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The association of microstructural connectivity in the brain and auditory modulation of representational momentum

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Abstract

Perceived displacement from an object's forward trajectory results in a representational momentum (RM) effect. In a behavioural task, participants watched a video of an actor reaching for/withdrawing from an object after hearing 'I'll take it' or 'I'll leave it', which was either congruent or incongruent with the subsequent action witnessed. The knowledge of other people's intentions through auditory cues and then the predictions of their actions have been found to create an effect on the strength of RM experienced. The degree to which this auditory information affects the RM effect differs for each individual. This variation could, at least partially, be due to the connectivity between parts of the brain which process auditory information, superior temporal sulcus (STS), and parts processing moving visual stimuli (area MT). Fractional anisotropy (FA) and tract-based spatial statistics (TBSS) analysis of diffusion tensor imaging (DTI) data was used to measure the microstructural connectivity of the areas of interest, which was then correlated with the RM data collected from the behavioural task. Results revealed no significant correlation between auditory modulation of RM effect and brain microstructural connectivity. However results were in line with previous research such as that by Kerzel (2005) and Hudson, Nicholson, Ellis and Bach (2015, submitted) by results being in the anticipated direction and some were approaching significance. Results from this study are integral to our understanding of people's social perception and can help aid therapies for those with neurological and psychiatric disorders.

Introduction

In order to successfully deal with moving objects in everyday life, the future trajectories of objects need to be anticipated when tracking objects, such as when visually isolating and tracking a moving car to effectively cross a busy road (Kerzel, 2005). This therefore, causes it to be a far more complex task than one might initially anticipate (Kerzel, 2005). A way to measure a person's predictions about the future trajectory of objects is to probe the errors made in their mental representation of physical rules (Kerzel, 2005). When participants are required to point out the finishing position of a moving object, participants will point further in the objects trajectory (Munger, Dellinger, Lloyd, Johnson-Reid, Tonelli, Wolf and Scott, 2006) and therefore displace its final position (Kerzel, 2005). This displacement of judgement in the position of the moving target, in the direction of the anticipated motion, is referred to as representational momentum (RM) (Hubbard, 2014). For example, if an object is moving horizontally, right to left and then disappears, the observer would indicate the object's ending position to be further left in its trajectory than its actual final position (Hubbard, 2014).

RM is seen as a positive distortion (Freyd and Finke, 1984) as a way to anticipate the successive action, as it is thought that the observer's cognitive system is unable to halt the represented motion immediately (Hubbard, 2014). Therefore, this causes a memory error in that direction to occur (Kerzel, 2005). In experimental settings, this can work with participants viewing a computer-generated series of still pictures (DeLucia and Maldia, 2006), implying motion in a constant direction (inducing stimuli) (Hubbard, 2014), or participants can view animated pictures designed to appear smooth as if watching a video (Thornton and Hayes, 2004), as first practiced by Hubbard and Bharucha (1988).

Originally, studies such as Hubbard's (1988; 1995), required the participants to give a pointing response to specify the final target position by moving the mouse cursor, with the screen co-ordinates then extrapolated from the hand's movement (Kerzel, 2005), or by physically touching the location on the screen (Hubbard, 2014). However, Goodale and Milner's (1992) neurophysiological theory suggested that the conscious perception processing of visual information, such as object location, is in another location to that of visual information for motor responses, for instance pointing (Kerzel, 2005). There are neurological processing delays between physical position and conscious perception, due to a 100ms timeframe for the brain to process visual information before it can be perceived (Kerzel, 2005). Therefore, extrapolating a position to be slightly ahead in trajectory might be the visuomotor system's solution to compensate for this delay (Nijhawan, 2002). Consequently, a perceptual response requiring only a verbal or symbolic response, such as pressing buttons to indicate their answer, is required to contrast this conflicting motor response (Kerzel, 2005).

Visuomotor processing has been investigated on a molecular level through single-cell studies on monkeys and has revealed that the superior temporal polysensory area (STP) receives input from the dorsal and ventral visual streams (Blakemore and Decety, 2001). This research has identified biological motion to respond selectively to specific cells (Blakemore and Decety, 2001). Subsequently, this research has been extended to humans, to explore if a specific neural network helps to promote this; for example Grossman, Donnelly, Price, Pickens, Morgan, Neighbor and Blake

(2000) conducted an fMRI study, comparing the activated brain regions from biological motion or coherent motion. The results found specifically the posterior region of the superior temporal sulcus (STS), to be activated in the ventral bank of the occipital extent (Grossman, et al., 2000). This was most prominently seen in the right hemisphere and left intraparietal cortex (Blakemore and Decety, 2001). Consequently, further research examining biological movement, such as hand, eye and mouth movement, has supported these findings, suggesting that the right posterior STS is crucial in biological motion detection (Blakemore and Decety, 2001). The STS is thought to be the human homologue for monkey area STP, receiving both dorsal and ventral visual stream information, for action and identification respectively. Therefore this can be interpreted as a clear crossing point for both action and identification object perception (Blakemore and Decety, 2001).

It has also been found that implied motion of static images can also have an equally similar effect, activating the regions specialised for visual motion processing (Blakemore and Decety, 2001). Furthermore, the sequential presentation of static images in different spatial locations can also result in the visual perception of apparent motion (Blakemore and Decety, 2001). Therefore the object appears to move along the shortest and most direct path, because the visual system has a bias towards creating the simplest interpretation (Blakemore and Decety, 2001). This was exemplified by Kourtzi and Kanwisher (2000), who found the occipito-temporal junction, including the medial temporal visual area, MT/V5, and the medial superior temporal area (MST), were activated when participants viewed static images of objects conveying dynamic motion, such as of a person about to throw a ball. However, they were not activated when viewing non-dynamic images such as a person sitting (Kourtzi and Kanwisher, 2000). Furthermore Blakemore and Decety (2001) found that simply observing biological movements can create activation in the premotor cortex in a somatotopic manner, evidencing that the specific regions activated in the premotor cortex to create these actions, are activated by witnessing them alone. These findings suggest that internal representation of dynamic information is stored, enabling the recollection of past movements, allowing future movements to be anticipated (Blakemore and Decety, 2001).

Indeed, there is a lot of evidence now from a range of neuroimaging techniques, such as fMRI (Grèzes, Costes and Decety, 1998), PET (Ruby and Decety, 2001), magnetoencephalogram (MEG) (Dittrich, Troscianko, Lea and Morgan, 1996) and transcranial magnetic stimulation (TMS) (Fadiga, Fogassi, Pavesi and Rizzolatti, 1995), suggesting that a number of brain regions including the premotor cortex, the posterior parietal cortex and the cerebellum, all activate while witnessing and mimicking others' actions and action generation (Blakemore and Decety, 2001).

Similarly, relative to the auditory cortical responses to external speech, self-produced speech is attenuated, which is thought to be due to this being predicted and so involves the cerebellum (Curio, Neuloh, Numminen, Jousmaki, and Hari, 2000). Stored within the cerebellum are representations of motor commands and the sensory consequences, action contexts and body kinematics (Curio, et al., 2000). The cerebellum and higher cortical regions have been hypothesised to monitor the communication between intended and achieved state (Blakemore and Decety, 2001). The processing of auditory intention is predominantly focused in the auditory cortex, which is further divided into subgroups of a core and belt region (Schirmer

and Kotz, 2006). The core region is organised tonotopically and therefore specific neurons within it are activated by specific frequencies and this information is then projected to the STS (Schirmer and Kotz, 2006). Assigning intentions to oneself and others can be described as “mentalising” (Kampe, Frith and Frith, 2003), a lower level form of Theory of Mind (Blakemore and Decety, 2001) and helps us understand signals in communication (Kampe, et al., 2003). It is considered a swift, automatic cognitive process (Kampe, et al., 2003) with a specific neural system (Vogeley, et al., 2001). Neuroimaging studies, such as Frith (2001) found the paracingulate cortex, the temporal poles and the STS are activated most regularly during mentalising.

To investigate these areas, this experiment used diffusion tensor imaging (DTI), also known as diffusion magnetic resonance imaging (dMRI) (Le Bihan, 2003) as recent advances in this technology permits the non-invasive (Soares, Marques, Alves and Sousa, 2013) measure of the brain’s local tissue microstructure (Le Bihan, Mangin, Poupon, Clark, Pappata, Molko and Chabriat, 2001). This is achieved by quantifying the three-dimensional diffusion of water (Alexander, Lee, Lazar and Field, 2007) molecules as well as the transport of ions (Geeter, Crevecoeur, Dupré, Hecke and Leemans, 2012) as a function of spatial positioning (Alexander, et al., 2007). A linear relationship between the transport of ions, eigenvalues of the conductivity, water molecules, and self-diffusion tensors, exists due mainly due to the constraints imposed by the extracellular space (Tuch, Wedeen, Dale, George and Belliveau, 2001). The degree, magnitude and orientation of anisotropy is determined by the diffusion tensor (Alexander, et al., 2007) and the mean diffusivity (MD) is used to measure the quantity of free water diffusion, which is hindered by diffusion barriers (Hübers, Klein, Kang, Hilker and Ziemann, 2012). This MD measure then establishes the eigenvalues average (Alexander, et al., 2007). The membrane density and fluid viscosity is inversely measured by MD and its direction is then averaged (Alexander, et al., 2007). Diffusion anisotropy identifies the extent to which the diffusivities are a function of the diffusion weighted (DW) encoding direction (Alexander, et al., 2007). The anisotropic diffusion profiles are created (Hübers, et al., 2012) due to the preference of diffusion, along axon fibres rather than perpendicular to axon fibres (Zhu, Zhang, Jian, Hu, Chen, Yang, Lv, Han, Guo and Liu, 2014). Diffusion anisotropy and principal diffusion direction gives estimates of the brain’s white matter connectivity patterns (Alexander, et al., 2007). Fractional anisotropy (FA), which measures which range between 0 and 1 (Alexander, et al., 2007), is used most commonly in this and works by amassing the amount of direction the diffusion of the water takes along the WM fibres (Hübers, et al., 2012). Axon density, diameter and degree of myelination have been found to have an influence on FA and MD (Beaulieu, 2009). Tractography uses DTI to determine the diffusion properties within a single voxel, it is possible to then evaluate the relationship in diffusion with other voxels and ultimately the entire WM fibre pathways (Zhu, et al., 2014). Consequently, it is possible to generate highly plausible, anatomical estimates of the human brain’s white matter trajectories (Alexander, et al., 2007).

By utilising these neuropsychological methods, it is possible to measure the brain regions involved in these processes, such as for analysis of visual motion using the extrastriate visual area medial temporal (MT) or medial superior temporal cortex (MST) (Kourtzi and Kanwisher, 2000) and even process apparent motion (Goebel, Khorram-Sefat, Muckli, Hacker and Singer, 1998). Other previous research such as that by Kourtzi and Kanwisher (2000) and Senior, Barnes, Giampietro, Brammer,

Bullmore, Simmons and David, (2000), also found activity in area MT and generally within the posterior regions such as V5 (Senior, Ward, and David, 2002). Through the innovation of brain imaging techniques, such as fMRI and DTI, more detailed questions about the precise neural substrates relating to RM are able to be assessed; investigating where in the brain RM effect is processed and if its links with auditory system has an effect (Senior, et al., 2002).

Therefore, based on previous research such as that by Grossman, et al. (2000), Kourtzi and Kanwisher (2000) and Schirmer and Kotz (2006), which highlights the significance of areas MT and STS in perception of biological apparent motion and auditory intention processing respectively, this experiment will investigate these areas for their microstructural connectivity in the brain and its correlation with RM effect. Through the use of a symbolic response by means of a probe stimulus to determine the RM effect so as to counteract effects from motor responses, as described in Kerzel's (2005) work above.

It is expected that the results will reveal a greater connectivity between areas STS and MT in participants who experience a greater modulation of the RM effect by auditory information. To test this hypothesis, a within-subjects design was used to assess auditory modulation of RM, this then correlates with diffusion-tensor image (DTI) measures of microstructural connectivity in white matter throughout the brain. If results are as expected, it would demonstrate that brain microstructural connectivity plays an important role in our effectiveness to make predictions about other's actions, suggesting that the strength of the connectivity in STS correlates with the effect of auditory stated intentions on expectations, developed from witnessing the object-hand interaction.

Method

Participants

Twenty eight participants (N = 28, 19 females, mean age of 23.5 years, *SD* = 9.2 years) psychology students were recruited from Plymouth University and received either a participation point or £4 for participation. All were native English speakers. Participants gave written informed consent prior to participation. The experiments adhered to the ethical guidelines of Plymouth University and the ESRC, in accord with the Helsinki declaration of human rights.

Materials

Diffusion tensor imaging

All participants had an MRI scan on a 1.5-Tesla Philips Intera scanner. A diffusion weighted single-shot spin-echo EPI sequence acquired the DTI data. The repetition time (TR) = 9543 ms, echo time (TE) = 66 ms and the reconstruction matrix = 96x96 mm, with a flip angle of 90 degrees. The order of acquisition was interleaved first odd then even at a transverse oblique orientation. Diffusion weighting was performed along 32 independent directions with 0.4mm gap and with a b-value of 1000 s/mm². The acquisition voxel size = 2.33x2.33x3 mm and reconstruction voxel size = 1.75x1.75x3 mm, with a field of view = 224mm. This also acquired a reference image (b=0 s/mm²).

Behavioural Data

M-Audio Microtrack 2 Digital Voice Recorder was used to record the audio stimuli and a Canon Legria HFS200 for the visual stimuli. The visual stimuli was then edited using MovieDek and Corel Paintshop Pro X6 and ran using Presentation software (NeuroBS), while the audio stimuli were delivered using a Logitech PC120 combined microphone and headphone set. The computers used were Viglen DQ67SW computer with a Philips Brilliance 221P3LPY display (resolution: 1920 X 1080, refresh rate: 60 Hz).

Visual Stimuli

The video starts with an object on the left of the screen and a right hand in a non-reaching, relaxed pose on the right side of the uniform black screen (as seen in Figure 1). Four reaches in total were filmed and put into a sequence with either safe objects, a glass, wine glass, plastic bottle or knife with blade pointing away from the hand; or pain inducing objects, a broken glass, broken wine glass, cactus and knife with its blade pointing towards the hand (Figure 2); and each sequence contained 29 frames. All the visual stimuli occupied a .07 x .12 degree visual angle on the screen and were presented at random positions, across trials, along the x-axis.

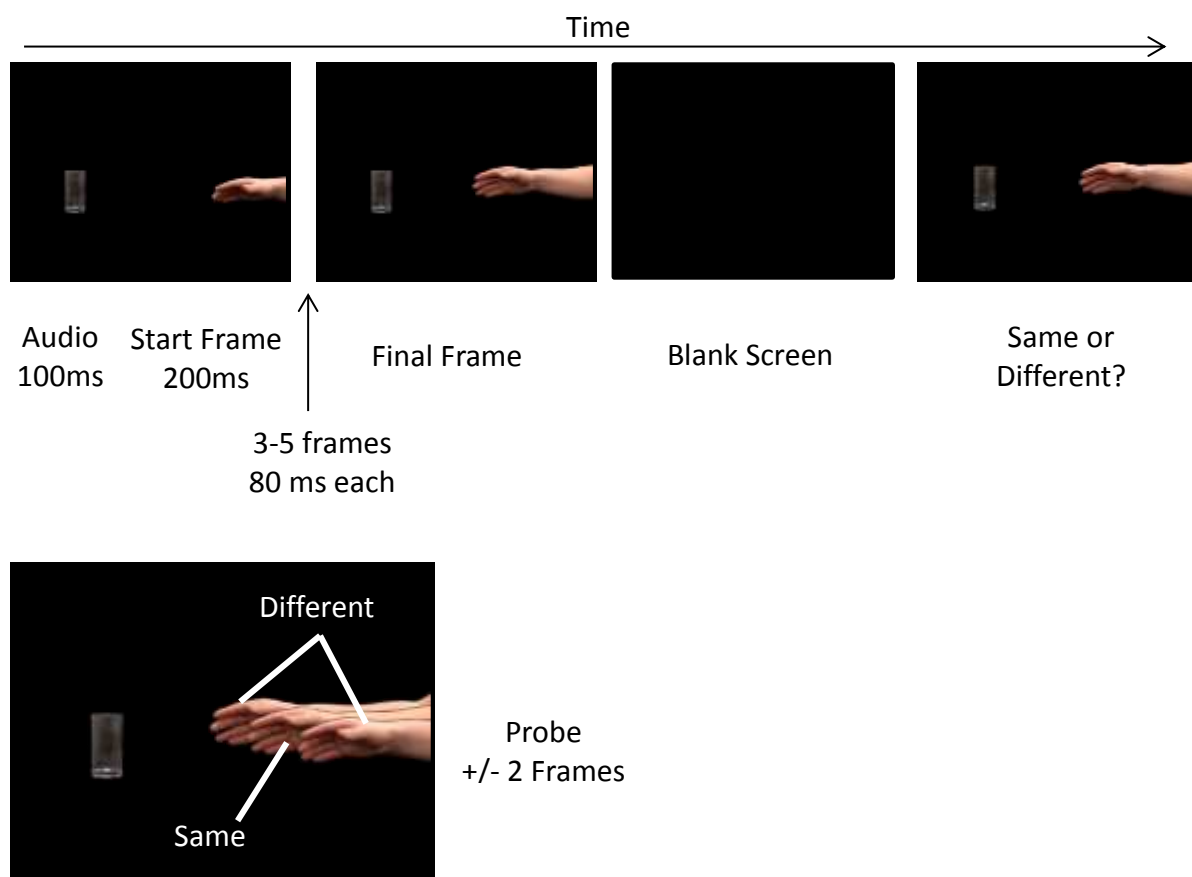


Figure 1: Trial sequence. An example of the trail sequence shown to participants.

Here, the actor is reaching towards an object, the unbroken glass, which is 'safe' to grasp. The final image has superimposed all three possible final probe stimuli, to show it could be in the 'same' position as the final position (centre); two frames in

front and therefore displaced forward in time and classed as 'different'; or two frames behind and therefore displaced backwards in time and again 'different'. If the action was a withdrawal from the object this mean displacement forward in time was instead even further from the object and displacement backwards in time were actually nearer the object.



Figure 2: Experimental stimuli. The different visual objects, randomly selected to appear in each trial. 'Safe' version to the left of each pair, above for the knife; and 'unsafe' equivalent version to the right of each pair, below for the knife. The knife's classification was its orientation to the hand; with the handle closest to the hand, 'safe', or the blade pointing to the hand, 'unsafe'.

Audio Stimuli

There were two auditory stimuli, one of an actor saying "I'll Take It" and the other "I'll Leave It", both for a duration of 1000ms. "I'll Take It" said with inflation and "I'll Leave It" with deflation to increase ecological validity in line with the auditory cortex's core region being organised tonotopically. They were both played through the headphones at 75% volume with a right bias by 50% to align with the position of the actor being to the right of the screen.

Design and Procedure

A within subjects design was used. Participants were asked to sit at a computer with the software already open and each was sat approximately 60cm from the screen. All participants were given a brief (Appendix A) and reminded that they were free to withdraw from the study at any time and none did so and all signed a consent form (Appendix B). Instructions were issued (full instructions available in Appendix C) with pictorial aids (Appendix D) and written instructions on the screen. The following is a short version of the instructions given:

"Each trial will start with a still image of a hand and an object. Through the earphones you will hear the actor say one of two intentions. He'll either say "I'll take it" or he'll say "I'll leave it". The movie is very quick, then you will see a blank screen, after which you will see a still image of the hand and the object. However, when it re-appears, the position of the hand can either be the same or different to the final position of the movie. If you think they are the same you don't do anything, you just wait a few seconds for the next trial to start. However, they could be in a different position. It could be nearer the object or further away from the object than the final position. In both of these cases it is different and you must press the spacebar with your left hand."

In the instructions, the hand and male voice in the audio cue was referred to as "he" and "the actor" to 'humanise' the video and promote the perception of an intentional agent.

Each trial then began with a fixation cross appearing in the middle of the screen and then a blank screen, for a total duration of 1000ms. The action sequence then started and showed the hand in a relaxed, non-reaching position to the right of the screen and an object to the left of the screen. The exact starting location was randomly chosen between frames 13 and 17 along the x-axis. A delay then occurred and was randomly selected to be between 1000ms and 3000ms. The participants were then presented with the auditory stimuli for 1000ms and either heard “I’ll take it” or “I’ll leave it”, incongruent of whether the object was painful or safe and randomly selected. The auditory intention was also either congruent or incongruent with the subsequent action witnessed. 200ms after, the action sequence started. Each frame in the action sequence lasted 80ms and was randomly selected to be 3 or 5 frames long on each trial. Participants then witnessed the actor reaching for/withdrawing from an object.

For 250 ms a blank screen was presented before the single frame probe stimulus reappeared on the screen. This was taken from the action sequence and stayed on the screen for 4000 ms or until a response was given by the participant. The single frame was the probe stimulus either in the same position as the final frame of the preceding action sequence, displaced one/two frame(s) forwards in time along its trajectory or displaced backwards in time. This resulted in five possible positions for the probe to appear in relative to the final position of the hand seen at the end of the sequence.

To indicate that the probe position was considered different from the hand’s final position seen in the action sequence, the participants were required to press the spacebar in the action sequence, and to give no response if viewed to be the same position.

A factorial design was used to present both levels of intention (“I’ll Take It” and “I’ll Leave It”), Action Direction (Reach and Withdrawal), and Probe Direction (-2, -1, 0, +1, +2). This was randomly selected on each trial and repeated 6 times (120 trials). There were also 10 catch trials where the probe was displaced 4 frames from the final position, however these trials were not further analysed. A debrief was issued to each participant at the end too (Appendix E).

Each participant’s RM score was determined by the percentage of trials in which the probe stimulus was reported as different from the final position of the action sequence and was then indexed by auditory information to create an auditory modulation score. This was determined by calculating the difference between the congruent RM and incongruent RM effects, congruent when the action witnessed and auditory information heard by the participant were the same; and incongruent when the action witness and auditory information heard were different.

An ANOVA revealed that the one frame displacement less readily detected and therefore had a weaker interaction with RM than two frame displacement, and that this was a statistically significant difference $F(1,27) = 59.73, p < .001, \eta_p^2 = .689$ (full statistical SPSS output available in Appendix F). This was also consistent with previous research by Hudson, Nicholson, Ellis and Bach (2015, submitted). Therefore the RM from the two frame displacement was used for analysis.

Diffusion tensor parametric maps

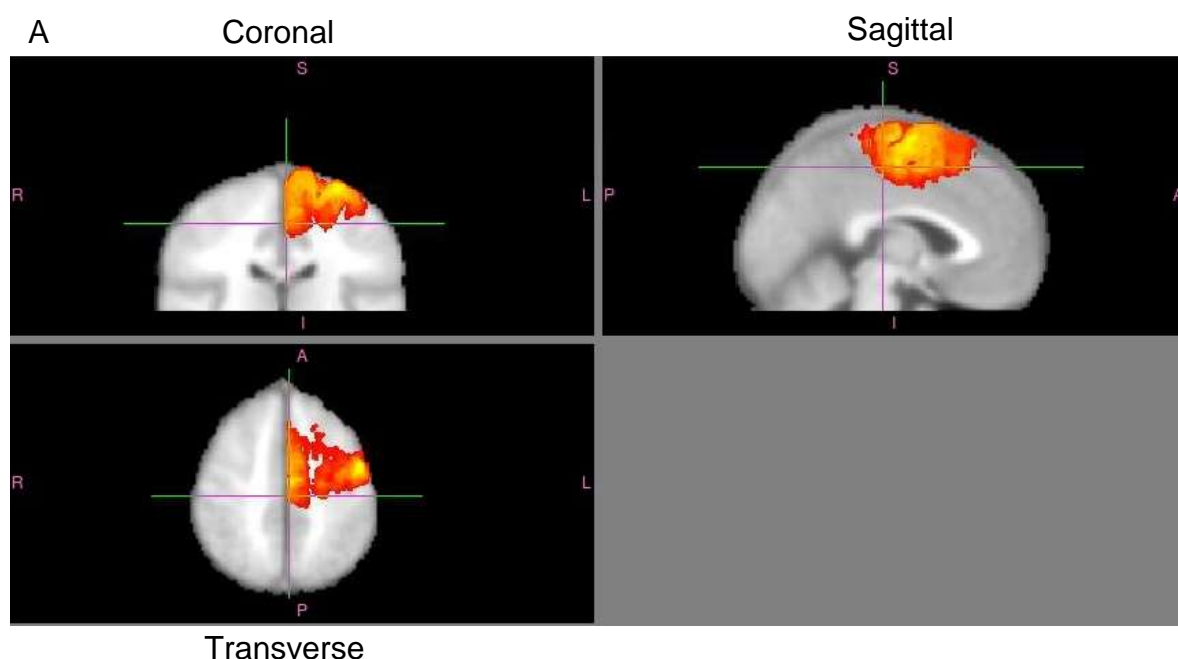
All DTI parametric maps were conducted using The Oxford Centre for Functional MRI of the Brain (FMRIB) software library (FSL v4.1.2) (Smith, et al., 2004) Using this software motion could be corrected for with Eddy current correction, diffusion tensor was fitted and whole-brain FA maps and mean diffusivity maps could be created.

DTI Data Processing and Analysis

Using FSL FDT (Jbabdi, Sotiropoulos, Savio, Grana, Behrens, 2012), the DTI data were processed, producing fractional-anisotropy (FA) images. The FA images were then analysed using tract-based spatial statistics (TBSS) (Smith, Jenkinson, Johansen-Berg, Rueckert, Nichols, Mackay, Watkins, Ciccarelli, Cader, Matthews and Behrens, 2006), which is part of FSL (Smith Jenkinson, Woolrich, Beckmann, Behrens, Johansen-Berg, Bannister, De Luca, Drobnyak, Flitney, Niazy, Saunders, Vickers, Zhang, De Stefano, Brady and Matthews, 2004). Using FSL Randomise (Winkler, Ridgway, Webster, Smith and Nichols, 2014), an individual measure of the RM by auditory modulation (AudMod) effect was regressed against FA data within a white-matter skeleton defined by TBSS to determine the relationship between auditory modulation of RM and brain structural connectivity.

Then to test the behavioural data against the skeletonised data a regression, using randomise (Winkler, et al, 2014), of the auditory modulation of RM against FA was run. The RM was then mean-centred (demean or standardize to z scores), as well as the FA data, to remove effects of overall level and focus solely on the relationship between the behavioural index and FA.

TBSS statistical analysis was also conducted on group comparison of high and low AudMod.



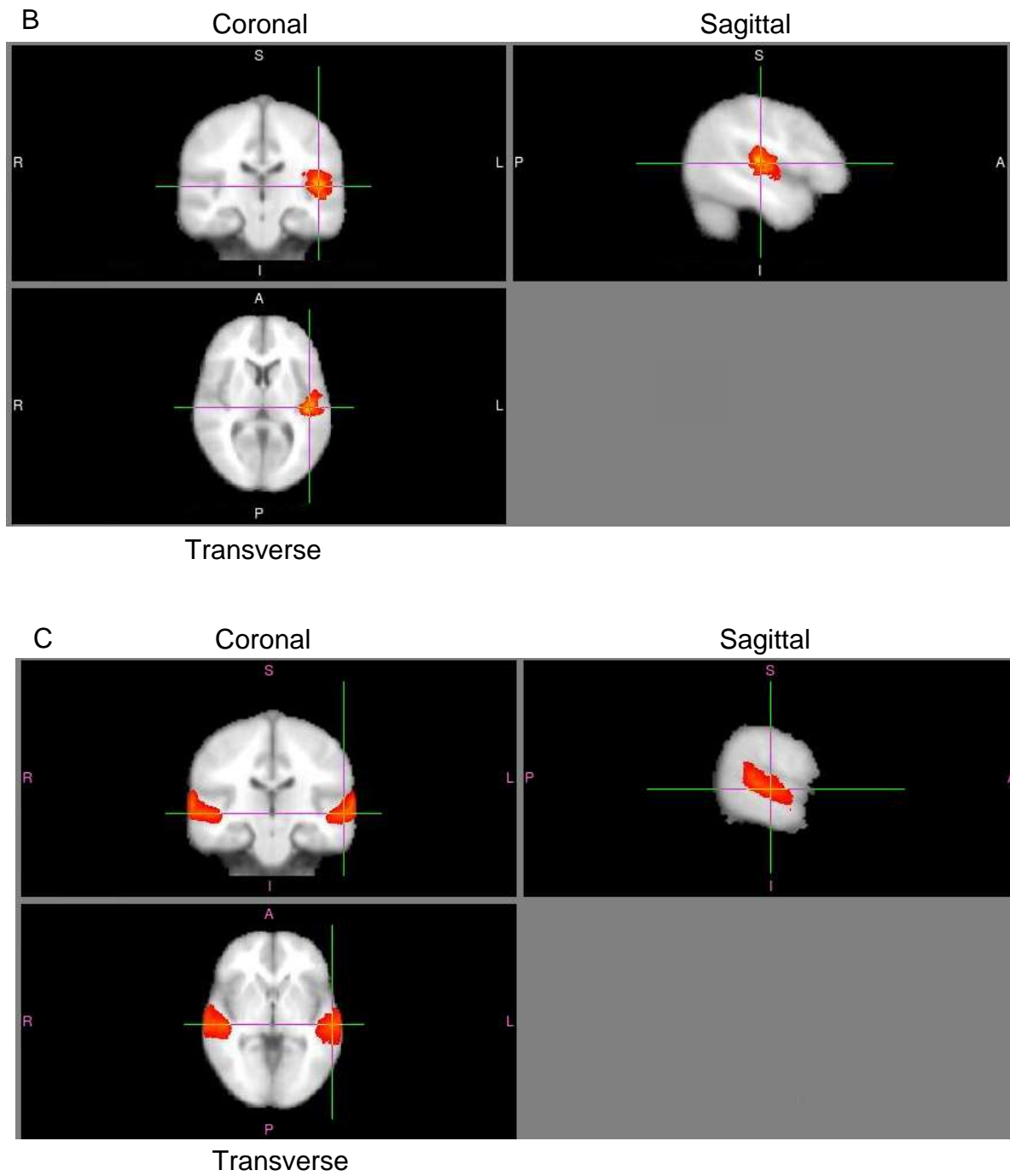


Figure 3: Indicates the primary area of interest, the premotor cortex, primary auditory cortex and the superior temporal gyrus, respectively.

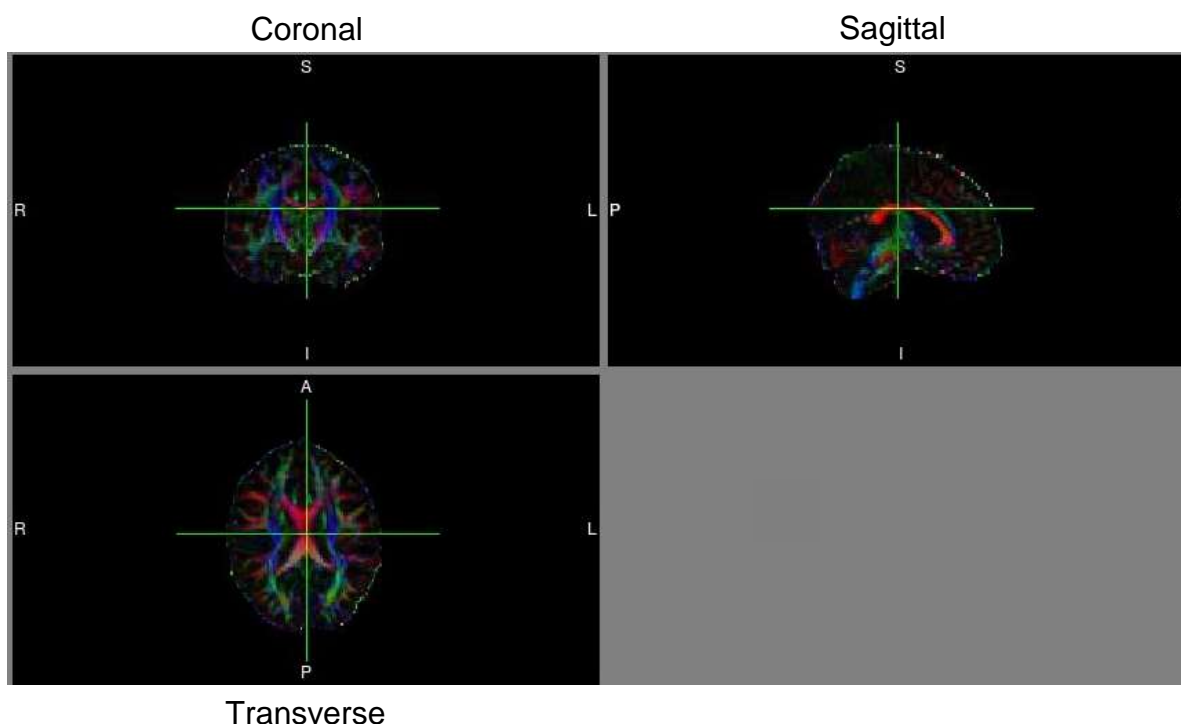


Figure 4: Mean FA analysis. FA scan for one participant to show all white matter diffusion pathways. Red indicates a diffusion pathway travelling left/right, blue head/foot, and green back/front ($n = 1$).

The mean FA was analysed first and individually for each participant so that this can be used for further statistical analysis to be performed. Figure 4 shows all the white matter pathways for participant 3 as an example of the output from this analysis.

Results

Representational Momentum Analysis

The relationship between action direction, RM scores and intention with the standard error bars, is illustrated in Figure 5.

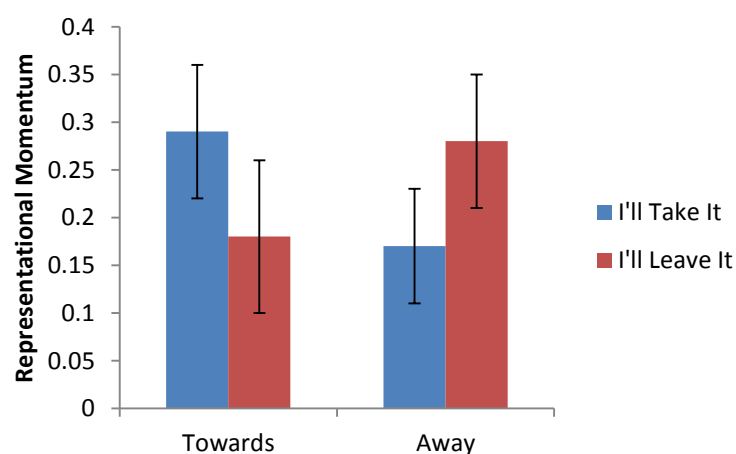


Figure 5: The graph shows the average RM effect experienced after the actor has said either “I’ll take it” or “I’ll leave it”, for reaches towards or withdrawals from the object ($n = 28$).

The data in Figure 5 shows that the size of the representational momentum effect was larger when the action direction was congruent with the actor's intentions, as seen by the outer bars, than when incongruent, as seen by the inner bars.

A Shapiro-Wilk's test, along with visual inspection of normal Q-Q plots, histograms and box plots revealed the data was approximately normally distributed and therefore it is normal distribution is assumed allowing for ANOVA testing (Descriptive statistics of these tests are available in Appendix G, histograms and normal Q-Q plots available upon request).

A three-way analysis of variance (ANOVA) was conducted on the repeated-measures factors: Intention ("I'll Take It" vs. "I'll Leave It"), Action Direction (reach vs. withdrawal) and Probe Direction (forward vs. backward) based on the percentage of trials which were reported as having a different probe stimulus final position. Those which were the same were not analysed. (Full SPSS output is available in Appendix H).

This revealed that the interaction between Intention, Action Direction and Probe Direction was statistically significant ($F(1,27) = 5.33$, $p = .029$, $\eta_p^2 = .165$). (Full details of statistical procedures are available in Appendix H).

DTI Analysis

In order to then run the TBSS statistical analysis, the Randomise (non-parametric permutation inference) statistics was run for the four comparisons of RM positive (RM+), RM negative (RM-), Auditory Modulated positive (AudMod+), Auditory Modulated negative (AudMod-). The results from this did not produce any significant ($p < 0.05$) voxels.

The statistical map of the voxels closest to significance is illustrated in Figure 6.

Of the statistical analysis for the four comparisons, the best analysis was AudMod+, as seen in Figure 6 A and B, which reached $p = 0.24$ although this is not statistically significant. The voxels are highlighted in red and are located around the supramarginal gyrus, the parietal lobe and the precentral gyrus within the right hemisphere.

The results of mean diffusivity for the four comparisons of RM+, RM-, AudMod +, AudMod-, also did not produce any significant ($p < 0.05$) voxels.

The statistical map of the voxels closest to significance is illustrated in Figure 7.

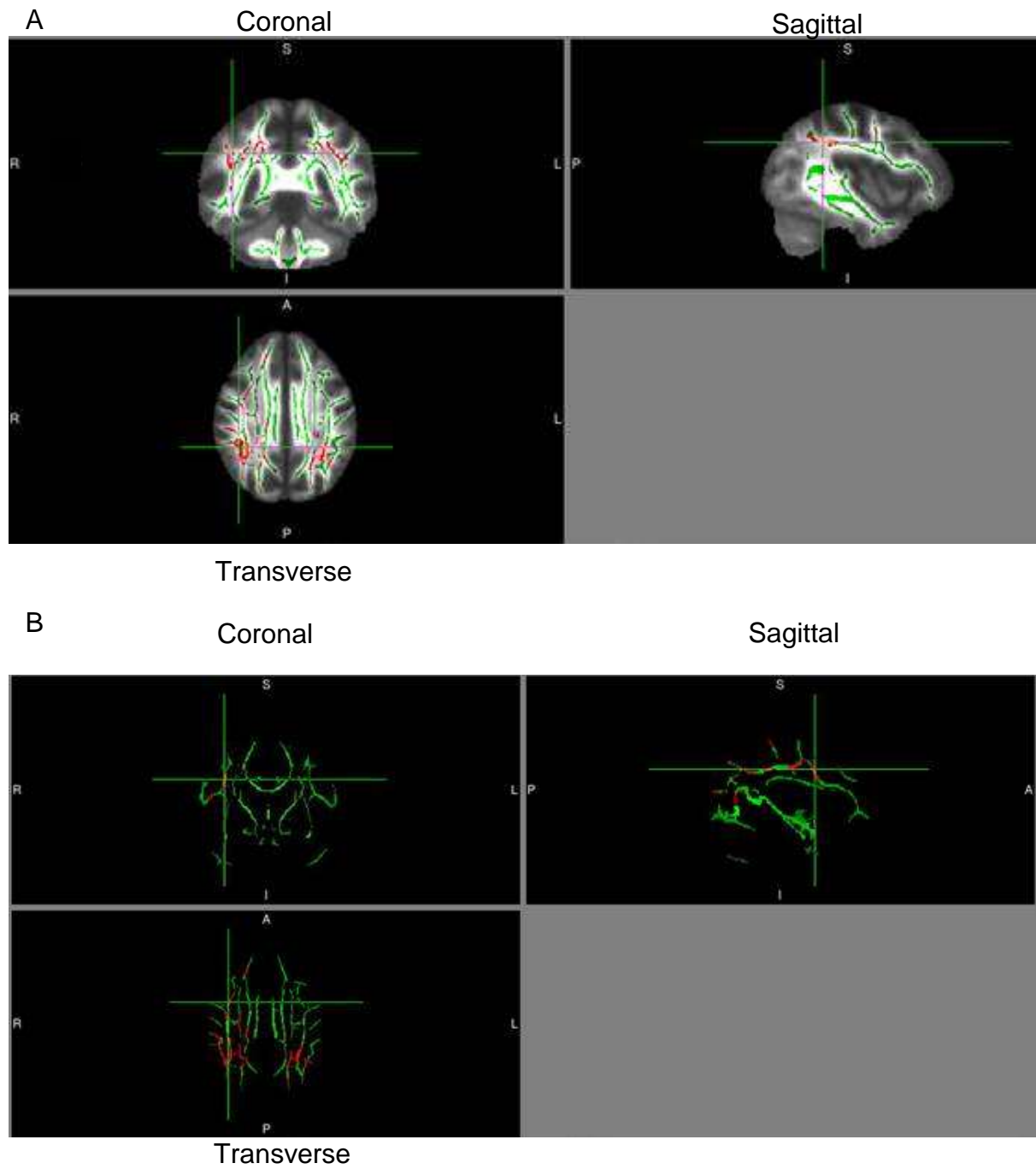


Figure 6 A and B: Randomise results for AudMod+. The statistical map showing the greatest number of nonsignificant voxels, ($n = 28$).

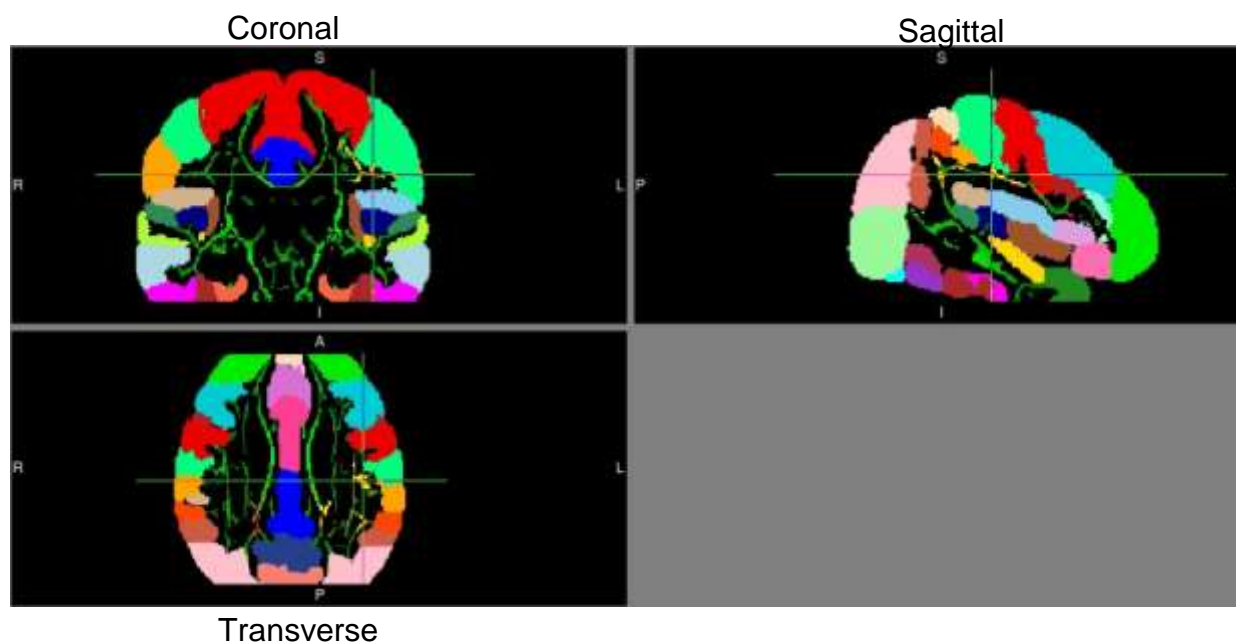
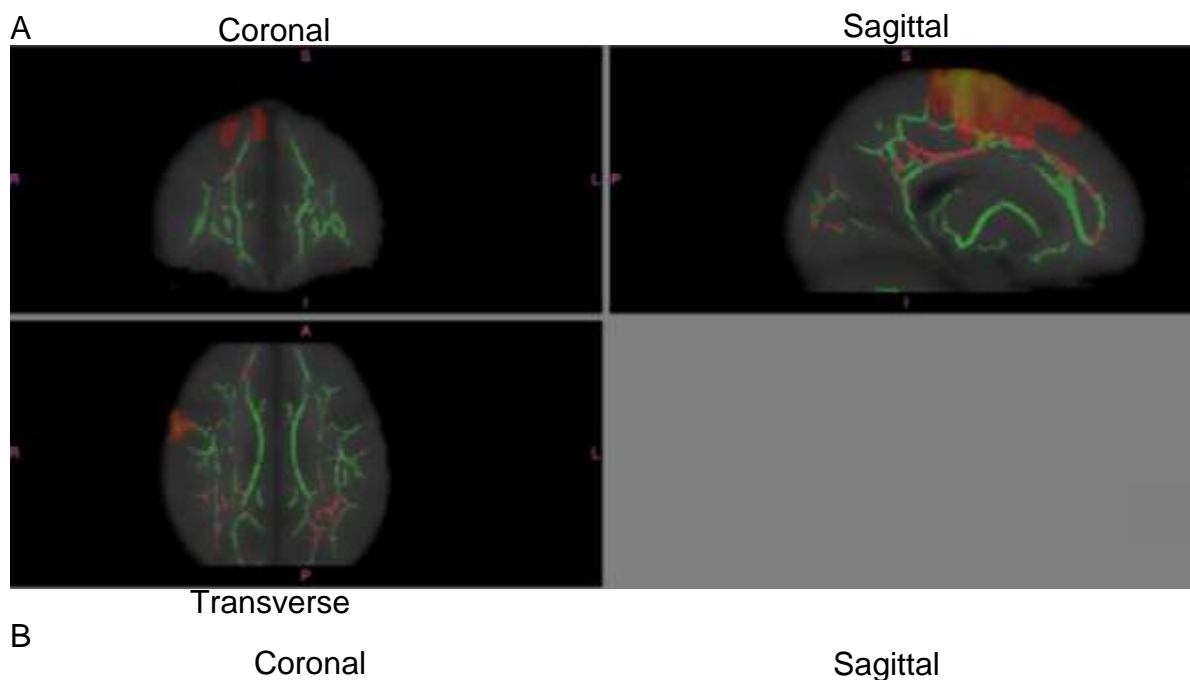
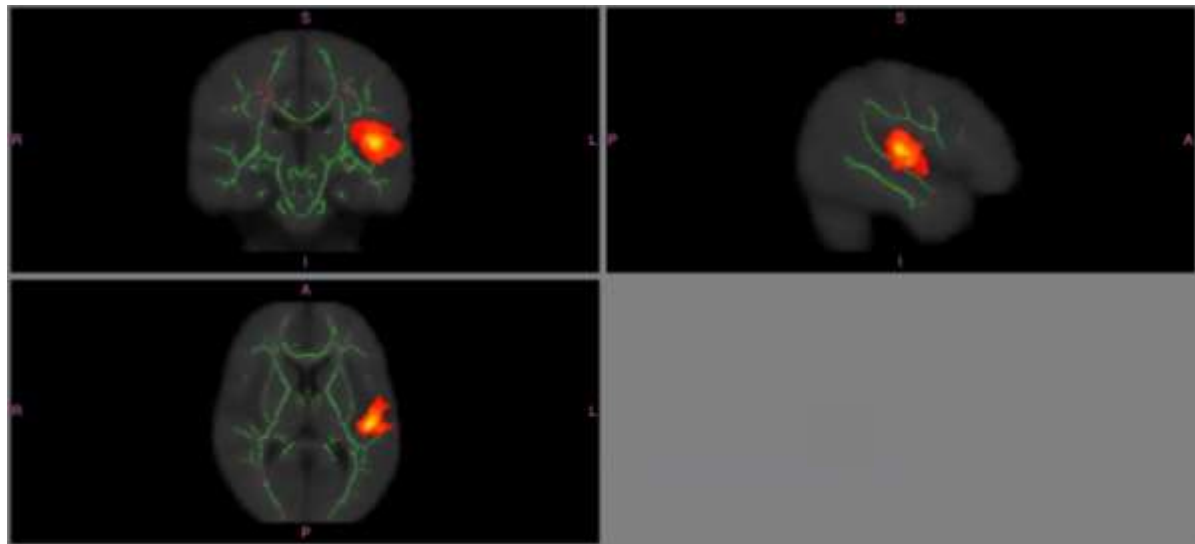


Figure 7: Mean Diffusivity. Mean diffusivity statistical map for AudMod- over structural atlases ($n = 28$).

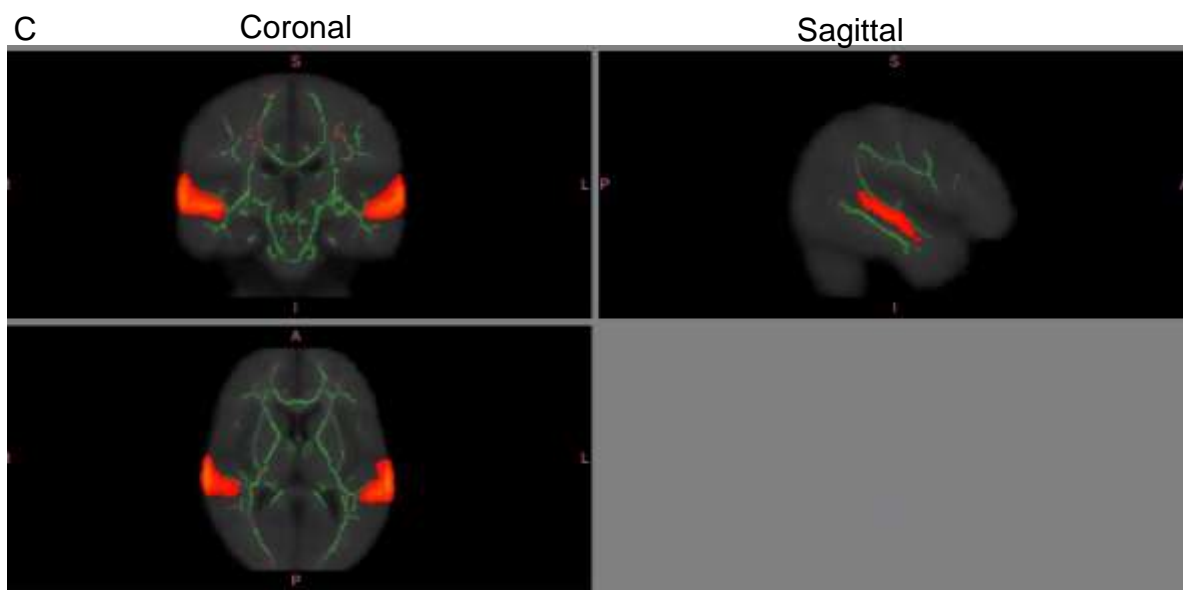
The statistical maps for all four comparisons revealed no significant voxels, however the AudMod – was very nearly significant, $p=0.07$, as seen in Figure 7 as a cluster of tracts in yellow. This could be seen as approaching significance. These very nearly significant voxels were particularly seen in the superior longitudinal fasciculus and postcentral gyrus.

Using a standard brain overlay and atlas, these results were overlaid against the highlighted areas of interest, illustrated in Figure 8.





Transverse



Transverse

Figure 8: Mean Diffusivity results over standard brain skeleton with areas of interest highlighted in red. Statistical map of the mean diffusivity results with a brain skeleton overlay and highlighted areas of interest ($n = 28$).

The data as seen in Figure 8 A motor cortex, B primary auditory cortex and C posterior superior temporal gyrus, identify the key connections between these areas.

TBSS analysis was also conducted on group comparison of high and low AudMod as illustrated in Figure 9.

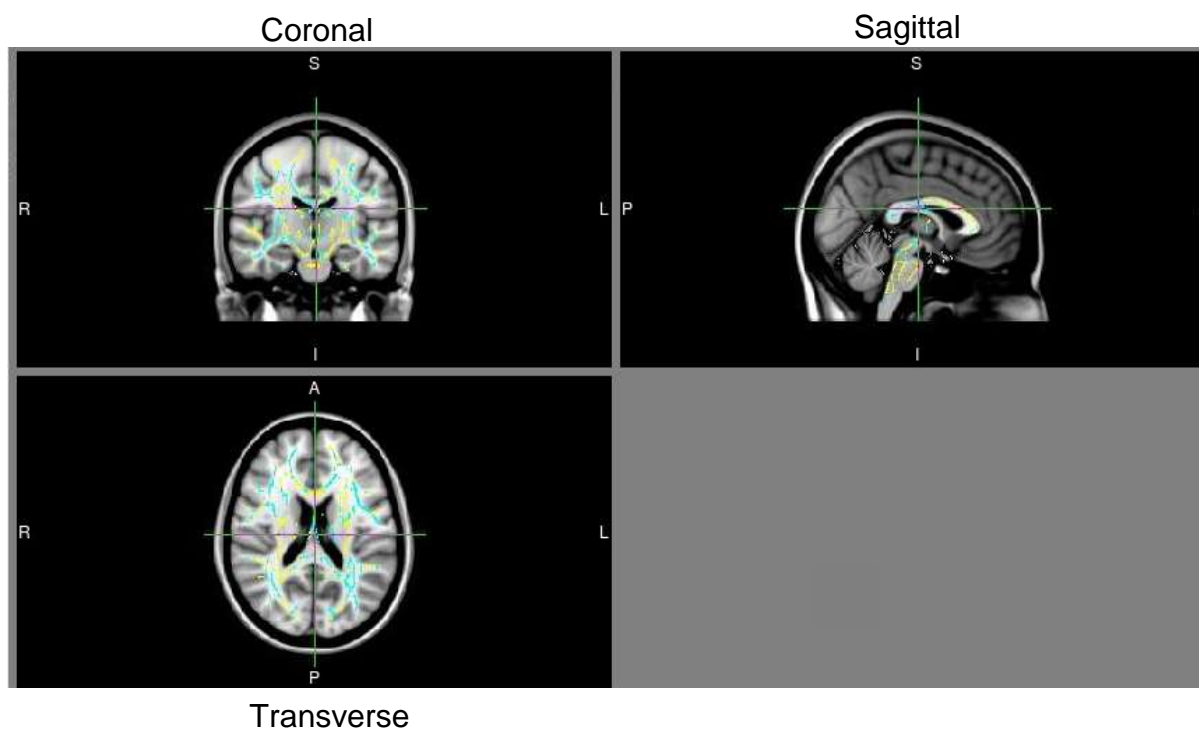


Figure 9: TBSS statistical map for group comparison of high and low AudMod. Statistical map highlighting the differences in connections between those who scored high AudMod and low AudMod ($n = 28$).

TBSS analysis of group comparison should highlight any connections which are different between those who had a low AudMod score, $<.19$, and those who had a high AudMod score, $>.28$. No statistically significant voxels were reported but the connections are highlighted in blue in Figure 9.

Discussion

The results on RM were consistent with previous research, such as that by Kerzel (2005), showing that there is a bias towards the future in perception of action, resulting in anticipation of the course of the action. The results also highlighted that this bias is influenced by knowledge of intentions, as seen in current research by Hudson, Nicholson, Ellis and Bach (2015, submitted). This was seen by an increased RM effect for movements towards an object after hearing the congruent intention "I'll take it", as well as for movement away with congruent intention of "I'll leave it". Compared to the lower RM for incongruent movement and intention, by movement towards an object after hearing the incongruent intention "I'll leave it", as well as for movement away with incongruent intention of "I'll take it". Therefore, actions congruent with auditory intention create a greater RM effect than actions incongruent with intention. This shows how the strength of RM effect is determined by action and intention congruency. Overall, these results demonstrate how our perceptions of other people's actions affect our anticipation of the objects future trajectory, through automatic incorporation of knowledge about other's intentions and low-level motion information.

Further to this, the relationship between the brain's microstructural connectivity and strength of effect of RM by auditory modulation was consistent with the experimental hypothesis. Showing that brain microstructural connectivity would play an important role in our effectiveness to make predictions about other's actions and that the strength of the connectivity in STS correlates with the effect of auditory stated intentions on expectations, developed from witnessing the object-hand interaction. This was highlighted by the increased structural connectivity within the motor cortex, primary auditory cortex and posterior superior temporal gyrus, which are responsible for motor control, auditory processing and language perception respectively, for participants with greatest auditory modulation of RM effect.

However, the correlation failed to reach significance which could be due to the relatively small sample size. Despite the lack of significance, the data was still in the anticipated regions, motor cortex, primary auditory cortex and posterior superior temporal gyrus, involved in motor control, auditory processing and language perception. Some of the data is also approaching significance, such as mean diffusivity for AudMod-. This therefore suggests that there could still be a correlation between RM by auditory modulation and brain microstructural connectivity. Further research on the dynamics of the relationship between RM by auditory modulation and brain microstructural connectivity is required.

Furthermore, the results were in line with previous research such as that by Grossman et al (2000), who found in their experiment that activation was biased and more pronounced to the right hemisphere compared to the left hemisphere. This is consistent with results seen in the AudMod+ through randomise. Their experimental results revealed this to be in the posterior STS when seeing biological motion, which is close to the activation seen in the supramarginal gyrus in these results and could explain the bias seen. This suggests that this area is integral in our mental processing of biological motion (Blakemore and Decety, 2001). The right hemisphere is also vital for processing emotionally oriented verbal information (Schirmer and Kotz, 2006). With the STS receiving both dorsal and ventral visual stream information, as well as auditory processing information, it is therefore a clear crossing point for both the action and identification of objects (Blakemore and Decety, 2001), as well as auditory perception (Schirmer and Kotz, 2006). However the audio stimuli were biased towards the right so it can be suggested that the increased activation for auditory modulation may be due this bias.

Furthermore, the statistical analysis between the two groups of those who experienced high AudMod compared to those who had low AudMod, revealed no statistical significance which means there is no significant difference of the white matter tractography between those two populations. This was not consistent with the experimental hypothesis. It would be expected that the results would identify a significant difference between the microstructural connectivity, showing those who experienced high AudMod to have greater structural connectivity between the areas of interest. This again could be a result of the relatively small sample size not giving an effective range.

A potential weakness of this study was participants' sensitivity to the probe and full involvement with the task. As mentioned in the method, there was an additional +/- 4 frame 'catch trial', designed to identify and exclude participants who were not sensitive to the task or not fully engaging with the task. If a participant's score was

less than 10% higher than in the experimental trials or less than one standard deviation from the group mean, they were originally to be excluded. However, for this experiment it would have entailed excluding six participants from an already very limited sample and so were kept in. This exclusion criteria is in line with previous research such as Hudson, Nicholson, Ellis and Bach (2015, submitted). However, this inclusion could cause less reliable results and could have contributed to the study's lack of significant results. Future studies would be advised to maintain this exclusion criterion whilst increasing sample size.

Additionally, a potential weakness was not having an equal amount of 'young adult' and 'older adult' participants. Previous research such as that by DeLucia and Mather (2006) have found that extrapolating motion occurs more slowly in older adults than young adults, and that the right dorsal cortical pathway activity for spatial processing, is reduced in older adults (Chen, Goedert, Murray, Kelly, Ahmeti and Barrett, 2011). In this experiment the majority of the participants were aged 19 or 20, giving a very unrepresentative sample of the general population as a whole. Further experimentation could involve a broader age range of participants, investigating group comparisons of the high and low age, comparing microstructural connectivity correlations with AudMod in these two age groups. This would be predicted to yield a better representation of the general public.

Furthermore, the participants were all psychology students who may have knowledge of what RM is and/or experienced the behavioural test before, receiving a debrief on what was being measured. This could have caused demand characteristics with participants trying to give the answer they think an experimenter would want, instead of their true judgement. Courtney and Hubbard (2008) found that even though RM occurred for both informed and uninformed participants, RM was greater for uninformed, showing that previous knowledge about it can have an effect in experimental settings.

Inferring intentions from auditory cues involves a series of highly complex brain mechanisms (Schirmer and Kotz, 2006). These results clearly suggest that our brains appear to be "hard-wired" to perceive motion (Blakemore and Decety, 2001) and are sensitive to intention cues (Schirmer and Kotz, 2006). This is because our brains have evolved to detect biological motion, enabling us to quickly spot this movement from a complex background, identify the source and categorise as threatening or enticing (Blakemore and Decety, 2001). From this we seemingly immediately are able to predict the future of this motion and consequently produce an appropriate response to it (Blakemore and Decety, 2001). Also, integrating this with knowledge of other's intentions helps us to deduce the mental states of those around us (Blakemore and Decety, 2001). These evolved adaptations have enabled humans to live successfully in social groups and develop fight/flight mechanisms for successful threat identification and response (Schirmer and Kotz, 2006).

Identifying these connections, as well as isolating them, can expand our comprehension of normal as well as dysfunctional social perception. It can also considerably advance our understanding and approach to treatment for people with neurological and psychiatric disorders. Particularly, it could help those who lack theory of mind, specifically autism, as well as for those with damage to the brain through injury or stroke.

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