay at the academy the interpreters underwent similar tests, with oral and written exams interleaved (one per week). The teachers had no insight into the findings from the study when grading the students. The language tests have been developed at the academy (which has been active in its role since 1957) by the language teachers, most of whom work part time as lecturers at Swedish universities.

Struggle

For this measure, the amount of effort needed to stay at the academy was rated for each interpreter by the head teacher (who had an overview of the different language divisions). The question (translated from Swedish) was: "Judge how large effort was needed for each participant to achieve the goals of the interpreter academy and to be allowed to stay in the program". The rating was done on a Likert scale of 1 (little effort) to 9 (large effort). No participant scored below 6 on this scale.

MR acquisition

Images were acquired at Umeå Center for Functional Brain Imaging (UFBI) on a GE Discovery MR 750, 3 T scanner with a 32 channel phased-array head coil. For T_1 -weighted imaging at pretest and posttest, a 3D fast spoiled gradient-echo (fSPGR) sequence was used ($TE = 3.2$ ms, $TR = 8.1$ ms, $TI = 450$ ms, flip angle = 12° , $FOV = 172 \times 250 \times 250$ mm³, matrix = $172 \times 256 \times 256$, bandwidth per pixel = 122 Hz, no parallel imaging, no surface coil intensity correction, 3D correction for gradient non-linearities).

MRI preprocessing

All scans were manually inspected for artifacts. No scan was rejected. The data volumes were then analyzed using the FreeSurfer imaging analysis suite (<http://surfer.nmr.mgh.harvard.edu/>; version 4.5). FreeSurfer is a semi-automatic software package that performs cortical reconstruction as well as volumetric segmentation of T_1 -weighted images. FreeSurfer uses intensity and continuity information from MR volumes to reconstruct and measure cortical thickness at each vertex of the brains surface (Dale et al., 1999; Fischl and Dale, 2000). Subcortical structures were volumetrically segmented in a separate analysis stream (Fischl et al., 2002, 2004a, 2004b). Images were then processed automatically within the longitudinal stream of FreeSurfer (Reuter et al., 2012). The longitudinal stream creates an unbiased (from the two timepoints) within-subject image (Reuter and Fischl, 2011), increasing reliability and statistical power compared to the regular FreeSurfer stream. FreeSurfer has shown an intra-class correlation of 0.994 for MPAGE sequences (Wonderlick et al., 2009) as well as high consistency of within-subject measurements of cortical thickness (Wang et al., 2008).

Data was blinded for time (i.e., pretest vs. posttest) and group (interpreters vs. controls), taken through the standard cross-sectional cortical reconstruction and volumetric segmentation processing, and then processed through FreeSurfer's longitudinal stream (version 4.5). Five subjects (pre and post for each participant) were randomly selected and manually checked for reconstruction steps and segmentation of the hippocampus. No manual alterations were needed.

Statistical analyses

Hippocampal volume estimates were exported to SPSS (version 17) and analyzed with a 2 (group; interpreters vs. controls) by 2 (time: pretest vs. posttest) by 2 (hemisphere; left vs. right) mixed ANOVA. The threshold for statistical significance was $p < .05$.

For each participant, a difference image (posttest–pretest) was calculated from the cortical thickness data. Specifically, the difference image was produced by subtraction of surface maps, where individual surface elements, which contain the cortical thickness data, are called vertices. Vertex-wise general linear model analyses were then performed to investigate group (interpreter vs. controls) differences in cortical thickness changes, which reduces to an independent-samples t -test on the difference images. These analyses were complemented with an independent t -test on cortical thickness at pretest to investigate potential group difference on baseline cortical thickness. The threshold for statistical significance was $p < .001$. The clusters-extent threshold was 100 vertices. Data was smoothed using a 3D gaussian kernel using FWHM 15 mm.

For each interpreter, the mean thickness differences of each cluster showing a statistically significant selective increase for interpreters as compared with controls were exported to SPSS. Pearson correlations, within the group of interpreters, were then computed between cortical thickness changes and the behavioral variables (struggle and proficiency). Hippocampal volume was also included in these analyses. The threshold for statistical significance was $p < .05$.

Results

Analyses of cortical areas (Fig. 1A) revealed that the groups displayed significantly ($p < .001$; cluster size > 100) different amounts of change in three left hemisphere regions; the dorsal MFG (MNIpeak = $-39\ 12\ 43$), IFG (MNIpeak = $-48\ 24\ 14$), and STG (MNIpeak = $-59\ -11\ -2$). Interpreters showed large increases in cortical thickness over time, whereas the controls displayed smaller decreases (Fig. 1C). No effects were found in the right hemisphere at this threshold. To further probe the laterality of the effect, a new analysis of the right hemisphere was conducted with the very liberal threshold of $p < .01$. At this level, smaller clusters of selective increases for interpreters as compared to controls were observed in the MFG and IFG, but not in the STG.

Hippocampal volumes also increased significantly more for interpreters than for controls, $F(1, 29) = 5.83$, $p = .022$. Hemisphere did not significantly modulate the group-related hippocampus increase, $F(1, 29) = 2.92$, $p > .098$, but the effect tended to be more pronounced in the right hippocampus (Fig. 1B). The groups did not differ significantly in terms of cortical thickness or hippocampal volume at pretest.

In the group of interpreters, individual differences in foreign language proficiency was positively related to changes in the right hippocampus ($r = .61$, $p = .020$) and the left STG ($r = .54$, $p = .049$; Fig. 2), but not to the observed frontal changes (p 's $> .82$). Change in cortical thickness of the frontal MFG region was however positively related

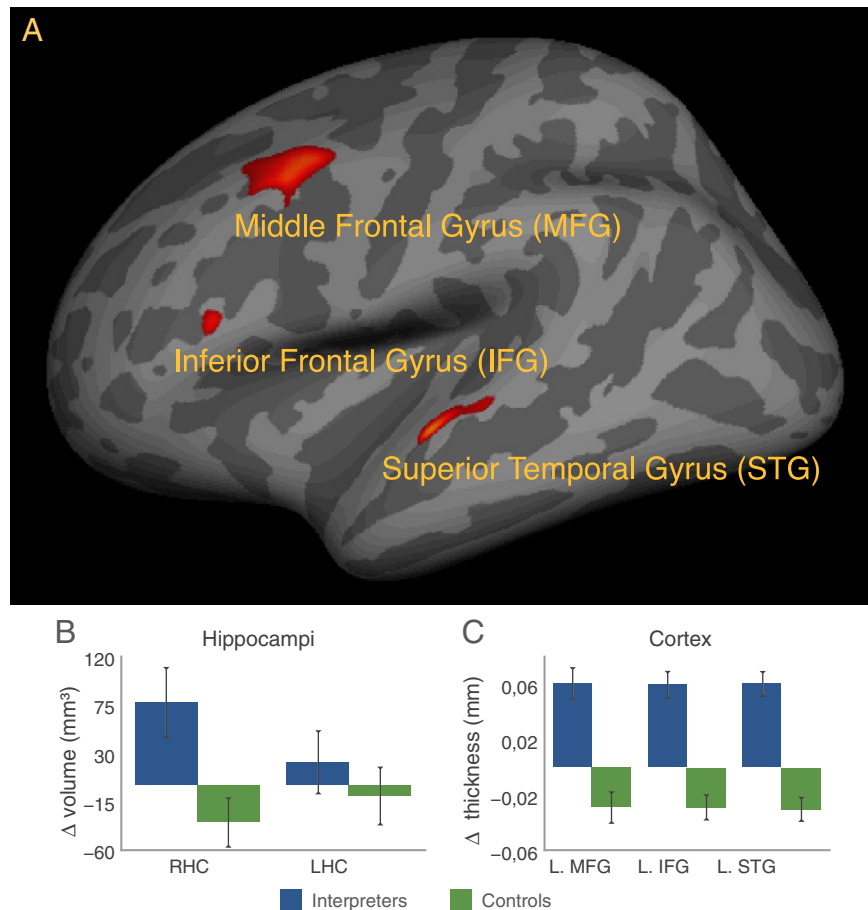


Fig. 1. Increases in cortical thickness and hippocampal volume accompany foreign language acquisition. (A) As compared with controls, conscript interpreters showed larger increases ($p < .001$; cluster size > 100) in the left middle frontal gyrus (MFG), inferior frontal gyrus (IFG), and superior temporal gyrus (STG). (B) Change (posttest value–pretest value) of right hippocampal volume (RHC) and left hippocampal volume (LHC) for interpreters and controls. (C) Changes in cortical thickness in the left MFG, IFG and STG.

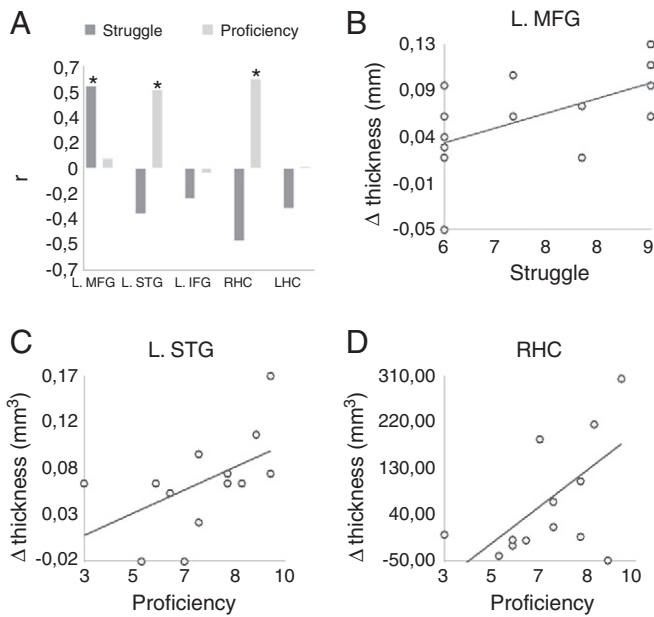


Fig. 2. (A) Pearson correlations between, on the one hand, language proficiency at posttest and teacher ratings of the effort exerted by the interpreters (struggle), and, on the other hand, changes in gray matter thickness and hippocampal volumes. (B) The association ($r = .56$, $p = .037$) between cortical thickness changes in the left middle frontal gyrus (L. MFG) and struggle. (C) A scatterplot of the association ($r = .54$, $p = .049$) between cortical thickness changes in the left mid-posterior superior temporal gyrus (L. STG) and proficiency. (D) Scatterplot of the association ($r = .61$, $p = .020$) between changes in the right hippocampus (RHC) volume and proficiency.

($r = .56$, $p = .037$) to teacher ratings of the effort exerted by the interpreters, such that those who struggled the most to reach the learning goals had the greatest expansion of MFG thickness (Fig. 2).

Discussion

Our findings provide evidence that learning a foreign language in adulthood changes the structure of language-related brain regions. To our knowledge this is the first time the effects of acquiring a completely foreign language has been measured in adults. The observed significant changes in cortical thickness were located in the fronto-temporal cortex of the left hemisphere. The IFG and STG regions are engaged by a variety of language-related tasks (Davis and Gaskell, 2009; Demonet et al., 2005; Hickok and Poeppel, 2007; Price, 2010). Specifically, the IFG is a key region of the articulatory network (e.g., Hickok and Poeppel, 2007), and has been linked to the mapping of meaning to new words (Ye et al., 2010). The STG is involved in acoustic-phonetic processes, such as spectrotemporal analysis (Demonet et al., 2005; Hickok and Poeppel, 2007; Price, 2010). The dorsal MFG region is a part of the articulatory network and may be involved in planning and control of articulatory processes (Hickok and Poeppel, 2007). The region also overlaps with premotor language areas implicated in providing top-down information to facilitate, for example, difficult speech perception (Meister et al., 2007). Interpreters also displayed larger hippocampus volume increases than controls; an effect that was pronounced in the right hemisphere. Although one could expect bi-lateral or left-sided changes, our results correspond well with some earlier findings. For example, Henke et al. (1999) reported that learning of association was related to activation in the right but not in the left hippocampus. A role of the hippocampus in rapid learning of new words is predicted by models of vocabulary acquisition (Davis and Gaskell, 2009). Our findings are in line with this

model, indicating that hippocampal plasticity may be an important part of the system's capacity for foreign language acquisition. The interpreters' strong focus on learning a large amount of novel words in a short time may have fostered the hippocampal changes, whereas more stable lexical representations in neocortical areas, such as the left inferior parietal lobe (Davis and Gaskell, 2009; Lee et al., 2007; Mechelli et al., 2004) or inferior temporal regions (Davis and Gaskell, 2009; Hickok and Poeppel, 2007), may be derived gradually from repeated encounters with new words.

The right hippocampus and the left STG were structurally more malleable in interpreters who acquired higher proficiency in the foreign language. To our knowledge, this is the first time that hippocampal volume changes observed longitudinally have been associated with individual differences in learning outcomes in humans. We speculate that these findings indicate that plasticity of these brain regions is an important part of what makes a language learner talented. Note that this suggestion is based on correlational evidence only. It is for example possible that individual differences in effort may have caused the individual differences in proficiency as well as in the increases in brain volume. We think that this particular interpretation is unlikely to be the case though. First, the interpreters were all highly motivated (they were exempt from regular conscription rules and could leave at any point; no one did) and working near the top of their capacity. The restriction in range of Fig. 2B illustrates this, with no interpreter going below 6 on a scale of 1 to 9 in rated struggle. Second, our measure of struggle showed a tendency towards a negative correlation with left STG and right hippocampal increase over time (Fig. 2A). Effort is likely to be an important component of this measure of struggle, and these results thus run counter to the notion that effort plays a key role in mediating the hippocampal change. Nevertheless, the suggestion that plasticity of the STG and the hippocampus are key components of what makes a language learner talented should be investigated in further studies.

The results also suggested that interpreters struggling relatively more to master the language displayed larger gray matter increases in the dorsal MFG. As noted, the dorsal MFG region overlaps with premotor language areas implicated in planning and top-down control of articulatory processes (Hickok and Poeppel, 2007; Meister et al., 2007). We speculate that for interpreters on the whole, and for those struggling relatively more to master a new language in particular, the demands on such top-down support should have been elevated, leading to increased cortical thickness.

The present results are partly inconsistent with a previous report relating improvements in foreign-language proficiency to changes in gray matter density of the left IFG in a group of English-speaking exchange students learning German in Switzerland (Stein et al., 2010). Specifically, we detected no such association between cortical thickness changes in the IFG and acquired proficiency in the group of interpreters. Nevertheless, we observed larger increases of cortical thickness in the left IFG for interpreters relative to controls. Taken together, the present results might suggest that the structural changes in the left frontal regions may reflect use- and demand-dependent changes rather than constitute the neural substrates of acquired language skill. In our results, plasticity of the temporal regions (STG and hippocampus) is clearly a stronger determinant of individual differences in efficient language learning than the frontal regions. Differences between the present study and the study reported by Stein et al. (2010) may partly explain the different results across the studies. These differences include knowledge of the foreign language prior to the study period (no prior knowledge in the present report vs. varying amounts of prior knowledge), intensity and nature of learning (intense formal education in the present report vs. 133–224 days of being in a foreign country), and the proficiency measure itself (an overall test of both written and oral skills in the present report vs. a written exam). These differences point to two very different learning situations: one involving exchange students with prior knowledge in German learning

more German in a real-life setting, the other including army interpreters learning a new language from scratch by highly intensive but traditional language studies. Future studies are needed for disentangling the effects of foreign-language acquisition in different contexts.

Though the present study has several advantages, including the longitudinal study of a group of individuals learning a new language from scratch at a high pace, these advantages also by default come with limitations, including the quasi-experimental design with a non-equivalent control group of young medical and cognitive science students. The sample of interpreters is not by any standards representative of the general population and they study at a rate that is unmatched in the Swedish educational system. We cannot exclude the possibility that the observed brain changes are reflections of general differences in the intensity of the studies between the two groups. In addition, we cannot exclude that other language-unrelated environmental or subject-specific factors are driving the present findings. Finally, without detailed measures of different aspects of language improvement, it is difficult to decisively determine the functional meaning of the different observed brain changes. Nevertheless, we think that several of our findings indicate that the identified volume changes reported in this paper reflect language acquisition. First, the control group was comparable to the interpreters on age, education, intelligence, emotional stability, cortical thickness, and hippocampal volumes at pretest. Second, gray matter volume increased selectively for interpreters in regions known to be involved in language processes. Third, behavioral variables tapping into language acquisition correlated with several of these volume changes, demonstrating brain–behavior relations within the group of interpreters. Therefore, we find it unlikely that language-unrelated environmental or subject-specific factors are driving the present findings. In this vein, we also note that all interpreters underwent basic soldier training during the three months preceding entry to the academy. Because these three months feature much more intense physical exercise than the limited soldier training at the academy, the conscripts typically decline or remain on the same level of physical ability during their stay at the interpreter academy. Thus, changes in physical fitness are also for this reason (in addition to the reasons noted above) unlikely to drive the reported effects.

We therefore suggest that adult foreign-language learning is accompanied by increases of gray matter volume in language-related brain regions. Plasticity of the hippocampus and the left STG might be important for learning a new language. Considering the hippocampus-related findings in particular, such experience-dependent neural changes may constitute a mechanism behind the delaying effect of bilingualism on the onset of late life diseases such as Alzheimer's (Craik et al., 2010). Replication of our findings in a randomized sample of younger adults from the general population is of importance. Future studies should also investigate the microscopic underpinnings of the observed changes, the long-term consequences of foreign-language acquisition, and whether foreign-language acquisition at more advanced stages of adulthood has similar effects.

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References

- Breitenstein, C., Jansen, A., Deppe, M., Foerster, A.F., Sommer, J., Wolbers, T., Knecht, S., 2005. Hippocampus activity differentiates good from poor learners of a novel lexicon. *Neuroimage* 25, 958.
- Craik, F.I.M., Bialystok, E., Freedman, M., 2010. Delaying the onset of Alzheimer disease: bilingualism as a form of cognitive reserve. *Neurology* 75, 1726.
- Dale, A.M., Fischl, B., Sereno, M.I., 1999. Cortical surface-based analysis. I. Segmentation and surface reconstruction. *Neuroimage* 9, 179–194.
- Davis, M.H., Gaskell, M.G., 2009. A complementary systems account of word learning: neural and behavioural evidence. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 364, 3773.
- Demonet, J.F., Thierry, G., Cardebat, D., 2005. Renewal of the neurophysiology of language: functional neuroimaging. *Physiol. Rev.* 85, 49.
- Draganski, B., Gaser, C., Busch, V., Schuierer, G., Bogdahn, U., May, A., 2004. Neuroplasticity: changes in grey matter induced by training. *Nature* 427 (6972), 311–312.
- Draganski, B., Gaser, C., Kempermann, G., Kuhn, H.G., Winkler, J., Büchel, C., May, A., 2006. Temporal and spatial dynamics of brain structure changes during extensive learning. *J. Neurosci.* 26, 6314–6317.
- Filaire, E., Sagnol, M., Ferrand, C., Maso, F., Lac, G., 2001. Psychophysiological stress in judo athletes during competitions. *J. Sports Med. Phys. Fitness* 41 (2), 263–268.
- Fischl, B., Dale, A.M., 2000. Measuring the thickness of the human cerebral cortex from magnetic resonance images. *Proc. Natl. Acad. Sci. U. S. A.* 97, 11050–11055.
- Fischl, B., Salat, D.H., Busa, E., Albert, M., Dieterich, M., Haselgrove, C., van der Kouwe, A., Killiany, R., Kennedy, D., Klaveness, S., Montillo, A., Makris, N., Rosen, B., Dale, A.M., 2002. Whole brain segmentation: automated labeling of neuroanatomical structures in the human brain. *Neuron* 33, 341–355.
- Fischl, B., Salat, D.H., van der Kouwe, A.J., Makris, N., Segonne, F., Quinn, B.T., Dale, A.M., 2004a. Sequence-independent segmentation of magnetic resonance images. *Neuroimage* 23 (Suppl. 1), S69–S84.
- Fischl, B., van der Kouwe, A., Destrieux, C., Halgren, E., Segonne, F., Salat, D.H., Busa, E., Seidman, L.J., Goldstein, J., Kennedy, D., Caviness, V., Makris, N., Rosen, B., Dale, A.M., 2004b. Automatically parcellating the human cerebral cortex. *Cereb. Cortex* 14, 11–22.
- Gaskell, M.G., Marslen-Wilson, W.D., 1997. Integrating form and meaning: a distributed model of speech perception. *Lang. Cognit. Process.* 12 (5/6), 613–656.
- Henke, K., Weber, B., Kniefel, S., Wieser, H.G., Buck, A., 1999. Human hippocampus associates information in memory. *Proc. Natl. Acad. Sci. U. S. A.* 96, 5884–5889.
- Hickok, G., Poeppel, D., 2007. The cortical organization of speech processing. *Nat. Rev. Neurosci.* 8, 393.
- Lee, H., Devlin, J.T., Shakeshaft, C., Stewart, H.L., Brennan, A., Glensman, J., Pitcher, K., Crinion, J., Mechelli, A., Frackowiak, R.S.J., Green, D.W., Price, C.J., 2007. Anatomical traces of vocabulary acquisition in the adolescent brain. *J. Neurosci.* 27 (5), 1184–1189.
- Mechelli, A., Crinion, J.T., Noppeney, U., O'Doherty, J., Ashburner, J., Frackowiak, R.S., Price, C.J., 2004. Neurolinguistics: structural plasticity in the bilingual brain. *Nature* 431, 757.
- Meister, I.G., Wilson, S.M., Deblieck, C., Wu, A.D., Iacoboni, M., 2007. The essential role of premotor cortex in speech perception. *Curr. Biol.* 17, 1692.
- Price, C.J., 2010. The anatomy of language: a review of 100 fMRI studies published in 2009. *Ann. N. Y. Acad. Sci.* 1191, 62.
- Raven, J., 2000. The raven's progressive matrices: change and stability over culture and time. *Cogn. Psychol.* 41, 1–48.
- Reuter, M., Fischl, B., 2011. Avoiding asymmetry-induced bias in longitudinal image processing. *Neuroimage* 57 (1), 19–21 (<http://reuter.mit.edu/papers/reuter-bias11.pdf>).
- Reuter, M., Schmansky, N.J., Rosas, H.D., Fischl, B., 2012. Within-subject template estimation for unbiased longitudinal image analysis. *Neuroimage* (in print, <http://dx.doi.org/10.1016/j.neuroimage.2012.02.084>).
- Spielberger, C.D., Gorsuch, R.L., Lushene, R.E., 1970. Manual for the State–Trait Anxiety Inventory. Consulting Psychologists Press, Palo Alto, CA.
- Stein, M., Federspiel, A., Koenig, T., Wirth, M., Strik, W., Wiest, R., Brandeis, D., Dierks, T., 2010. Structural plasticity in the language system related to increased second language proficiency. *Cortex* 1–8.
- Wang, X., Bauer, W., Chiaia, N., Dennis, M., Gerken, M., Hummel, J., Kane, J., Kenmuir, C., Khuder, S., Lane, R., Mooney, R., Bazeley, P., Apkarian, V., Wall, J., 2008. Longitudinal MRI evaluations of human global cortical thickness over minutes to weeks. *Neurosci. Lett.* 441, 145–148, <http://dx.doi.org/10.1016/j.neulet.2008.06.013>.
- Wonderlick, J.S., Ziegler, D.A., Hosseini-Varnamkhasti, P., Locascio, J.J., Bakkour, A., van der Kouwe, A., Triantafyllou, C., Corkin, S., Dickerson, B.C., 2009. Reliability of MRI-derived cortical and subcortical morphometric measures: effects of pulse sequence, voxel geometry, and parallel imaging. *Neuroimage* 44, 1324–1333, <http://dx.doi.org/10.1016/j.neuroimage.2008.10.037>.
- Ye, Mestres-Misse, A., Rodriguez-Formells, A., Münte, T.F., 2010. Two distinct neural networks support the mapping of meaning to a novel word. *Hum. Brain Mapp.* 3 (7).