Increased gray-matter volume in the right angular and posterior parahippocampal gyri in loving-kindness meditators

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Abstract

Previous voxel-based morphometry (VBM) studies have revealed that meditation is associated with structural brain changes in regions underlying cognitive processes that are required for attention or mindfulness during meditation. This VBM study examined brain changes related to the practice of an emotion-oriented meditation, namely, loving-kindness meditation (LKM). A 3T MRI scanner captured images of the brain structures of 25 men, 10 of whom had practiced LKM in the Theravada tradition for at least 5 years. Compared with novices, more gray-matter volume was detected in the right angular and posterior parahippocampal gyri in LKM experts. The right angular gyrus has not been previously reported to have structural difference associated with meditation and its specific role in theory of mind and cognitive empathy suggest the uniqueness of this finding to LKM practice. These regions are important for affective regulation associated with empathic response, anxiety, and mood. At the same time, gray matter volume in the left temporal lobe in the LKM experts appeared greater, an observation that has also been reported in previous MRI meditation studies on meditation styles other than LKM. Overall, the findings of our study suggest that the experience with LKM may influence brain structures associated with affective regulation.

Keywords: Temporo-parietal Junction; Voxel-based Morphometry; Metta Meditation; Empathy; Affective Regulation
Introduction

It is well known that the human brain is a malleable organ. This suggests that intense training can induce structural changes in those brain regions that are needed to produce the trained behavior (Draganski & May, 2008). Indeed, scientists have coined the term “neuroplasticity” to describe the fact that the human brain changes in response to experiential learning. The classic study of London taxi drivers is one of the best illustrations of experience-induced neuroplastic change. In their study, Maguire et al. (2000) demonstrated that experience navigating London streets was associated with significantly larger bilateral posterior hippocampi. The hippocampus is known to be a spatial navigation centre (Maguire et al., 1998). Along similar lines, Aydin et al. (2007) found that math experts have higher gray-matter density in the parietal cortex than do controls. In fact, the parietal cortex is known for its involvement in arithmetic calculations and visuospatial processing (Dehaene et al., 1999).

Meditation is a process of training mental states, and such experiential learning may affect the human brain. Lazar et al. (2005) were the first to investigate the relationship between meditation and structural brain changes. They found that expert Insight meditators had a thicker prefrontal cortex and right anterior insula than novice meditators. Since then, other studies have reported differences in brain structures between experts and novices in a number of meditation practices, including Zen (Grant et al., 2010; Pagnoni & Cekic, 2007), Insight (Hölzel et al., 2008), concentrative practices and open awareness (Vestergaard-Poulsen et al., 2009), and a mixed style (Luders et al., 2009). Zen experts have a thicker anterior cingulate cortex (ACC) compared with novices (Grant et al., 2010). The ACC actively helps people focus and refocus attention voluntarily in response to distraction and so may help Zen
meditators maintain their state of “emptiness” (Pagnoni et al., 2008). In Insight experts, the right anterior insula is cortically thicker than in novices (Lazar et al., 2005). The insula is important for interoceptive awareness that connects us with our subjective internal states (Hölzel et al., 2008). Some studies have reported that cortical thickness/gray matter volume is associated with years/hours of meditation practice (Lazar et al., 2005; Holzel et al., 2008) while other studies have failed to identify any relationships between these two variables (Luders et al., 2009; Vestergaard-Poulsen et al., 2009).

In general, scientific studies have focused on types of meditation that train attention regulation to produce a calm mind. Therefore, it should be no surprise that they have found differences in the brain regions in the attention system. Following this line of thought, meditation that focuses on affective processing should have an effect on the emotion-processing system. If meditation really can change how the brain processes emotions, the finding could influence how clinicians design interventions for clinical affective dysregulation.

Loving-kindness meditation (LKM) is a form of meditation that trains emotion regulation. LKM practitioners explicitly cultivate positive feelings, generating an emotional state that is full of unconditional love, compassion, and empathy toward the self and others, without any discursive thoughts (Salzberg, 1995). Previous research has shown that a short LKM practice in the laboratory was sufficient to induce “feelings of social connection and positivity towards strangers on both explicit and implicit levels” (Hutcherson et al., 2008). Further, after completing a 12-week focused-attention meditation (FAM) and LKM intervention, college students had significantly less anxiety and negative affect (Sears & Kraus, 2009). LKM’s unique focus on cultivating positive emotions and heartfelt care for self and others makes it a
valuable technique to counteract negative symptoms like anhedonia and blunted affect from which people with schizophrenia suffer (Garland et al., 2010; Johnson et al., 2009). But despite the potential value of LKM in reducing negative emotions and improving mental well-being and social connectedness, it has received only sparse scientific attention. In particular, it is important to understand how LKM might affect brain structure, yet this has remained unexplored. To date, only a few fMRI studies have looked at the neural correlates of LKM. Lutz et al. (2008) had LKM experts and novices listen to neutral and emotional (including positive and negative) human vocalizations during meditation and rest states, respectively. They found significantly higher activation in LKM experts than novices during meditation than in the rest state (i.e., state-by-group interactions) in the amygdala and temporo-parietal junction (TPJ), which is constituted by the inferior parietal lobule (IPL), superior temporal gyrus (STG), and posterior superior temporal sulcus (pSTS) during all sounds; in limbic regions like the insula and cingulate cortices during emotional sounds; and in the insula during negative sounds. These results are unified on the networks important for social cognition, for instance, theory of mind and empathy (Decety & Lamm, 2007; Saxe & Kanwisher, 2003). Hence, this has led to speculation that long-term practice of LKM may enhance mentation toward human voices and emotion sharing (Lutz et al., 2008). In their follow-up study, Lutz et al. (2009) further investigated the relationship between the brain and the cardiovascular system on the same group of subjects as they listened to emotional sounds during the compassion state. The neural activity in the right insula, somatosensory cortices, right IPL, and premotor areas was found to be positively associated with heart rate; also, this positive association was especially stronger in LKM experts than in novices during the compassion state. These data suggest that LKM training may change brain representations toward
affective stimuli, and that these functional brain changes may be coupled with the visceral system.

To verify the possibility that devoted cultivation of positive emotion and compassion could bring about changes in brain structures, on top of that provided by mindfulness training, we adopted automated voxel-based morphometry (VBM) to examine differences in gray-matter volume between LKM experts and novices on a whole-brain voxel-by-voxel basis. In general, meditation practitioners usually commence their practice in forms that train attention or mindfulness, and then move on to the forms of practice they want to pursue. Different forms of meditation are thought to reinforce one another. Therefore, we hypothesized that LKM experts would have more gray-matter volume than novices not only in brain regions previously indicated for attention or mindfulness meditation, but also in those regions related to social cognition and affective processing as reviewed above, such as the right TPJ (including the IPL, STG, and pSTS) and the amygdala. Furthermore, we examined the relationship between hours of meditation practice and gray matter volume in our LKM experts.

**Materials and Method**

**Participants**

Twenty-five healthy Chinese men participated in this study, 10 of whom were LKM experts, while the remaining 15 were novices without long-term meditation experience. Both groups were matched on age and education levels. The experts were recruited from the Buddhist meditation network in Hong Kong and had at least 5 years of LKM practice based on the Theravada tradition. To control for any possible confounding variance introduced by different motivation of meditation practice, for
the comparison group for the LKM experts, we used novices interested in meditation and had undergone a total of 7-hour training of basic meditation self-practice. The home-based meditation self-practice was carried out based on the written instruction for practising concentration/calming/kindness-cultivation skills prepared by our co-investigator, Venerable Jing Yin who himself is an expert in meditation. The instruction was similar to that offered by the Venerable Dr. M. Ricard, who has much experience practicing and teaching meditation. All subjects were right-handed, measured with the Edinburgh Handedness Inventory (Oldfield, 1971). Subjects had no history of traumatic brain injury, medical conditions, or psychiatric disorders that could affect their brain structure at the time of study. All subjects gave their written informed consent to take part in this study, which was approved by the Institutional Review Board of The University of Hong Kong/Hospital Authority Hong Kong West Cluster.

**Image acquisition**

High-resolution MRI brain images were acquired via a 3.0 Tesla Philips Medical Systems Achieva scanner with an 8-channel SENSE head coil. A three-dimensional, T1-weighted, magnetization-prepared rapid-acquisition gradient-echo (MP-RAGE) sequence was used, with 164 contiguous sagittal slices, 1 mm thick, time to repetition (TR) = 7 ms, time to echo (TE) = 3.2 ms, flip angle = 8°, field of view (FOV) = 164 mm, matrix = 256 x 240 mm, voxel size = 1 x 1 x 1 mm.

**Image processing (VBM-Dartel)**

The MRI images were processed using the VBM8 toolbox (Christian Gaser; http://dbm.neuro.uni-jena.de/vbm/download/) within the SPM8 (Wellcome...
Department of Cognitive Neurology, London, UK; http://fil.ion.ucl.ac.uk/spm) in MATLAB 7.7.0 (Mathworks Inc., Natick, MA, USA). Default settings were used unless otherwise specified. Each MRI image was first displayed in SPM8 to screen for artifacts or gross anatomical abnormalities. For better registration, the orientation of images was adjusted to match the template, and the image origin was manually set to a position as close to the anterior commissure as possible. In the spatial normalization step, the high-dimensional Dartel normalization approach (VBM-Dartel) was chosen (Ashburner, 2007). This deformation technique has much better normalization power across individuals by improving intersubject alignment, especially for small inner structures (Yassa & Stark, 2009), and it is more sensitive to regional differences, for example, in the hippocampus (Bergouignan et al., 2009). It is thought to be a better alternative to the standard VBM-SPM normalization approach (Ashburner & Friston, 2000). To preserve the actual gray-matter values locally and account for individual differences in global brain size, modulated gray-matter segments were generated by multiplying them with the nonlinear components derived from the normalization matrix instead of the linear components. The covariance between all normalized modulated images was visualized using a boxplot and covariance matrices to check for homogeneity and thus inspect for outliers. Finally, the normalized modulated images were smoothed with a standard Gaussian kernel of 8 mm full width at half maximum (FWHM). Smoothing rendered the data more normally distributed, so that the assumption of parametric statistical comparisons was not violated (Worsley et al., 1996). Normalized and bias-corrected images of all subjects were also obtained and further averaged to create a study-specific template for visualizing the result.

**Statistical analysis**
A series of statistical analyses were performed on the smoothed, normalized, and modulated gray-matter images in SPM8. Two-sample independent $t$-tests tested for group differences in whole-brain gray-matter volume between experts and novices. An absolute threshold masking of 0.1 was used, meaning that only voxels with gray-matter values greater than 0.1 were counted. Global normalization was not needed in the statistical model because we applied the correction directly to the data during the modulation step using the nonlinear (instead of linear) component, as recommended in the VBM8 manual. Clusters were considered significant at the combined voxel-extent threshold of an uncorrected voxel level of $p < 0.01$ and cluster extent > 530 voxels, as determined based on Monte Carlo simulations with AlphaSim equivalent to $p < 0.05$, corrected for multiple comparisons. A more lenient corrected $p < 0.1$ was then adopted to detect trend-level results, which corresponded to $p < 0.01$ and cluster extent > 463 voxels. To further examine the relationship between the duration of meditation training and gray matter volume, correlation analysis was conducted between hours of meditation practice and average gray matter volume extracted from the significant cluster(s) using the REX toolbox in the LKM experts (Susan Whitfield-Gabrieli; http://web.mit.edu/swg/software.htm).

Results

Demographics

Table 1 presents the demographic information for all subjects. The LKM experts were matched with the novices by age [$t(23) = 0.651, p > 0.5$] and years of education [$t(23) = -1.704, p > 0.1$]. The experts had 6,456.2 hours of experience in LKM practice on average.

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Table 1 about here

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VBM-Dartel

When LKM meditators were compared with novices, more gray-matter volume was detected in the right angular gyrus (BA 39; Figure 1a, Table 2a) and right posterior parahippocampal gyrus (BA 36; Figure 1b, Table 2a) at a significant level (corrected \( p < 0.05 \)). With a more lenient threshold, more gray matter was also detected in the left inferior and middle temporal gyrus (BA 20 and 21; Figure 1c, Table 2a) at a trend level (corrected \( p < 0.1 \)). The same results stayed even after controlling for age and years of education. Novices had no regions with significantly more gray matter than the LKM experts, even after controlling for age or years of education (Table 2b). The same results stayed when another group of subjects who did not have any experience in meditation (i.e. zero hours) was used as the control comparison group (for details please see supplementary material).

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Figure 1 & Table 2 about here

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Results of the correlation analysis showed that meditation hours of the LKM experts was negatively related (at trend-level) to the gray matter volume of the right angular gyrus \( (r = -0.618, p = 0.057) \) and the left MTG \( (r = -0.593, p = 0.071) \), but not with the right parahippocampal gyrus \( (r = -0.079, p = 0.828) \). When the effect of age and education were removed, only the correlation between meditation hours and the gray matter volume of the right angular gyrus remained significant \( (r = -0.761, p = 0.028) \).
Discussion

This study examined the effect of experience in LKM meditation on brain morphometry in expert Chinese male meditators. We used the VBM-Dartel intersubject alignment (VBM-Dartel) to minimize the threat of registration errors. The LKM experts appeared to have more gray matter in the left temporal lobe (ITG and MTG) at a trend level. Previous meditation research has reported similar results in the left ITG (Hölzel et al., 2008; Luders et al., 2009). Thus, this finding may be attributable to the general effect of meditation practice. At the same time, we found that the LKM experts had significantly more gray matter than novices in the right angular and right posterior parahippocampal gyri. It is noted that not all hypothesized regions (identified based on previous fMRI studies on normal controls) had more gray-matter volume in LKM experts than novices, no matter how lenient a threshold was used. This observation suggests that mechanisms involved in structural and functional changes are likely different. An alternative explanation is that the neural correlates of social cognition in LKM experts may differ from those in the participants of these fMRI studies. The structural difference in the right angular gyrus was not observed in previous MRI studies on focused-attention or mindfulness meditation. Because of the specific role of the right angular gyrus in theory of mind and cognitive empathy, we consider this finding to be unique to LKM. All these structural differences cannot be explained by individual variations in global brain volume, age, or years of education. Previous reports have suggested that LKM is associated with a reduction in anxiety and negative affect (Goldin & Gross, 2010; Johnson et al., 2009; Sears & Kraus, 2009). Taking these findings together, we speculate that the enlarged right angular and right parahippocampal gyri (and the left temporal lobe at a trend level) in LKM experts may play a role in counteracting
anxiety and negative affect.

**Right angular gyrus**

The finding of an enlarged right angular gyrus is novel. Previous studies on Insight, Zen, and Tibetan Buddhism and a mixed style of meditation practice have demonstrated increased gray matter in the insula, hippocampus, inferior temporal lobe, cingulate cortex, prefrontal regions, brain stem, and some other regions (Grant et al., 2010; Hölzel et al., 2008; Lazar et al., 2005; Luders et al., 2009; Pagnoni & Cekic, 2007; Vestergaard-Poulsen et al., 2009), but none have reported gray matter changes in the parietal structures. Although a recent longitudinal study reported an increase in gray-matter concentration in the left TPJ after 8 weeks of mindfulness-based stress reduction (MBSR) training, this cluster in fact peaked in the left middle temporal gyrus (MNI coordinates: -50, -48, 20) (Holzel et al., 2011), whereas the peak coordinates of our angular gyrus cluster were on the right side and were more posterior and superior (41, -63, 46). On the other hand, diffusion tensor imaging (DTI) offers in-vivo examination of white matter connectivity. A recent study has revealed greater connectivity in the left superior longitudinal fasciculus (SLF) and its temporal component (tSLF) in meditators who practiced different forms of meditation, compared to control subjects (Luders et al., 2011). Since the SLF connects together the frontal and the temporo-parietal regions, the finding of Luder et al.’s (2011) study lays ground for the speculation of some changes in the parietal lobe associated with meditation. However, the nature and mechanisms of the coupling of the parietal and the fronto-temporal activity for affective regulation in people practising LKM meditation awaits verification in future research.

The right angular gyrus may be related to meditation practices that involve LKM
in multiple ways. It is one of the main regions that form the TPJ, which has been repeatedly implicated in social cognition such as theory of mind and empathy (Decety & Lamm, 2007). In particular, the right TPJ is believed to be selectively recruited to understand others’ thoughts, desires, and feelings (Saxe & Wexler, 2005). Together with the medial temporal lobe and ventromedial prefrontal cortex, it forms a cognitive system important for cognitive empathy. In particular, the role of the right TPJ in the self–other distinction is fundamental to the mentalizing ability central to cognitive empathy (Saxe & Kanwisher, 2003); this may be important for understanding the affective states of others and for sharing compassionate loving kindness to truly recognize the wisdom that all human beings are equal and to appreciate oneness with others (Salzberg, 1995).

Lutz et al. (2008) observed that LKM experts had more activity than novices in the right angular gyrus of the TPJ and a number of other brain regions when listening to emotional human vocalizations during compassion meditation. The authors reasoned that long-term LKM may enhance emotion sharing and perspective taking, especially since the increase was strongly modulated by meditation expertise. Their follow-up study further highlighted the importance of the right angular gyrus/IPL in LKM because of the stronger coupling between its activity and heart rate during the compassion state in LKM experts than in novices (Lutz et al., 2009). These findings are in line with our observation of increased gray matter in the right angular gyrus with LKM practice.

The increased gray-matter volume of the right angular gyrus in LKM experts corroborates the previous beneficial findings of LKM on affective processing (Garland et al., 2010; Johnson et al., 2009; Sears & Kraus, 2009), leaving room for speculating on the potential therapeutic effect of LKM on counteracting affective
disturbances. On the other hand, we found a negative correlation between hours of meditation practice and the gray matter volume of angular gyrus in the LKM experts. Previous VBM studies on meditation experts have shown inconsistent results on the relationship between brain structure and duration of meditation practice (Lazar et al., 2005; Holzel et al., 2008; Luders et al., 2009; Vestroigard-Poulsen et al., 2009).

Previous fMRI studies have revealed an ‘inverted U-shape’ relationship between meditation expertise and neural activity. For example, Brefczynski-Lewis et al. (2007) observed that experts with an average of 19,000 hours of practice, relative to meditation novices, showed stronger BOLD signals in the attentional default network. However, BOLD signals in the same regions were weaker for those experts who have an average of 44,000 hours of practice. This inverted U-shaped function may be explained by the process of skill acquisition—a pattern that has been observed in others domains of expertise (Doyon et al., 2002). It is also consistent with the description in meditation texts that practice of concentration meditation will become less effortful as one becomes more skillful at the practice. We speculate that, based on the prediction set forth by the inverted U-shape pattern, it is entirely possible that a positive relationship is revealed during the early stage of meditation practice (e.g. < 2,000-5,000 hours). Further research to verify the direction of the relationship between duration of meditation practice and gray matter volume may consider a longitudinal design or employing cohorts at various levels of meditation expertise.

**Right posterior parahippocampal gyrus**

The finding of an enlarged posterior parahippocampal gyrus is unique to LKM in our study. No gray-matter change was found in this region in previous structural studies on focused-attention or mindfulness meditation. The parahippocampal gyrus,
together with the temporopolar area, cingulate cortex, orbitofrontal cortex, and insula, forms the paralimbic system (Brodmann, 1909, 1994). Having dense connections with the limbic system, especially the amygdala, the paralimbic system is an important transition area that supports communication between the limbic system and the neocortex (Mesulam, 2000), which is important for a range of higher order cognitive affective functions, such as emotion/mood regulation, self-control, and motivational behavior (Kiehl, 2006). As proven by effective connectivity analysis, the parahippocampal gyrus has strong interactions with the amygdala (Stein et al., 2007). Abnormalities such as decreased gray-matter volume or altered activity in these two regions are linked with various conditions of emotional dysfunction such as depression (Gilbert et al., 2010), bipolar disorder (Chen et al., 2011), and schizophrenia (Gradin et al., 2011). A recent study that revealed gender-related differences in neural activity toward the compassion experience is in line with our findings. Pictures of human suffering selectively activated the parahippocampal gyrus and the occipital regions in male participants (Mercadillo et al., 2011). Another VBM study on Insight meditators with a relatively high male composition (80%) also reported higher gray-matter volume in the right medial temporal (hippocampus) and left temporal (ITG) lobes (Hölzel et al., 2008).

**Left temporal lobe**

The left temporal lobe has repeatedly been reported to have structural and functional changes associated with meditation. Insight experts had significantly more gray matter in the left ITG than novices, and their ITG size positively correlated with hours of meditation practice (Hölzel et al., 2008). Another study on the common effects of different meditation styles on brain structure also found more gray matter in
the left ITG when the statistical threshold was lowered (Luders et al., 2009). The temporal lobe was further found to be activated during the mindfulness meditation state (Holzel et al., 2007). It appears that the temporal lobe is involved in the experience of the mindful state and “insight into the unity of all reality” (Hölzel et al., 2008). Luders et al. (2011) have also observed that meditators (who practiced various forms of meditation) showed higher connectivity in the left tSLF, which traverses through the left middle/superior temporal lobe. This finding corroborates our observation that experts have increased gray matter volume in the left temporal lobe. Future studies should be conducted to examine whether there is enhanced connectivity in the tSLF/SLF in LKM meditators, and if yes how this enhanced connectivity relates to the enlargement of the left temporal lobe. These data suggest that the left temporal lobe is not exclusively implicated in a specific style of meditation, but instead is involved in various styles ranging from attention to mindfulness to LKM. Caution must be taken, however, to interpret this structural difference, since it appeared as a trend-level result in both the current and previous studies (Luders et al., 2009).

Limitations

This study has several limitations. First, the sample size of LKM experts was rather small because of the difficulty with subject recruitment. Insufficient power may have led to the negative findings in some emotion-related brain regions, e.g. the medial orbitofrontal cortex and the insula. The level of expertise of our LKM experts may also explained these negative findings because specific neural changes may take place at different stages of LKM practice and levels of LKM competence. These speculations may be verified in future longitudinal studies of large sample sizes.
Second, like other cross-sectional studies comparing brain structure between experts and novices, we cannot definitively say that long-term LKM caused the gray-matter differences observed in this study, or that people with these brain differences are more inclined to practice LKM. Longitudinal studies are needed to explore the causal relationship between LKM practice and brain structure. Third, the current finding has yet to be generalized to female LKM experts, since this study recruited only male LKM experts. The purpose of recruiting men was to avoid potential gender confounds, especially since this is the first exploratory study of LKM and brain structure. Future studies may recruit female participants or both genders to address this limitation.

**Conclusions**

This study found that LKM experts had significantly more gray-matter volume in the right angular gyrus, which may be unique to the effect of LKM training. Neuroscience studies have linked the right angular gyrus (a part of the right TPJ) with empathy for others during meditation. Our LKM experts also had more gray-matter volume in the right posterior parahippocampal gyrus. It is part of the paralimbic system that works with the limbic and neocortical regions to regulate emotional or empathic responses, and this may be specific to men. Although more gray matter was also detected in the left temporal lobe in LKM experts at a trend level, this difference may not be specific to LKM since it has also been observed in other meditation styles. Despite some limitations, our findings provide an important initial clue that LKM may be associated with increased gray-matter volume in regions important for emotion regulation. Future research should investigate the neural processes and mechanisms underlying LKM training to examine its therapeutic potential as an intervention for affective dysregulation.
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Table 1. Descriptive statistics of subject demographics and questionnaire data

<table>
<thead>
<tr>
<th></th>
<th>LKM experts</th>
<th>LKM novices</th>
<th>( p )-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
</tr>
<tr>
<td>Age</td>
<td>50.2</td>
<td>10.5</td>
<td>47.7</td>
</tr>
<tr>
<td>Years of education</td>
<td>14.0</td>
<td>4.1</td>
<td>16.9</td>
</tr>
<tr>
<td>Meditation hours</td>
<td>6456.2</td>
<td>6040.6</td>
<td>---</td>
</tr>
<tr>
<td>(range in hours)</td>
<td>(588 – 14600)</td>
<td>---</td>
<td>---</td>
</tr>
</tbody>
</table>

Note: The \( p \)-values represent group differences between LKM experts and novices using independent-samples \( t \)-tests (two-tailed).
Table 2. Increased gray matter volumes in LKM experts compared to novices as revealed by VBM-Dartel

<table>
<thead>
<tr>
<th>Contrast</th>
<th>Brain regions (Brodmann area)</th>
<th>Peak coordinates</th>
<th>Corrected t</th>
<th>Cluster size</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) experts &gt; novices</td>
<td>Right angular gyrus (39)</td>
<td>41 -63 46</td>
<td>0.015</td>
<td>4.87</td>
</tr>
<tr>
<td></td>
<td>Right posterior parahippocampal gyrus (36)</td>
<td>18 -10 -27</td>
<td>0.049</td>
<td>3.7</td>
</tr>
<tr>
<td></td>
<td>Left inferior temporal gyrus (20)</td>
<td>-48 -45 -8</td>
<td>0.091^</td>
<td>3.83</td>
</tr>
<tr>
<td></td>
<td>Left middle temporal gyrus (21)</td>
<td>-51 -31 -9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(b) experts &lt; novices</td>
<td>no suprathreshold voxels</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Notes: The corrected p-value was determined by combining the voxel-level and cluster-level thresholds by AlphaSim. (a) Experts had significantly more gray matter volume than novices in the right angular and right posterior parahippocampal gyri, while more gray matter volume was also detected in the left temporal lobe (the inferior and middle temporal gyri) at trend-level only^\. (b) No significant group differences were detected for the opposite contrast (experts < novices). Controlling for years of education did not affect the results. Coordinates are in MNI space. BA: Brodmann area.
Figure 1. Increased gray matter volumes in LKM experts compared to novices as revealed by VBM-Dartel

Notes: On the left side of Fig.1 are the group differences (LKM experts > novices) overlaid on the average of the bias-corrected images of all subjects. On the right side of Fig.1 are the glass brains showing all the clusters that survived corrected $p < 0.05$ or $p < 0.1$. Significant effects ($p < 0.05$, corrected) were detected in the (a) right angular and (b) posterior parahippocampal gyri. Trend-level effect ($p < 0.1$, corrected) was detected in the (c) left temporal lobe. No significant group differences were found for the opposite contrast (LKM experts < novices). Controlling for age or years of education did not affect the results. BA: Brodmann area.
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Figure 1. Increased gray matter volumes in LKM experts compared to novices as revealed by VBM-Dartel

Notes: On the left side of Fig. 1 are the group differences (LKM experts > novices) overlaid on the average of the bias-corrected images of all subjects. On the right side of Fig. 1 are the glass brains showing all the clusters that survived corrected $p < 0.05$ or $p < 0.1$. Significant effects ($p < 0.05$, corrected) were detected in the (a) right angular and (b) posterior parahippocampal gyri. Trend-level effect ($p < 0.1$, corrected) was detected in the (c) left temporal lobe. No significant group differences were found for the opposite contrast (LKM experts < novices). Controlling for age or years of education did not affect the results. BA: Brodmann area