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# BNST neurocircuitry in humans

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#### ABSTRACT

Anxiety and addiction disorders are two of the most common mental disorders in the United States, and are typically chronic, disabling, and comorbid. Emerging evidence suggests the bed nucleus of the stria terminalis (BNST) mediates both anxiety and addiction through connections with other brain regions, including the amygdala and nucleus accumbens. Although BNST structural connections have been identified in rodents and a limited number of structural connections have been verified in non-human primates, BNST connections have yet to be described in humans. Neuroimaging is a powerful tool for identifying structural and functional circuits in vivo. In this study, we examined BNST structural and functional connectivity in a large sample of humans. The BNST showed structural and functional connections with multiple subcortical regions, including limbic, thalamic, and basal ganglia structures, confirming structural findings in rodents. We describe two novel connections in the human brain that have not been previously reported in rodents or non-human primates, including a structural connection with the temporal pole, and a functional connection with the paracingulate gyrus. The findings of this study provide a map of the BNST's structural and functional connectivity across the brain in healthy humans. In large part, the BNST neurocircuitry in humans is similar to the findings from rodents and non-human primates; however, several connections are unique to humans. Future explorations of BNST neurocircuitry in anxiety and addiction disorders have the potential to reveal novel mechanisms underlying these disabling psychiatric illnesses.

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# Introduction

Elucidating the neural basis of common psychiatric disorders, such as anxiety and addiction, can guide the development of novel preventions and therapeutics. Complex states likely result from alterations in underlying neurocircuitry, and both structural and functional measures of connectivity show promise as disease biomarkers. Neuroimaging methods provide a powerful tool for examining neural circuits *in vivo* and progress has been made in identifying the neurocircuitry of anxiety (Shin and Liberzon, 2010) and addiction (Koob and Volkow, 2010). However, most investigations have focused on larger brain regions due to concerns about the ability of neuroimaging methods to measure smaller structures. With advances in imaging technology and analytic techniques, the exploration of circuits involving smaller brain regions is now possible.

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http://dx.doi.org/10.1016/j.neuroimage.2014.01.017 1053-8119/© 2014 Elsevier Inc. All rights reserved. A prime candidate for this type of investigation is the bed nucleus of the stria terminalis (BNST), a small structure in the basomedial forebrain. Research in rodents has established that the BNST mediates sustained anxiety responses (Davis et al., 1997; Hammack et al., 2004; Lungwitz et al., 2012; Sullivan et al., 2004; Waddell et al., 2006). Preliminary evidence also links BNST function to anxiety in nonhuman primates (Fox et al., 2008; Kalin et al., 2005) and humans (Alvarez et al., 2011; Grupe et al., 2013; Hasler et al., 2007; Somerville et al., 2010, 2013). BNST function also mediates reward-seeking and addictive behaviors in rodents (Dumont et al., 2005; Kash et al., 2008; Koob and Le Moal, 2008; Leri et al., 2002; Silberman and Winder, 2013) and humans (O'Daly et al., 2012).

Specific neural circuits—rather than specific brain regions—are crucial for complex behaviors, as recently demonstrated using optogenetics (Jennings et al., 2013; Kim et al., 2013). Most of our knowledge about BNST structural connectivity comes from tracer studies in rodents, which have shown that the BNST has extensive connections to other limbic regions—including the amygdala, hypothalamus, hippocampus, periaqueductal gray, and infralimbic cortex (Dong and Swanson, 2004a,b, 2006a,b,c; Dong et al., 2001b)—and striatal regions, including the nucleus accumbens and ventral tegmental area (Dong et al.,





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2001b). In primates, however, surprisingly little is known about BNST neurocircuitry. Tract-tracing studies in non-human primates have focused predominantly on relationships between the BNST and other limbic structures (Price and Amaral, 1981). In a single study using functional connectivity in humans and non-human primates, Oler et al. (2012) demonstrated that the BNST is functionally connected with the central nucleus of the amygdala, consistent with previously demonstrated rodent and non-human primate anatomical connections (Dong et al., 2001a). The BNST is much larger and more developed in humans than in rodents (Lesur et al., 1989), suggesting that BNST circuits may be altered in humans; however, to our knowledge, no studies have examined BNST structural or functional connectivity across the whole human brain. In the present study, we used diffusion tensor imaging (DTI) and resting state functional MRI (rs-fMRI) methods to identify patterns of BNST structural and functional connectivity in humans.

#### Materials and methods

#### Participants

We selected 82 DTI scans and 99 rs-fMRI scans of healthy controls with no psychiatric illnesses from two ongoing studies for this analysis. Scans were selected based on the following criteria: 1) the participant had no current or past psychiatric disorders, as determined by the Structured Clinical Interview for the DSM-IV (SCID I-P) (First et al., 2002); 2) participants were not on any psychotropic medications (within the past 6 months); and 3) the scan was determined to have good data quality (see quality methods below). Sixty-one participants overlapped between the DTI and rs-fMRI analyses. Participants included in this analysis were 17–57 years old (mean  $\pm$  SD = 30.6  $\pm$  11.3 years), 47.7% female, and 84.7% right-handed. Participants represented a variety of ethnicities including Caucasian (66.9%), African-American (26.2%), Asian (5.4%), and other (1.5%). The Vanderbilt University Institutional Review Board approved the study and written informed consent was obtained from each participants.

# BNST delineation

The BNST is a small (approximately 190 mm<sup>3</sup> in humans, compared to the amygdala at approximately 1800 mm<sup>3</sup>) cluster of nuclei located in the basomedial forebrain. Due to the small size of the BNST and its close proximity to other subcortical gray matter nuclei (Lesur et al., 1989), the boundaries of the BNST are often difficult to delineate on standard T1-weighted (T1W) anatomical images. To overcome this challenge and accurately delineate the boundaries of the BNST in the

human brain, we collected an ultra high-resolution anatomical image at 7 Tesla (T) ( $400 \times 400$  matrix, voxel size = .6 mm  $\times$  2.93 mm  $\times$ .6 mm, gap = 1 mm, number of slices = 16, TE = 59 ms, TR = 9534 ms) in a single 42 year old Caucasian male participant using gradient spin echo magnetic resonance imaging (GRASE) and a sequence specifically designed to optimally resolve the BNST in contrast to nearby structures by creating clear contrast between gray matter, white matter, and cerebrospinal fluid (CSF) (Fig. 1). The partial-brain GRASE image was resampled (.6 mm isotropic), coregistered to the participant's T1-weighted (T1W) whole-brain image using SPM8, normalized to standard MNI space by applying normalization parameters created during T1-to-MNI normalization in SPM8, and carefully visually inspected to ensure accurate normalization (Supplementary Fig. 1). To standardize the analysis across scans, we created a single BNST template mask from the normalized high-resolution GRASE image. The BNST was manually traced using 3DSlicer (version 3.4; www.slicer.org) (Fedorov et al., 2012), a software package that provides simultaneous visualization in all orientations. Tracing was performed by JUB and confirmed by SNA and JAC. The anatomical location of the BNST was identified based on a standard brain atlas (Mai et al., 2008). The BNST was initially traced in the coronal view, with the axial and the sagittal views used for confirmation. The GRASE sequence used for the 7 T scan, combined with the high resolution, provided excellent gray/white/CSF separation that was essential for identifying the boundaries of the BNST. The anterior boundary of the BNST was defined as 3 slices (1.8 mm) anterior to the slice containing the anterior commissure. The posterior boundary was defined by the most anterior portion of the internal segment of the globus pallidus. The medial border was defined by the fornix and the lateral border was defined by the internal capsule. The superior border was defined by the lateral ventricle. The inferior border was defined anteriorly by the anterior commissure and posteriorly by the hypothalamus. Although it was not possible to exactly identify each participant's BNST from the T1W images, we visually inspected the placement of the BNST mask on each individual's structural T1W image in 3-D slicer. To assess placement, we checked the BNST mask against three anatomical boundaries that are visible on the T1W images: the anterior commissure, the internal capsule, and the fornix. If the normalization of the BNST mask is accurate, we would expect the BNST mask to sit within those boundaries on each participant's image. The anterior commissure should provide the ventral border for the anterior BNST, the internal capsule should provide the lateral border for the middle portion of the BNST, and the fornix should provide the medial boundary for the lower portion of the BNST. Although the lateral ventricle is also visible, the gray matter/CSF contrast was insufficient to clearly assess the boundary. Based on the visual inspection of the BNST mask according



Fig. 1. The human bed nucleus of the stria terminalis (BNST). The human brain is shown as an illustration (Gray, 1918) with the BNST highlighted in yellow. For reference, a similar slice is shown for fixed tissue (Mai et al., 2008). The traced BNST mask used for this study is outlined in yellow (right) on a 7 T gradient spin echo (GRASE) magnetic resonance image.



Fig. 2. The traced BNST mask is shown in yellow on a template brain (top row) and on four individual participant brains (rows 2 through 5). The anatomical landmarks used to confirm correct placement within known boundaries are shown in green (internal capsule), orange (fornix), and blue (anterior commissure).

to the visible boundaries, the BNST mask appeared to be appropriately sized and within the boundaries of the BNST for all participants (see Fig. 2 for examples).

# Structural connectivity data-image acquisition

Diffusion MRI data were acquired on two identical 3 T Philips Achieva MRI scanners (Philips Healthcare, Inc.). Whole-brain diffusion weighted images were acquired using a pulsed-gradient spin echo, echo-planar imaging (single-shot EPI) pulse sequence and the following parameters:  $96 \times 96$  matrix; voxel size = 2.5 mm isotropic; number of slices = 50; TE = 65 ms; TR = 8.5 s; SENSE acceleration factor = 2. We acquired 92 diffusion directions with a *b* value of 1600 s/mm<sup>2</sup> and one T2-weighted volume with a *b* value of 0 s/mm<sup>2</sup>. High-resolution T1W anatomical images were collected with the following parameters:

FOV = 256 mm; number of slices = 170; voxel size = 1 mm isotropic; gap = 0 mm.

# Structural connectivity data-image preprocessing

Diffusion weighted data were preprocessed and analyzed using the FMRIB Software Library (FSL, version 4.1.4; Oxford Centre for Functional MRI of the Brain (FMRIB), UK; http://www.fmrib.ox.ac.uk/fsl/) and Matlab (Version R2010, The MathWorks, Inc., Natick, MA). Diffusion data were corrected for eddy current distortions and motion using the Eddy Current Correction tool within the FMRIB FDT toolbox (version 2.0), skull stripped using the FMRIB Brain Extraction tool (BET) (Smith, 2002), and visually inspected for processing artifacts (e.g., skull stripping failure). Diffusion tensors were fitted at each voxel using the FMRIB FDT toolbox. Diffusion data were selected from an original

sample of 135 participants. Scans were first carefully visually inspected for acquisition artifacts (i.e., ghosting, water-fat shift artifacts), and 45 diffusion scans were excluded as a result of artifact detection. Next, 8 participants were excluded for excessive motion, which was defined as greater than 5 mm or 3° of motion in any direction across the 14 min, 36 s diffusion series. Finally, preprocessed scans were visually inspected for processing failures (e.g., skull stripping failure), and all failures at this stage were corrected. This resulted in a final sample of 82 high quality DTI scans in the final analysis.

#### Structural connectivity data-probabilistic tractography

Because we were interested in describing connectivity across the entire human brain, we used an agnostic exploratory approach with respect to potential BNST connectivity, selecting 54 bilateral target regions (108 total) from the Harvard-Oxford Cortical (n = 47 targets) and Subcortical (n = 7 targets) Probabilistic Atlases (Desikan et al., 2006) representing the entire brain. Probabilistic tractography was used to determine the likelihood of structural connections between the BNST and each target region. Because anatomical tracer studies have shown predominantly ipsilateral connections between the BNST and other gray matter regions (Coolen and Wood, 1998; Sun et al., 1991; Wood and Swann, 2005), separate tractography analyses were conducted for the left and right hemispheres. The few studies which have examined contralateral projections identified only small, midline structures not available in the Harvard-Oxford atlases, such as the midbrain and brainstem nuclei, and hypothalamus (Dong and Swanson, 2006c; Dong et al., 2000). For each hemisphere, the BNST was seeded for probabilistic tractography to the 54 cortical and subcortical target regions using the following parameters: 5000 streamline samples per voxel, 0.5 mm step lengths, and curvature threshold = 0.2. Standard FSL procedures effectively constrain tractography results by excluding streamlines that enter areas of high uncertainty (i.e., low fractional anisotropy) or are forced to make anatomically improbable decisions (e.g., making a sharp turn or looping back); therefore, additional thresholding of fractional anisotropy values was not performed. The number of tractography streamlines passing from each BNST seed voxel into each target region was recorded. To eliminate spatial overlap between targets, target regions were thresholded at 50% probability and warped to each participant's native diffusion space for probabilistic tractography analysis. The template BNST mask was also warped to each participant's native diffusion space. Because DTI-based tractography methods tend to lose fibers along the track pathways and underestimate connectivity for longer tracts, we applied a distance correction. The distance correction accounts for increased difficulty in hitting targets based on distance from the seed by multiplying the number of target hits by the average distance of the tract. To account for the effect of both seed and target size on accuracy, seed-to-target probability maps were corrected for size of each target region and individual differences in BNST size. Finally, to minimize the effect of outliers, the seed-to-target probability maps were thresholded at the 5th and 95th percentiles of the mean (i.e., trimmed mean).

# Structural connectivity data-validation analyses

We performed two validation analyses: 1) we tested for probabilistic tractography streamlines within the stria terminalis, and 2) we tested connectivity in *a priori* positive and negative control regions selected from the Harvard-Oxford Probabilistic Atlas target masks.

The stria terminalis is a distinct white matter pathway that provides the major connection between the amygdala and the BNST (Fig. 3). Because we would expect to observe tractography streamlines coursing from the BNST through the stria terminalis, we conducted a region of interest analysis within the stria terminalis. The stria terminalis was traced in 3D Slicer (http://www.slicer.org) (Fedorov et al., 2012) with respect to its known anatomical boundaries (Mai et al., 2008). Tracing was performed by JUB and confirmed by SNA and JAC. The stria terminalis was initially traced in the coronal view and confirmed in the sagittal view. The stria terminalis was identified as beginning at the BNST and tracing of the full white matter pathway was performed by following the movement of the white matter tract from slice to slice, ensuring separation from the fornix. The amygdala marked the end of the stria terminalis tracing. The contiguous connection of the pathway was confirmed in sagittal slices. While significant measures were taken to accurately identify the stria terminalis, we acknowledge that manual tracing of this small white matter path may be prone to error.

Each participant's probabilistic tractography pathway map, created as a result of the BNST-to-targets analysis, was thresholded for error  $(\leq 1\%)$ , warped to MNI space and averaged into a group map. The probabilistic tractography group mask was thresholded at >50% group overlap and masked with the traced stria terminalis mask (Fig. 3). There was a 100% overlap between the group streamline map and our traced stria terminalis mask, indicating that every stria terminalis voxel had probabilistic tractography streamlines running through it and confirming that, on the whole, tractography streamlines were following appropriate anatomical pathways. In order to examine consistency across participants, each individual's probabilistic tractography pathway map was masked with the traced stria terminalis mask, using a stringent individual level thresholding (<1% of total tractography streamlines sent). Almost all (94%) of individuals showed tractography streamlines running through the stria terminalis, again confirming that on the whole tractography streamlines followed appropriate anatomical pathways.

Next, we performed a control region analysis. We chose the amygdala as the positive control region because anatomical studies in rodents and non-human primates have described extensive



Fig. 3. The stria terminalis mask (blue) and BNST mask (red) are shown on a 3-dimensional template brain (left). The group DTI streamlines map, masked by the stria terminalis mask, is shown in green on a 3-dimensional template brain (middle). Each voxel of the stria terminalis mask overlapped with the group streamlines map, demonstrating that tractography streamlines were coursing through the entire stria terminalis. For reference, a histological section of the stria terminalis is shown (right).

connections between the BNST and amygdala (Coolen and Wood, 1998; Price and Amaral, 1981). Because there are so few primate tracer studies, we selected the negative control region based on known structural brain connections with the amygdala, a region with similar connections as the BNST. The middle frontal gyrus served as the negative control region because it has only sparse connections with the amygdala (Ghashghaei et al., 2007). The amygdala (positive control) was significantly connected with the BNST, while the middle frontal gyrus (negative control) was not significantly connected, demonstrating that probabilistic tractography can accurately discriminate between highly likely and highly unlikely structural connections.

# Functional connectivity data-image acquisition

Seven minutes of rs-fMRI data was obtained approximately 20 min after entering the 3 T scanner, following T1W structural image collection, but before DTI data collection (see Structural connectivity data image acquisition). Participants were instructed to relax and close their eyes, but not fall asleep. Functional images were acquired using an echo-planar imaging sequence with the following parameters: volumes = 203; TR = 2 s; TE = 34 ms; SENSE = 1.8; FOV = 240 mm; and matrix = 80 × 80. Each volume contained 28 4 mm slices (acquisition voxels = 3 mm × 3 mm × 4 mm) and provided whole-brain coverage. No tasks were performed prior to the collection of the rsfMRI data.

#### Functional connectivity data-image preprocessing

Data were preprocessed in SPM8 (http://www.fil.ion.ucl.ac.uk/spm/ software/spm8/). Each participant's T1W structural image was segmented into gray matter, white matter, and cerebrospinal fluid using the Voxel-Based Morphometry, 8.0, toolbox (http://dbm.neuro.unijena.de/vbm) and gray matter images were normalized to the Montreal Neurological Institute (MNI) gray matter template. Functional data were slice time corrected, motion corrected, coregistered to the segmented gray matter image, and normalized using parameters derived from normalization of the gray matter image. Images were then resampled to 3 mm  $\times$  3 mm  $\times$  3 mm. Given the small size of the BNST and need for precision in the connectivity analyses, only minimal spatial smoothing was applied (3-mm FWHM). Resting state data were selected from an original sample of 135 participants (same initial sample as diffusion data), using a five-step process to check for image quality. The resting state data were not available at the time of analysis for seven participants. FMRI data were initially selected based on ratings from an in-house quality assurance toolbox used in a previous study (Woodward et al., 2012). The threshold values for poor quality were based on subjective rater agreement of poor quality images on a training dataset of 84 participants, classification based on a fuzzy clustering algorithm and validation on an independent dataset. The thresholds for poor quality are: signal-to-noise ratio (<29), percent standard deviation (>5), percent standard deviation histogram (>.78), percent drift (>1.18), percent fluctuation (>.51), and spatial correlation variance ratio (>.19). Four participants (3%) were removed based on poor quality data. Next, scans were manually inspected and excluded for visual artifacts; 16 participants were excluded due to artifacts. Next, motion was assessed, and any participants with motion greater than 2 mm or 2° in any direction were excluded; eight participants were excluded due to motion. Finally, normalization of the structural and functional data was inspected; one participant was excluded due to poor quality normalization. These exclusions resulted in a final sample of 99 participants with high quality rs-fMRI data.

# Functional connectivity data-connectivity analyses

The CONN toolbox (Whitfield-Gabrieli and Nieto-Castanon, 2012), implemented in Matlab, was used to estimate functional connectivity for each participant. The right and left BNST masks were entered as seed regions. For each participant, the blood-oxygenation-level-dependent (BOLD) time series was estimated as the average time series for all voxels in the left and right BNST seed masks separately. Time series at each voxel had white matter, cerebrospinal fluid, and motion-related signals removed via regression (Behzadi et al., 2007; Chai et al., 2012) and were filtered to 0.1–1.0 Hz to retain the frequencies relevant for connectivity estimation. Global signal was not removed given concerns about the impact of removing global signal on resting state correlations (Murphy et al., 2009; Saad et al., 2012). Temporal correlations were estimated between the average time course from each seed region and all voxels in the brain, producing beta images for each seed region for each participant. The resulting beta images were used for all subsequent analyses.

For consistency with the structural connectivity analyses, average positive connectivity for each of the 54 target regions from the Harvard-Oxford Cortical and Subcortical Probabilistic Atlases (Desikan et al., 2006) (Table 1) was estimated. Target regions were thresholded at 50% probability to remove overlap between regions. Positive connectivity maps were created for each participant. Average connectivity between the BNST and each target region was extracted using SPM8.

To explore the spatial pattern across each voxel in the brain, we also conducted a voxel-wise functional connectivity analysis. The left and right BNST were the seed regions for the left and right hemispheres, respectively.

#### Statistical analysis of connectivity

Structural and functional connectivity values are inherently descriptive, preventing any determination of whether a specific region is definitively connected to the BNST. For this initial characterization of BNST connectivity, we took a conservative approach with the goal of determining the target regions with the highest likelihood of structural or functional connectivity. We performed a bootstrap analyses (10,000 permutations) to identify the 95% confidence interval around the mean and defined a significant likelihood of a connection as a connectivity value greater than the upper limit of the 95% confidence interval (structural connectivity = .077; functional connectivity = .117). Furthermore, to ensure that significant values for target regions were not driven by a small percentage of participants, only significant regions where more than 50% of participants were above the threshold value are reported. For the whole-brain functional connectivity analysis, we used a conservative t-value of >8.0 and a cluster threshold of 20 voxels (540 mL) to identify significant clusters.

#### Spatial pattern of connectivity

To explore the spatial pattern of BNST structural connectivity within each significant target, we conducted post-hoc probabilistic tractography analyses. Each target identified as having a significant likelihood of connection with the BNST was seeded for probabilistic tractography to the BNST (5000 streamline samples per voxel, 0.5 mm step lengths, curvature threshold = 0.2, with correction for distance), and the number of tractography streamlines passing from each target seed voxel into the BNST was recorded. Each participant's target-to-BNST probability maps were thresholded at the 5th and 95th percentiles of the mean to exclude outlier values, warped to MNI space, and averaged across participants in order to observe the average spatial pattern of BNST structural connectivity across the group.

To explore the spatial pattern of BNST functional connectivity, we conducted a functional connectivity analysis within each significant target region. BNST functional connectivity was conducted for each participant. Individual participant BNST maps were entered into a one-sample *t*-test and masked by the significant target regions in order to illustrate the average spatial pattern of BNST functional connectivity.

# Table 1

Mean connectivity values and % connectivity by target region.

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International production of the section of the sec	Right angular gyrus	0.0073	0%	0.1019	34%
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Left control operatum contro0.00210.108381Her control operatum contro0.01260.20.1114392Hey control operatum contro0.01260.20.1125425Rept control operatum contro0.0270420.0772282Rept control contro0.0270420.0772282Rept control contro0.0270420.0772282Rept control contro0.0270420.0774245Rept control contro0.02660.0774245245Rept control contro0.04661380.0774245Rept control contro0.04661380.0774245Rept control contro0.04671380.078295Rept control operatum contro0.02711380.1167332Rept control plect contro0.02811380.1390975Rept control plect contro0.03221380.0190235Rept control plect contro0.03221380.0190235Rept foronal plect contro0.03221380.0190245Rept infector foronal proc particle0.02722730.0286375Rept infector foronal proc particle0.02722730.0286375Rept infector foronal proc particle0.02722730.0286375Rept infector foronal proc particle0.02737750.0286375Rept infector foronal proc particle0.02742730.028637	Right caudate	0.1108	<b>87</b> %	0.2646	88%
logic and a portulation doma         0.045         B         0.055         244           left cinguits grows, posterior         0.025         23         0.1114         953           left cinguits grows, posterior         0.0270         45         0.0125         225           left cinguits grows, posterior         0.0270         45         0.0774         245           left cinguits grows, posterior         0.0270         45         0.07754         245           left cinguits cinguits cinguits         0.0125         0.05         0.07754         245           left cinguits cinguits         0.0255         0.05         0.07754         245           Replit forind recluit cines         0.0466         135         0.01169         355           Replit forind in recluit cines         0.0231         0.46         0.1135         0.055           Replit forind in recluit cines         0.0231         0.46         0.1135         0.055           Replit forind in recluit cines         0.0232         0.45         0.0139         275           Replit forind in recluit cines         0.0171         45         0.136         0.057           Replit forind recluit cines         0.0270         0.55         0.0113         0.057	Left central operculum cortex	0.0072	1%	0.1065	38%
Let: tigguard gyns, attention0.042 0.0259280.1112 0.1125493 423let: conglar gyns, posterior0.0279630.1125423Right conglar gyns, posterior0.0270410.0772245Right conglar gyns, posterior0.02650.50.0777224Right conglar gyns, posterior0.02660.50.0777225Right conglar gyns, posterior0.02660.50.0777225Right conglar gyns, posterior0.02661330.1140887Right conglar gyns, posterior0.04661330.1140887Right formal optical cortex0.04671230.0140887Right formal optical cortex0.04281230.1142987Right formal optical cortex0.04281240.135305Right formal optical cortex0.04281240.135305Right formal optical cortex0.04282470.139561Right formal optical gyns, pars opercularis0.0277250.139561Right formal optical gyns, pars opercularis0.0737250.1224445Right finderic formal gyns, pars opercularis0.073730.108305Right finderic formal gyns, pars opercularis0.073730.108305Right finderic formal gyns, pars opercularis0.073740.108305Right finderic formal gyns, pars opercularis0.073750.108305Right finderic formal gyns	Right central operculum cortex	0.0045	0%	0.0885	28%
bill integring integring         0.005         2.62         0.115         9.72           bigh integring integring, poterior         0.0270         4.7         0.0072         2.83           Left cancel cortex         0.0400         118         0.0747         2.25           Left cancel cortex         0.0400         205         0.1835         4.93           Left frontal medial cortex         0.0475         3.7         0.1167         3.75           Left frontal medial cortex         0.0428         2.2         0.1142         407           Left frontal orbital cortex         0.0428         1.2         0.1142         407           Right frontal orbital cortex         0.0428         1.2         0.1135         363           Right frontal orbital cortex         0.0428         1.4         0.1036         407           Right frontal orbital cortex         0.0428         1.4         0.1036         407           Right frontal orbital cortex         0.0428         1.4         0.1036         407           Right frontal orbital cortex         0.0428         1.5         0.1131         363           Right frontal orbital cortex         0.0427         2.7         1.113         363           Right frontal orbital cortex	Left cingulate gyrus, anterior	0.0243	5% 2%	0.1212	44%
Dely compute prox. product over0027047. 47.01972282. 283.Right consol cortex0.025667. 	Left cingulate gyrus, posterior	0.0126	2% 6%	0.1125	59% 179
and number         opposite	Right cingulate gyrus, posterior	0.0230	0% 19	0.0972	42% 28%
nether consist carbon0.0256620.07702.22Right frontal methal cortex0.035511%0.11854967Right frontal perchain cortex0.032511%0.1140383Right frontal operculam cortex0.02155.30.0560202Right frontal operculam cortex0.02155.40.0258224Right frontal operculam cortex0.02155.40.0139377Right frontal operculam cortex0.05232480.1133457Right frontal operculam cortex0.05272480.1039377Right frontal opercularis0.05277470.1396457Right frontal opercularis0.05277470.1391458Left Heiser frontal grows pars opercularis0.0577750.1224458Left heiser frontal grows pars opercularis0.0577750.1038397Left heiser frontal grows pars opercularis0.0577750.1038375Right inforcat monol grows, part singularis0.0577750.1038375Right inforier temporal grows, anterior0.05652350.0596307Right inforier temporal grows, part singularis0.0577750.1038375Right inforier temporal grows, part singularis0.0571750.1089375Right inforier temporal grows, part singularis0.05762350.1089375Right inforier temporal grows, part singularis0.0571750.1089375 <td< td=""><td>Left current cortex</td><td>0.0270</td><td>11%</td><td>0.0372</td><td>26%</td></td<>	Left current cortex	0.0270	11%	0.0372	26%
Inth frammal medial contex         0.0400         20%         0.1385         49%           Left frontal operculum contex         0.0425         11%         0.1107         33%           Left frontal operculum contex         0.0426         13%         0.1149         38%           Left frontal operculum contex         0.0215         5,6         0.0560         29%           Left frontal operculum contex         0.0141         10%         0.1086         43%           Left frontal operculum contex         0.0134         14%         0.1396         45%           Left frontal operculum contex         0.0131         45%         0.1396         55%           Left frontal operculum contex         0.0131         45%         0.1319         56%           Left frontal groups parts         0.257         84%         0.1294         42%           Left frontal groups parts apprendiation         0.0256         73%         0.03986         30%           Left frontal groups parts apprendiation         0.0353         1.28         0.03981         33%           Left frontal groups parts apprendiation         0.0333         1.28         0.03984         33%           Left frontal groups parts apprendiation         0.0270         10%         0.0384 <t< td=""><td>Right cureal cortex</td><td>0.0256</td><td>6%</td><td>0.0707</td><td>27%</td></t<>	Right cureal cortex	0.0256	6%	0.0707	27%
ngh funcai neutial cortex         0.0335         11%         0.1107         33%           Righ fronial operculuut cortex         0.0466         13%         0.1149         38%           Righ fronial operculuut cortex         0.0428         12%         0.0148         48%           Righ fronial orbital cortex         0.0431         10%         0.1048         43%           Righ fronial orbital cortex         0.0431         10%         0.1038         43%           Righ fronial orbital cortex         0.0623         24%         0.1038         43%           Righ fronial orbital cortex         0.0623         14%         0.1039         43%           Righ fronial orbital cortex         0.0171         44         0.1039         44%           Left history groups         0.2577         84         0.1244         44%           Left history groups and groups ancreation         0.0257         75         0.1284         33%           Left history groups ancreation         0.0277         75         0.1284         33%           Left history groups ancreation         0.0277         10%         0.0490         33%           Left history groups ancreation         0.0277         10%         0.0496         33%           Left h	Left frontal medial cortex	0.0460	20%	01385	49%
Left final operation cortex         0.0466         138         0.149         385           Left final orbital cortex         0.0215         5%         0.06969         2%           Left final orbital cortex         0.0248         128         0.1106         433           Left final orbital cortex         0.0381         128         0.1135         375           Left final pole         0.0382         124         0.1135         375           Left final pole         0.0382         124         0.1086         335           Left final pole         0.037         76         0.1086         335           Left final proceampes         0.0276         56         0.0219         445           Left final proceampes         0.0276         56         0.0219         455           Left final proceampes         0.0276         56         0.0219         455           Left finatric montal grups, pars opercularis         0.0276         28         0.0129         455           Left finatric montal grups, pars opercularis         0.0276         27         0.038         0.0139         355           Left finatric montal grups, pars opercularis         0.0277         75         0.0996         355           Left finitric mon	Right frontal medial cortex	0.0325	11%	0.1107	33%
Right fording004281280.04280.280.04280.04280.04280.01420.0530.04280.01420.0530.	Left frontal operculum cortex	0.0466	13%	0.1149	38%
Left function characterization of the section of t	Right frontal operculum cortex	0.0215	5%	0.0969	29%
Right functional point0.06410.064.3%Right functional point0.06232.4%0.11353.6%Right functional point0.01344.4%0.13063.5%Right functional point0.247277%0.13196.6%Right functional gram, pars opercularis0.01714.5%0.01244.4%Right functional gram, pars opercularis0.01714.5%0.12134.6%Right functional gram, pars opercularis0.01714.5%0.12134.6%Right function frontal gram, pars opercularis0.12742.7%0.1284.6%Right function frontal gram, pars opercularis0.12742.7%0.1284.6%Right function frontal gram, pars opercularis0.0272.7%0.1284.6%Right function frontal gram, pars opercularis0.0272.7%0.1083.7%Right function frontal gram, pars opercularis0.0272.7%0.1043.7%Right function frontal gram, pars opercularis0.0272.7%0.1043.7%Right function frontal gram, pars opercularis0.0272.7%0.1043.7%Right function frontal gram, pars opercularis0.0212.7%0.1043.7%Right function frontal gram, pars opercularis0.0222.6%0.1043.7%Right function frontal gram, pars opercularis0.0222.6%0.0083.3%Right function frontal gram, pars opercularis0.0222.6%0.0083.3%Right function frontal gram, pars	Left frontal orbital cortex	0.0428	12%	0.1142	40%
Left monit pole0.06232.4%0.113536%Left heschly gyns0.01344.50.103640%Left heschly gyns0.01714.50.108635%Left hisporampus0.252784%0.122942%Left inforior frontal gyns, pars opercularis0.02565.50.121942%Left inforior frontal gyns, pars opercularis0.01714.50.111336%Left inforior frontal gyns, pars trangularis0.1742.2%0.129443%Left inforior frontal gyns, pars trangularis0.05377.70.108636%Left inforior temporal gyns, anterior0.06362.3%0.08822.6%Left inforior temporal gyns, anterior0.02171.6%0.10402.5%Left inforior temporal gyns, interior0.02171.6%0.10402.5%Left inforior temporal gyns, interport0.02171.6%0.10402.5%Left inforior temporal gyns, interport0.02171.6%0.10403.5%Left inforior temporal gyns, interport0.02171.6%0.10403.5%Left inforior temporal gyns, interport0.02171.6%0.10403.5%Left inforior temporal gyns, interport0.02167.5%0.00643.5%Left inforior temporal gyns, interior0.02249.5%0.01063.5%Left inforior temporal gyns, gync inforior0.02449.5%0.09663.2%Left inforior temporal gyns, gync inforior0.02449.5%0.0106 <t< td=""><td>Right frontal orbital cortex</td><td>0.0341</td><td>10%</td><td>0.1096</td><td>43%</td></t<>	Right frontal orbital cortex	0.0341	10%	0.1096	43%
Bight fordar0.03821%0.0397%Right Fisch's gravs0.01714%0.1306358Right Fisch's gravs0.24727%0.1319686Right fisch's gravs0.227284%0.122444%Et if inferior frontal gravs, pars opercularis0.01714%0.113136%Right finiter frontal gravs, pars transgalaris0.02565%0.122443%Right inferior frontal gravs, pars transgalaris0.02567%0.108637%Right inferior frontal gravs, pars transgalaris0.02567%0.108637%Left inferior frontal gravs, pars transgalaris0.02567%0.108637%Left inferior transport gravs, termporoaccipital0.02605%0.088427%Right inferior transport gravs, termporoaccipital0.02605%0.089427%Left inferior transport gravs, termporoaccipital0.02605%0.089437%Left inferior transport gravs, termporoaccipital0.02647%0.100641%Left inferior transport gravs, termporoaccipital0.02647%0.010641%Left inferior transport gravs, termporoaccipital0.02747%0.010641%Left inferior transpor	Left frontal pole	0.0623	24%	0.1135	36%
Låft Heschi sjørns0.01344%0.130640%Lätt hippocangus0.04727%0.131956%Lätt hippocangus0.2555%0.121942%Lätt hippocangus0.02565%0.121942%Lätt hirdrich frontal gyrus, par opercularis0.02565%0.121942%Lätt hirdrich frontal gyrus, par trangularis0.127432%0.129443%Lätt hirdrich frontal gyrus, par trangularis0.0577%0.109630%Lätt hirdrich temporal gyrus, anterior0.05177%0.098630%Lätt hirdrich temporal gyrus, parterior0.053712%0.008630%Lätt hirdrich temporal gyrus, parterior0.053712%0.008635%Lätt hirdrich temporal gyrus, posterior0.053712%0.019428%Lätt hirdrich temporal gyrus, posterior0.0595%0.019637%Right infort temporal gyrus, posterior0.0295%0.100631%Lätt hirdracalcarine cortex0.045416%0.100633%Lätt hirdracalcarine cortex0.045415%0.010633%Lätt hirdracalcarine cortex0.01332%0.010631%Lätt hirdracalcarine cortex0.02647%0.020835%Lätt hirdracalcarine cortex0.02760%0.028435%Lätt hirdracalcarine gyrus0.02647%0.028331%Lätt hirdracalcarine gyrus0.03760.5%0.102645% </td <td>Right frontal pole</td> <td>0.0382</td> <td>1%</td> <td>0.1039</td> <td>37%</td>	Right frontal pole	0.0382	1%	0.1039	37%
Right Heschir's gruss0.01714%0.108635%Left hippocampus0.25784%0.122444%Bight hippocampus0.25784%0.123444%Left inferior frontal gruss, pars opercularis0.01714%0.111336%Bight inferior frontal gruss, pars triangularis0.5377%0.108839%Eft inferior frontal gruss, pars triangularis0.05677%0.089226%Right inferior frontal gruss, pars triangularis0.027010%0.089226%Right inferior temporal gruss, pars procecipital0.02605%0.014435%Right inferior temporal gruss, parsoccipital0.02605%0.010831%Right inferior temporal gruss, temporoccipital0.02537%0.114237%Right inferior temporal gruss, temporoccipital0.02547%0.100831%Right inferior temporal gruss, temporoccipital0.02547%0.010031%Right inferior temporal gruss, temporoccipital0.02547%0.010031%Right inferior temporal gruss, temporoccipital0.02444%0.010031%Right inferior temporal gruss, temporoccipital0.02449%0.09442%Right inferior temporal gruss, temporoccipital0.02444%0.069032%Right inferior temporal gruss, anterior0.02044%0.069035%Right inferior temporal gruss, gruss of0.02044%0.06962%Right inferior temporal	Left Heschl's gyrus	0.0134	4%	0.1306	40%
Left hippocamps0.2477%0.13966Left hirfor fortal gyrus, par operularis0.02565%0.121942%Left hirfor fortal gyrus, par operularis0.02765%0.121942%Left hirfor fortal gyrus, par trangularis0.127422%0.129443%Left hirfor tortal gyrus, par trangularis0.0577%0.109639%Left hirfor tortang gyrus, parts insigularis0.0577%0.096139%Left hirfor tortang gyrus, parts insigularis0.0377%0.009635%Left hirfor tortang gyrus, parts insigularis0.0210.0380.0380.03833%Left hirfor tortang gyrus, parts insigularis0.0265%0.038433%Left hirfor tortang gyrus, parts insigularis0.0212%0.009631%Left hirfor tortang gyrus, parts insigularis0.02212%0.03933%Left hirfor tortang gyrus, parts insigularis0.0212%0.03933%Left hirfor tortang gyrus, parts insigularis0.0244%0.03932%Left hirfor tortang gyrus, parts inferior0.0244%0.03932%Left hirfor tortang gyrus, parts inferior0.0244%0.03932%Left hirfor tortang gyrus0.0369%0.03632%Left hirfor tortang gyrus0.0369%0.03632%Left hirfor tortang gyrus0.0369%0.03632%Left hirfor tortang gyrus0.0369%0.036	Right Heschl's gyrus	0.0171	4%	0.1086	35%
Right Inpocantpus0.25794%0.122494%Leit Infrior fontal gyrus, pars operularis0.01714%0.111336%Leit Infrior fontal gyrus, pars tinagularis0.05377%0.109839%Right Infrior fontal gyrus, pars tinagularis0.05377%0.098226%Leit Infrior temporal gyrus, anterior0.06120.0710.089226%Leit Infrior temporal gyrus, pars tinagularis0.07210%0.098226%Leit Infrior temporal gyrus, posterior0.027010%0.014035%Leit Infrior temporal gyrus, temporoccipital0.02605%0.014033%Leit Infrior temporal gyrus, temporoccipital0.02605%0.104033%Leit Intracalarine cortex0.02787%0.100631%Leit Intracalarine cortex0.02787%0.100633%Leit Intracalarine cortex0.02787%0.100633%Leit Intracalarine cortex0.02749%0.030622%Leit Intracalarine cortex0.01532%0.039633%Leit Intracalarine cortex0.01931%0.096635%Leit Intracalarine cortex0.02647%0.039635%Leit Intracalarine cortex0.03760%0.13635%Leit Intracalarine0.03760%0.13635%Leit Intracalarine cortex0.03760%0.13635%Leit Intracalarine0.03815%0.046635%<	Left hippocampus	0.2472	77%	0.1319	56%
Left inferior frontal gyrus, pars opercularis0.02565%0.121942%Left inferior frontal gyrus, pars trangularis0.127432%0.129443%Left inferior frontal gyrus, pars trangularis0.65623%0.099630%Left inferior temporal gyrus, anterior0.062623%0.099630%Left inferior temporal gyrus, anterior0.033312%0.040435%Left inferior temporal gyrus, pars trangularis0.035312%0.040435%Left inferior temporal gyrus, pars temporoccipial0.038513%0.103527%Right inferior temporal gyrus, temporoccipial0.02212%0.014433%Left inferior temporal gyrus, temporoccipial0.02247%0.016631%Left infractakerine cortex0.02249%0.096432%Left infractakerine cortex0.02144%0.066631%Left infractakerine cortex0.02249%0.096432%Left infractakerine cortex0.01741%0.068131%Left infractakerine cortex0.01744%0.016041%Right infracta Corpical cortex, inferior0.02249%0.068331%Left infractakerine cortex0.01779%0.126245%Left infractakerine0.01779%0.12645%Left infractakerine0.01750.5%0.106031%Left infractakerine0.01750.5%0.102645%Left infractakerine<	Right hippocampus	0.2527	84%	0.1224	44%
Right inferior frontal gyrus, part strangularis         0.171         4%         0.1113         365           Lift inferior frontal gyrus, part strangularis         0.0537         7%         0.108         397           Right inferior frontal gyrus, part strangularis         0.0537         7%         0.108         397           Right inferior temporal gyrus, parterior         0.0312         10%         0.0892         265           Lift inferior temporal gyrus, partoroccipital         0.037         7%         0.1040         353           Lift inferior temporal gyrus, personaccipital         0.0270         10%         0.1040         353           Lift inferior temporal gyrus, temporoccipital         0.0260         5%         0.0894         337           Lift inferior temporal gyrus, temporoccipital         0.0265         7%         0.1060         313           Lift intracalcranic cortex         0.0258         7%         0.1060         337           Right inferior         0.0173         2%         0.0264         2%         0.0606         325           Lift atracal corbial cortex, inferior         0.0173         1%         0.066         335           Lift atracal corbial cortex, inferior         0.0173         1%         0.0264         355	Left inferior frontal gyrus, pars opercularis	0.0256	5%	0.1219	42%
Ich inforior frontal gyrus, pars triangularis0.127432%0.129443%Ight inforior frontal gyrus, part triangularis0.05577%0.109839%Ich inforior temporal gyrus, anterior0.035312%0.098128%Ight inforior temporal gyrus, posterior0.035312%0.098128%Ight inforior temporal gyrus, posterior0.038513%0.104035%Ich inforior temporal gyrus, temporooccipital0.02665%0.089433%Ight inforior temporal gyrus, temporooccipital0.02212%0.114237%Ight inforior temporal gyrus, temporooccipital0.02212%0.106031%Ich instalar cortex0.02212%0.103033%Ight intriacticante cortex0.0241%0.096427%Ight intriacticante cortex0.01741%0.096427%Ight intriacticante cortex0.01741%0.096131%Ich instal gyrus0.02944%0.016031%Ich ingual gyrus0.01979%0.098035%Ich ingual gyrus0.01979%0.028241%Ich indiad gyrus, staterior0.038515%0.108033%Ich indiad frontal gyrus, staterior0.038515%0.102738%Ich indiad gyrus0.01972%0.108032%Ich indiad frontal gyrus0.01972%0.108032%Ich indiad frontal gyrus0.01972%0.108032% <td>Right inferior frontal gyrus, pars opercularis</td> <td>0.0171</td> <td>4%</td> <td>0.1113</td> <td>36%</td>	Right inferior frontal gyrus, pars opercularis	0.0171	4%	0.1113	36%
Right inferior frontal gruss, pars triangularis         0.0537         7%         0.1098         39%           Lit inferior temporal gruss, anterior         0.0312         10%         0.0992         26%           Lit finefroir temporal gruss, posterior         0.0333         12%         0.0981         28%           Right inferior temporal gruss, posterior         0.0270         10%         0.1040         35%           Lit finefroir temporal gruss, perfor         0.0270         10%         0.1040         35%           Lit finefroir temporal gruss, perfor         0.0270         5%         0.0894         33%           Lit finisolar cortex         0.0270         5%         0.0894         33%           Lit finisolar cortex         0.0271         2%         0.1142         37%           Right inferior temporal gruss, perfor         0.0274         9%         0.0096         32%           Lit fatratal occipital cortex, inferior         0.0174         1%         0.0994         32%           Lit fatratal occipital cortex, superior         0.0224         9%         0.0966         32%           Lit fatratal occipital cortex, superior         0.0133         1%         0.0981         31%           Lit fatratal occipital cortex, superior         0.0167         <	Left inferior frontal gyrus, pars triangularis	0.1274	32%	0.1294	43%
Left inforie temporal gyrus, anterior0.06262.3%0.099630%Left inforie temporal gyrus, streinor0.03311.2%0.09812.8%Left inforie temporal gyrus, sposterior0.027010%0.10403.5%Left inforie temporal gyrus, sposterior0.03851.3%0.10352.7%Left inforie temporal gyrus, temporoccipital0.02805%0.08843.3%Left inforie temporal gyrus, temporoccipital0.02212%0.11423.7%Left instale cortex0.02287%0.10063.1%Left instale cortex0.01332%0.009442.7%Left instale cortex, inferior0.01741.5%0.009663.2%Left instale cortex, inferior0.01741.5%0.009663.2%Left instale cortipial cortex, inferior0.02249%0.098913.1%Left instale cortipial cortex, inferior0.02647%0.08903.5%Left instale gyrus0.02647%0.08933.1%Left middle temporal gyrus, anterior0.03581.5%0.10273.8%Left middle temporal gyrus, anterior0.03582.0%0.11354.1%Left middle temporal gyrus, streinor0.01255%0.10213.3%Left middle temporal gyrus, posterior0.01255%0.10213.2%Left middle temporal gyrus, posterior0.01255%0.10213.2%Left middle temporal gyrus, posterior0.01265%0.02812.2%<	Right inferior frontal gyrus, pars triangularis	0.0537	7%	0.1098	39%
Right inferior temporal gyrus, spoterior         0.0312         10%         0.0892         26%           Left inferior temporal gyrus, posterior         0.0270         10%         0.1040         35%           Right inferior temporal gyrus, temporooccipital         0.0280         5%         0.0884         33%           Left inferior temporal gyrus, temporooccipital         0.0280         5%         0.0884         33%           Left insular cortex         0.0221         2%         0.1060         31%           Left insular cortex         0.0454         16%         0.1090         33%           Right intracalcarine cortex         0.0153         2%         0.1090         33%           Right intracalcarine cortex, inferior         0.0124         9%         0.0906         22%           Right interaclocipital cortex, inferior         0.0204         4%         0.1060         41%           Right interaclocipital cortex, superior         0.0130         1%         0.0986         33%           Right indiag gyrus         0.0264         7%         0.0283         31%           Left middle frontal gyrus, superior         0.0197         9%         0.1206         46%           Left middle temopal gyrus, superior         0.0125         5%         0.1025	Left inferior temporal gyrus, anterior	0.0626	23%	0.0996	30%
Left Inferior temporal gyrus, posterior         0.0353         12%         0.0981         28%           Right inferior temporal gyrus, posterior         0.0270         10%         0.1040         53%           Left inferior temporal gyrus, posterior         0.0280         5%         0.0084         33%           Left insular cortex         0.0221         2%         0.1142         37%           Right inferior temporal gyrus, posterior         0.0106         31%         16%         0.1000         33%           Left insular cortex         0.0454         16%         0.1000         33%           Right inferior cortex         0.0174         15%         0.0944         27%           Left lateral occipital cortex, superior         0.0124         9%         0.0996         32%           Left lateral occipital cortex, superior         0.0204         4%         0.0980         33%           Left inguita gyrus         0.0264         7%         0.0893         31%           Left middle temporal gyrus, anterior         0.0385         15%         0.1026         44%           Left middle temporal gyrus, anterior         0.0197         2%         0.1031         30%           Left middle temporal gyrus, posterior         0.0197         2% <td0< td=""><td>Right inferior temporal gyrus, anterior</td><td>0.0312</td><td>10%</td><td>0.0892</td><td>26%</td></td0<>	Right inferior temporal gyrus, anterior	0.0312	10%	0.0892	26%
Right inferior temporal gyrus, protoroccipial         0.0270         10%         0.0400         35%           Right inferior temporal gyrus, temporoccipial         0.0260         5%         0.0894         33%           Right inferior temporal gyrus, temporoccipial         0.0221         2%         0.0106         31%           Right inferior cortex         0.0238         7%         0.1066         31%           Left instal cortex         0.0454         16%         0.0090         30%           Left intracalcarine cortex         0.0153         2%         0.0096         32%           Right intracalcarine cortex, inferior         0.0124         9%         0.0944         27%           Right lateral occipital cortex, superior         0.0133         1%         0.0981         31%           Right ingal gyrus         0.0264         7%         0.0893         31%           Left indiad cristal cortex, superior         0.01369         9%         0.1202         41%           Right indiad gyrus         0.0264         7%         0.0893         31%           Left middle frontal gyrus         0.0167         6%         0.1206         46%           Left middle frontal gyrus, susterior         0.0125         5%         0.1206         46%	Left Inferior temporal gyrus, posterior	0.0353	12%	0.0981	28%
Lett interior temporal gyrus, temporoaccipital         0.0385         13%         0.1035         27%           Ight inferior temporal gyrus, temporoaccipital         0.020         5%         0.0894         33%           Left insular cortex         0.021         2%         0.1142         37%           Ight insular cortex         0.0454         16%         0.1030         33%           Left intracalcarine cortex         0.0454         16%         0.1030         33%           Left intracalcarine cortex, inferior         0.0174         1%         0.0944         27%           Right intracalcarine cortex, inferior         0.0204         9%         0.0906         32%           Left lateral occipital cortex, superior         0.0204         4%         0.1060         41%           Right infigital gyrus         0.0369         9%         0.0890         35%           Left middle frontal gyrus         0.0264         7%         0.0893         31%           Left middle frontal gyrus         0.0076         0%         0.1206         46%           Left middle frontal gyrus, anterior         0.0355         5%         0.1057         33%           Left middle temporal gyrus, posterior         0.0173         4%         0.1012         36%	Right inferior temporal gyrus, posterior	0.0270	10%	0.1040	35%
Right interior temporal gyrus, temporoccipital         0.0260         5%         0.0894         33%           Right insular cortex         0.0221         2%         0.1106         31%           Right insular cortex         0.0258         7%         0.1006         33%           Right intracalcarine cortex         0.0153         2%         0.1009         33%           Right intracalcarine cortex, sinerior         0.0174         1%         0.0906         32%           Left lateral occipital cortex, sinerior         0.0224         9%         0.0906         32%           Left lateral occipital cortex, sinerior         0.0224         9%         0.0980         35%           Left insular cortical cortex, sinerior         0.0264         7%         0.0880         35%           Left middle frontal gyrus         0.0264         7%         0.0890         35%           Left middle temporal gyrus, anterior         0.0285         15%         0.1027         38%           Left middle temporal gyrus, posterior         0.0197         2%         0.1037         30%           Left middle temporal gyrus, posterior         0.0197         2%         0.1013         30%           Left middle temporal gyrus, posterior         0.0197         2%         0.1013 <td>Left inferior temporal gyrus, temporooccipital</td> <td>0.0385</td> <td>13%</td> <td>0.1035</td> <td>27%</td>	Left inferior temporal gyrus, temporooccipital	0.0385	13%	0.1035	27%
Left insular cortex         0.0221         2%         0.1142         37%           kiph insular cortex         0.0258         7%         0.1006         31%           Left intracalcarine cortex         0.0153         2%         0.1009         30%           Left lateral occipital cortex, inferior         0.0174         1%         0.0904         27%           Right intracalcarine cortex, inferior         0.0224         9%         0.0906         32%           Left lateral occipital cortex, superior         0.0133         1%         0.0981         31%           Left hareal occipital cortex, superior         0.0139         1%         0.0980         35%           Right Ingual gyrus         0.0264         7%         0.0893         31%           Left middle frontal gyrus         0.0076         0%         0.1202         41%           Right middle temporal gyrus, anterior         0.0138         20%         0.1205         41%           Right middle temporal gyrus, superior         0.0125         5%         0.1013         30%           Left middle frontal gyrus         0.0197         2%         0.1013         30%           Left middle temporal gyrus, posterior         0.0197         4%         0.1050         32%	Right inferior temporal gyrus, temporooccipital	0.0260	5%	0.0894	33%
Ngmt insluid cortex         0.0258         75         0.1006         312           Left intracalcarine cortex         0.0153         2.%         0.1009         30%           Right intracalcarine cortex         0.0174         1%         0.0944         2.7%           Right lateral occipital cortex, inferior         0.0224         9%         0.0906         32%           Left lateral occipital cortex, superior         0.0204         4%         0.0600         41%           Left lateral occipital cortex, superior         0.0193         1%         0.0981         31%           Left intradicarine cortex         0.0197         9%         0.0980         35%           Left intradicarine cortex         0.0197         9%         0.1202         41%           Kight middle frontal gyrus         0.0076         0%         0.1206         46%           Left middle temporal gyrus, anterior         0.0385         15%         0.1077         38%           Left middle temporal gyrus, posterior         0.0125         5%         0.1050         32%           Left middle temporal gyrus, posterior         0.0173         4%         0.1027         38%           Left middle temporal gyrus, posterior         0.0173         0.0866         26%	Left insular cortex	0.0221	2%	0.1142	37%
Left mitracacarine cortex         00494         10%         0.1030         33%           Left lateral occipital cortex, inferior         0.0153         2%         0.1090         30%           Left lateral occipital cortex, inferior         0.0224         9%         0.09066         32%           Left lateral occipital cortex, superior         0.0193         1%         0.0981         31%           Left lateral occipital cortex, superior         0.0369         9%         0.0980         35%           Left ingual gyrus         0.0369         9%         0.0893         31%           Left middle frontal gyrus         0.0137         9%         0.1202         41%           Right middle frontal gyrus, anterior         0.0385         15%         0.1027         38%           Left middle temporal gyrus, anterior         0.0135         15%         0.1027         38%           Left middle temporal gyrus, suterior         0.0132         30%         0.4068         30%           Left middle temporal gyrus, suterior         0.0133         0%         0.1027         38%           Left middle temporal gyrus, temporoccipital         0.0173         4%         0.102         36%           Left middle temporal gyrus, anterior         0.0132         0.41%         <	Right insular cortex	0.0258	1%	0.1006	31%
Nght Initadiatanine Cottex         0.0133         2.6         0.1009         30.6           Left lateral occipital cortex, inferior         0.0174         1%         0.0906         32%           Right lateral occipital cortex, superior         0.0193         1%         0.0981         31%           Right lateral occipital cortex, superior         0.0193         1%         0.0981         31%           Left instand occipital cortex, superior         0.0193         1%         0.0980         35%           Right ingual gyrus         0.0264         7%         0.0893         31%           Left middle frontal gyrus, anterior         0.0076         0%         0.1206         46%           Left middle temporal gyrus, anterior         0.0175         5%         0.1027         38%           Left middle temporal gyrus, posterior         0.0125         5%         0.1050         32%           Right middle temporal gyrus, posterior         0.0133         0%         0.0951         28%           Left middle temporal gyrus, temporoccipital         0.0133         0%         0.0951         28%           Right noidiel temporal gyrus, temporoccipital         0.0133         0%         0.0951         28%           Right pracingulate gyrus         0.0408         11% <td>Left Intracalcarine cortex</td> <td>0.0454</td> <td>16%</td> <td>0.1030</td> <td>33%</td>	Left Intracalcarine cortex	0.0454	16%	0.1030	33%
Left lateral occipital cortex, inferior       0.0174       1.8       0.0994       27.8         Left lateral occipital cortex, superior       0.0224       9%       0.0906       32%         Left lateral occipital cortex, superior       0.0224       4%       0.09981       31%         Left literal occipital cortex, superior       0.0193       1%       0.0981       31%         Left ingual gyrus       0.0369       9%       0.0893       31%         Left middle frontal gyrus       0.0197       9%       0.1202       41%         Right middle frontal gyrus, anterior       0.0385       15%       0.1027       38%         Left middle temporal gyrus, anterior       0.0197       2%       0.1013       30%         Left middle temporal gyrus, anterior       0.0133       0%       0.0951       22%         Right middle temporal gyrus, superior       0.0173       4%       0.1012       36%         Left middle temporal gyrus, temporoccipital       0.0173       4%       0.0951       28%         Left occipital fusiform gyrus       0.0483       15%       0.0866       26%         Left occipital pole       0.0242       6%       0.0978       28%         Left occipital pole       0.0242       6%	Right Intracalcarine cortex	0.0153	2%	0.1009	30%
Nght atterat occipital cortex, superior         0.0224         9A         0.0900         52A           Left lateral occipital cortex, superior         0.0193         1%         0.0981         31%           Left ingual gyrus         0.0264         7%         0.0893         31%           Left ingual gyrus         0.0197         9%         0.02980         35%           Right riddle frontal gyrus         0.0197         9%         0.1206         46%           Left middle frontal gyrus, anterior         0.00588         20%         0.1135         41%           Right middle temporal gyrus, anterior         0.0185         15%         0.1027         38%           Left middle temporal gyrus, sosterior         0.0125         5%         0.1013         30%           Left middle temporal gyrus, posterior         0.0133         0%         0.0988         28%           Left occipital fusiform gyrus         0.0408         11%         0.0888         28%           Left occipital fusiform gyrus         0.0408         11%         0.0888         28%           Left occipital fusiform gyrus         0.0408         11%         0.0933         31%           Left occipital fusiform gyrus         0.0408         11%         0.0943         31% <td>Right lateral occipital cortex, inferior</td> <td>0.0174</td> <td>1/6</td> <td>0.0944</td> <td>21/6</td>	Right lateral occipital cortex, inferior	0.0174	1/6	0.0944	21/6
Left and corpital cortex, superior         0.0193         1%         0.0980         31%           Left lingual gyrus         0.0369         9%         0.0980         35%           Left lingual gyrus         0.0369         9%         0.0980         35%           Right lingual gyrus         0.0076         7%         0.0893         31%           Left middle frontal gyrus         0.0076         0%         0.1206         46%           Left middle temporal gyrus, anterior         0.0385         15%         0.1027         38%           Left middle temporal gyrus, posterior         0.0125         5%         0.1050         32%           Right middle temporal gyrus, posterior         0.0173         4%         0.1102         36%           Right middle temporal gyrus, temporococipital         0.0173         4%         0.1013         30%           Left oxcipital fusiform gyrus         0.0483         15%         0.0866         26%           Right orcipital pole         0.0214         6%         0.0951         28%           Left oxcipital fusiform gyrus         0.0408         11%         0.0888         28%           Right paracingulate gyrus         0.0208         2%         0.132         31%           Left oxcip	Loft lateral occipital cortex, interior	0.0224	5%	0.0900	JZ/0 /19/
Inglin lateral occupital control         Doll 35         1 /8         Dolbain         5 /8           Left lingual gyrus         0.0264         7%         0.0893         31%           Left middle frontal gyrus         0.0076         0%         0.1202         41%           Right middle frontal gyrus, anterior         0.0658         20%         0.1105         41%           Right middle temporal gyrus, anterior         0.0385         15%         0.1027         38%           Left middle temporal gyrus, posterior         0.0125         5%         0.1013         30%           Left middle temporal gyrus, posterior         0.0133         0%         0.0951         28%           Left cocipital fusiform gyrus         0.0408         11%         0.0886         26%           Right middle temporal gyrus, temporooccipital         0.0133         0%         0.0978         28%           Left occipital fusiform gyrus         0.0408         11%         0.0886         26%           Right occipital pole         0.0184         2%         0.0943         31%           Left paracingulate gyrus         0.00067         21%         0.1020         29%           Right paracingulate gyrus         0.00667         21%         0.1020         29%	Right lateral occipital cortex, superior	0.0204	1%	0.0081	21%
Lith mignal grus         0.000         0.000         0.0000         0.0000           Left middle frontal grus         0.0197         9%         0.1202         41%           Left middle frontal grus         0.0076         0%         0.1206         46%           Left middle temporal grus, anterior         0.0658         20%         0.1135         41%           Right middle temporal grus, posterior         0.0197         2%         0.1007         38%           Left middle temporal grus, posterior         0.0197         2%         0.1013         30%           Left middle temporal grus, temporoccipital         0.0173         4%         0.1012         36%           Right middle temporal grus, temporoccipital         0.0133         0%         0.0951         28%           Left occipital fusiform grus         0.0483         15%         0.0866         26%           Right middle temporal grus, temporoccipital         0.0184         2%         0.0978         28%           Left occipital pole         0.0242         6%         0.0978         28%           Left paracingulate grus         0.0208         2%         0.1382         51%           Left paracingulate grus         0.0208         2%         0.1382         51% <t< td=""><td>Left lingual ovrus</td><td>0.0369</td><td>9%</td><td>0.0980</td><td>35%</td></t<>	Left lingual ovrus	0.0369	9%	0.0980	35%
Left middle frontal gyrus         0.007         9%         0.1202         41%           Right middle frontal gyrus         0.0076         0%         0.1206         46%           Left middle temporal gyrus, anterior         0.0385         15%         0.1027         38%           Left middle temporal gyrus, posterior         0.0125         5%         0.1030         32%           Right middle temporal gyrus, posterior         0.0197         2%         0.1013         30%           Left middle temporal gyrus, posterior         0.0197         2%         0.1013         30%           Left middle temporal gyrus, posterior         0.0173         4%         0.1102         36%           Right middle temporal gyrus, temporooccipital         0.0173         4%         0.010866         26%           Right occipital fusiform gyrus         0.0408         11%         0.0888         28%           Left occipital pole         0.0124         6%         0.0978         28%           Left pallidum         0.2134         100%         0.1123         41%           Left paracingulate gyrus         0.0208         2%         0.1382         51%           Right paracingulate gyrus         0.0208         2%         0.1206         29%	Right lingual gyrus	0.0264	7%	0.0893	31%
Right middle frontal gyrus       00076       0%       0.1206       46%         Left middle temporal gyrus, anterior       0.0558       20%       0.1135       41%         Right middle temporal gyrus, posterior       0.0125       5%       0.1027       38%         Left middle temporal gyrus, posterior       0.0125       5%       0.1050       32%         Right middle temporal gyrus, posterior       0.0197       2%       0.1013       30%         Left middle temporal gyrus, temporoccipital       0.0173       4%       0.1102       36%         Right middle temporal gyrus, temporoccipital       0.0133       0%       0.0951       28%         Left orcipital fusiform gyrus       0.0483       15%       0.0866       26%         Right occipital fusiform gyrus       0.0448       11%       0.0888       28%         Left occipital pole       0.0242       6%       0.0978       28%         Left pallidum       0.2134       100%       0.1123       41%         Right paracingulate gyrus       0.0109       0%       0.1208       51%         Left paratingulate gyrus       0.0109       0%       0.1200       29%         Right paracingulate gyrus       0.0667       21%       0.1020       <	Left middle frontal gyrus	0.0197	9%	0.1202	41%
Left middle temporal gyrus, anterior       0.0658       20%       0.1135       41%         Right middle temporal gyrus, noterior       0.0385       15%       0.1027       38%         Left middle temporal gyrus, posterior       0.0125       5%       0.1050       32%         Right middle temporal gyrus, posterior       0.0197       2%       0.1013       30%         Left middle temporal gyrus, temporooccipital       0.0173       4%       0.1102       36%         Right middle temporal gyrus, temporooccipital       0.0133       0%       0.0951       28%         Left occipital fusiform gyrus       0.0483       15%       0.0866       26%         Right occipital pole       0.0242       6%       0.0978       28%         Left occipital pole       0.0184       2%       0.0943       31%         Left pallidum       0.2134       100%       0.1123       41%         Right occipital pole       0.0109       0%       0.1208       51%         Right paracingulate gyrus       0.00667       21%       0.1020       29%         Right parahippocampal gyrus, anterior       0.0667       21%       0.1027       39%         Left parahippocampal gyrus, posterior       0.0598       23%       0.108	Right middle frontal gyrus	0.0076	0%	0.1206	46%
Right middle temporal gyrus, anterior       0.0385       15%       0.1027       38%         Left middle temporal gyrus, posterior       0.0125       5%       0.1050       32%         Right middle temporal gyrus, posterior       0.0197       2%       0.1013       30%         Left middle temporal gyrus, temporooccipital       0.0173       4%       0.1102       36%         Right middle temporal gyrus, temporooccipital       0.0133       0%       0.0951       28%         Left occipital fusiform gyrus       0.0483       15%       0.0866       26%         Left occipital fusiform gyrus       0.0408       11%       0.0888       28%         Left occipital pole       0.0242       6%       0.0978       28%         Left paraingulate gyrus       0.0184       2%       0.0943       31%         Left paraingulate gyrus       0.0208       2%       0.1382       51%         Right paracingulate gyrus       0.0109       0%       0.1210       40%         Left parahippocampal gyrus, anterior       0.0663       24%       0.1067       39%         Left parahippocampal gyrus, posterior       0.0598       23%       0.09915       29%         Left paraihippocampal gyrus, posterior       0.0628       28%	Left middle temporal gyrus, anterior	0.0658	20%	0.1135	41%
Left middle temporal gyrus, posterior       0.0125       5%       0.1050       32%         Right middle temporal gyrus, posterior       0.0197       2%       0.1013       30%         Left middle temporal gyrus, temporoccipital       0.0133       0%       0.0951       28%         Right middle temporal gyrus, temporoccipital       0.0483       15%       0.0866       26%         Right occipital fusiform gyrus       0.0408       11%       0.0888       28%         Left occipital fusiform gyrus       0.0408       11%       0.0888       28%         Left occipital pole       0.0242       6%       0.0978       28%         Right occipital pole       0.0173       90%       0.1208       51%         Left occipital pole       0.0184       2%       0.0943       31%         Left paracingulate gyrus       0.0208       2%       0.1382       51%         Left paratinguotate gyrus       0.0208       2%       0.1382       51%         Left paratinguotate gyrus, anterior       0.0667       21%       0.1020       29%         Right paratinpocampal gyrus, anterior       0.0663       24%       0.1067       39%         Left paratinpocampal gyrus, posterior       0.0598       23%       0.0998<	Right middle temporal gyrus, anterior	0.0385	15%	0.1027	38%
Right middle temporal gyrus, posterior       0.0197       2%       0.1013       30%         Left middle temporal gyrus, temporooccipital       0.0173       4%       0.1102       36%         Right middle temporal gyrus, temporooccipital       0.0133       0%       0.0951       28%         Left occipital fusiform gyrus       0.0483       15%       0.0866       26%         Right occipital fusiform gyrus       0.0408       11%       0.0888       28%         Left occipital pole       0.0242       6%       0.0978       28%         Left occipital pole       0.0242       6%       0.0943       31%         Left pallidum       0.2134       100%       0.1123       41%         Right paracingulate gyrus       0.0208       2%       0.1382       51%         Left paracingulate gyrus       0.01067       21%       0.1020       29%         Left paracingulate gyrus       0.0667       21%       0.1020       29%         Left parahippocampal gyrus, anterior       0.0663       28%       0.0998       30%         Left parahippocampal gyrus, posterior       0.0598       28%       0.0998       30%         Left parietal operculum cortex       0.0181       5%       0.0994       31% <td>Left middle temporal gyrus, posterior</td> <td>0.0125</td> <td>5%</td> <td>0.1050</td> <td>32%</td>	Left middle temporal gyrus, posterior	0.0125	5%	0.1050	32%
Left middle temporal gyrus, temporooccipital       0.0173       4%       0.1102       36%         Right middle temporal gyrus, temporooccipital       0.0133       0%       0.0951       28%         Left occipital fusiform gyrus       0.0483       15%       0.0866       26%         Right occipital fusiform gyrus       0.0408       11%       0.0888       28%         Left occipital pole       0.0242       6%       0.0978       28%         Left pallidum       0.2134       100%       0.1123       41%         Left paracingulate gyrus       0.0208       2%       0.1382       51%         Left paracingulate gyrus       0.00667       21%       0.1020       29%         Right parahippocampal gyrus, anterior       0.0667       21%       0.1089       39%         Left parahippocampal gyrus, posterior       0.0588       23%       0.1089       39%         Right parahippocampal gyrus, posterior       0.0582       28%       0.0915       29%         Right parietal operculum cortex       0.0181       5%       0.0102       35%         Right parietal operculum cortex       0.0181       5%       0.0102       35%         Right parietal operculum cortex       0.0189       37%       0.1002 </td <td>Right middle temporal gyrus, posterior</td> <td>0.0197</td> <td>2%</td> <td>0.1013</td> <td>30%</td>	Right middle temporal gyrus, posterior	0.0197	2%	0.1013	30%
Right middle temporal gyrus, temporooccipital       0.0133       0%       0.0951       28%         Left occipital fusiform gyrus       0.0483       15%       0.0866       26%         Right occipital fusiform gyrus       0.0408       11%       0.0888       28%         Left occipital pole       0.0242       6%       0.0978       28%         Right occipital pole       0.0184       2%       0.0943       31%         Left pallidum       02134       100%       0.1123       41%         Right pallidum       0.1719       90%       0.1208       51%         Left paracingulate gyrus       0.0109       0%       0.1210       40%         Left paracingulate gyrus, anterior       0.0667       21%       0.1020       29%         Right parahippocampal gyrus, anterior       0.0633       24%       0.1067       39%         Left parahippocampal gyrus, posterior       0.0598       23%       0.0998       30%         Left parietal operculum cortex       0.01181       5%       0.0915       29%         Right parietal operculum cortex       0.0180       0%       0.0944       31%         Left parietal operculum cortex       0.0598       24%       0.0996       36%	Left middle temporal gyrus, temporooccipital	0.0173	4%	0.1102	36%
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Left pallidum       0.2134       100%       0.1123       41%         Right pallidum       0.1719       90%       0.1208       51%         Left paracingulate gyrus       0.0208       2%       0.1382       51%         Right paracingulate gyrus       0.0109       0%       0.1200       40%         Left parahippocampal gyrus, anterior       0.0667       21%       0.1020       29%         Right parahippocampal gyrus, anterior       0.0633       24%       0.1067       39%         Left parahippocampal gyrus, posterior       0.0598       23%       0.1089       39%         Right parietial operculum cortex       0.0181       5%       0.0915       29%         Right parietial operculum cortex       0.0108       0%       0.0944       31%         Left planum polare       0.0598       24%       0.0996       36%         Left planum polare       0.0118       5%       0.0915       29%         Right planum polare       0.0598       24%       0.0996       36%         Left planum polare       0.0598       24%       0.0996       36%         Left planum temporale       0.0233       9%       0.1164       40%         Right planum temporale	Right occipital pole	0.0184	2%	0.0943	31%
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Left paracingulate gyrus       0.0208       2%       0.1382       51%         Right paracingulate gyrus       0.0109       0%       0.1210       40%         Left parahippocampal gyrus, anterior       0.0667       21%       0.1020       29%         Right parahippocampal gyrus, posterior       0.0633       24%       0.1067       39%         Left parahippocampal gyrus, posterior       0.0598       23%       0.1089       39%         Right parahippocampal gyrus, posterior       0.0828       28%       0.0998       30%         Left parietal operculum cortex       0.01181       5%       0.0915       29%         Right parietal operculum cortex       0.0108       0%       0.0994       31%         Left planum polare       0.0895       37%       0.1002       35%         Right planum polare       0.0598       24%       0.0996       36%         Left planum temporale       0.0598       24%       0.0996       36%         Left planum polare       0.0233       9%       0.1164       40%         Right planum temporale       0.0307       10%       0.0963       30%         Left postcentral gyrus       0.0164       0%       0.1037       36%	Right pallidum	0.1719	90%	0.1208	51%
Kignt paracingulate gyrus     0.0109     0%     0.1210     40%       Left parahippocampal gyrus, anterior     0.0667     21%     0.1020     29%       Right parahippocampal gyrus, anterior     0.0633     24%     0.1067     39%       Left parahippocampal gyrus, posterior     0.0598     23%     0.1089     39%       Right parahippocampal gyrus, posterior     0.0828     28%     0.0998     30%       Left parietal operculum cortex     0.0108     0%     0.0944     31%       Left planum polare     0.0895     37%     0.1002     35%       Right planum temporale     0.0233     9%     0.1164     40%       Right planum temporale     0.0307     10%     0.0963     30%       Left planum temporale     0.0307     10%     0.0164     30%	Left paracingulate gyrus	0.0208	2%	0.1382	51%
Left parahippocampal gyrus, anterior       0.0667       21%       0.1020       29%         Right parahippocampal gyrus, anterior       0.0633       24%       0.1067       39%         Left parahippocampal gyrus, posterior       0.0598       23%       0.1089       39%         Right parahippocampal gyrus, posterior       0.0628       28%       0.0998       30%         Left parietal operculum cortex       0.0181       5%       0.0915       29%         Right parietal operculum cortex       0.0108       0%       0.0944       31%         Left planum polare       0.0895       37%       0.1002       35%         Right planum polare       0.0598       24%       0.0996       36%         Left planum temporale       0.0233       9%       0.1164       40%         Right planum temporale       0.0307       10%       0.0963       30%         Left postcentral gyrus       0.0164       0%       0.1037       36%	Right paracingulate gyrus	0.0109	0%	0.1210	40%
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Ngin paramper yrds, postrior         U020         25%         0.0996         30%           Left parietal operculum cortex         0.0181         5%         0.0915         29%           Right parietal operculum cortex         0.0108         0%         0.0944         31%           Left planum polare         0.0895         37%         0.1002         35%           Right planum polare         0.0233         9%         0.1164         40%           Right planum temporale         0.0307         10%         0.0963         30%           Left postcentral gyrus         0.0164         0%         0.1037         36%	Right parahippocampal gyrus, posterior	0.0396	23/0 79%	0.1009	20% 23%
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Right planum temporale         0.0307         10%         0.0963         30%           Left postcentral gyrus         0.0164         0%         0.1037         36%	Left planum temporale	0.0233	9%	0.1164	40%
Left postcentral gyrus 0.0164 0% 0.1037 36%	Right planum temporale	0.0307	10%	0.0963	30%
1 00 00 000 000 000 000 000 000 000 000	Left postcentral gyrus	0.0164	0%	0.1037	36%

Table 1 (continued)

Harvard-Oxford cortical and subcortical target masks	DTI connectivity value	% Subjects with DTI connectivity	RS-fMRI connectivity value	% Subjects with RS connectivity
Right postcentral gyrus	0.0187	2%	0.0881	29%
Left precentral gyrus	0.0180	6%	0.1103	33%
Right precentral gyrus	0.0224	9%	0.0980	30%
Left precuneous cortex	0.0196	2%	0.0935	32%
Right precuneous cortex	0.0187	2%	0.0854	28%
Left putamen	0.1663	93%	0.1387	<b>60</b> %
Right putamen	0.1437	84%	0.1453	55%
Left subcallosal cortex	0.0971	<b>52</b> %	0.1249	44%
Right subcallosal cortex	0.1239	56%	0.1092	38%
Left sup frontal gyrus	0.0457	13%	0.1203	39%
Right sup frontal gyrus	0.0257	5%	0.1059	37%
Left superior temporal gyrus, anterior	0.0482	12%	0.0982	28%
Right superior temporal gyrus, anterior	0.0480	9%	0.0898	31%
Left superior parietal lobule	0.0441	16%	0.0787	25%
Right superior parietal lobule	0.0262	5%	0.0797	25%
Left supplementary motor cortex	0.0136	0%	0.0924	33%
Right supplementary motor cortex	0.0120	2%	0.0905	27%
Left supracalcarine cortex	0.0415	11%	0.0793	25%
Right supracalcarine cortex	0.0400	12%	0.0797	25%
Left supramarginal gyrus, anterior	0.0104	0%	0.1032	33%
Right supramarginal gyrus, anterior	0.0143	2%	0.0911	29%
Left supramarginal gyrus, posterior	0.0179	4%	0.1042	33%
Right supramarginal gyrus, posterior	0.0164	2%	0.1066	37%
Left temporal fusiform cortex, anterior	0.0904	22%	0.0826	27%
Right temporal fusiform cortex, anterior	0.1630	29%	0.0958	27%
Left temporal fusiform cortex, posterior	0.0603	13%	0.0930	28%
Right temporal fusiform cortex, posterior	0.0584	22%	0.0950	29%
Left temporal occipital fusiform gyrus	0.0360	12%	0.0888	28%
Right temporal occipital fusiform gyrus	0.0338	11%	0.0834	26%
Left temporal pole	0.1191	60%	0.0995	33%
Right temporal pole	0.0934	40%	0.0952	27%
Left thalamus	0.1233	83%	0.1458	57%
Right thalamus	0.0895	<b>59</b> %	0.1446	<b>63</b> %

The bold values reach the significance criterion (95th percentile) or the % subjects criterion (> 50%).

#### Amygdala subnuclei connectivity

The amygdala is composed of multiple distinct subnuclei, and human imaging studies have confirmed differential patterns of structural and functional connectivity across amygdala subnuclei (Bach et al., 2011; Etkin et al., 2009; Mishra et al., 2013; Roy et al., 2009). Anatomical tracer studies in both rodents and non-human primates have demonstrated that the BNST has different patterns of connectivity with amygdala subnuclei (Coolen and Wood, 1998; Dong et al., 2001a; Price and Amaral, 1981). For example, the BNST has strong, dense connections with the centromedial subnucleus of the amygdala (Price and Amaral, 1981), but weaker, more diffuse connections with other amygdala subnuclei (Dong et al., 2001a). To determine whether the same pattern exists in humans we performed two analyses. Amygdala subnuclei were identified using a probabilistic atlas (Amunts et al., 2005), thresholded at 50% with each voxel assigned to the subnuclei with the greatest probability of membership. Structural and functional connectivity between the left and right BNST and the ipsilateral amygdala subnuclei were calculated. First, we tested whether each subnucleus had a significant likelihood of connectivity using the critical values from the previous bootstrap analyses. Second, we directly tested for differences in the strength of connectivity between the three subnuclei by comparing pairs of subnuclei using permutation t-tests (10,000 permutations,  $\alpha$  = .05). Tests were performed using an in-house script written in R (R Core Development Team, 2008) according to standard methods (Good, 2000).

# Sex differences

The BNST is sexually dimorphic in rodents (Hines et al., 1985, 1992) and may also be dimorphic in humans (Allen and Gorski, 1990; Chung et al., 2002); however, very little research has investigated whether dimorphic differences translate to altered BNST connectivity. Sex differences in structural and functional connectivity were tested using permutation *t*-tests (10,000 permutations,  $\alpha = .05$ ). To minimize the potential for type I error due to multiple testing, analyses were restricted to the regions that were identified as having as significant probability of being connected with the BNST in the previous structural and functional analyses.

# Results

#### Structural and functional connectivity of the BNST

Of the 108 target regions tested using structural connectivity, 17 regions showed significant likelihood of structural connectivity with the BNST (Figs. 4A, C). As expected, these included several regions of the basal ganglia (accumbens, caudate, putamen, and pallidum), limbic system (amygdala, subcallosal cortex, and hippocampus), and thalamus, indicating evolutionarily-conserved connections across species. We also identified a connection with the temporal pole which has not been previously described in rodents.

Of the 108 target regions tested using functional connectivity, 11 regions showed significant likelihood of functional connectivity with the BNST (Figs. 4B, D). These included several regions of the basal ganglia (accumbens, caudate, putamen, and pallidum), limbic system (hippocampus), and thalamus, replicating findings using anatomic tracer studies in rodents as well as our DTI findings. Functional connectivity identified one novel target region of the BNST, the paracingulate gyrus.

In order to further explore functional connectivity patterns across the entire brain, we conducted a post-hoc voxel-wise functional connectivity analysis. The findings from the whole-brain functional connectivity analysis were consistent with the results from the target region analysis. Significant BNST connectivity was observed with the basal ganglia, hippocampus, thalamus, and paracingulate gyrus. The whole-brain approach also identified some additional regions not shown in the target region approach, including other limbic regions (amygdala,



**Fig. 4.** Structural and functional connectivity of the bed nucleus of the stria terminalis (BNST) in the human brain. Voxel-wise connectivity maps shown on a template brain illustrate spatial patterns of structural (A) and functional connectivity (B) within regions identified as having significant likelihood of connectivity with the BNST. Color bars indicate strength of connectivity with lighter colors representing stronger connectivity. Using DTI (n = 82) and rs-fMRI (n = 99) to assess structural and functional BNST connectivity, respectively, a varied pattern of BNST spatial connectivity is demonstrated within each larger target region. Bar graphs show mean connectivity values by region for structural (C) and functional (D) analyses, with error bars representing the standard error of the mean. The vertical dotted line indicates the threshold of significant likelihood of connectivity as determined using bootstrap methods (10,000 permutations, >95% confidence interval of the mean). Target regions were determined to have a significant likelihood of connectivity values passed the threshold for significance (structural connectivity >.077, functional connectivity >.117), and 2) at least 50% of individual connectivity values passed the threshold for significant functional connectivity (C) and 11 regions passed both threshold criteria for significant structural connectivity (C) and 11 regions passed both threshold criteria for significant functional connectivity (D). Note: \*Amygdala = positive control region in the structural connectivity analysis; \*\* Middle frontal gyrus = negative control region in the structural connectivity analysis;

subcallosal cortex, parahippocampal gyrus, and anterior insula), prefrontal cortex regions (anterior cingulate cortex, medial frontal gyrus, superior frontal gyrus, inferior frontal gyrus, and middle frontal gyrus), posterior cingulate cortex, calcarine fissure, precuneus, and precentral gyrus (Fig. 5).

# Spatial pattern of connectivity

Next, because target regions were relatively large and distinct patterns of connectivity may exist within each region, we explored the spatial pattern of BNST connectivity by performing post-hoc



Fig. 5. Exploratory voxel-wise functional connectivity findings. The results of this voxel-wise analysis were consistent with the results from the target region analysis, identifying large clusters within each of the significant target regions. The voxel-wise analysis also revealed significant functional connectivity within regions which were not identified using the target region approach, including limbic regions (amygdala, subcallosal cortex, parahippocampal gyrus, and anterior insula), prefrontal cortex regions (anterior cingulate cortex, medial frontal gyrus, superior frontal gyrus, inferior frontal gyrus, and middle frontal gyrus), posterior cingulate cortex, calcarine fissure, precuneus, and precentral gyrus.

analyses within each of the significant target regions. Each target region showed a distinct spatial pattern of structural connectivity with the BNST, ranging from low to high connectivity (Fig. 4A). Functional connectivity also showed a distinct spatial pattern of connectivity within each target region (Fig. 4B). Several regions showed a similar spatial pattern of connectivity across both structural and functional analyses; for example, the head of the caudate and the medial thalamus showed stronger structural and functional connectivity than the tail of the caudate and the lateral thalamus, respectively.

Amygdala subnuclei-structural and functional connectivity

In rodents, the BNST is differentially connected with the subnuclei of the amygdala (Coolen and Wood, 1998; Dong et al., 2001a; Price and



**Fig. 6.** Differential structural and functional connectivity of amygdala subnuclei. An illustration of the three amygdala subnuclei is shown on a template brain in coronal, sagittal, and axial slices (A). Bar graphs show strength of structural (B, left) and functional (B, right) bed nucleus of the stria terminalis (BNST) connectivity by amygdala subnuclei, with error bars representing the standard error of the mean. The centromedial amygdala had greater structural connectivity with the BNST compared to both the laterobasal and superficial subnuclei (p's < .001) (B, left). BNST functional connectivity was greater for the left and right superficial subnuclei, compared with the left and right laterobasal subnuclei (left: p < .001, right: p = .002) and the left centromedial subnucleis (p = .026) (B, right).

Amaral, 1981); therefore we identified which subnuclei showed evidence for connectivity and directly tested for differences in connectivity across the three subnuclei (centromedial, superficial, and laterobasal). All three subnuclei had a significant likelihood of structural connectivity and the centromedial and superficial subnuclei also had a significant likelihood of functional connectivity. Directly testing for differences in strength of structural connectivity revealed that BNST structural connectivity was significantly greater for the centromedial amygdala (Fig. 6), compared to both the basolateral and superficial subnuclei, consistent with anatomical tracer studies. BNST functional connectivity was significantly greater for the left and right superficial subnucleus, compared with the left and right laterobasal subnucleus and the left centromedial subnucleus. The centromedial nucleus trended towards significantly greater connectivity than the laterobasal in the right hemisphere.

### Sex differences

Across species, the BNST has sexually dimorphic regions which are larger in males than females (Allen and Gorski, 1990; Chung et al., 2002; Hines et al., 1985, 1992). However, the implications of larger volume for connectivity in humans are unknown. We tested for sex differences in structural and functional connectivity in the regions that showed significant connectivity with the BNST. For structural connectivity, 76% of the regions had greater connectivity in females (Table 2). In contrast, for functional connectivity, the left putamen had greater connectivity in males than females, and the right thalamus had significantly greater connectivity in females than males. Because differences in motion could have contributed to the observed sex differences, we compared the two groups on six motion parameters. Males and females had similar motion for both the DTI and rs-fMRI scans (all p > .10).

Table 2	
Sex differences in structural and functional connectivity.	

	Male mean (SD)	Female mean (SD)	p-value			
Structural connectivity target region						
Left accumbens	.35 (.14)	.51 (.18)	<.001			
Right accumbens	.28 (.14)	.41 (.25)	.005			
Left amygdala	.34 (.15)	.44 (.23)	.020			
Right amygdala	.22 (.10)	.34 (.19)	.001			
Left hippocampus	.20 (.15)	.30 (.21)	.027			
Right hippocampus	.21 (.16)	.30 (.17)	.013			
Left pallidum	.19 (.08)	.25 (.25)	.004			
Right pallidum	.15 (.06)	.20 (.08)	.002			
Left caudate	.18 (.05)	.23 (.06)	.001			
Right caudate	.10 (.03)	.12 (.03)	.002			
Left putamen	.14 (.05)	.19 (.09)	.002			
Right putamen	.12 (.05)	.17 (.07)	<.001			
Left thalamus	.12 (.04)	.13 (.05)	.088			
Right thalamus	.08 (.02)	.10 (.04)	.062			
Left temporal pole	.11 (.08)	.13 (.09)	.283			
Left subcallosal cortex	.08 (.07)	.12 (.09)	.045			
Right subcallosal cortex	.10 (.09)	.15 (.12)	.065			
Functional connectivity target region						
Left accumbens	.26 (.14)	.24 (.18)	.413			
Right accumbens	.23 (.16)	.25 (.15)	.715			
Left caudate	.25 (.10)	.27 (.15)	.424			
Right caudate	.26 (.14)	.25 (.15)	.747			
Left hippocampus	.13 (.06)	.13 (.08)	.738			
Right pallidum	.13 (.07)	.11 (.08)	.284			
Left paracingulate gyrus	.14 (.09)	.14 (.10)	.996			
Left putamen	.16 (.08)	.12 (.08)	.032			
Right putamen	.13 (.08)	.16 (.10)	.182			
Left thalamus	.14 (.07)	.15 (.09)	.509			
Right thalamus	.13 (.06)	.16 (.09)	.047			

The bold values indicate regions with significant differences.

#### Discussion

The goal of this study was to describe the structural and functional connectivity of the BNST in humans. Using DTI and rs-fMRI, we provide a preliminary characterization of human BNST neurocircuitry. The BNST was structurally and functionally connected with multiple subcortical regions, including limbic, thalamic, and basal ganglia structures, replicating structural findings in rodents (Dong and Swanson, 2004a, 2006a; Dong et al., 2001b). We also identified two novel connections that have not been previously reported in rodents or non-human primates; the BNST was structurally connected with the temporal pole and was functionally connected with the paracingulate gyrus. The identification of BNST circuitry lays a critical foundation for future studies investigating the neural circuits mediating anxiety and addiction in humans.

Structural and functional findings showed convergence in the accumbens, thalamus, hippocampus, pallidum, caudate, and putamen. This convergence is consistent with previous studies showing that white matter tracts connect commonly identified resting state functional networks (Greicius et al., 2009; Hagmann et al., 2008; van den Heuvel et al., 2009). Given both structural and functional evidence for connectivity, we propose that these regions form the key nodes of a BNST circuit in humans. However, there were also regions that did not show convergence across the connectivity analyses. For example, the amygdala and subcallosal cortex regions showed significant structural, but not functional, connectivity in the primary target region analysis. One possibility for the difference in findings is the conservative statistical approach used to determine connectivity, which required that average connectivity value reach a specific threshold and that at least half of the participants' values also reach that threshold. Both the amygdala and subcallosal cortex met the first criterion, based on average values, but fell just short of the participant-specific criterion (see Table 1); both regions also had clusters with significant connectivity in the exploratory voxel-wise analysis. Another possibility is that functional connections between some regions may be best observed under conditions of stress or anxiety. For example, a recent study in rodents illustrated that the effects of severing structural connections between the BNST and amygdala were only observable following administration of an anxiogenic drug and were not observable at baseline (Cai et al., 2012). Finally, it is possible that some of the observed structural connections may not reflect glutamateric projections but may instead reflect increased GABA projections, which have an unclear effect on fMRI signal (Arthurs and Boniface, 2002).

One of the best-established connections of the BNST is with the central nucleus of the amygdala (CeA). Structural connections have been well-described in both rodents and non-human primates (Coolen and Wood, 1998; Decampo and Fudge, 2013; Dong et al., 2001a; Price and Amaral, 1981). Although a description of structural connections is currently lacking in humans, functional connectivity was recently demonstrated using rs-fMRI (Oler et al., 2012). Here, we confirm those findings and also provide evidence of structural connections between the CeA and BNST in humans. Furthermore, we show that BNST structural connections with the CeA are stronger than connections with the superficial and basolateral nuclei, although we find evidence for structural connectivity across all three subnuclei, similar to non-human primates (Decampo and Fudge, 2013). The lower levels of structural connectivity in the superficial and basolateral subnuclei likely contributed to the amygdala showing the second highest strength of connectivity with the BNST, instead of the first. The distinct pattern of connectivity across amygdala subnuclei has been well-established and may suggest that these subnuclei should be examined separately. We also extended the findings from the previous study by showing functional connectivity between the BNST and the superficial subnucleus of the amygdala. Given that the BOLD signal reflects inputs to a region as well as local processing (Logothetis and Wandell, 2004), the functional connectivity

may reflect connectivity among the amygdala subnuclei in addition to BNST-amygdala connectivity.

While the BNST-amygdala relationship often receives the most attention, the accumbens is also considered to be a part of the 'extended amygdala', a cluster of nuclei that includes the central nucleus of the amygdala, the BNST, and the accumbens (Alheid and Heimer, 1988). In the present study, the BNST-accumbens connection was the strongest structural connection and second strongest functional connection. The structural finding is consistent with anatomical tracer studies in rodents that also show strong structural connectivity (Dong and Swanson, 2004b; Wood and Swann, 2005); however, evidence for the functional role of that connection is lacking. The link between the BNST and accumbens is especially exciting given that both structures have a prominent role in addiction neurocircuitry (Koob and Volkow, 2010).

Of interest, there were two regions that showed BNST connectivity in humans that have not been described in rodents or primatesthe temporal pole and the paracingulate gyrus. The temporal pole is a paralimbic region that has bidirectional connections with the basomedial forebrain (Olson et al., 2007). In humans, the medial portion of the temporal pole-the area which showed highest BNST connectivity in our spatial analysis—is akin to the agranular insular cortex in rodents, which has strong connections with the BNST (Reynolds and Zahm, 2005). The paracingulate gyrus showed functional connectivity with the BNST. This finding is intriguing in light of growing evidence that the prefrontal cortex figures prominently in anxiety and addiction disorders (Davidson and Irwin, 1999; Etkin, 2010; Goldstein et al., 2002; Kim et al., 2011; Koob and Volkow, 2010; Shin and Liberzon, 2010). However, the paracingulate gyrus was not structurally connected to the BNST, consistent with previous findings that functional connectivity is not constrained by structural paths (Honey et al., 2009; Koch et al., 2002). Given the lack of direct structural connections, it is likely that the functional connectivity between the BNST and paracingulate gyrus is indirect and transmitted through other brain regions, such as the subcallosal cortex. While these novel connections are intriguing, cautious interpretation is recommended until they are replicated.

Sexually dimorphic brain regions are of special interest given sex differences in the prevalence of anxiety disorders (Lewinsohn et al., 1998; McLean et al., 2011) and addiction (Becker and Hu, 2008). Indeed in rodents, the BNST has been proposed to play an important role in gender-dependent effects of stress on learning (Bangasser, 2013). In the present study we identified several gender differences in BNST structural connectivity, with greater connectivity in females. In contrast, there were few differences in functional connectivity. As described earlier, there are several possible explanations for the differences between the structural and functional findings including the role of context (i.e., resting state vs. anxiety task), and the fact that structural connections may reflect increased GABA projections (Polston et al., 2004), which have an unclear effect on fMRI signal (Arthurs and Boniface, 2002).

This study has several limitations which may be addressed in future research. First, we used a single BNST mask, based on a male participant, for all participants. The use of a single region of interest mask is common in DTI and resting state analyses (Amunts et al., 2005), even for sexually dimorphic brain regions such as the amygdala (Lombardo et al., 2012). This approach allowed us to standardize our analysis across individuals; however, the approach may lack sensitivity to individual differences in anatomy. Although it was not possible to exactly identify the BNST on the T1W structural images, we were able to check the placement of the BNST mask using several anatomical landmarks that are visible on the T1W. One possible implication of using a single mask is that some individuals may have voxels outside of the mask that are truly part of the BNST and other individuals may have voxels inside the mask that are not truly part of the BNST. The implication for either of these cases is decreased power to detect true BNST connections; therefore, the results presented here should be considered preliminary and possibly conservative. Future studies should use the high contrast provided by

the GRASE sequence and the high resolution provided by the 7 T MRI to create a probabilistic atlas of the BNST across a wide range of individuals. Second, we used an MRI atlas (Harvard-Oxford) for our target regions. This atlas does not contain masks for a number of small structures which have been shown to be connected to the BNST in rodents, such as the hypothalamus, substantia nigra, and substantia innominata. Third, DTI studies are susceptible to a proximity bias, whereby there is a greater likelihood to detect connections with more proximal regions. We reduced the likelihood of this bias using a distance correction. Furthermore, although we did observe connectivity with multiple proximal regions, these regions (i.e. accumbens, caudate, putamen, and thalamus) have also been detected in vivo with anatomical tracer studies and in the functional connectivity analysis, which does not suffer from proximity bias. Also, other proximal regions which do not show connectivity with tracer studies also did not show connectivity here (e.g., cingulate gyrus). Fourth, for this initial study of BNST connectivity, we used a relatively conservative statistical approach. The combination of stringent statistical thresholds and the use of target regions may have limited our ability to detect regions with moderate or spatially restricted connectivity with the BNST. Future studies will be needed to confirm and extend these findings.

To our knowledge, this is the first study to characterize BNST structural and functional connectivity in humans. Given the key role that the BNST plays in anxiety and addictive disorders, these results lay the foundation for future studies of psychiatric illness.

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# **Conflict of interest statement**

The authors declare no competing financial interests.

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