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Date

Psychosocial Personality Measures and their Relation to the Social Brain Hypothesis: a DTI and VBM Study

by

Stephen Andrew Lapierre

Adviser

Dr. James K. Rilling

Department of

Anthropology

Dr. James K. Rilling

_____

Dr. Melvin Konner

_____

Dr. Hiram Maxim

_____

4/14/2010

_____

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An abstract of
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Abstract

Psychosocial Personality Measures and their Relation to the Social Brain

Hypothesis: a DTI and VBM Study

By Stephen Andrew Lapierre

Why do humans have larger brains than their non-human primate cousins? One of the most widely accepted explanations for this perceived difference in cranial capacity between humans and other primates is the Social Brain Hypothesis. This theory posits that as the number of individuals in social groups and the complexity of interactions between these individuals increases, the brain must expand to meet the processing requirements neccesary for maintaining these social relationships. Using diffusion tensor imaging (DTI) and voxel-based morphometry (VBM), this study will test the theoretical plausibility of the Social Brain Hypothesis by measuring differences in gray matter volume and white matter tract integrity throughout the brain.

Psychosocial Personality Measures and their Relation to the Social Brain Hypothesis: a DTI and VBM Study

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Table of Contents

Introduction

If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down.

- Charles Darwin

Human behavior is compelling to study because of complexity in relation to the behavior of most other species, including non-human primates. As a species, humans demonstrate a remarkable capacity for problem solving and innovation which is rarely observed among other animals. These incredible abilities involve abstract reasoning and conscious decision making, which are highly evolved in humans compared to other species (Adolphs 2003). Although humans and non-human primates share a common evolutionary trajectory, and, as is the case with chimpanzees, nearly 98.4% of genetic information (Sibley, Comstock, Ahlquist 1990), the evolution of the human lineage nearly six million years ago (Vigilant et al 1991) signaled marked anatomical and behavioral changes within the primate order. Perhaps the most profound anatomical change during this period was the drastic increase in cranial capacity. By greatly expanding the brain, specifically the neocortex, humans experienced a revolution in thought – they now possessed the neural machinery to plan, coordinate, and execute behaviors which are much more complex than behaviors seen in other species.

However, what exactly does “more complex” behavior entail? Although most people attribute many behaviors to be “uniquely” human, primates do share several behavioral homologues with humans. Several studies (Tomasello et al 2000; Premack & Woodruff 1978) have demonstrated that chimpanzees, the closest genetic relative to humans, demonstrate a rudimentary grasp of understanding the perspective of others in their social groups, a skill which nearly all humans are competent at by the age of 5 or 6 (O’Connell & Dunbar 2003). Additionally, it has been shown that macaques possess “mirror neurons” which fire when an animal performs a behavior or observes that same behavior produced by another animal (Rizzolatti et al 2004). This may form the basis of imitative learning in non-human primates, but it remains unclear whether or not these animals are participating in “true” imitation (Tomasello 1996), where the animal understands how each step in a process yields a certain product or result, or “action level” imitation (Byrne & Russon 1998), where animals merely copy and produce a rote sequence of actions. Additional lines of inquiry tend to suggest that humans are also more capable of manipulating information about individuals in their social groups and are capable of maintaining larger social groups than non-human primates (Dunbar 1998). Thus, is it apparent that while humans and non-human primates demonstrate a capacity for similar behaviors, humans

particularly excel at tasks which involve abstraction and problem solving compared to other primates, particularly in the social domain.

These dissimilarities in behavior between humans and non-human primates may be largely a product of greater neocortical volume in humans relative to non-human primates. Most observable from the intensive study of endocasts, fossilized molds made of dirt and rock which form inside of a skull, the large differences in cranial capacity between humans and other primate species are striking. Endocasts provide scientists and scholars valuable information regarding the general size and structure of an organisms' brain. Evidence from endocasts suggests that *australopithecines*, the first ancestors of modern humans, had a cranial capacity between 400-500 cubic centimeters (cc) (Tobias 1965). This more or less corresponds to the average cranial capacity of modern day chimpanzees (Haug 1987), suggesting that *australopithecines* and chimpanzees possessed similar cognitive abilities.

Homo habilis, the first member of the genus *Homo*, had a cranial capacity of about 600 cubic centimeters (cc) (Leakey 1965), while *Homo erectus*, the predecessor to *Homo habilis*, had a cranial capacity of about 1000 cc (Rightmire 2003). Modern day humans, or *Homo sapiens sapiens*, have a cranial capacity which is about 1350 cc, triple the volume of chimpanzees and *australopithecines*. It is widely

accepted that humans diverged from chimpanzees about six million years ago (Vigilant et al 1991) and that *australopithecines* were extant as long ago as four million years (Leakey et al 1998). This means that humans have experienced a nearly threefold increase in cranial capacity during this four million year period. Considering the brain is among the most metabolically expensive organs to maintain in the body (Aiello & Wheeler 1995), an extremely strong ecological selection pressure must have acted upon the brain to expand rapidly at the onset of the *Homo* lineage.

What selective pressure would cause the human lineage to experience such a sudden increase in cranial capacity over such a short period of evolutionary time? Among the leading theories for explaining this expansion in brain size is the Social Brain Hypothesis. This hypothesis posits that as the number of individuals in human social groups and the complexity of social interactions increases, the brain expanded in volume in order to keep up with the cognitive demands of an increasingly social world (Dunbar 1998). Central to Dunbar's theory is the notion that group size places restriction on neocortex size. The processing capacity of the brain thus reflects the number of individuals a person can maintain an active relationship at any one time, which, for humans, is around 150 individuals. This theory implicates increasing social demands along the human lineage

as the necessary selective pressure for driving the expansion of the neocortex, and, the production of complex, human behaviors.

Several lines of inquiry lend credence to the Social Brain Hypothesis. First, analysis indicates that anthropoid (i.e. prosimians, monkeys, prosimians) primates are grouped into grades when neocortex size is correlated to group size. Apes, have the largest neocortices, followed by monkeys and prosimians, respectively. This suggests that apes have greater ability to understand and manipulate social information compared to monkeys and prosimians. Rates of "tactical deception" (Byrne 1995) among primates have also been shown to correlate positively with neocortex size. Another compelling line of evidence in support of the Social Brain Hypothesis comes from the prolonged juvenile stage in primates compared to other mammalian species. It has been shown in primates that neocortex size in adults correlates positively to the length of adolescence (Joffe 1997). Together, this evidence suggests that increases in social processing capacity in the human lineage necessitated the development of larger neocortices. Thus, the Social Brain Hypothesis offers a viable explanation for the substantial increase in brain size observed in humans compared to non-human primates.

The Social Brain Hypothesis provides a valuable framework for understanding how increased social complexity might have selected

for larger brain size. Individuals who had greater social intelligence than their peers would, in theory, achieve higher reproductive rates, and, as a result, higher levels of fitness. Their genes would survive, gradually increasing neocortical size over vast periods of evolutionary time. Unfortunately, as useful as this paradigm is for speculating about increases in brain size throughout anthropoid evolution, the Social Brain Hypothesis does not provide a working definition for what constitutes social intelligence, in either primates or humans. That is one of the primary aims of this proposal – to define social intelligence through four psycho-social domains. These domains are: empathy, which is the ability to understand the emotions of others; emotion perception, defined as the ability to accurately identify and comprehend physical signals exhibited by conspecifics; emotion regulation, defined as being able to control emotion; and emotional-social intelligence (ESI), which will be used as a general indicator of social competency.

This study will investigate the relationship between these psychosocial domains and neuroanatomical variation in human populations to determine, theoretically speaking, whether or not the Social Brain Hypothesis is plausible. There are four hypothesizes regarding gray matter volume and two involving white matter connectivity. Empathy measures obtained from the Bar-On EQ-i will be

correlated to gray matter volume in the anterior insula and anterior cingulate cortex. Neuroticism scores from the NEO PI-R will be correlated to gray matter volume in the orbitofrontal cortex and amygdalas. Total score on the Bar-On EQ-i will be correlated to gray matter volume in the ventromedial prefrontal cortex, amygdales, insula, and primary somatosensory cortices. Gray matter volume in the amygdala and right superior temporal sulcus will be correlated to total scores on the Reading Mind in the Eyes task. Interpersonal scores on the Bar-On EQ-i will be correlated to gray matter volume in the dorsomedial prefrontal cortex and right temporoparietal junction (TPJ). Additionally, fractional anisotropy (FA) values along the uncinate fasciculus from the amygdala to the orbitofrontal cortex will be correlated to Neuroticism scores on the NEO PI-R. Lastly, FA values along the inferior fronto-occipital fasciculus will be correlated to total score on the Reading Mind in the Eyes task. Understanding how these abilities contribute to social intelligence may provide crucial insight into how natural selection shapes human behavior and how evolutionary processes affect the development of the human brain.

Methods

Data Collection

The data analyzed in this thesis was collected previously as part of a study designed to investigate the neural bases of individual variation in cooperative behavior.

Screening process

All individuals who participated in this study were eighteen to twenty-two year old males currently enrolled as undergraduates in either Emory College or Gouzieta Business School. Upon contacting the lab manager for the Laboratory for Darwinian Neuroscience, potential subjects were emailed a screening form and a consent form. The screening form was used to identify suitable candidates for participation who had no history of mental illness, drug abuse, claustrophobia, or metal implants. Individuals who failed to meet the necessary screening criteria were excluded from participation in the study. Consent forms were used to inform participants of their rights as well as potential risks encountered during scanning. Following successful completion of the screening process, subjects were contacted by the lab manager and informed of their scanning time.

Pre-scan preparation

Subjects are told to report to the Laboratory for Darwinian Neuroscience approximately one hour before each scanning session in order to complete preparations for the scan. Each participant provides a saliva sample for genotyping analysis and practices the Prisoner's Dilemma task they will perform in the scanner. After completing the tutorial, subjects' vital signs (blood pressure, temperature, pulse) are measured and recorded by a research assistant. In a double blinded procedure, participants then self-administer an intranasal spray containing oxytocin (OT), vasopressin (AVP), or placebo (used in functional data collection and analysis). The research assistant then leads the subject to the scanner located at the Biomedical Imaging Technology Center (BITC) within Emory University Hospital.

Scanning

Upon arrival at the scanner, subjects vital signs are re-measured to insure the intranasal spray produced no adverse side effects. Next, participants have a blood sample drawn by researchers from the Laboratory of Comparative Human Biology. Finally, before starting the scan, subjects practice the Prisoner's Dilemma task again, responding with the same controller they will use once scanning begins.

The subject is instructed to remove any metallic items (belts, cell phones, coins, ect.) and is positioned in the scanner by the BITC lab

technician. Scanning sessions typically last between an hour and an hour and a half and involve three different types of image acquisition. Typically, at the beginning of the scan, structural images are the first to be acquired. Subsequently, functional images are acquired while subjects play four rounds of the Prisoner's Dilemma Game, either against human or computer opponents. Lastly, after all functional volumes have been acquired, diffusion tensor imaging (DTI) scans are performed.

Post Scan

At the conclusion of each scan, research assistants escort the subject from BITC at Emory University Hospital back to the Laboratory for Darwinian Neuroscience. A post scan question and answer session is performed by the principal investigator (Dr. James K. Rilling), and participants are debriefed about the methods used during the experiment. Subjects are paid approximately one-third of what they earned while playing the Prisoner's Dilemma Game during the scanning session and another sixty dollars following the completion of various personality measures on a different day. These these include the NEO PI-R, TCIR, Bar-On EQ-i, Reading Mind in the Eyes, and PONS.

TBSS

Tract-Based Spatial Statistics (TBSS) is the preferred method for

running statistical analyses on diffusion tensor imaging (DTI) data (Smith 2006). There are six steps involved between DTI image acquisition and parametric statistical tests.

First, FA (functional anisotropy) images, the preferred DTI images used for TBSS analysis, are created (Smith 2002). The unprocessed DTI data from the Siemens 3T scanner at Emory University Hospital is corrected for eddy currents and slight head movements. Next, a brain mask is created using B=0 (non diffusion weighted images). Lastly, dtifit is used to fit the FA image onto the diffusion tensor model.

After the initial step of creating the FA images, subjects FA images are combined in an empty folder prior to running TBSS. When FA images from all subjects are placed into this folder, the first TBSS script (tbss_1_preproc *.nii.gz) is run. This script places all FA images in a new directory called FA. Additionally, the original data acquired from the scanner is placed into a folder named origdata. Lastly, the script runs the command slicedir, which opens a webpage to view each subject's input image and check for major problems.

The next step in TBSS involves nonlinear registration (Anderson 2007a, Anderson 2007b). FA images from all subjects are transformed into a common 1x1x1 mm voxel standard space. Subjects FA images can be registered to a specified target, to the FA image most representative of all subjects, or to the standard image generated from

the average of every subjects FA image.

TBSS then takes the nonlinear transformed images from the previous step and transforms them into a standard space. Each FA is affine-aligned with the target image and placed in 1x1x1 mm MNI152 space. Now that each subjects FA image has been transformed into a common stererotaxic space, the script (tbss_3_postreg -S) assimilates every image into 4D file called all_FA. This file is placed in the subdirectory stats, which was also created by the tbss_3_postreg -S script. Using the file all_FA, the mean FA for all subjects is calculated, resulting in a new file named mean_FA. Placed in the FA skeletonisation program, mean_FA is used to generate the file mean_FA_skeleton. The original FA images from each subject have now been fit to a common space suitable for running statistical analyses.

One final step is required before running statistics in TBSS. The script tbss_4_prestats 0.2 is used to define the specific voxels which will be used in statistical tests. Following the running of this script, the skeletonised FA data is ready for statistics.

The final step in TBSS is running statistical analyses. This determines, through a voxelwise analysis, which voxels along the FA skeleton correlate significantly with the covariates being tested. TBSS is used for evaluating positive and negative correlations of every covariate in a list with all voxels on a normalized skeleton.

VBM

Voxel-based morphometry (VBM) is the preferred method for measuring regional gray matter volume differences in the brain (Ashburner 2000). The first step in VBM is to transform and register each subject's structural data (T1 images) into a standard space. T1 images from each subject are matched as accurately as possible to the template image by estimating the best possible 12-parameter affine transformation. The second step of registration accounts for nonlinear shape differences between subjects. When completed, the spatially normalized images should have a high resolution (1x1x1) so that partial voluming (voxels which contain a mixture of gray and white matter) is reduced or eliminated.

Next, using a mixture model cluster analysis technique, spatially normalized images are separated into gray matter, white matter, and cerebrospinal fluid. Using an isotropic Gaussian kernel, the spatially normalized gray matter images are smoothed, resulting in more normally distributed data. This step is necessary because the original images contain mostly values clustered close to either zero or one, neither of which is desirable for running accurate statistical tests. By smoothing the data and creating a more even distribution of values, the validity of statistical tests rises precipitously.

Once all structural images used in the analysis have been registered to a normalized space and following spatial smoothing, data is ready to undergo statistical testing. General linear models (GLMs) are employed to determine whether or not gray matter changes correlate significantly to the covariates being investigated. The most common tests used are *t* and *F* tests. VBM is used for measuring the positive and negative correlations between a list of covariates and all voxels segmented into gray matter.

NEO PI-R

The Neo PI-R is a psychological personality inventory that utilizes the Five Factor Model of human personality. The Five Factor Model comprises the dimensions of personality that are believed to contribute to the complexity of the human psyche. These domains are Neuroticism, a relative measure of negative affect; Extraversion, which is defined as gregariousness and personal assertiveness; Openness to experience, which involves active imagination, attentiveness to feelings, and intellectual curiousity; Agreeableness, which is the ability to be agreeable during social interactions; Conscientiousness, which is defined as the tendency to act based on ones conscience.

When administered, each subject receives a NEO PI-R Item Booklet, a scoring sheet, and No. 2 pencil. Subjects are told to

complete the 240 question inventory. Upon completion, a research assistant profiles and scores each subjects survey. This information is then entered into a Microsoft Excel spreadsheet, where preprogrammed macros (abbreviated set of commands for quickly processing and organizing data) calculate the final domain scores for each of the five personality factors.

Bar-On EQ-i

The Bar-On EQ-i is a general measure of emotional-social intelligence. Reuben Bar-On, the creator of the measure, posits that in general, individuals who have ESI (emotional-social intelligence) were better able to cope with and adapt to environmental demands. He defines emotional social intelligence through five domains: Intrapersonal, which encompasses self-awareness and self-expression; Interpersonal, defined as social awareness and competency in interpersonal relationships; Stress management, the ability to manage and regulate emotions; Adaptability, which is the capacity to adjust to new circumstances; and General Mood, or how one feels about themselves.

Subjects were instructed to complete the Bar-On EQ-i on a computer located in the Laboratory for Darwinian Neuroscience. Following completion of the survey, scores are submitted to an online scoring center. After each subjects survey has been graded, research

assistants request the scores and record the data on Microsoft Excel.

Reading Mind in the Eyes

Reading Mind in the Eyes is a test which was developed in order to gauge how accurately an individual is able to identify non-verbal emotional cues. Subjects are instructed to look at the pictures on the computer screen and try to ascertain the emotional state of the individual in the picture. A participant chooses their response onscreen, and at the end of the test a score is given, with higher scores indicating an increased capacity for accurately identifying facial expressions and lower scores suggesting a decreased ability to recognize facial emotions.

Results

Voxel-based morphometry (VBM)

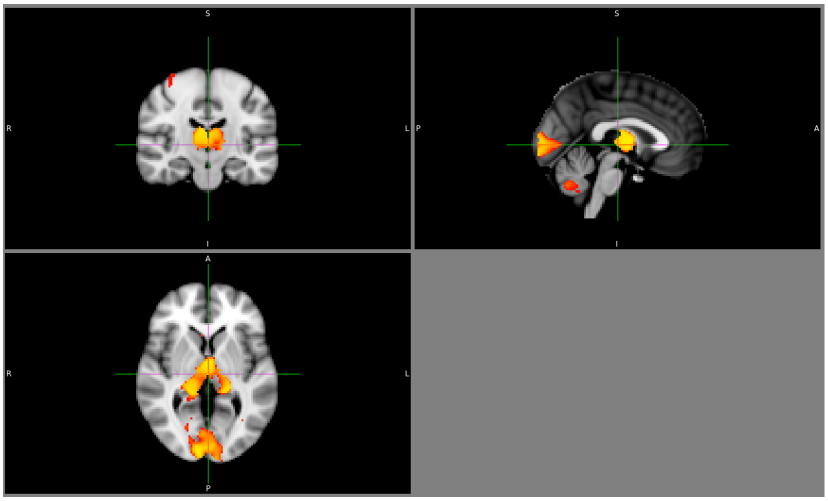
Empathy

Hypothesis : Individuals who have higher Bar-On EQ-i Empathy scores, a measure of the ability to understand how others feel, will have higher gray matter volume in the anterior cingulate cortex, anterior insula, right temporal pole, right fusiform gyrus, right caudate nucleus, and right subcallosal gyrus.

Positive Correlations

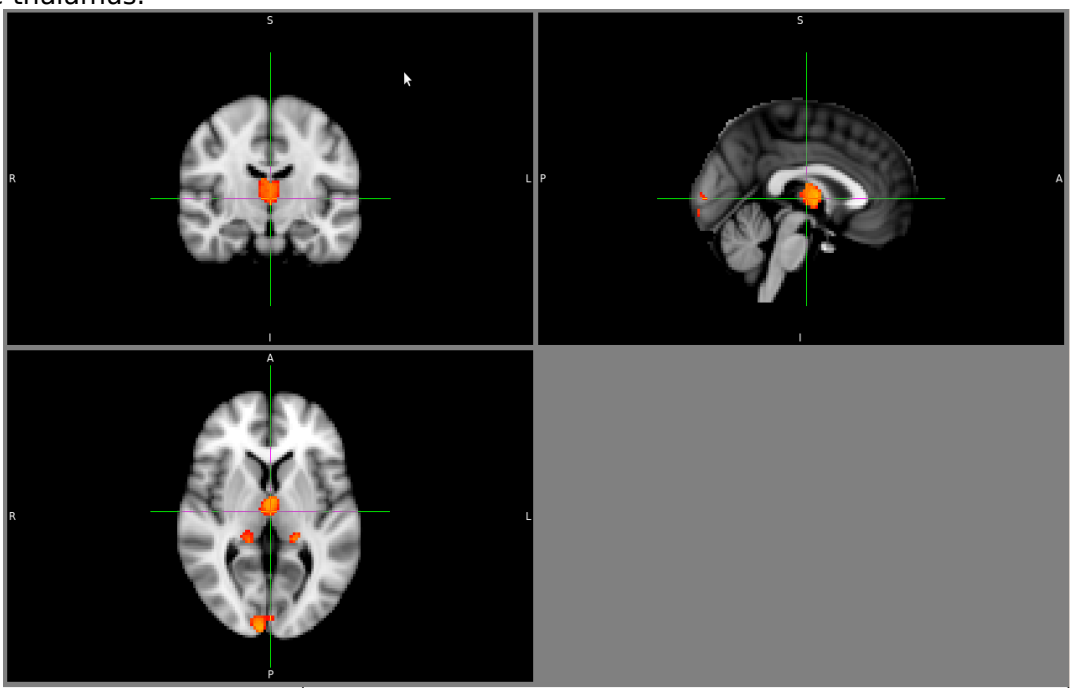
Contrasting with the *a priori* hypothesis, higher gray matter volume was not observed in any hypothesized regions of interest. Rather, Bar-On Empathy scores correlated positively ($p<.05$) with gray matter volume in the thalamus, occipital lobe, and cerebellum.

Figure1: Positive correlations ($p<.05$) between Bar-On EQ-i Empathy scores and gray matter volume in the thalamus, cerebellum, and occipital lobe.



At a more stringent threshold (p<.01), significant positive correlations of gray matter volume with Bar-On EQ-i Empathy scores were observed in the occipital lobe, right medial dorsal (MD) nucleus of the thalamus, bilateral anterior nuclei of the thalamus, and bilateral ventral posterolateral (VPL) nuclei of the thalamus.

Figure 2: Positive correlations (p<.01) between Bar-On EQ-i Empathy scores and gray matter volume in the occipital lobe, right medial dorsal nucleus of the thalamus, bilateral anterior nuclei of the thalamus, and bilateral ventral posterolateral nuclei of the thalamus.



Negative Correlations

In addition to the above positive correlations, it was observed that Bar-On EQ-i Empathy scores correlated negatively (p<.05) with gray matter volume within the left precentral sulcus, left superior frontal gyrus, and left cingulate gyrus.

Figure 3: Negative correlations (p<.05) between Bar-On EQ-i Empathy scores and gray matter volume in the precentral sulcus and left superior frontal gyrus.

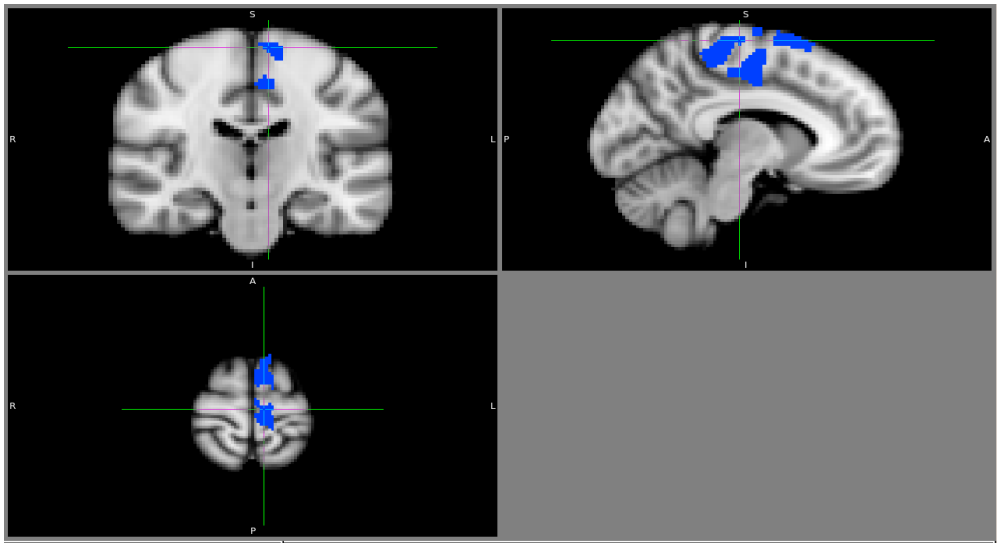
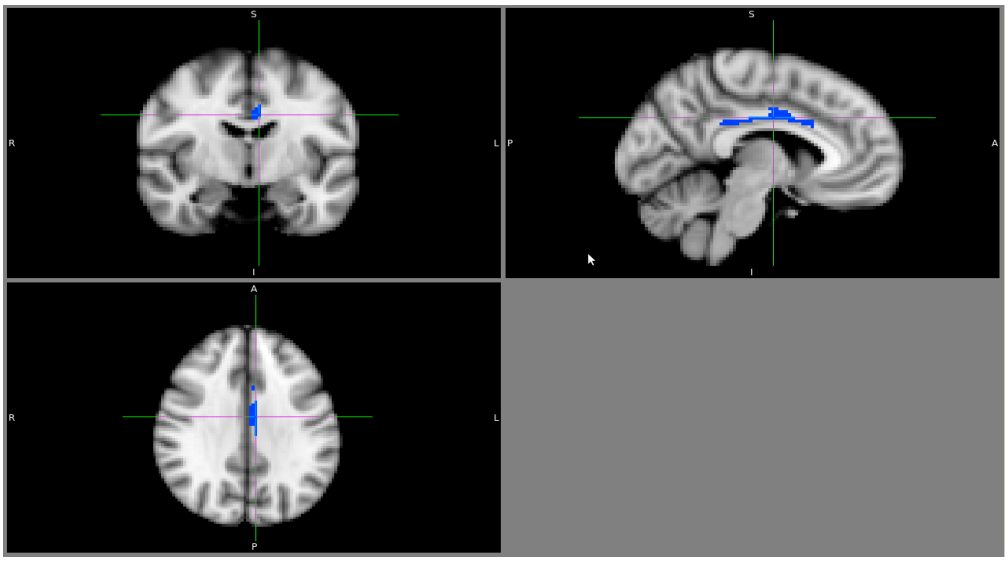


Figure 4: Negative correlation (p<.05) between Bar-On EQ-i Empathy scores and gray matter volume in the left cingulate gyrus.



Emotion Regulation

Hypothesis: Individuals who have higher NEO PI-R Neuroticism scores, a measure of negative affect, will have lower gray matter volume in the anterior cingulate cortex and orbitofrontal cortex.

Positive Correlations

In line with the *a priori* hypothesis, NEO PI-R Neuroticism scores correlate negatively ($p<.05$) with gray matter volume in the right anterior cingulate cortex and left orbitofrontal cortex.

Figure 5: Negative correlation ($p<.05$) between NEO PI-R Neuroticism scores and gray matter volume in the right anterior cingulate cortex.

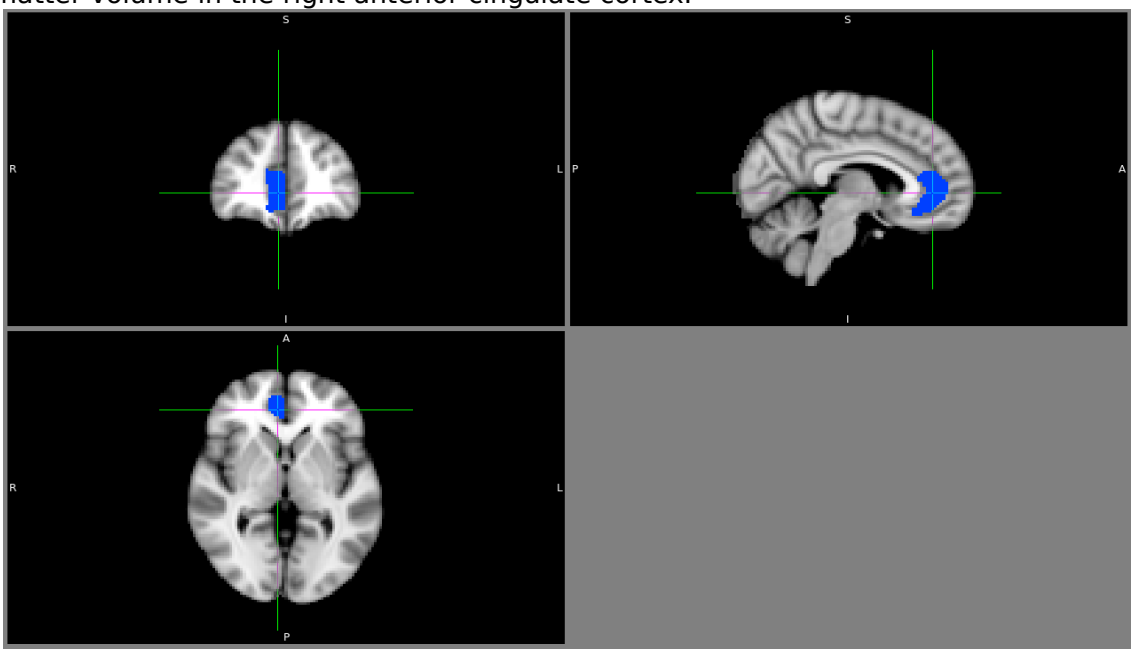
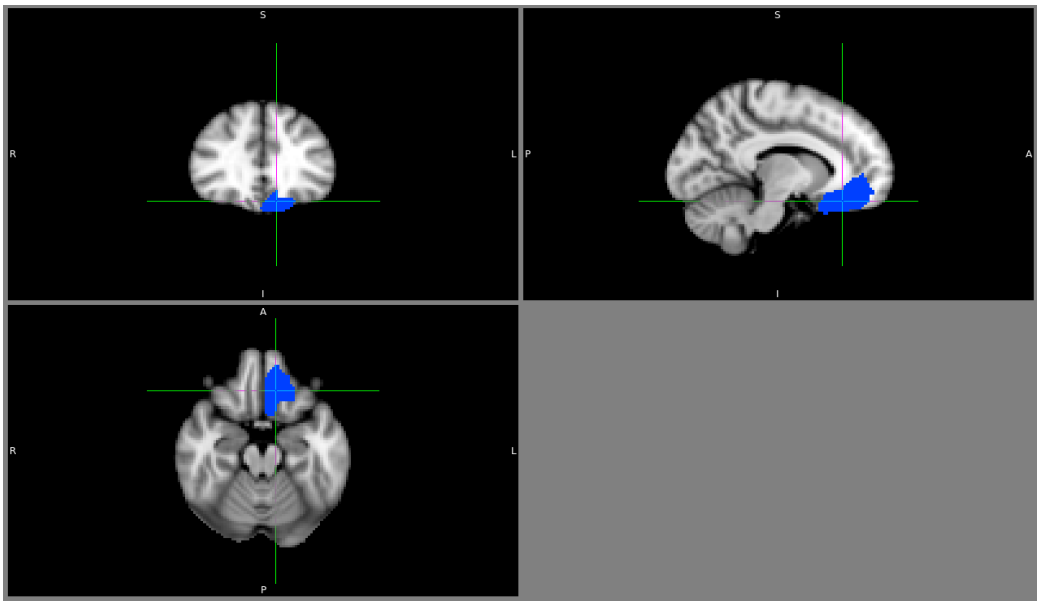


Figure 6: Negative correlation (p<.05) between NEO PI-R Neuroticism scores and gray matter volume in the left orbitofrontal cortex.



Also, negative correlations with NEO PI-R Neuroticism scores were observed in these same regions under a more stringent threshold (p<.01)

Figure 7: Negative correlation (p<.01) between NEO PI-R Neuroticism scores and gray matter volume in the right anterior cingulate cortex.

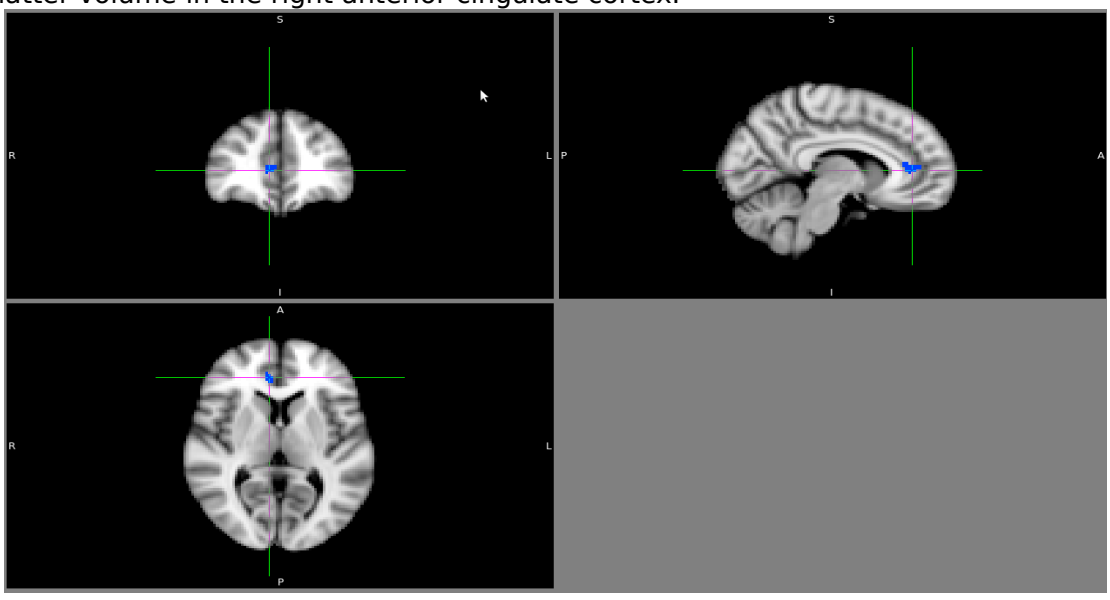
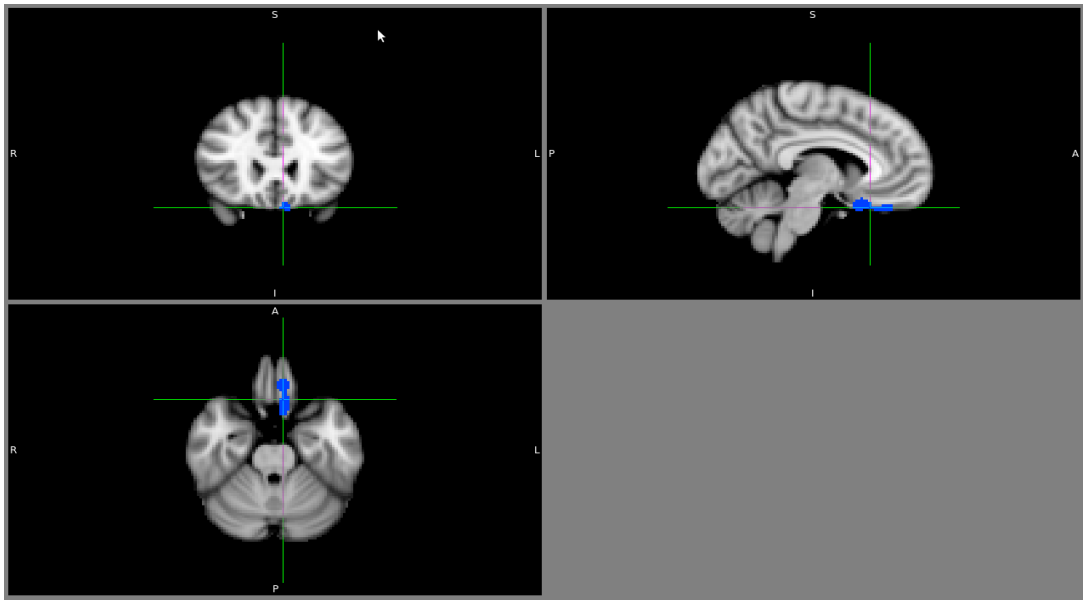


Figure 8: Negative correlation (p<.01) between NEO PI-R Neuroticism scores and gray matter volume in the left orbitofrontal cortex.



Emotional-social Intelligence (ESI)

Hypothesis: Individuals who have higher total scores on the Bar-On EQ-i, a general measure of the ability to function well in social environments, will have higher gray matter volume in the ventromedial prefrontal cortex (vmPFC), anterior insula, amygdala, and primary somatosensory cortex.

Positive Correlations

None of the hypothesized regions of interest showed significant positive or negative correlations with Bar-On EQ-i total score. However, significant positive correlations (p<.05) were discovered in the occipital lobe and medial dorsal nucleus of the thalamus.

Figure 9: Positive correlation (p<.05) between Bar-On EQ-i total scores and gray matter volume in the occipital lobe.

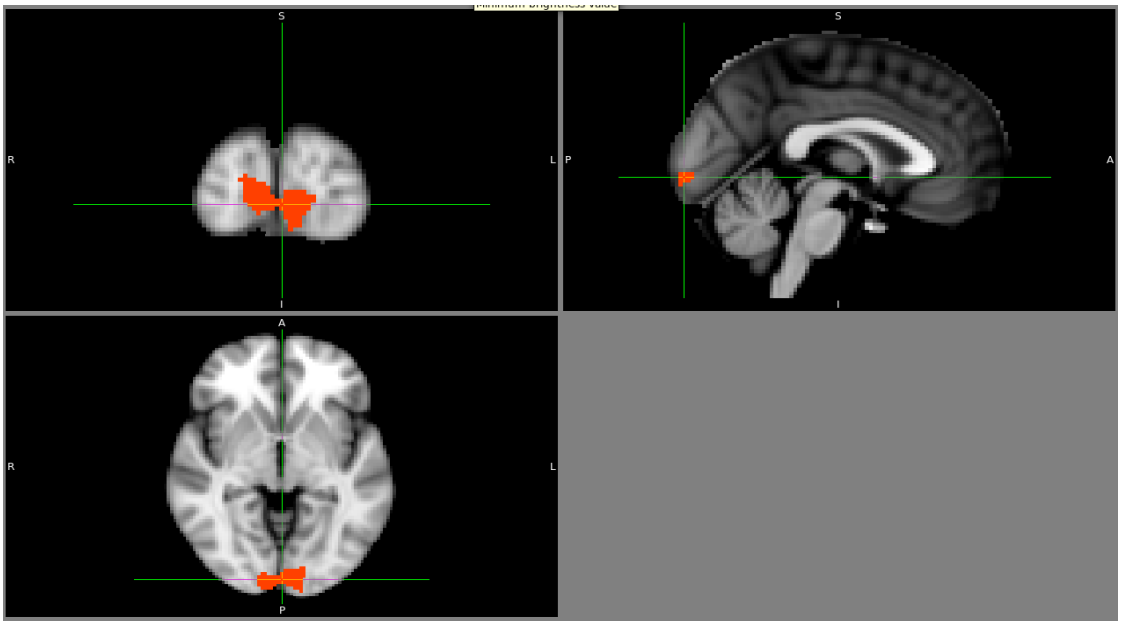
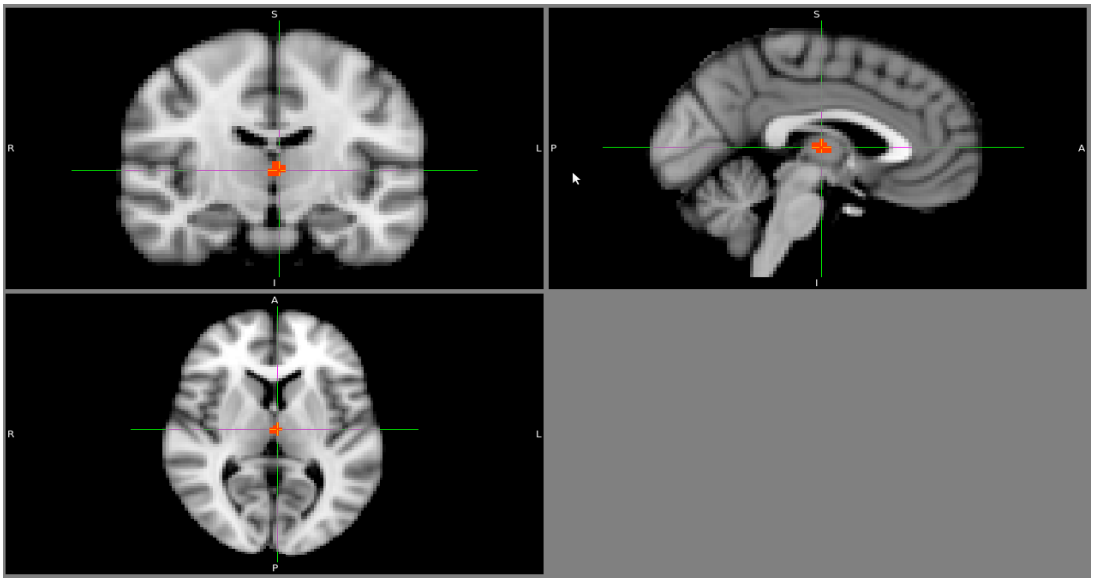


Figure 10: Positive correlation (p<.01) between Bar-On EQ-i total scores and gray matter volume in the medial dorsal nucleus of the thalamus.



Negative Correlations

Analysis of imaging data also revealed that Bar-On EQ-i total

score correlated negatively (p<.05) with gray matter volume in the right anterior cingulate cortex, right superior temporal gyrus, right posterior insula, and right temporal pole.

Figure 11: Negative correlation (p<.05) between Bar-On EQ-i total scores and gray matter volume in the right anterior cingulate cortex.

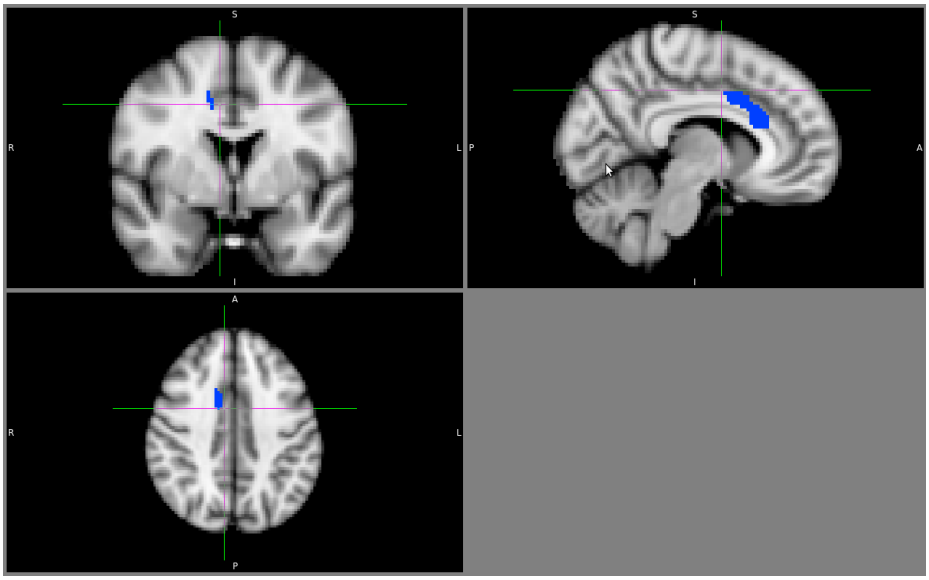


Figure 12: Negative correlation (p<.05) between Bar-On EQ-i total scores and gray matter volume in the right superior temporal gyrus.

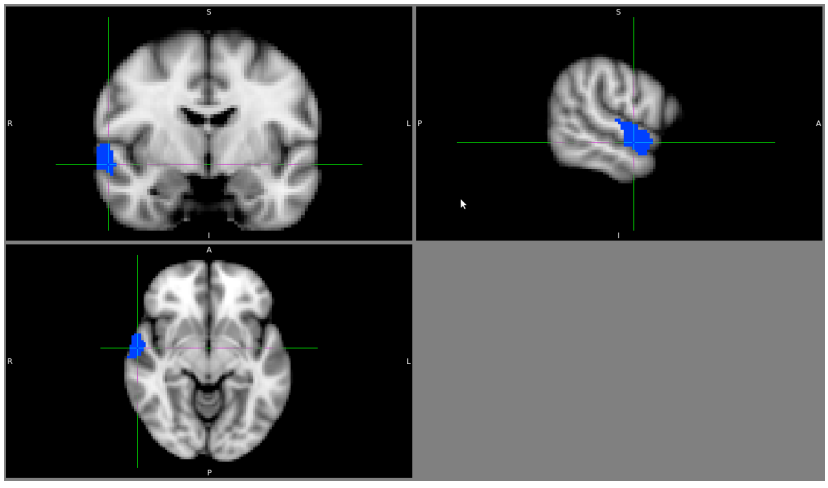


Figure 13: Negative correlation (p<.05) between Bar-On EQ-i total scores and gray matter volume in the right posterior insula.

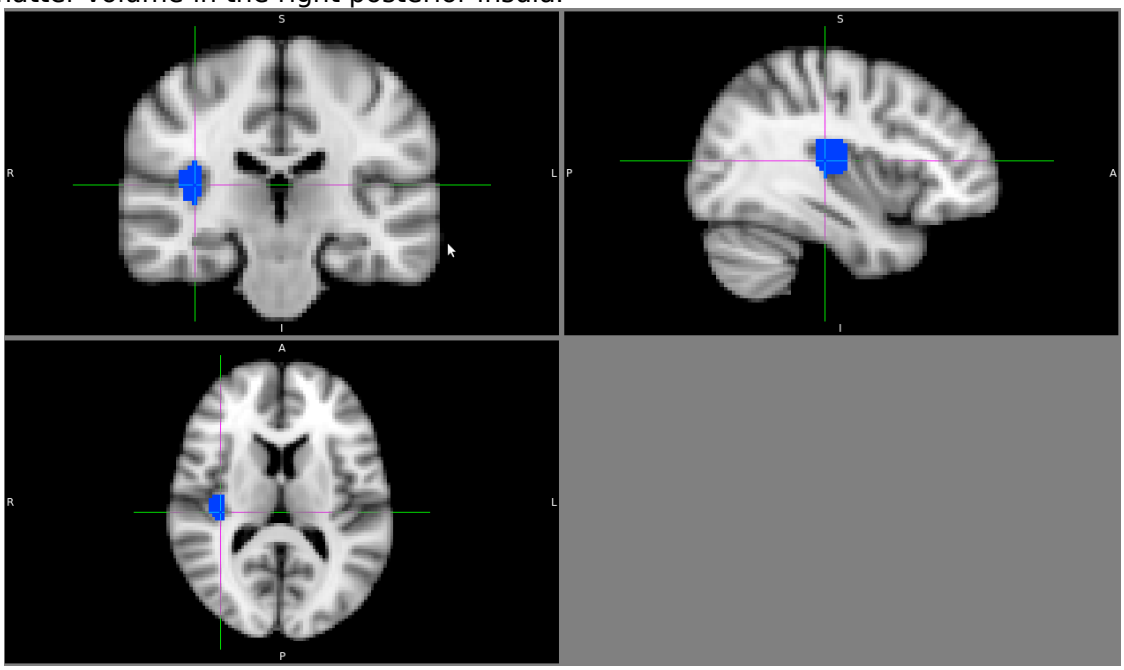
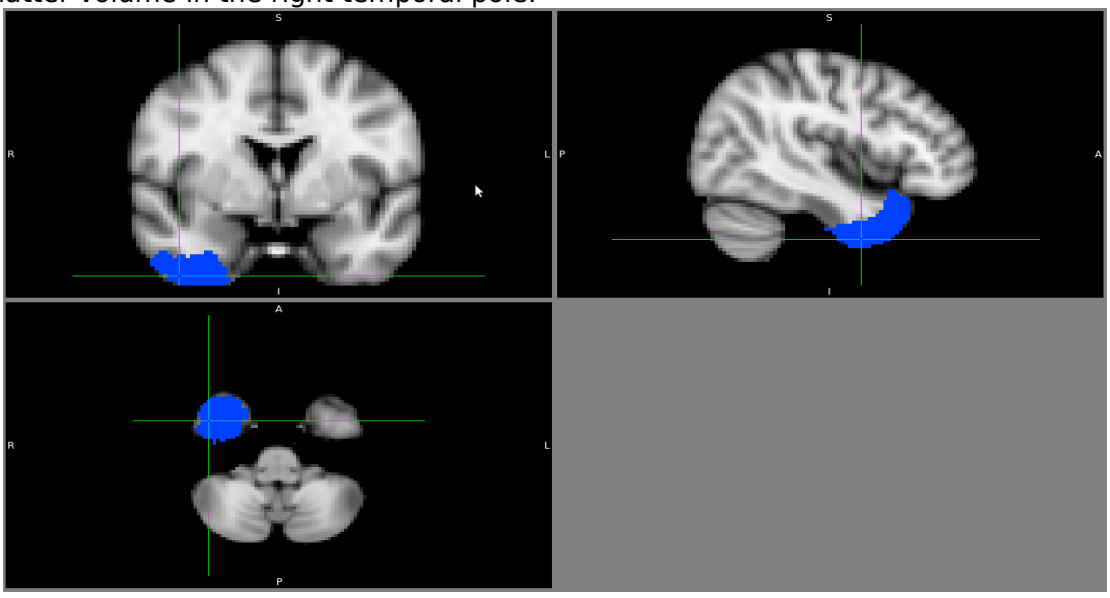


Figure 14: Negative correlation (p<.05) between Bar-On EQ-i total scores and gray matter volume in the right temporal pole.



Under a more stringent threshold (p<.05), significant negative correlations were observed in the right superior temporal gyrus and right temporal pole.

Figure 15: Negative correlation (p<.01) between Bar-On EQ-i total scores and gray matter volume in the right superior temporal gyrus.

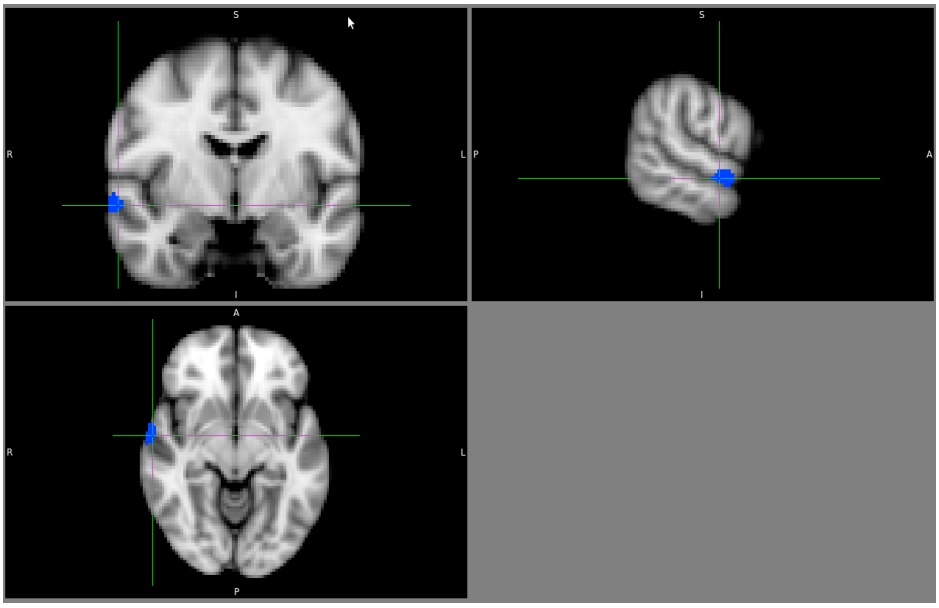
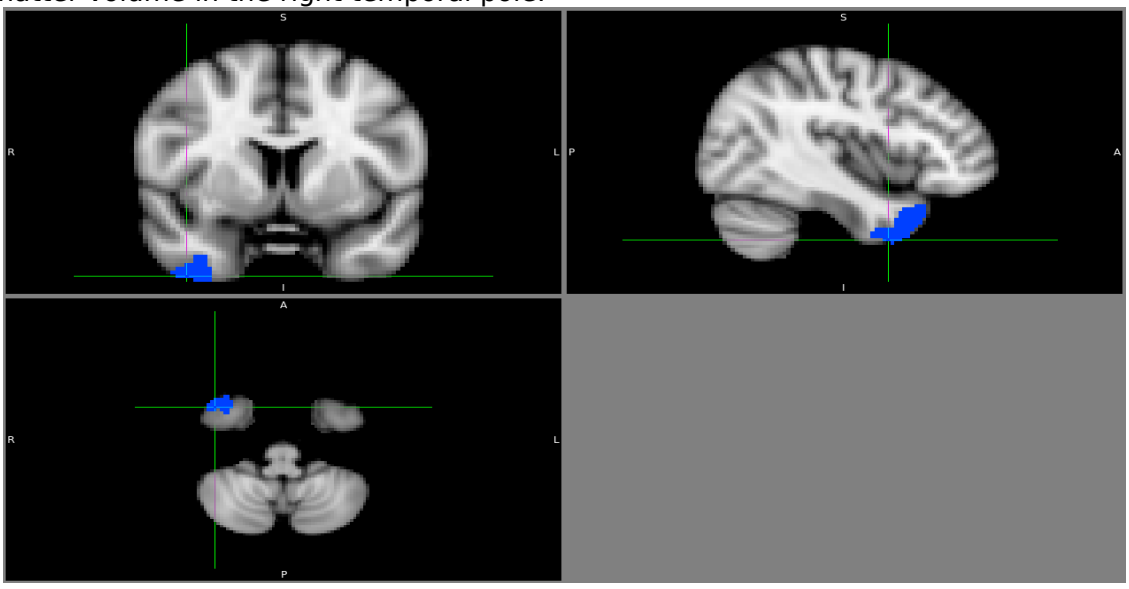


Figure 16: Negative correlation (p<.01) between Bar-On EQ-i total scores and gray matter volume in the right temporal pole.



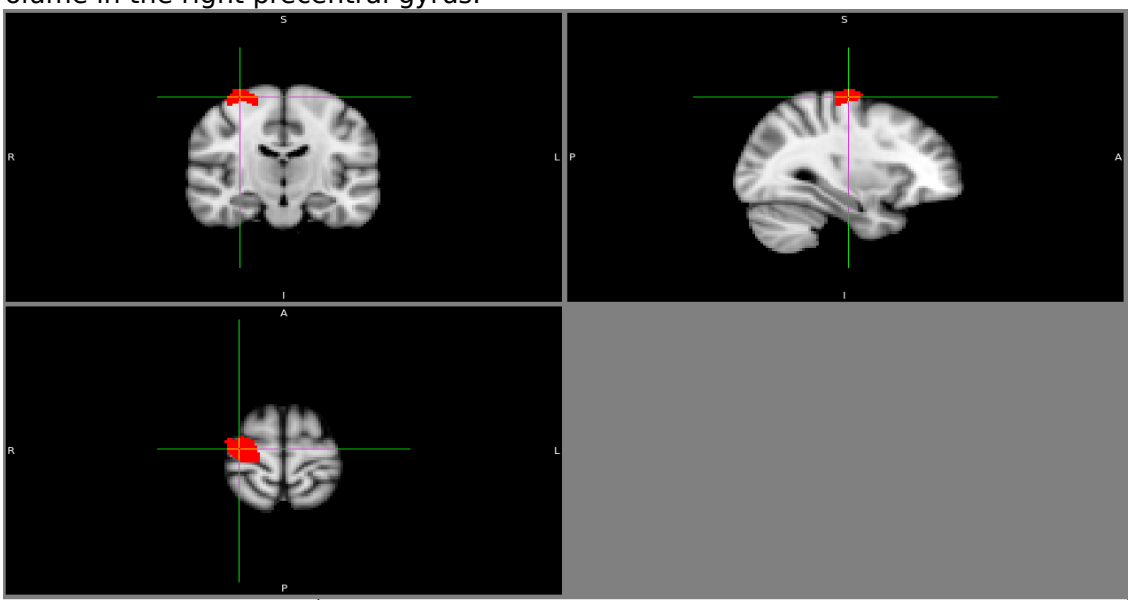
Emotion Perception

Hypothesis: Individuals who have higher scores on the Reading Mind in the Eyes task, which measures the ability accurately understand facial expressions of others, will have higher gray matter volume in the superior temporal sulcus and amygdala.

Positive correlations

A priori regions of interest showed no significant positive or negative correlations with Reading Mind in the Eyes (RMIE) total scores. However, RMIE total scores did show positive correlation (p.<05) with gray matter volume in the right precentral gyrus.

Figure 17: Negative correlation (p<.05) between RMIE total score and gray matter volume in the right precentral gyrus.



TBSS (Tract-based Spatial Statistics)

Neuroticism

Hypothesis: Individuals with higher NEO PI-R Neuroticism scores, a measure of negative affect, will have lower fractional anisotropy (FA) values along the uncinate fasciculus between the orbitofrontal cortex and amygdala.

Negative Correlations

TBSS revealed negative correlations ($p<.05$) between NEO PI-R Neuroticism scores and FA values along the left uncinate fasciculus in the medial frontal lobe and left inferior longitudinal fasciculus.

Figure 18: Negative correlation between NEO PI-R Neuroticism scores and FA values along the left uncinate fasciculus in the medial frontal lobe.

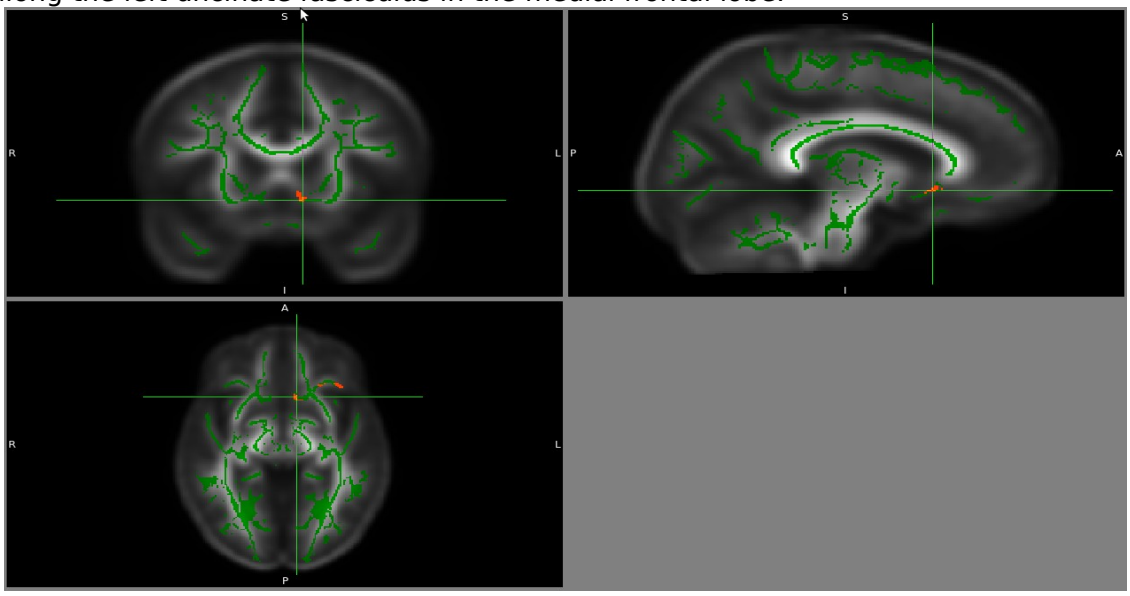
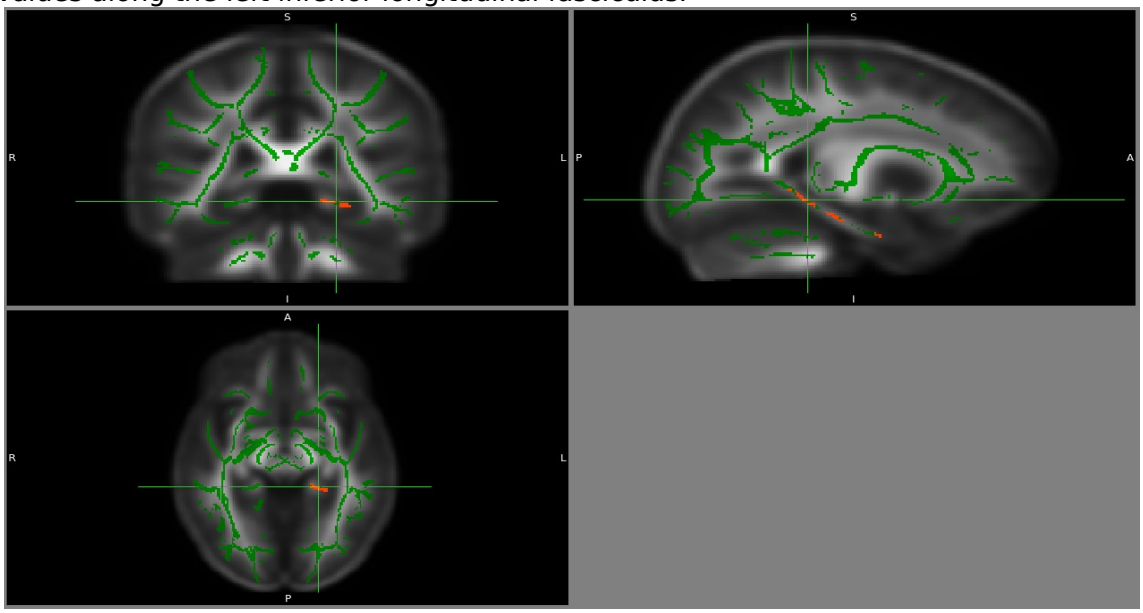


Figure 19: Negative correlation (p<.05) between NEO PI-R Neuroticism scores and FA values along the left inferior longitudinal fasciculus.



Emotion Perception

Hypothesis: Individuals who have higher scores on the Reading Mind in the Eyes task (RMIE), which measures the ability accurately understand facial expressions of others, will have higher FA values along the inferior frontal-occipital fasciculus (IFOF).

Negative Correlations

TBSS revealed no significant positive correlations along the IFOF. However, negative correlations (p<.05) were observed along the left IFOF in the frontal lobe, right temporal pole, and left temporal pole.

Figure 20: Negative correlation (p<.05) between RMIE total scores and FA values along the left IFOF in the frontal lobe.

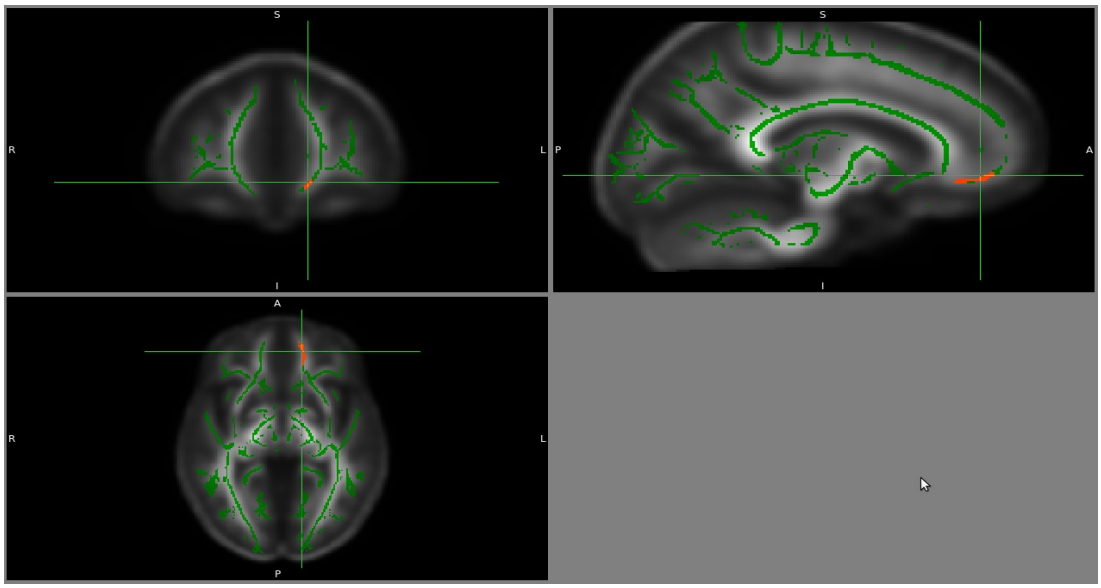


Figure 21: Negative correlation (p<.05) between RMIE total scores and FA values in the right temporal pole.

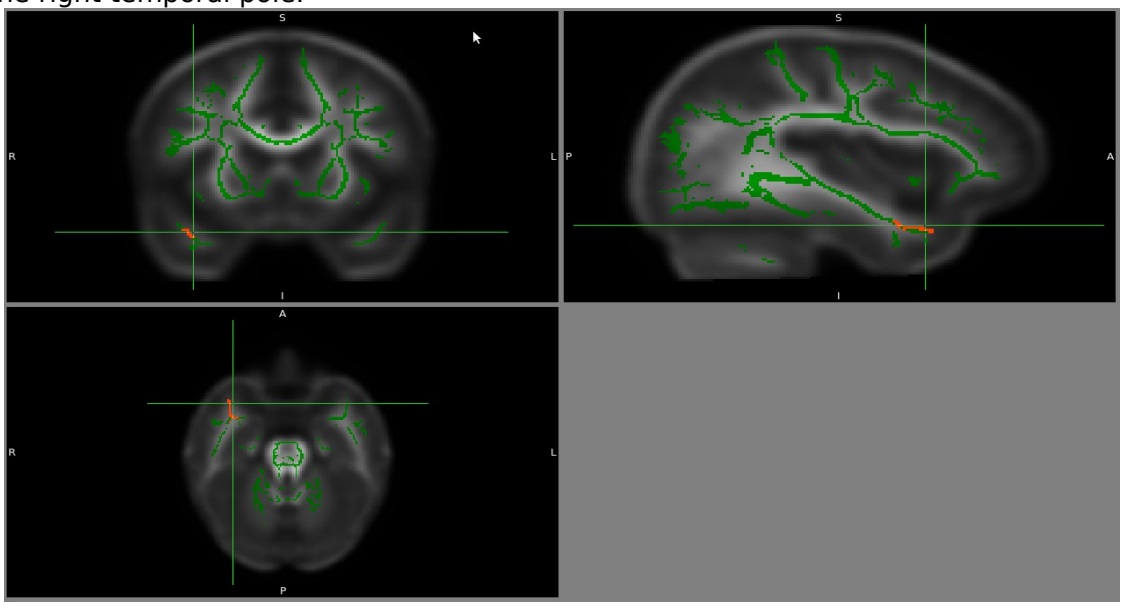


Figure 22: Negative correlation (p<.05) between RMIE total scores and FA values in the left temporal pole.

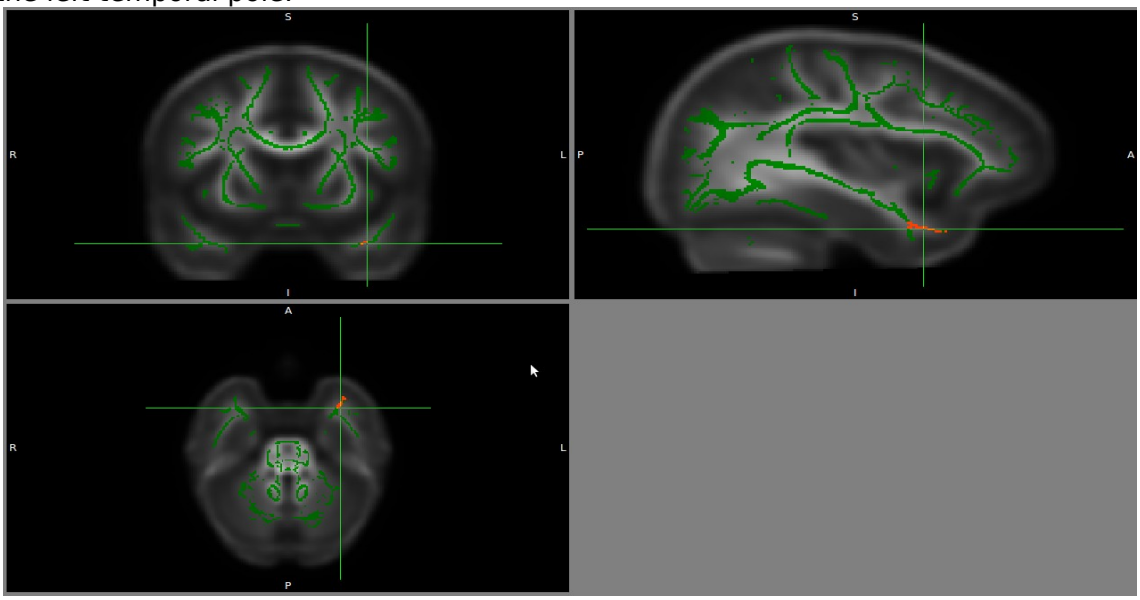


Table 1: Positive correlations between Bar-On Empathy scores and gray matter volume using VBM.

Region of Interest	P value	Spatial Extent (in voxels)	Max tStat (x, y, z)
Anterior nuclei of the thalamus	0.01	276	(45, 60, 39)
Right medial dorsal nucleus of the thalamus	0.01	120	(42, 51, 43)
Ventral posterolateral nuclei of the thalamus	0.01	126	(55, 46, 41)

Table 2: Negative correlations between Bar-On Empathy scores and gray matter volume using VBM.

Region of Interest	P value	Spatial Extent (in voxels)	Max tStat (x, y, z)
Left cingulate gyrus	0.05	172	(49, 65, 50)
Left precentral gyrus	0.05	1181	(50, 57, 63)

Table 3: Negative correlations between NEO PI-R Neuroticism scores and gray matter volume using VBM.

Region of Interest	P value	Spatial Extent (in voxels)	Max tStat (x, y, z)
Left orbitofrontal cortex	.05 .01	830 153	(47, 82, 22) "
Right anterior cingulate cortex	.05 .01	619 54	(41, 82, 39) "

Table 4: Positive correlations between Bar-On EQ-i total scores and gray matter volume using VBM.

Region of Interest	P value	Spatial Extent (in voxels)	Max tStat (x, y, z)
Medial dorsal nuclei of the thalamus	0.05	31	(45, 55, 39)
Occipital lobe	0.05	453	(47, 14, 35)

Table 5: Negative correlations between Bar-On total scores and gray matter volume using VBM.

Region of Interest	P value	Spatial Extent (in voxels)	Max tStat (x, y, z)
Right anterior cingulate cortex	0.05	388	(39, 77, 47)
Right superior temporal sulcus	.05 .01	450 83	(17, 62, 28) "
Right posterior insula	0.05	261	(26, 54, 42)
Right temporal pole	0.05 .01	1562 395	(26, 69, 14) "

Table 6: Positive correlation between Reading Mind in the Eyes score and gray matter volume using VBM.

Region of Interest	P value	Spatial Extent (in voxels)	Max tStat (x, y, z)
Right precentral gyrus	0.05	448	(43, 49, 74)

Table 7: Negative correlations between NEO PI-R Neuroticism scores and FA values using TBSS.

Region of Interest	P value	Spatial Extent (in voxels)	Max tStat
Left uncinate fasciculus	0.05	109	(122, 163, 119)
Left inferior longitudinal fasciculus	0.05	388	(109, 113, 105)

Table 8: Negative correlations between Reading Mind in the Eyes total score and FA values using TBSS.

Region of Interest	P value	Spatial Extent (in voxels)	Max tStat
Left inferior frontal-occipital fasciculus	0.05	116	(99, 184, 119)
Left temporal pole	0.05	75	(120, 156, 95)
Right temporal pole	0.05	67	(52, 144, 99)

Discussion

Empathy

In contrast to studies which implicate primarily cortical structures in generating feelings of empathy, findings from this study suggest that gray matter volume within three thalamic nuclei (anterior, medial dorsal, ventral posterior lateral) may also play a key role in triggering empathic responses. Imaging data shows that gray matter volume within bilateral anterior ($p<.005$), bilateral ventral posterior lateral ($p<.01$), and right dorsal medial ($p<.01$) thalamic nuclei correlate positively with Empathy scores as measured by the Bar-On EQ-i, a statistically validated measure of emotional and social intelligence (Bar-On 2006).

Several findings indicate that the medial dorsal (MD) nuclei of the thalamus may play a crucial role in empathic responses via their role in interoceptive awareness of bodily states (Craig 2003). Afferent fibers from all bodily tissues providing crucial information regarding pain, temperature, touch, and visceral conditions terminate in the lamina I, a cell column located in the dorsal horn of the spinal cord. The lamina I neurons project to various sites in the upper brain stem, most notably the parabrachial nucleus, which is involved in the integration and control of all the body's homeostatic inputs (Saper 2002). Interestingly, lamina I neurons also have direct projections to the

medial dorsal nucleus of the thalamus, which sends efferent projections to the anterior cingulate cortex (aCC) (Craig 1995). Functional imaging studies, most notably those done by Singer *et al*., demonstrated that the aCC (as well as the anterior insula) was activated during both the conscious experience of pain and while watching a loved one experience painful stimulation (Singer et al 2004). This is direct evidence that the cortical substrates activated during interoceptive awareness of painful stimuli and subjective feelings of empathy are roughly the same. Literature on connectivity between thalamo-cortical structures combined with evidence from this study suggests that gray matter volume within the medial dorsal nuclei of the thalamus plays a key role in modulating empathic responses. It does not, however, explain the mechanism by which the medial dorsal nucleus of the thalamus affects the anterior cingulate cortex.

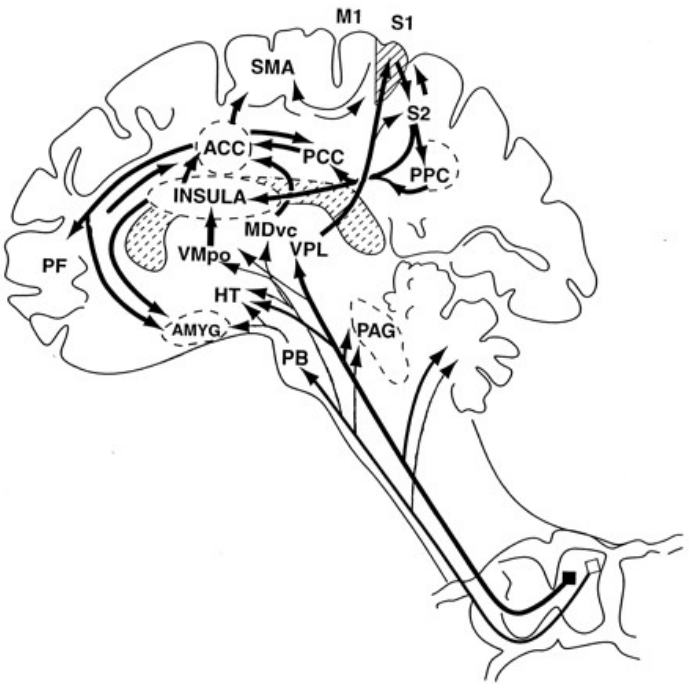


Figure 1: Schematic diagram of ascending sensory pathways and their connectivity in the brain (Price 2000).

Craig (2003) also posited that the ventral posterior medial nucleus of the thalamus, which receives afferent enervation from lamina I neurons, is also involved in relaying interoceptive information to the insula, a cortical area embedded in the lateral sulcus (Sylvian fissure) between frontal and temporal lobes. This region did not show significant increases in gray matter volume in a positive correlation with empathy scores as measured by the Bar-On EQ-i. Rather, the thalamic nuclei directly lateral to the ventral posteromedial nucleus of the thalamus, the ventral posterolateral nucleus, was shown to have increases in gray matter bilaterally when positively correlated to

empathy scores on the Bar-On EQ-i. In contrast to the ventral posterior medial nuclei, which receives inputs from lamina I and projects efferent fibers to the insula (Craig 1995), it has been documented that the ventral posterolateral nuclei receives sensory information from the spinothalamic tract (Gerhart et al 1980) and sends projections to primary somatosensory cortex (Price 1999). Contrasting with previous findings published by Singer *et al.*, a study which does not implicate primary somatosensory cortex in empathic responses to observed pain, recent functional imaging evidence indicates that the somatosensory cortex is involved the detection of painful stimuli as well as subjective feelings of empathy (Bufalari et al 2007, Lamm et al 2007b). Similar to the medial dorsal nuclei, the ventral posterolateral nuclei of the thalamus may play a large role in empathic responses. But the processes through which gray matter changes in the thalamus may affect empathic responses produced in the primary somatosensory cortex remains uninvestigated.

The voxels with the most significant positive correlation to Bar-On EQ-I empathy scores were heavily localized in the anterior nucleus of the thalamus. This nucleus is enervated by the mammillothalamic tract, which has its origins in the mammillary bodies, a structure located at the anterior-inferior end of the fornix (Guillery 1955). Several studies of mammillary body and mammillothalamic tract

pathology have documented that these structures are largely responsible for the ability to accurately recall episodic memories (Kopelman 1995, Yoneoka et al 2004, Tsivilis 2008). Functioning in episodic memory and having large efferent connections to the anterior nuclei of the thalamus via the mammillothalamic tract, evidence suggests these anterior thalamic nuclei may function in the recollection of explicit memories. However, it seems unlikely that the anterior nucleus contributes to empathic responses by aiding in the remembrance of specific events, as empathy is generated in circumstances where individuals are unfamiliar with one another (Chismar 2004).

Findings for this aim were largely unexpected based on the available neuroanatomical and functional research on empathy. Functionally, the bilateral anterior insula and anterior cingulate cortex are heavily implicated in the production of empathic responses (Singer et al 2004). Yet results from both positive and negative correlations of Bar-On EQ-i empathy score to gray matter volume did not yield regional differences in these cortical regions. Structurally, evidence from neurodegenerative disorders, specifically frontotemporal lobar degeneration (FTLD), demonstrated that individuals with lower empathy scores on the Interpersonal Reactivity Index (IRI) had decreased gray matter volume in the right temporal pole, right

fusiform gyrus, right subcollosal gyrus, and right caudate nucleus (Rankin et al 2006). Again, however, there were no significant gray matter volume correlations, either positive or negative, noted in these regions. Lesion studies also suggest that distinct cortical substrates, specifically in the frontal lobe, may be involved in feelings of empathy. In a study done by Shamay-Tsoory *et al*., it was found that empathic responses were weakened by selective lesions to the right ventromedial prefrontal cortex (Shamay-Tsoori et al 2003). Correlated both positively and negatively to Bar-On EQ-i empathy scores, this region did not demonstrate any discernable changes in gray matter volume.

These findings suggest that increased gray matter volume in the medial dorsal, ventral posterolateral, and anterior nuclei of the thalamus may result in enhanced empathic abilities. Yet the reason why increased thalamic volume in these nuclei may contribute to an improved ability to empathize with others remains uninvestigated.

Bar-On EQ-i Total Score – Emotional-Social Intelligence (ESI)

The ventromedial prefrontal cortex (vmPFC) is widely regarded as an important cortical region for the rational decision making (Damasio 1996). It has been demonstrated that individuals who suffer damage or lesions in this area lose the capacity to make rational

decisions. The most famous example of ventromedial prefrontal damage is Phineas Gage, a railroad worker who suffered a catastrophic accident in 1848 when a tamping iron shot through the front of his skull (Damasio 1994). Amazingly, Gage survived the accident, but his colleagues observed marked changes in his temperament and disposition following this event, including irrationality and poor decision making. This was the first evidence to suggest that the ventromedial prefrontal cortex functioned in the ability to make rational decisions. In addition to irrational decision making, Damasio (1996) demonstrated that individuals with lesions to the vmPFC showed a diminished capacity for experiencing or expressing their emotions. Thus, it appears that the ventromedial prefrontal cortex also serves as an integration center for emotions and feelings. Not surprisingly, then, the vmPFC is the principle cortical structure thought to be responsible for important governing aspects of emotional-social intelligence (ESI) (Bar-On 2006). Together, these findings suggest a link between the inability to experience emotions and irrational decision making. This forms the basis of what Damasio refers to as "The Somatic Marker Hypothesis".

The Somatic Marker Hypothesis posits that during decision making, the brain must assess rewards and consequences inherent in making certain choices. During situations of uncertainty or ambiguity,

it would be grossly inefficient for the brain to try and ascertain the outcome of a situation through logical cognitive mechanisms. Instead, the brain relies on forming salient emotional associations to specific situations, deemed somatic markers, which are utilized during instances where rapid, accurate decisions are required.

This is accomplished in one of two ways. First, the so called "body-loop", states that the sensory information the brain receives from the body is utilized in facilitating a sequence of physiological responses leading to accurate decision making. More simply put, the emotional reaction solicited by various somatic markers informs the brain how to make a quick, rational decision. The second way the Somatic Marker Hypothesis is thought to work is referred to as the "as if" loop. In this scheme, the brain simulates how the body would feel in a given situation in the absence of bodily sensation. Paraplegics, who have a complete absence of sensation in their bodies, are thought to use this mechanism for making informed rational decisions in certain scenarios.

According to the Somatic Marker Hypothesis, the cortical areas largely responsible for processing the emotions involved in rational decision making are the insula, amygdala, and primary somatosensory cortices. These cortical regions all have efferent projections to the ventromedial prefrontal cortex. Functional imaging studies

demonstrate that insular cortex is activated during changes in bodily states such as touch, pain, or visceral sensation (Craig 2009, Ploghaus et al 1999, Craig 2003). Furthermore, Craig (2003, 2009) contends that while interoceptive awareness of bodily states is mapped onto the insular cortex, a subsequent re-representation of sensory information in the anterior insula is largely responsible for the conscious experience of bodily conditions. It seems that conscious awareness of internal feeling states is crucial in guiding risk taking behaviors, as neuroeconomics research indicates that the anterior insula appears to play an important role in decision making during situations of uncertainty or ambiguity (Huettel et al 2006).

Research indicates that the amygdala is functionally implicated in responses (both conditioned and unconditioned) to emotionally salient environmental stimuli, particularly those which evoke feelings of fear, anxiety (Whalen 1998, 2004), or distrust (Adolphs et al 1998). Additionally, amygdala over-activity has been documented in persons who experience social phobias (Phan et al 2006) and amygdala under-activity in autism spectrum disorders (Baron-Cohen et al 1999), suggesting this structure plays an important role in processing social information.

It has been demonstrated that damage to or impairment of these structures can also lead to deficits in decision making similar to

those observed in ventromedial prefrontal lesions (Bechara et al 1994, Bar-On et al 2003). However, there were found to be no positive correlations between total score on the Bar-On EQ-i and gray matter volume in the insula, amygdala, or primary somatosensory cortices. Rather, the voxels with the most significant positive correlation ($p<.05$) to Bar-On total score were found in the visual cortex and medial dorsal nucleus of the thalamus.

A recent diffusion tensor imaging (DTI) study of humans and macaques illustrates the connectivity between the mediodorsal nucleus of the thalamus and various frontal lobe regions involved in executive control (Klein et al 2010). These areas include the orbitofrontal cortex, anterior cingulate cortex, ventrolateral prefrontal cortex, and dorsolateral prefrontal cortex. Although there is no clear consensus as to the exact function of each of these cortical regions, they are postulated to be involved in a variety of processes including impulse control (Weiger and Bear 1988), responses to rewarding stimuli (Shultz et al 2000), error detection (Carter et al 1998), empathy (Singer et al 2004), spatial and object recognition (Goldman-Rakic 1995), and working memory (Petrides 1996). There is currently no literature pertaining to volumetric changes in gray matter within the medial dorsal nucleus of the thalamus or the effects of such a change on the functioning of cortical regions with which it shares connectivity.

Emotion Regulation

In concordance with the *a priori* hypotheses, this study found that gray matter volume within the orbitofrontal cortex and anterior cingulate cortex correlated negatively with NEO PI-R Neuroticism scores. Reductions in gray matter volume were most heavily localized within the right anterior cingulate cortex ($p<.01$) and left orbitofrontal cortex ($p<.01$). Also, fractional anisotropy (FA) values along the left uncinate fasciculus ($p<.05$) in the inferior frontal lobe were negatively correlated to NEO PI-R Neuroticism scores.

It is hypothesized that the ability to inhibit negative emotions and regulate impulsive aggression is controlled by the interactions between the orbitofrontal cortex, the anterior cingulate cortex, and the amygdala (Davidson et al 2000). Suppression of general negative affect was believed to be controlled via inhibitory connections from the orbitofrontal cortex and anterior cingulate cortex to the amygdala. The inability of these two cortical regions to properly control responses generated from the limbic system is thought to characterize several psychopathological disorders, including Williams syndrome (Meyer-Lindenberg et al 2005), borderline personality disorder (New et al 2007), and impulsive aggressive disorder (New et al 2004). Thus, it appears that a proper homeostasis between the orbitofrontal cortex, anterior cingulate cortex, and amygdala is fundamental to human

social cognition, as abnormalities in this network may surface in the form of aberrant social behavior.

Several lines of evidence document the role of the orbitofrontal cortex in emotion regulation. Studies in rats, non-human primates, and humans demonstrate that lesions to the orbitofrontal cortex impair the extinction of Pavlovian conditioned responses (Ledoux et al 1993). In addition, selective lesions to orbitofrontal cortex appear to reduce the effectiveness of reversal learning (Damasio et al 1997). Corroborating these findings is neurophysiological research which indicates that extinguishing conditioned responses and effective reversal learning may be mediated via projections from orbitofrontal cortex and anterior cingulate cortex to the amygdala (Kringelbach et al 2004). A PET study conducted by Abercrombie *et al.* validates these hypothesized connections by revealing a functional coupling between OFC, ACC, and amygdala (Abercrombie et al 1996).

Within this regulatory circuit, orbitofrontal cortex has been associated with assessing the reward attached to primary and secondary reinforcers while the amygdala is implicated in responses to emotionally salient environmental stimuli (Whalen 1998, 2004). The interaction between these two structures is thought to be instrumental in combining social judgments about possible rewards with sensory representations of a stimulus. Structural abnormalities in the

orbitofrontal cortex (as in the lesion studies above) may interfere with this process, resulting in a functional decoupling with the amygdala. As a result, lower gray matter volume in this region may facilitate a reduced ability to eliminate conditioned responses and cause impairments in reversal learning, making it difficult to break the association between negative emotions and a stimulus.

Other lines of evidence suggest that the orbitofrontal cortex is involved in the suppression of negative affect. Research on neuropathology revealed that individuals with damage localized in the orbitofrontal cortex experience more spontaneous outbursts of anger than persons with no damage to the OFC (Weiger & Bear 1988). Another intriguing line of evidence indicating the orbitofrontal cortex is involved in aspects of emotion regulation comes from an fMRI study by Meyer-Lindenberg *et al*. (2005). In this study, it was found that the orbitofrontal cortex (as well as the anterior cingulate cortex) was activated in an attempt to attenuate responses generated by the amygdala in persons with Williams Syndrome.

Subsequent findings have further clarified the role of the orbitofrontal cortex in emotion regulation, specifically in controlling impulsive aggression (Buckholz et al 2008). It was found that in carriers of the MAOA-L allele, orbitofrontal cortex showed greater functional coupling with the amygdala than in individuals with the

MAOA-H allele. This was thought to occur as a result of structural (reduced gray matter volume) and functional impairments (attenuated activation) in the anterior cingulate cortex, a medial prefrontal region connected to both orbitofrontal cortex (Ongur & Price 2000) and amygdala (Carmichael & Price 1995). As a result of regulatory problems in the anterior cingulate cortex, it is thought that the orbitofrontal cortex is engaged differentially more in order to provide additional support in suppressing amygdala responses. These findings provide evidence in support of the hypothesized top-down executive control of emotion in limbic structures by the orbitofrontal cortex.

Anterior cingulate cortex is the other cortical region thought to be essential in the ability to regulate negative affect. Many imaging studies point to the suspected role of the anterior cingulate cortex in emotion regulation. In a PET study conducted by Abercrombie *et al*., correlations of localized glucose metabolism support the hypothesized coupling between the anterior cingulate cortex and amygdala (Abercrombie et al 1996). An fMRI study also demonstrates that the anterior cingulate cortex (as well as the orbitofrontal cortex) is activated when viewing angry facial expressions or during the intentional provocation of anger in subjects during scanning (Kimbrell et al 1999), probably to attenuate responses generated by the amygdala (Nomura et al 2004, Monk et al 2008).

Additionally, the anterior cingulate cortex, especially the anterior-ventral affective portion, is activated during an fMRI study where persons were instructed to willfully inhibit sexual arousal when viewing erotic pictures (Beauregard et al 2001). When viewing erotic stimuli in the absence of any conscious inhibition, subjects were found to activate a variety of limbic structures, including the right amygdala, right temporal pole, and hypothalamus. However, when instructed to suppress feelings of sexual arousal in response to observing erotic stimuli, activations were noted in the right superior frontal gyrus and right anterior cingulate gyrus. These findings suggest that the anterior cingulate cortex is particularly involved in the assessment of emotional input during the control of affective responses (Devinsky et al 1995).

Genetic research indicates that structural changes in the anterior cingulate cortex may result from allelic variation in both the 5-HTTLPR polymorphism of the serotonin transporter gene and monoamine oxidase A (MAOA), which is involved in presynaptic release and enzymatic clearance of serotonin and norepinephrine during ontogeny. In a landmark study by Meyer-Lindenberg *et al*., it was shown that carriers of the short allele for the 5-HTTLPR polymorphism had reduced gray matter volume in the subgenual ACC and amygdala (Meyer-Lindeberg et al 2005). Carriers of this allele also showed increased synaptic levels of 5-HTTLPR (Canli et al 2006). Functionally, in carriers

of the 5-HTTLPR short allele, subgenual ACC and amygdala showed weak functional coupling with one another, suggesting reduced subgenual ACC inhibition on the amygdala. It has been demonstrated that individuals who are carriers of the short allele of the 5-HTTLPR polymorphism are especially prone to anxiety (Schinka et al 2004) and depression (Lotrich & Pollock 2004), mood disorders associated with a general inability to control negative affect.

Carriers of the short allele for MAOA (MAOA-L) have also demonstrated reduced gray matter volume in the perigenual anterior cingulate cortex (Buckholz et al 2008) while additional evidence from animal studies suggests increased synaptic serotonin and norepinephrine may result from possessing a MAOA-L allele (Cases et al 1995). Behavioral research done in both animal populations and humans indicates that MAOA-L is associated with impulsive aggression, heightened fear responses, and increased rage (Brunner et al 1993, Kim et al 1997).

As noted above, the anterior cingulate cortex is intimately connected to both the orbitofrontal cortex and amygdala. Furthermore, the anterior cingulate cortex is the area of the brain with the highest density of serotonin receptors (Varnas et al 2004). Thus, converging evidence seems to suggest that reductions in gray matter volume within the anterior cingulate cortex in carriers of the short

allele of the 5-HTTLPR serotonin transporter and MAOA-L may result from a failure to clear serotonin and norepinephrine from the synaptic cleft during critical developmental stages early in life (Buckholz et al 2008). Because the anterior cingulate has the highest density of serotonin receptors in any part of the brain, it may be particularly susceptible to this effect, ultimately resulting in profound negative effects upon emotion regulation circuitry.

Diffusion tensor imaging (DTI) evidence also suggests that the uncinate fasciculus plays a role in emotion regulation via connections between the orbitofrontal cortex, anterior cingulate cortex, and amygdala (Ghashghaei et al 2007). Lower FA (fractional anisotropy) values in the uncinate fasciculus, specifically in the left inferior frontal lobe, may reflect a reduction in connectivity between prefrontal cortex and the amygdala. Although no studies have yet demonstrated the left uncinate to be involved in regulating emotion, research has shown that the right uncinate fasciculus may be involved in the modulation of affective responses. Evidence from generalized social anxiety disorder (Phan et al 2009) and bipolar disorder (McIntosh et al 2008) have also documented lower FA values in the right uncinate fasciculus, providing evidence that this tract does in fact play a role in regulating emotional responses.

Voxel-based morphometry (VBM) evidence from this study

suggests that decreased gray matter volume in the left orbitofrontal cortex and right anterior cingulate cortex negatively correlates to higher Neuroticism scores on the NEO PI-R. Research done on these structures elucidates the role they play in regulating various aspects of negative emotion, including anger, impulsivity, and depression. Evidence also highlights their function in eliminating conditioned responses and facilitating reversal learning, abilities critical for the proper regulation of emotion.

Emotional Perception

Regions within the conventionally defined boundaries of the superior temporal sulcus are thought to play a role in the perception of motion. Single-cell electrode recording studies in macaques have demonstrated that neurons in the middle temporal (MT) area of the superior temporal sulcus are selectively activated in response to different types of visual manipulations, such as changes in direction, brightness, or rotations (Tanaka et al 1986). Additionally, selective bilateral lesions of the MT have been shown to impair responsiveness to subtle changes in movement (Pasternak & Merigan 1994). Evidence also suggests that the superior temporal sulcus plays an important role in the perception of eye gaze. In a study by Campbell et al 1990, macaques that had bilateral lesions to the superior temporal sulcus

were not as adept at accurately perceiving eye gaze as animals with no lesions. Thus, even in our non-human primate relatives, homologues of the superior temporal sulcus are evolved for the dynamic perception of motion, in particular changes in eye gaze direction.

Human studies also implicate the superior temporal sulcus in processing changes in movement, particularly facial expression. In a novel study done by Narumoto and colleagues, fMRI results implicated the right superior temporal sulcus (rSTS) in the processing and recognition of facial emotions (Narumoto et al 2001). Additionally, voxel based morphometry (VBM) showed that the superior temporal sulcus of autistic children has reduced gray matter volume (Boddaert et al 2004). This finding suggests that the superior temporal sulcus may play an important role in the comprehension of facial expression needed for proper social functioning, an ability not present in persons afflicted with autism.

The amygdala, which is predominantly involved in threat processing, has been shown to be involved in the processing of fearful facial expressions through research done on individuals with bilateral amygdala lesions (Adolphs et al 1999). What makes this finding even more interesting is the fact that the amygdala is activated during the masked presentation of fearful facial expressions during which the

subject is completely unaware of these images (Whalen et al 1998), suggesting that presentation of implicit stimuli can evoke activation. fMRI studies also demonstrate that the amygdala responds differently to variation in the intensity of facial emotions (more fearful/less fearful), indicating an evaluative role for emotionally salient stimuli (Perret et al 1996). Several PET studies demonstrate that the right amygdala is activated in experiments in which a participant was told to gaze directly into the eyes of a volunteer (Decety et al 1997, Kawashima et al 1999). In contrast, autistic subjects had no amygdala activation while looking into the eyes to try and determine the emotions or feelings of another (Baron-Cohen et al 2000). Autistic individuals are unable to properly infer the emotional states of others through visual cues, leading to profound deficits in social competency. This evidence suggests that the amygdala is involved in evaluating the emotional salience of facial information, including expressions and eye gaze. Functional impairments of this ability, either through lesions or neurodevelopmental disorders such as Autism, have been shown to have negative effects upon social processing.

Although literature on the subject indicates that these two regions are heavily involved in the comprehension of facial emotions, VBM findings from this study did not reveal any positive or negative correlations between Reading Mind in the Eyes scores and gray matter

volume. Further research is necessary to determine whether or not neocortical structural variation is responsible for differences in emotion perception.

Conclusions

Evidence from this study indicates that differences in gray matter volume and connectivity in the brain may contribute to variation in social behavior between individuals. Persons with higher Empathy scores on the Bar-On EQ-i exhibited increased gray matter volume in the medial dorsal, anterior, and ventral posterolateral nuclei of the thalamus while higher total scores on the Bar-On EQ-i (an indicator of emotional-social intelligence) positively correlated to gray matter volume in the medial dorsal nuclei of the thalamus. Additionally, voxel-based morphometry revealed that individuals with higher NEO PI-R Neuroticism scores showed decreased gray matter volume in the left orbitofrontal cortex and right anterior cingulate cortex.

Literature documents the hypothesized role of each of these cortical stuctures in proper social functioning, providing corroborating evidence in support of the results (empathy, emotion regulation, emotional-social intelligence) obtained in this study. Furthermore, these findings provide evidence in support of current theoretical understandings of the Social Brain Hypothesis. According to this

theory, in a competitive social setting, positive social attributes (greater empathy, greater overall emotional-social intelligence) might, in theory, allow an animal to be better at actively maintaining social relationships, conferring that organism fitness benefits. Selection for these attributes might be more intense in primates with the most complex social groups, such as apes, or in larger social groups, as these abilities are essential for survival. Positive selection for increased social ability may, as a result, facilitate increased gray matter volume in certain areas of the brain, driving cortical evolution throughout the primate lineage.

Today, emerging technologies such as voxel-based morphometry (VBM) and diffusion tensor imaging (DTI) permit the *in vivo* examination of neural substrates involved in social functioning. These methods provide useful analytical tools for the investigation of anthropological theories such as the Social Brain Hypothesis. In the future, these techniques will prove invaluable in studies of human cortical evolution and comparative neuroanatomy between humans and non-human primates.

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