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Auditory and Sensorimotor Resting State Networks in Children Preceding and Following Overt Speaking

by

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Abstract

Measuring the impact of a task on resting state networks (RSNs) is important for understanding their relative strength and stability. Little is known about RSN stability in adults and less is known about RSN stability in children. The effect of an active task on RSNs was measured on fourteen children using functional magnetic resonance imaging (fMRI). The auditory, sensorimotor, and default mode RSNs and the speech network were measured before, during, and immediately following overt speaking. The results indicated that before overt speaking, these RSNs were stronger with greater areas of activation compared to immediately following the task. The speech network showed a shift from right- to left- activation, from rest to speech, respectively. These results demonstrate the importance of studying task effects on RSNs and contribute to understanding neural development in healthy children. This research provides a basis for clinical applications in terms of identifying treatment effects on RSNs.

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Introduction

Detecting differences in brain activity between a resting condition and a task-orientated condition has been the premise of functional neuroimaging since its advent. Primarily, the focus has been on correlating brain activation patterns with specific task-driven conditions. For example, unique brain activation patterns have been described during tasks such as repetitive finger movements, viewing pictures, or speaking. Studies like these are aimed at acquiring a better and more complete understanding of typical brain function (Hammeke *et al.*, 1994, Deyoe, *et al.*, 1996, Olman, Pickett, Schallmo, & Kimberley, 2012). More recently, researchers have focussed on brain activity associated with non-task states or resting states. Of particular interest are regions of activation detected during rest that conversely "deactivate" during task-driven conditions (Greicius, Krasnow, Reiss, & Menon, 2003, Fransson, 2005). Brain regions that are active during rest are known as resting state networks (RSNs). Beckmann, DeLuca, Devlin, and Smith (2005) define RSNs as "neuronal baseline activity of the human brain in the absence of deliberate and/or externally stimulated neuronal activity" (p. 1001). A number of RSNs have been identified, including the auditory network, sensorimotor network, and default mode network (Shirer, Ryali, Rykhlevskaia, Menon, & Greicius, 2012). Little is known about the contribution of the RSNs to overall function in adults and even less is known about these networks in children (Fair *et al.*, 2008, Supekar *et al.*, 2010, de Bie *et al.*, 2012). Moreover, stability of RSNs is not well understood nor are the effects of task-driven activity on these networks. However, researchers are beginning to compare RSNs acquired prior to with those following a task-driven condition in adults (Tung *et al.*, 2013, Sami & Miall, 2013, Albert, Robertson, & Miall, 2009, Waites, Stanislavsky, Abbott, & Jackson, 2005). Of particular interest in the present study were the auditory and the sensorimotor RSNs because of their potential overlap with overt speaking (de Bie *et al.*, 2012, de Luca, Beckmann, De Stefano, Matthews, & Smith, 2006, Beckmann *et al.*, 2005). The aim of the present study was to further characterize the auditory and sensorimotor RSNs in children and to determine whether or not there was an impact on these networks immediately following overt speaking.

Networks of Interest

The current study was an exploratory investigation of RSNs in children with a focus on the following networks: (1) auditory RSN, (2) sensorimotor RSN, (3) default mode RSN, and (4) task-driven speech network. The auditory RSN has been reported to include the following brain regions: Heschl's gyrus, superior temporal gyrus, insula, and thalamus (Beckmann *et al.*, 2005, Shirer *et al.*, 2012). The sensorimotor RSN has been reported to include the following brain regions: precentral gyrus, postcentral gyrus, supplemental motor area, cerebellum, and thalamus (Beckmann *et al.*, 2005, Shirer *et al.*, 2012). These RSNs also have been reported as a collective RSN that includes both auditory and sensorimotor elements; this collective RSN was reported to include the following regions: cingulate, precentral gyrus, superior temporal gyrus, thalamus, and hippocampus (de Luca *et al.*, 2006). One RSN known as the default mode network (DMN) has been characterized in adults to include the following brain regions: posterior cingulate cortex, ventral anterior cingulate cortex, precuneus, inferior parietal cortex bilaterally, orbitofrontal cortex, medial prefrontal cortex, left dorsolateral prefrontal cortex, left parahippocampal gyrus, left inferolateral temporal cortex, nucleus accumbens, and the hypothalamus/midbrain (Greicius *et al.*, 2003). Previous investigators have characterized the role of the DMN as serving in “self-referential” or “introspective” mental activity (Gusnard, Akbudak, Shulman, & Raichle, 2001, Johnson *et al.*, 2002, Uddin, Iacoboni, Lange, & Keenan, 2007) and social cognition (Supekar *et al.*, 2010, Schilbach *et al.*, 2006). The task-driven speech network is reported to include areas of the left inferior frontal gyrus, superior temporal lobe, premotor cortex, precentral gyrus, supramarginal gyrus, and the cerebellum (Guenther, 2006, Fridriksson *et al.*, 2009). The extent to which the auditory RSN, sensorimotor RSN, and DMN correspond to functional task networks is not fully understood in adults and is even less well understood in children.

Development of RSNs in Children

RSNs have recently been characterized in infants and preterm human brains; although networks were not identical to their adult counterparts they demonstrated resemblance to adult RSNs (Doria *et al.*, 2010, Fransson *et al.*, 2007, Liu, Flax, Guise, Sukul, & Benasich, 2008). Doria *et al.* (2010) studied the RSNs in three groups of preterm infants [early preterm (29-32.2 weeks), preterm (33-36.6 weeks), and term-equivalent preterm (39.4-43.3 weeks)] and compared them to the RSNs observed in full-term infants. Their results indicated that preterm infants often had disintegrated networks at 30 weeks, but full-term infants exhibited similar networks to those observed in adults (Doria *et al.*, 2010). Liu *et al.*, (2008) showed that sensorimotor RSNs in sleeping infants (11.8-13.8 months) had less functional connectivity between the two hemispheres of the brain and more intrahemispheric connectivity.

A number of investigators have begun to examine the developmental trajectory of RSNs (Lee, Morgan, Shroff, Sled, & Taylor, 2013, de Bie *et al.*, 2012, Jolles, van Buchem, Crone, & Rombouts, 2011, Fair *et al*., 2009, Zielinski, Gennatas, Zhou, & Seeley, 2010). A study conducted by Lee *et al.* (2013) described the development of RSNs of preterm infants (<32 weeks gestational age) to four years of age. The results showed large regions of connectivity in infants and more localized connectivity by ages two and four years (Lee *et al.*, 2013). Fair *et al*. (2009) examined developmental trajectories of RSNs of children into adulthood. The developmental pattern of four RSNs (fronto-parietal, cingulo-opercular, DMN, and cerebellar) in healthy participants aged 7-31 years, indicated that these networks changed from strong short distance connections and weak long distance connections to stronger long distance connections; however if the short distance connections changed, they did in the direction of weakening with age (Fair *et al*., 2009, Zielinski *et al*., 2010, Fair *et al.*, 2008, Supekar *et al.*, 2010).

Other characteristics and developmental patterns of RSNs also have been described in a seminal study examining RSNs in children five to eight years of age (de Bie *et al.*, 2012). de Bie *et al.* (2012) imaged awake children and showed that networks involved in fundamental roles including sensory and motor-related processing, comprised mature functional connectivity patterns. In contrast, networks involved in higher cognitive roles (e.g., DMN) demonstrated immature and segmented networks (de Bie *et al*., 2012). de Bie *et al*. (2012) described a decomposition of the DMN into four component maps. Notably, when the four component maps were combined they resembled an adult-like DMN (de Bie *et al.*, 2012). Moreover, the precuneus was found in each of the four decomposed components of the DMN (de Bie *et al.*, 2012). Importantly the precuneus has been shown in previous research to be a focal brain region of the DMN (Fransson & Marrelec, 2008). In another study examining RSNs, Jolles *et al*. (2011) compared RSNs of children ages 11 to 13 years with young adults ages 19 to 25 years. In general, they reported that functional connectivity in the majority of networks was more wide-ranging in children than in adults (Jolles *et al*., 2011). Jolles *et al*. (2011) also found different developmental patterns of functional connectivity for the auditory network and those networks associated with higher-order functions than the connectivity patterns for less complex functions, such as visual or sensorimotor. The authors' interpretation of these findings was that the auditory and higher-order cognitive networks were not entirely refined and continued to develop into adulthood (Jolles *et al*., 2011). Together, current literature provides evidence that the development of RSNs may transition from weaker networks with large undefined areas of connectivity to stronger networks with more clearly defined proximal and distal regions. In addition, there appears to be different developmental trajectories for RSNs associated with basic functions and those networks associated with more complex roles (Lee *et al*., 2013, de Bie *et al*., 2012, Jolles *et al*., 2011, Fair *et al*., 2009, Supekar *et al.*, 2010).

Pre-Post Resting Task Effects

A few researchers have examined resting states before and after a task in adults (Tung *et al*., 2013, Sami & Miall, 2013, Albert *et al*., 2009, Waites *et al*., 2005, Wang *et al.*, 2012, Peltier *et al.*, 2005). These studies reported either increased or decreased functional connectivity in the post-task resting condition but varied in their examination of pre-post resting states through variable experimental designs and analyses, which might have contributed to differing results. A study conducted by Waites *et al*. (2005) demonstrated very specific areas of increased functional connectivity following a word generation task; specifically an increase in the connectivity of the medial frontal cortex with the posterior cingulate and the right middle frontal gyrus with the left middle frontal gyrus. Peltier *et al.* (2005) showed that following a muscle-fatiguing task the functional connectivity between hemispheres decreased. Of note, Peltier *et al.* (2005) also reported that fatiguing tasks differ in their activation pattern by showing an increase in activation during the task initially and a subsequent decrease in activity with fatigue. This alternate pattern of activation makes a fatiguing task a variant of more typical activation patterns examined with conventional active tasks (e.g., finger tapping) and therefore, may influence resting conditions differently when comparing RSNs before and after a task. Furthermore, Tung *et al*. (2013) demonstrated that the interhemispheric functional connectivity of the sensorimotor cortex was greater in the resting state following a one-hand button pushing task than in a resting state prior to the task and that this difference lasted for 5-10 minutes after task completion. In the same study Tung *et al*. (2013) demonstrated that the signal amplitude fluctuation also increased significantly following the button pushing task and that this difference was present for a minimum of 15 minutes following task completion. Sami & Miall (2013) expanded the work of Albert *et al*. (2009) and reported differing patterns of the effect of an active task on a post-task resting state for conditions that did or did not involve a learning component. These authors demonstrated that tasks with a learning component increased the functional connectivity strength of the post-task resting state. In contrast, tasks without a learning component decreased the functional connectivity strength of the post-task resting state (Sami & Miall, 2013).

To summarize, some researchers have shown increased functional connectivity in RSNs, whereas others report decreased RSN connectivity following a task. These findings are often region specific. There is some evidence to support increased functional connectivity in a post-task resting state when the task involves an aspect of learning and decreased functional connectivity when the learning component of a task is absent.

Current Study

The present study was an exploratory investigation of the stability of the auditory and sensorimotor RSNs in children. To examine their stability, the auditory and sensorimotor networks were compared in two separate resting conditions; one before and one immediately after an overt speaking task. The primary question was: Are the auditory and sensorimotor RSNs detected before an overt speaking task equal to the auditory and sensorimotor RSNs following an overt speaking task? The prediction was that these RSNs would differ and that the RSNs detected prior to the speaking task would be stronger and demonstrate more activation than those detected after speaking. The DMN was used as a control. Therefore, the DMN was expected to exhibit the same pattern and degree of activation prior to and following a speech task. A secondary aim of the current study was to describe the patterns of activation/deactivation of these same RSNs during overt speaking. The assumption was that the auditory and sensorimotor RSNs would exhibit deactivation in the speech condition. Moreover, it was of interest to identify the speech network during the speech condition and contrast this network across conditions.

Methods

Imaging data were collected from fourteen participants (four females), ages five to ten years old (Mean = 8 yrs). Inclusion criteria included: (a) English as the first and only language, (b) right handedness, (c) hearing within normal limits, and (d) no history of speech, language, or learning disabilities. Right-handedness was determined using the Edinburg Handedness Inventory (Oldfield, 1971). Determination of normal hearing was examined with a hearing screening at 500 dB HL, 1000 dB HL, and 2000 dB HL. School records and parent reports were used to rule out speech, language, and learning disabilities. The Health Research Ethics Boards at the University of Alberta and University of Texas-San Antonio approved this study.

Design or Procedure

During a home visit parental consent and child assent were obtained. Participants were screened for hearing and handedness and educational reports were obtained from parents. Additionally, the home visit included an MR safety screen, orientation to neuroimaging, and training of each child for the phonation tasks to be produced while in the scanner. Recordings from these practice sessions were used to quantify the consistency of the productions performed outside and inside the scanner. The home visit also served as a time for the children to ask questions and look at pictures of the procedure (e.g., the magnet, head coil, earphones, and room setup).

Once at the magnetic resonance imaging (MRI) centre a radiologist conducted a second MR safety screening on all the participants. The participants were familiarized with the MR scanner and shown where to look during rest conditions. During data collection one parent remained in the scanner room with their child and was instructed to touch the child on his or her arm during the entire procedure.

Children participated in three conditions: a pre-speech resting condition, a speech condition, and a post-speech resting condition. During the pre-speech resting condition participants were instructed to rest with their eyes open and to look at a blank wall via a mirror. The resting condition occurred for five minutes and was followed by the speech condition. During the speech condition four speech tasks were performed including the production of: (a) ‘ah’ at conversational loudness for approximately 2 seconds, (b) ‘ah’ at internally perceived twice-conversational loudness for approximately 2 seconds, and (c) the words ‘heat’ and (d) ‘hoot’ for less than 1 second per token. Auditory cues were presented via headphones and indicated when the children should produce either a phonation or a word. These cues were pre-recorded for consistency of stimulus presentation and timing of the participant response. Responses during the speech tasks were measured using a MRI-safe unidirectional microphone and recorded on a separate computer that was time-locked to the scanner. This allowed for the determination of the exact time of vocalization and the relative sound amplitude (in voltage) post data collection. Two tasks were block randomized within a trial. For example, ‘ah’ at conversational loudness (speech task 1) and ‘ah’ at twice-conversational loudness (speech task 2) were blocked together. Similarly, the words ‘heet’ (speech task 1) and ‘hoot’ (speech task 2) were blocked together. Within a trial, each phonation or speech token was produced twelve times for a total of 24 speech productions per trial. A maximum of three trials of each block grouping were completed, for a maximum total of six speech trials (72 speech productions). The post-speech resting condition was block randomized within the speech trials as shown in Table 1; the three trials were presented sequentially.

Table 1. Task order across three trials within a block.

Task Order	Trial 1	Trial 2	Trial 3
First	Speech Task 1	Speech Task 2	Post-speech Resting Condition
Second	Speech Task 2	Post-speech Resting Condition	Speech Task 1
Third	Post-speech Resting Condition	Speech Task 1	Speech Task 2

Participants were instructed for the post-speech condition to rest with their eyes open and to look at a blank wall via a mirror just like in the pre-speech resting condition. Each post-speech resting condition was 32 s in duration for a maximum total duration (six trials) of 192 s (3.2 minutes).

Data Collection

A 3.0 T Siemens MRI scanner was used to collect functional magnetic resonance imaging (fMRI) data and anatomical scans. The scan order for conditions was based on the block design, as seen in Table 1, and was followed by the anatomical scans. All images were acquired continuously including those obtained during overt productions of phonation and speech. A gradient-echo echo-planar imaging (GE-EPI) pulse sequence was used. The parameters for EPI data collection were as follows: a repetition time (TR) of 2000 ms, an echo time (TE) of 30 ms, a flip angle (FA) of 90 degrees, a field of view (FoV) of 256×256 mm, 3 mm slices, 34 slices collected with no gap, and a voxel size of 2 x 2 x 3 mm^3. During EPI data collection, 157 volumes were collected for phonation conditions and 180 volumes for the initial resting state condition. Parameters for the MPRAGE T1 weighted structural images were as follows: a TR of 2200 ms, a TE of 2.72 ms, a FA of 13 degrees, a FoV of 256x256 mm, 208 slices collected with no gap, and a voxel size of 1 x 1 x 1 mm^3.

Data Analysis

The fMRI images collected were first pre-processed (e.g. slice re-alignment and normalization) using Statistical Parametric Mapping Eight (SPM8, http://www.fil.ion.ucl.ac.uk/spm) software; realignment was completed using the

INRIAlign toolbox in SPM8. Following pre-processing, the data were analyzed using an independent components analysis (ICA), which is a common method reported in the literature for locating RSNs in infants, children, and adults (Calhoun, Adali, Pearlson, & Pekar, 2001, de Bie *et al.*, 2012, Fransson *et al.*, 2007, Beckmann *et al.*, 2005, Greicius *et al.*, 2003). The ICA separates networks by finding correlated voxels and assumes that the sources for these activations mix linearly; in other words, the stronger the source activation the stronger the resulting signal. The ICA also assumes that networks are non-Gaussian and independent from one another (Poldrack, Mumford, & Nichols, 2011, Calhoun & Adali, 2006). The ICA analysis yields components or voxels that are correlated with one another as either temporally independent or spatially independent (Poldrack *et al.*, 2011). The ICA method offers high sensitivity and specificity for resting state fMRI, which makes it a desirable method of data analysis for this study (Beckmann *et al.*, 2005, Poldrack *et al.*, 2011). The ICA analysis in this study was carried out using the group ICA toolbox software (GIFT, http://mialab.mrn.org/software). The Infomax algorithm was used within the ICA analysis for component determination. The total number of components that GIFT produces is selected by the researcher; however GIFT can estimate the number of components within a data set prior to an ICA analysis. Rather than selecting an arbitrary number of components for the ICA to produce, the number of components was first estimated using GIFT and this estimation was used to guide the number of meaningful components produced in the current analysis. Reliability of the component isolation process was increased by using Icasso, a software program that runs ICA multiple times to yield the best estimate of the output components (Rachakonda, Egolf, & Calhoun, 2011). Using this protocol, an ICA was conducted on each of the three conditions: 1) resting condition prior to the speech task (Rest-Pre), 2) speech condition, 3) the resting condition following the speech task (Rest-Post). Once the component maps were obtained a combination of the Component Labeller Utility in GIFT and visual inspection were used for identification of the desired components. Only the components that corresponded to the auditory and sensorimotor network, DMN, and speech network were of interest. The Component Labeller utilized a set of RSN templates for component labelling based on the work of Shirer *et al.* (2012). Once the components were labelled they were inspected visually to ensure labels were applied appropriately and to decide which components to analyze statistically. In a few instances multiple components were identified following ICA as networks of interest. One component for each network within a condition was selected and brought forward for statistical analysis, as agreed upon by consensus of the researchers, based on visual inspection with reference to the RSN templates of Shirer *et al.* (2012).

Statistical Analysis

Once component maps were isolated, statistical analysis was carried out using SPM8 software. One sample *t*-tests were completed on each network identified, in each condition (Rest-Pre, speech, Rest-Post), to determine statistical significance of activation or deactivation. Based on the hypotheses, statistical significance of activation and deactivation in the speech condition was tested for each network. Two sample *t*-tests were used to contrast areas of significant activation of networks between conditions.

Results

Following the ICA an *auditory network*, a *sensorimotor network,* and a *speech network* were identified. However, the DMN was not identified as one network rather it was identified as two streams, a *dorsal DMN* and a *ventral DMN*, and was therefore analyzed separately. Whereas all networks were identified for the Rest-Pre and speech conditions, neither a *speech network* nor a *ventral DMN* were identified in the Rest-Post condition.

It was hypothesized that activation in the Rest-Pre condition would be stronger and demonstrate more activation than in the Rest-Post condition for the *auditory* and *sensorimotor networks*. To explore this, first the significant areas of mean activation in the Rest-Pre and Rest-Post conditions were determined. Figures 1-5 show the selected networks isolated using GIFT. For a detailed description of significant coordinates described for Figures 1-5, refer to Table 2, Appendix A page 43. Networks were statistically significant (one-way *t*-test) at the $p < 0.05$ level, using a family wise error (FWE) and a cluster threshold of 10.

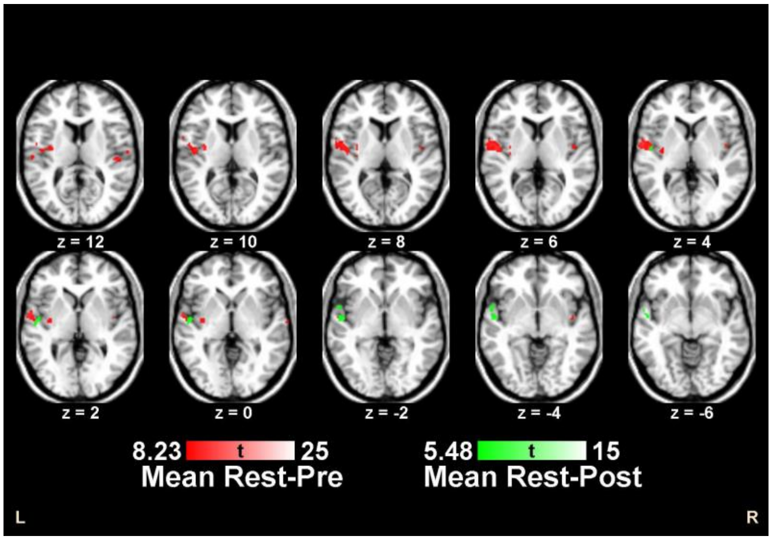

Figure 1. Mean activation of the auditory network in the Rest-Pre and Rest-Post conditions. Mean activation of the *auditory network* in the Rest-Pre and Rest-Post conditions based on *t* scores ($p < 0.05$ FWE, cluster threshold 10).

As can be seen in Figure 1 and Table 2, the mean activation associated with the *auditory network* in the Rest-Pre condition revealed activation in the bilateral postcentral gyri, precentral gyri, left superior temporal gyrus, left claustrum, and right insula. In contrast, Post-Rest activation was found in the left superior temporal gyrus.

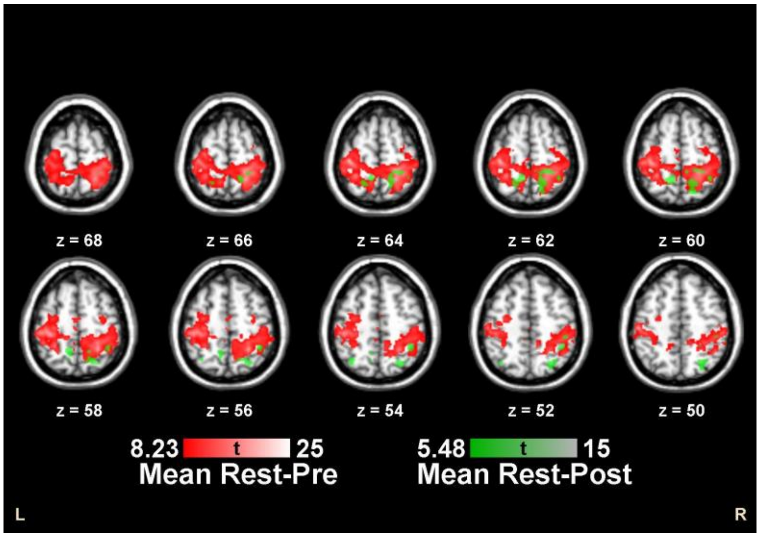

Figure 2. Mean activation of the sensorimotor network in the Rest-Pre and Rest-Post conditions. Mean activation of the *sensorimotor network* in the Rest-Pre and Rest-Post conditions based on *t* scores ($p < 0.05$ FWE, cluster threshold 10).

As can be seen in Figure 2 and Table 2, the mean activation associated with the *sensorimotor network* in the Rest-Pre condition revealed activation in the bilateral postcentral gyri, precuneus, and paracentral lobule. In contrast, Rest-Post activation was found in the bilateral precuneus, superior parietal lobule, paracentral lobule, inferior parietal lobule, and parietal sub-gyral (Brodmann Area (BA) 40).

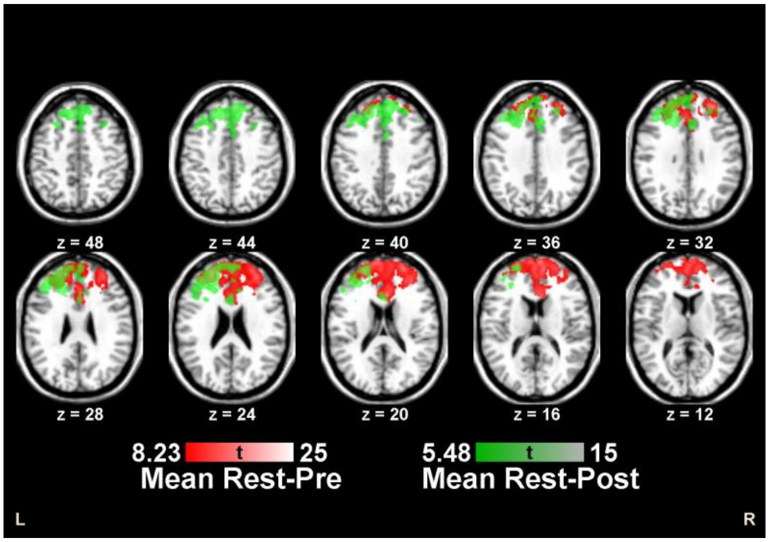

Figure 3. Mean activation of the dorsal DMN in the Rest-Pre and Rest-Post conditions. Mean activation of the *dorsal DMN* in the Rest-Pre and Rest-Post conditions based on t scores ($p < 0.05$ FWE, cluster threshold 10).

As can be seen in Figure 3 and Table 2, the mean activation associated with the *dorsal DMN* in the Rest-Pre condition revealed activation in the bilateral superior frontal gyri, anterior cingulate and middle frontal gyri. In contrast, Rest-Post activation was found in the bilateral middle frontal gyri, superior frontal gyri, and cingulate.

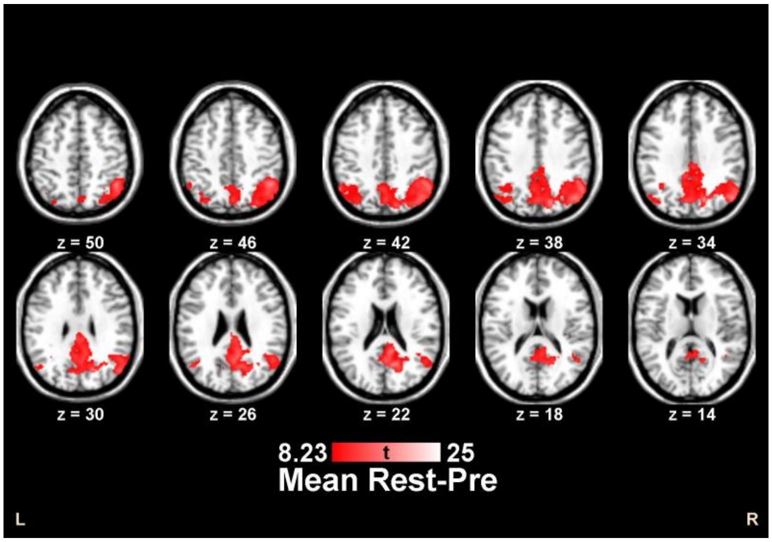

Figure 4. Mean activation of the ventral DMN in the Rest-Pre condition. Mean activation of the *ventral DMN* in the Rest-Pre condition based on *t* scores ($p < 0.05$ FWE, cluster threshold 10).

Figure 4 and Table 2 show the mean activation associated with the *ventral DMN* in the Rest-Pre condition revealed activation in the bilateral angular gyri, middle temporal gyri, cuneus, and inferior parietal lobule. Note that the *ventral DMN* was not detectible in the Rest-Post condition.

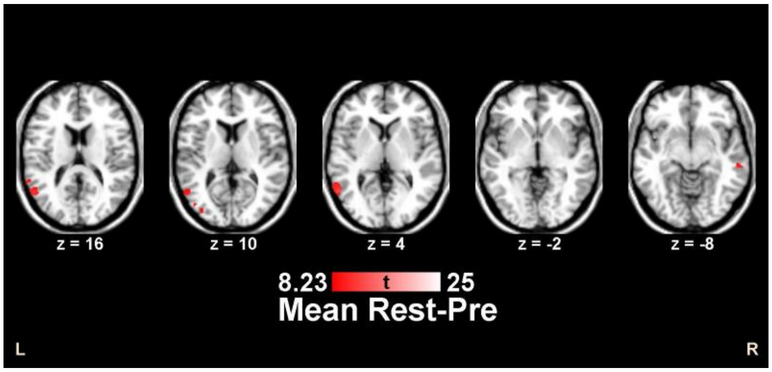

Figure 5. Mean activation of the speech network in the Rest-Pre condition. Mean activation of the *speech network* in the Rest-Pre condition based on *t* scores ($p < 0.05$ FWE, cluster threshold 10).

As can be seen in Figure 5, the mean activation associated with the *speech network* in the Rest-Pre condition revealed activation in the bilateral superior temporal gyri and left middle temporal gyrus. Table 2 shows additional areas of mean activation in the left supramarginal gyrus, left middle occipital gyrus, and right middle temporal gyrus. Note that the *speech network* was not detectible in the Rest-Post condition.

In order to further examine the hypothesis that the *auditory* and *sensorimotor networks* would be stronger and demonstrate more activation in the Rest-Pre condition than in the Rest-Post condition, the selected RSNs were compared between these two conditions. The *auditory*, *sensorimotor*, and *dorsal DMN* were the RSNs compared in the Rest-Pre condition with the Rest-Post condition and resulted in significant activation differences ($p < 0.05$ FWE, cluster threshold 10). The results of these comparisons are displayed below in Figure 6 and in Table 3, Appendix A page 44.

The *auditory network* (Table 3 and Figure 6, image A) demonstrated increased activity in the bilateral precentral gyri, postcentral gyri, superior temporal gyri, and right middle frontal gyrus for Rest-Pre compared to Rest-Post (red). Table 3 shows additional areas of activation in the right superior frontal gyrus and right middle temporal gyrus. The auditory network demonstrated increased activity in the right superior frontal gyrus for Rest-Post compared to Rest-Pre (green). Table 3 shows additional areas of activation in the left superior frontal gyrus, left middle frontal gyrus, left precentral gyrus, right inferior frontal gyrus and right superior temporal gyrus.

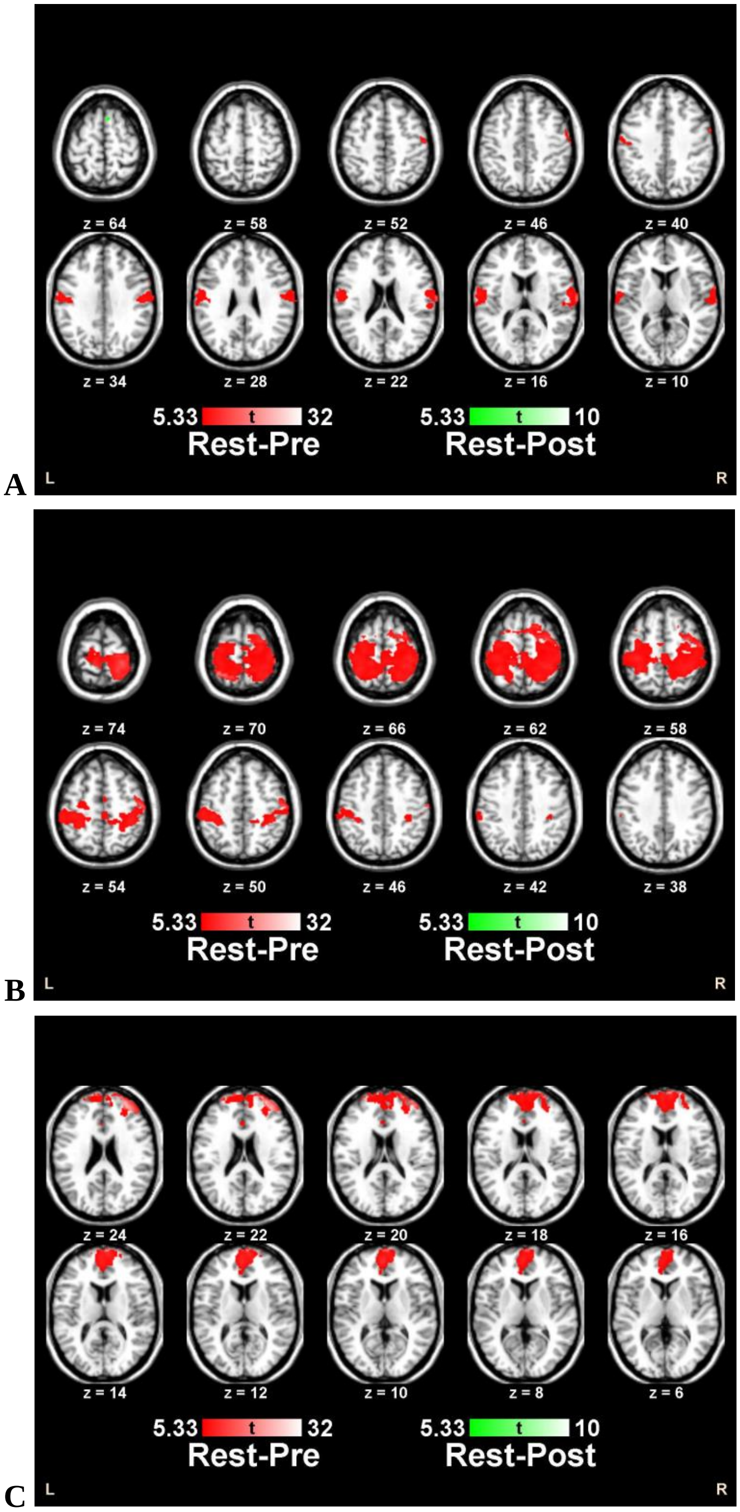

Figure 6. RSNs in the Rest-Pre condition compared to the Rest-Post condition. Activation is displayed based on *t* scores ($p < 0.05$ FWE, cluster threshold 10). The red scale represents the areas Rest-Pre > Rest-Post and the green scale represents Rest-Post > Rest-Pre. A- *auditory network*, B- *sensorimotor network*, C- *dorsal DMN*.

The *sensorimotor network* (Table 3 and Figure 6, image B) showed increased activation in the bilateral superior frontal gyri, middle frontal gyri, precentral gyri, postcentral gyri, and cingulate for Rest-Pre compared to Rest-Post. Table 3 shows additional areas of activation in the bilateral medial frontal gyri, left superior parietal lobule, right superior temporal gyrus, right lingual gyrus, and right uncus. There were no statistically significant differences for the sensorimotor network in the Rest-Post > Rest-Pre comparison.

The *dorsal DMN* of Rest-Pre compared to Rest-Post, reported in Table 3 and shown in image C of Figure 6 (red), had activation in the bilateral medial frontal gyri and anterior cingulate. Table 3 shows additional areas of activation in the bilateral superior frontal gyri, middle frontal gyri, right uncus, right precentral gyrus, right superior parietal lobule, right lingual gyrus, right cuneus, right cerebellum, and inferior brainstem. The dorsal DMN demonstrated a statistical difference in the right middle frontal gyrus for Rest-Post compared to Rest-Pre as shown in Table 3.

Areas of activation and deactivation during the speech condition were then explored. It was hypothesized that the RSNs would exhibit deactivation in the task condition. RSNs identified during the speech condition with significant ($p < 0.05$ FWE, cluster threshold 10) areas of activation and deactivation are displayed in Figure 7 and in Table 4, Appendix A pages 45 and 46.

As can be seen in Table 4a and Figure 7 (image A), the activation associated with the *auditory network* was in the bilateral transverse temporal gyri, precentral gyri, postcentral gyri, and cingulate. Table 4a shows additional areas of activation in the cerebellum bilaterally, left middle temporal gyrus, left medial frontal gyrus, left middle occipital gyrus, left precuneus, and right superior frontal gyrus. In contrast, deactivation was found in the bilateral caudate, left anterior cingulate, left supramarginal gyrus, and right parahippocampus. Table 4a shows additional areas of deactivation in the left posterior cingulate, left superior temporal gyrus, right lingual gyrus, right anterior cingulate, and right cingulate.

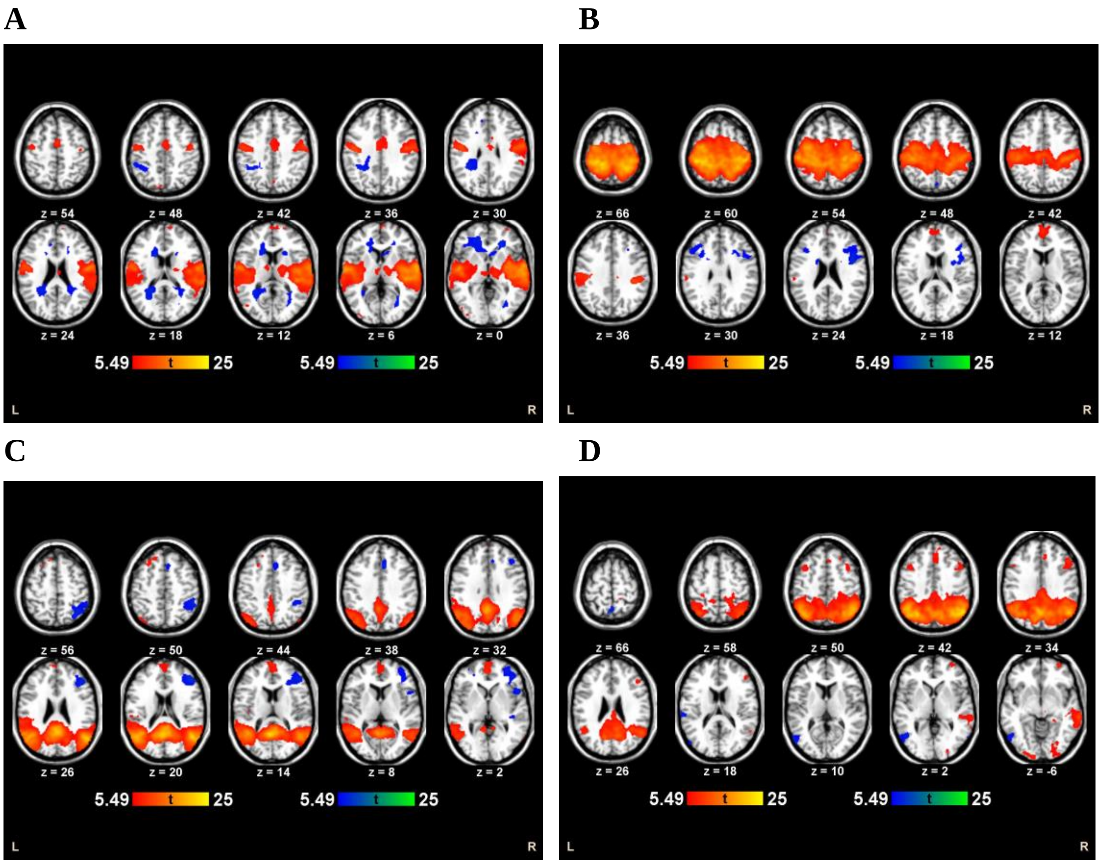

Figure 7. Areas of activation and deactivation for the RSNs in the speech condition. The red-yellow scale shows the activation of each network in the speech condition and the blue-green scale shows the deactivation of each network in the speech condition. Both scales are based on *t* scores ($p < 0.05$ FWE, cluster threshold 10). A- *auditory network*, B- *sensorimotor network*, C- *dorsal DMN*, D- *ventral DMN*.

As can be seen in Table 4a and Figure 7 (image B), the activation associated with the *sensorimotor network* revealed activation in the bilateral postcentral gyri, precentral gyri, inferior parietal lobule, medial frontal gyri, and superior frontal gyri. Table 4a shows additional areas of activation in the left superior temporal gyrus. In contrast, deactivation was found in the bilateral middle frontal gyri, left caudate body, and right precentral gyrus. Table 4a shows additional areas of deactivation in the left cuneus, left cingulate, left precuneus, right claustrum, and right thalamus.

The activation associated with the *dorsal DMN*, reported in Table 4b and shown in image C of Figure 7, revealed activation in the bilateral middle temporal gyri, posterior cingulate, anterior cingulate, and left superior frontal gyrus. Table 4b shows additional areas of activation in the left inferior temporal gyrus and left medial frontal gyrus. In contrast, deactivation was found in the right middle frontal gyrus, right inferior frontal gyrus, right cingulate, right superior frontal gyrus, right superior parietal lobule, and right superior temporal gyrus. Table 4b shows additional areas of deactivation in the left middle frontal gyrus, left inferior frontal gyrus, left globus pallidus, right inferior parietal lobule and right insula.

As can be seen in Table 4b and Figure 7 (image D), the activation associated with the *ventral DMN* revealed activation in the bilateral lingual gyri, middle frontal gyri, superior frontal gyri, superior parietal lobule, inferior parietal lobule, precuneus, right middle temporal gyrus, right superior frontal gyrus, and right cingulate. Table 4b shows additional areas of activation in the bilateral precentral gyri, cerebellum, left inferior occipital gyrus, left middle temporal gyrus, right parahippocampus, right medial frontal gyrus, right angular gyrus, right superior temporal gyrus, right temporal sub-gyral, and right sub-lobar, extra-nuclear. In contrast, deactivation was found in the bilateral precuneus, left middle temporal gyrus, and left superior temporal gyrus. Table 4b shows additional areas of deactivation in the bilateral fusiform gyri, left middle occipital gyrus, left superior parietal lobule, right inferior temporal gyrus, and right middle temporal gyrus.

The *speech network* identified during the speech condition is shown in Figure 8, with significant activation ($p < 0.05$ FWE, cluster threshold 10, red-yellow) in the bilateral anterior cingulate, left superior temporal gyrus, left inferior frontal gyrus, left cingulate, left insula, left thalamus, right fusiform gyrus, and right cerebellum. Table 5, Appendix A page 47, shows an additional area of activation in the right inferior occipital gyrus. Areas of deactivation for the speech network during the speech condition also are shown in Figure 8 (blue-green) and comprised the left parieto-occipital sulcus, right superior frontal gyrus, right middle frontal gyrus, right precentral gyrus, right postcentral gyrus, right parahippocampus, right temporal sub-gyral (BA 20), right insula and right caudate body. Table 5 shows additional areas of deactivation in the left middle occipital gyrus, left superior occipital gyrus, left lingual gyrus, left posterior cingulate, right anterior cingulate, right medial frontal gyrus, right fusiform gyrus, and right claustrum. For a detailed description of significant coordinates described for Figure 8, refer to Table 5.

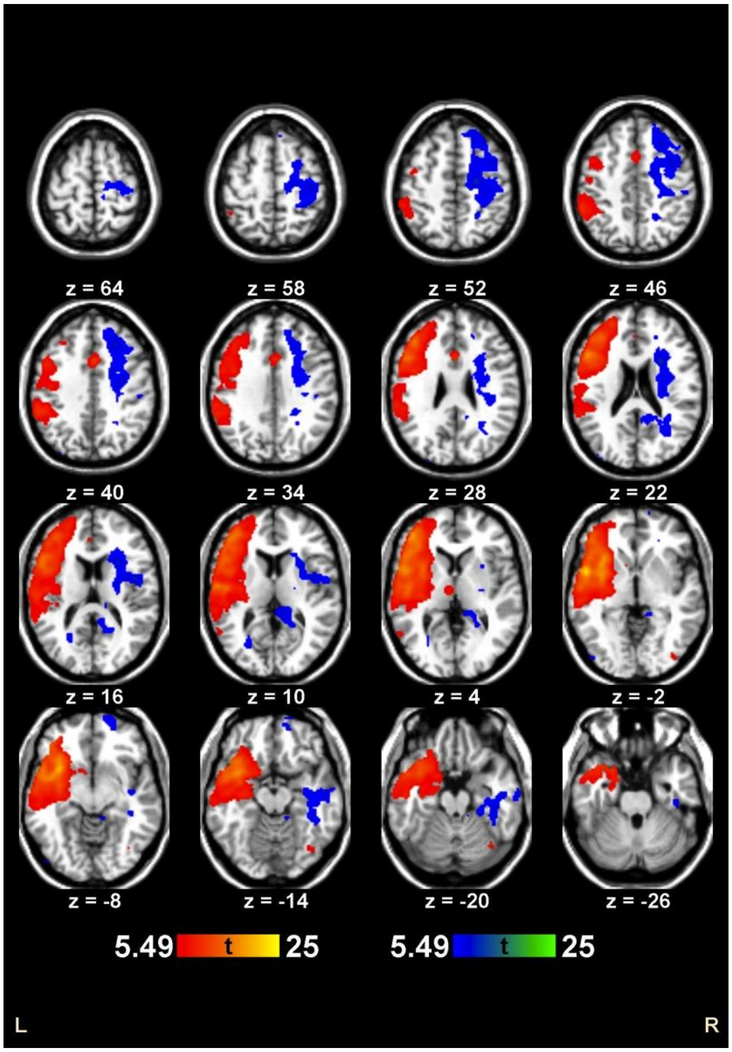

Figure 8. Areas of activation and deactivation for the speech network in the speech condition. The red-yellow scale shows the activation of the *speech network* in the speech condition and the blue-green scale shows the deactivation of the *speech network* in the speech condition. Both scales are based on *t* scores ($p < 0.05$ FWE, cluster threshold 10).

Secondary Analysis

Even though the primary purpose of the current study was to explore the nature of RSNs prior to and immediately after a speaking task perturbation, it is worthy to know what is happening to the *speech network* across the three conditions (Rest-Pre, speech, Rest-Post). As noted, earlier, the *speech network* could not be identified in the Rest-Post condition. Subsequently, a follow-up analysis was conducted on the *speech network* in the Rest-Pre condition and the *speech network* in the speech condition.

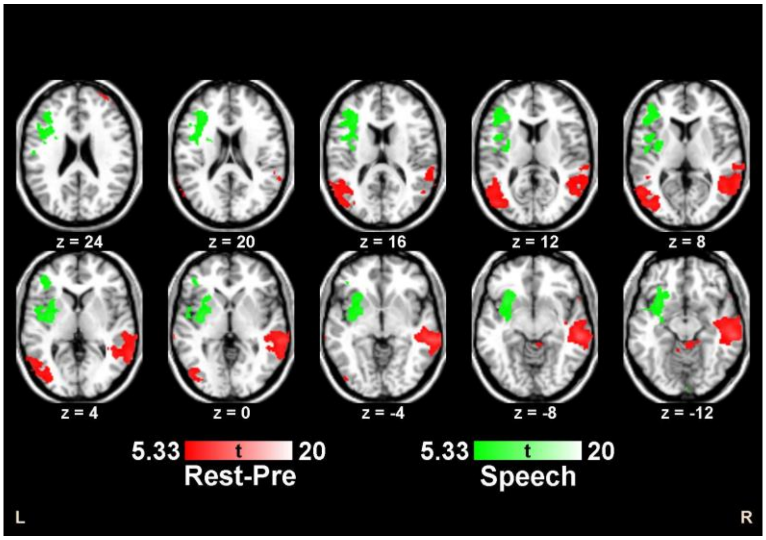

Figure 9. Speech network in the Rest-Pre condition compared to the speech condition. Activation of the *speech network* is shown based on *t* scores ($p < 0.05$ FWE, cluster threshold 10), the red-yellow scale represents Rest-Pre > speech and the green scale represents speech > Rest-Pre.

As seen in Figure 9, the *speech network* in the Rest-Pre condition compared to the speech condition shows greater activation for the Rest-Pre condition in the bilateral middle temporal gyri, cerebellum, and right medial frontal gyrus, ($p < 0.05$ FWE, cluster threshold 10, red). Table 6, Appendix A page 48, shows additional areas of activation in the bilateral precuneus, left superior temporal gyrus, right precentral gyrus, right postcentral gyrus, right paracentral lobule, right inferior parietal lobule, right posterior cingulate, right middle frontal gyrus, right superior frontal gyrus, and right insula. In contrast, the *speech network* shows greater activation in the speech condition than in the Rest-Pre condition in the left precentral gyrus, left middle frontal gyrus, left putamen, and left insula. Table 6, shows additional areas of activation in the left lingual gyrus, left medial frontal gyrus, right uncus, right superior frontal gyrus, right inferior frontal gyrus, right superior temporal gyrus, right middle temporal gyrus, right inferior temporal gyrus and inferior brainstem. For a detailed description of significant coordinates described for Figure 9, refer to Table 6.

Discussion

The present study examined the auditory, sensorimotor, and default mode RSNs before, during and after speech tasks in children. The main findings were (1) the auditory and sensorimotor networks were stronger with a general trend of more areas of activation in a rest condition before a speech task than in a rest condition immediately following a speech task, (2) the DMN also demonstrated increased strength and more areas of activation in a rest condition before a speech task than in a rest condition following a speech task and was therefore not an appropriate control network, (3) the RSNs during the speech condition demonstrated areas of both activation and deactivation, (4) the speech network in the speech condition exhibited a strong left unilateral network, and (5) the speech network in a rest condition before a speech task showed largely right sided activation when compared to a speech network during a speech condition.

Pre-Post Resting Task Effects

The results indicated that activation in the Rest-Pre condition was stronger with more areas of activation than in the Rest-Post condition for all three RSNs examined. Notably, the auditory network demonstrated the most areas of increased activation in the Rest-Post > Rest-Pre comparison. One explanation for this finding is that the auditory feedback loop (Guenther, 2006) continued to be engaged following speech production and thus contributed to the increased activation in the Rest-Post condition. The sensorimotor network had no significant areas of activation unique to the Rest-Post condition compared to the Rest-Pre condition. As expected by the primary hypothesis, this finding showed that in the Rest-Post condition the sensorimotor network was less robust than in the Rest-Pre condition. The dorsal DMN only demonstrated one statistical difference in the right middle frontal gyrus for the Rest-Post > Rest-Pre comparison. This finding is similar to the findings reported by Waites *et al*. (2005) who reported increased activation in the right middle frontal gyrus following a language task; as measured by an increase a functional connectivity with the left middle frontal gyrus. The Rest-Pre > Rest-Post comparison for the auditory, sensorimotor and dorsal default mode networks all demonstrated a pattern of greater activation when compared to the Rest-Post > Rest-Pre comparison (Figure 6). This also can be seen in a visual comparison of the mean activation of the Rest-Pre RSNs compared to the mean activation of the Rest-Post RSNs as displayed in Figures 1-3. As all three networks, including the DMN, were perturbed by the speaking task; the DMN did not serve as a good control network. Perhaps the DMN was not an appropriate control network because the DMN is still undergoing refinement in children. Overall these findings suggest that RSNs immediately following a task were weaker with fewer areas of activation than prior to a task. This finding is consistent with the work of Sami & Miall (2013), which demonstrated diminished connectivity following a task if there was no learning aspect within the task.

An implication of these findings is that resting state conditions immediately following a task are influenced by the task itself, which has been reported previously. For example Tung *et al*. (2013) found that pressing buttons, a frequent type of response system utilized in imaging studies, impacted resting conditions. In their work, Tung *et al*. (2013) demonstrated increased connectivity following a task, which is not consistent with the current findings; underscoring the importance of determining the effects of task-type and task-complexity on resting states. It also is important to consider the order of resting state and task conditions in the experimental design, as well as the potential impact of the response modality on resting states.

Examining task effects on post-task resting conditions in children has potential implications for the development and monitoring of treatment methods in clinical pediatric populations. Despite the relatively recent emergence of research describing RSNs in healthy children, some studies have compared RSNs in clinical versus healthy children. There is evidence that varying RSNs are different in pediatric clinical populations (e.g., pediatric bipolar disorder, fetal alcohol spectrum disorder, and depression) than in healthy controls (Wu *et al.*, 2013, Wozniak *et al.*, 2013, Gaffrey, Luby, Botteron, Repovs, & Barch, 2012). The current study demonstrates that there is an impact on these RSNs following a task; similar to other studies demonstrating treatment and training effects using RSNs in children (Rocca *et al.*, 2013, Jolles, van Buchem, Crone, & Rombouts, 2013). The knowledge that these RSNs are different in clinical populations and can be influenced by a task supports the proposition that these RSNs are prospective tools for both the assessment of clinical populations, as well as for the development and monitoring of treatment effects in the clinical realm.

A point of consideration for this analysis is that the resting state following the task was shorter (32 s for each block combined to a maximum total of 3.2 min) in length than the resting condition prior to the task (5 min). However, even with a shorter post-task resting condition the auditory, sensorimotor, and dorsal default mode RSNs were still detectable and demonstrated enough analytical power to measure their respective mean activation maps. Further research is necessary to determine the length of time that a resting state following a task is impacted in children and also if this finding is consistent with varying tasks and across all RSNs, age groups, and populations.

Patterns of Activation During Speaking

RSNs in the speech condition demonstrated a pattern of both activation and deactivation. Although, this is in disagreement to the original hypothesis that RSNs would demonstrate deactivation there are a couple possible explanations for this finding. First, areas of activation demonstrated within these networks during a speaking task are comparable to those areas expected to activate during a speech task. Such areas include superior temporal gyri and precentral gyri (Guenther, 2006). A speech task in and of itself requires input from both the auditory and sensorimotor systems, as well as output from the sensorimotor system (Guenther, 2006, Price, 2012); therefore activation of these networks is reasonable. Another possible explanation is found in previous research demonstrating that cognitive complexity of a task can impact the resulting deactivation (McKiernan, Kaufman, Kucera-Thompson, & Binder, 2003, Persson, Lustig, Nelson, & Reuter-Lorenz, 2007). These researchers demonstrated that a task with greater cognitive demand resulted in an increase in deactivation (McKiernan *et al.*, 2003, Persson, *et al.*, 2007). Arguably, speech is a fairly complex system requiring both feedback and feed forward control systems (Guenther, 2006); however, in healthy controls without a speech disorder, correct productions of cued speech requires a minimal cognitive load. This may have impacted the amount/magnitude of deactivation observed in the current study, although future research is needed to test this claim more explicitly. Another potential factor may be the age of the participants within this study. For example, Persson *et al*. (2007) examined the differences in deactivation seen between two different age cohorts (young and old adults). These authors demonstrated that young adults (M = 21.7 years) had increased deactivation for a higher cognitive load task than the old adults (M = 68.1 years). Although Persson *et al*. (2007) did not include children in their study, their results suggest that the amount of deactivation may change with age and cognitive load; therefore suggesting the need to explore these manipulations further in pediatric populations.

As mentioned earlier, some networks, chiefly the DMN in the speech condition, was found fragmented into multiple components. The fragmented pattern of the DMN in a resting condition has previously been shown in children (de Bie *et al.*, 2012). The current data did demonstrate some fragmentation of the DMN in the Rest-Pre condition; moreover this fragmentation was exacerbated by the implementation of a speaking task, as indicated by the largest number of fragments during the speech condition. Although, this finding was not under direct examination in the current study, it suggests that the DMN during a task may decrease in cohesiveness and provides important information regarding the potential development of RSNs in children.

As predicted the speech network during the speech condition demonstrated activation in the superior temporal gyrus, inferior frontal gyrus, and cerebellum and is consistent with the literature (Guenther, 2006). The speech network during the speech condition demonstrated a predominantly left unilateral network apart from right cerebellum, right inferior occipital gyrus, and right fusiform gyrus. Notably, the deactivation shown in Figure 8 was primarily in the right hemisphere. These results are in line with current understanding that the speech production system is primarily a left hemisphere dominant task (Price, 2012).

Secondary Analysis: Speech Networks

In the exploratory comparison of the speech network, between the resting condition before and during an overt speaking task, a shift in activation was observed. More specifically, there was largely right sided activation for Rest-Pre > speech and largely left sided activation for speech > Rest-Pre. As previously mentioned, the speech production network is primarily a left hemisphere dominant task however, data from the current study demonstrate that in a resting condition prior to speaking the speech network has more right hemisphere activation. One possible explanation for this finding is that the areas that were active in the resting condition but not during the task are complementary areas for processing speech information but do not play as dominant of a role in speech production. For example, speech comprehension is linked to the production of speech but was not essential during the overt speaking task and as a result areas related to the comprehension of speech demonstrated activation in the Rest-Pre > speech comparison. More specifically, areas including the middle temporal gyrus and precuneus were activated in the speech network for the Rest-Pre > speech comparison. Both of these areas play a more predominant role in the comprehension of speech than its production (Price, 2012). Another possible explanation for this finding is that the speech network is bilateral in the resting condition and with the commencement of speaking the left hemisphere, which is dominant for speaking, takes over. More research is required to explore this phenomenon in order to provide further insight into the observed right-to-left hemisphere shift from rest to speaking. The distinct shift in in the speech network may have possible implications and applications for individuals with speech disorders. This finding is unique to the literature and is pivotal for advancing the current understanding of speech networks. The trade-off suspected of a bilateral to a left dominant speech network activation pattern has major implications for our understanding of speech development both in healthy children and children with speech disorders.

Limitations and Conclusions

The limitations of the current study included the shorter duration of Rest-Post than Rest-Pre, as well as the limitations of the comparisons completed regarding the networks chosen. As mentioned previously, some networks were found fragmented into multiple components while others were not found in the

Rest-Post condition, which limited the comparisons conducted in analysis. When a network fragmented, only one component was brought forward for statistical analysis, which may have influenced the comparisons and activation/deactivation patterns observed. Future research that integrates multiple components for their inclusion in statistical analysis would further clarify RSN stability in children. In addition the sample was not balanced by gender, as females were not equally represented. A future study that takes a more balanced account of both males and females would allow for a more representative description of healthy children. Furthermore, the sample size of this study was small which may have influenced findings through some loss of statistical power.

Notably, the networks analyzed in this paper do not represent all networks separated by ICA. For example, higher visual networks across all three conditions were also identified, in addition to a number of other networks, such as the executive control networks, which were found in at least one or more conditions. Since the DMN did not serve as a good control in this analysis, future research could consider using a different control network; one that may not be directly impacted by the task. More specifically, in the current work the experimental conditions completed were not visual tasks. As such, a visual network may serve as a better control as it has no relation to the task condition; if not it will provide evidence that demonstrates all RSNs are influenced by tasks regardless of the relationship between the network and tasks performed. Finally, the current study did not employ a secondary group to which the results could be compared and evaluated. Future research that includes a comparison group for analyses, such as a clinical group or a comparative group who perform differing tasks would be beneficial to examine TASK X GROUP interaction effects. For example, comparing the influence of different tasks on RSNs could be explored with one group of children doing overt speaking, one doing covert speaking, and one doing pattern recognition; this would further clarify the findings of the current study.

In conclusion, auditory, sensorimotor, and dorsal default mode networks were found to demonstrate greater robustness in a rest condition before an overt speech task than immediately after. Also, the RSNs studied exhibited patterns of both activation and deactivation during the speech condition underscoring the necessity of these networks during a speech task. Finally, the speech network demonstrated a mainly right-sided activation pattern in the resting condition prior to speaking in comparison with the speech condition; which shifted to the left-hemisphere when speaking. The findings of this study suggest that RSNs in children can be delineated, although in a more fragmented form than adults, and are impacted by preceding task demands. The present findings demonstrate that RSNs provide unique information about brain connectivity in children and as such, have the potential to be influential evaluation tools in detecting neurobiological mechanisms underlying pathology that are perhaps sensitive to behavioural intervention.

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Appendix A

Table 2. Areas of mean activation in the Rest-Pre and Rest-Post conditions for five networks. Activation is significant with $p < 0.05$ FWE and a cluster threshold of 10. BA, Brodmann Area; R, Right; L, Left; Sup, Superior; Mid, Middle; Inf, Inferior; Lob, Lobule; Ant, Anterior.

Network	Rest-Pre							Rest-Post						
	Region	**BA**	**Cluster size (Voxels)**	**Peak *t* score**	**Coordinates**			**Region**	**BA**	**Cluster size (Voxels)**	**Peak *t* score**	**Coordinates**		
Auditory	L Sup Temporal	22	151	16.73	-51	-10	4	L Sup Temporal	22	51	8.04	-54	-10	-2
	L Sup Temporal	22		12.95	-63	-1	4	L Sup Temporal	22		6.93	-60	5	-5
	L Claustrum	N/A		12.31	-33	-10	10							
	R Insula	13	13	12.23	45	-22	10							
	R Postcentral	43	34	11.99	69	-13	19							
	R Postcentral	43		9.92	60	-10	16							
	L Postcentral	2	22	11.13	-69	-19	28							
	L Postcentral	3		10.53	-63	-13	31							
	L Postcentral	43		9.59	-66	-13	22							
	R Insula	13	12	10.19	45	-7	4							
	R Precentral	6	13	10.08	45	5	22							
Sensorimotor	L Postcentral	3	2380	24.04	-39	-25	64	L Precuneus	7	71	8.73	-9	-46	61
	L Postcentral	2		23.32	-54	-22	49	L Precuneus	7		7.54	-21	-55	61
	R Paracentral Lob	5		20.53	21	-37	64	L Precuneus	7		6.96	-12	-52	55
	L Precuneus	7	18	11.85	-18	-49	49	R Paracentral Lob	5	190	7.33	18	-37	61
								R Sub-gyral	40		7.29	27	-40	61
								R Precuneus	7		7.24	27	-70	49
								L Sup Parietal Lob	7	21	7.15	-39	-67	52
								R Inf Parietal Lob	40	43	6.87	39	-46	52
								R Inf Parietal Lob	40		6.77	36	-46	61
								R Inf Parietal Lob	40	12	6.08	57	-43	43
Dorsal DMN	R Ant Cingulate	33	2075	22.85	3	23	19	L Sup Frontal	9	1887	10.68	-24	50	25
	R Mid Frontal	9		18.47	30	44	31	L Mid Frontal	8		9.96	-21	35	37
	L Sup Frontal	9		18.24	-9	65	19	L Cingulate	32		9.91	-21	23	31
								R Mid Frontal	9	16	6.40	36	38	28
								R Mid Frontal	8	20	6.14	42	26	40
								R Mid Frontal	9		5.69	45	23	31
								R Mid Frontal	8		5.65	48	20	40
Ventral DMN	R Cuneus	7	2006	20.80	15	-73	37	**N/A**						
	R Inf Parietal Lob	40		18.91	45	-55	52							
	R Inf Parietal Lob	40		18.46	51	-52	40							
	L Angular	39	264	18.19	-57	-58	43							
	L Mid Temporal	39		12.58	-51	-64	25							
	L Angular	39		12.35	-36	-73	40							
Speech	L Mid Temporal	21	88	13.89	-60	-61	4	**N/A**						
	L Mid Temporal	39		13.05	-57	-61	16							
	L Mid Temporal	39		11.42	-48	-64	13							
	L Supramarginal	40	10	12.76	-60	-49	31							
	L Sup Temporal	22	13	11.62	-63	-46	13							
	R Mid Temporal	21	22	11.60	57	-31	-8							
	L Mid Occipital	19	14	10.23	-48	-79	13							
	L Mid Occipital	18	12	9.55	-39	-85	7							
	L Mid Occipital	19		8.71	-36	-88	16							

Table 3. RSNs areas of significant activation in the Rest-Pre condition compared to the Rest-Post condition. Activation is significant with $p < 0.05$ FWE and a cluster threshold of 10. BA, Brodmann Area; R, Right; L, Left; Sup, Superior; Mid, Middle; Inf, Inferior; Med, Medial; Lob, Lobule; Ant, Anterior.

Network	**Rest-Pre > Rest-Post**							**Rest-Post > Rest-Pre**						
	Region	**BA**	**Cluster size (Voxels)**	**Peak *t* score**	**Coordinates**			**Region**	**BA**	**Cluster size (Voxels)**	**Peak *t* score**	**Coordinates**		
Auditory	R Postcentral	43	472	23.53	69	-13	19	R Sup temporal	38	72	9.69	27	8	-32
	R Mid temporal	21		19.40	69	-10	-2	R Sup temporal	38		9.24	42	5	-38
	R Precentral	6		16.77	66	2	10	R Inf frontal	47		9.01	39	20	-26
	R Mid temporal	21	12	17.60	72	-19	-8	L Precentral	6	23	9.26	-42	2	61
	L Sup temporal	42	380	14.22	-69	-10	7	L Mid frontal	6		7.20	-39	8	55
	L Postcentral	43		11.76	-69	-7	16	L Mid frontal	6		6.68	-33	-1	64
	L Precentral	6		11.40	-66	2	16	L Sup frontal	6	20	7.43	0	20	64
	R Sup frontal	10	19	9.43	9	71	-8							
	R Sup frontal	11		8.26	9	68	-17							
	R Sup frontal	10		6.20	27	68	-8							
Sensorimotor	R Postcentral	5	3479	21.39	24	-37	73	No significant clusters						
	L Sup Parietal Lob	7		20.91	-33	-49	70							
	R Precentral	4		19.20	21	-25	73							
	R Sup Temporal	38	13	8.89	36	11	-29							
	R Sup Temporal	38		6.48	45	14	-26							
	R Uncus	28	11	7.44	21	-1	-29							
	R Lingual	18	24	6.95	12	-73	7							
	L Med Frontal	6	25	6.58	-6	-10	55							
	R Med Frontal	6		6.13	3	-7	52							
Dorsal DMN	R Med Frontal	10	942	31.90	3	68	13	R Mid Frontal	10	14	9.30	48	50	-14
	R Sup Frontal	9		29.43	27	53	25							
	R Sup Frontal	9		26.20	21	62	22							
	L Mid Frontal	10	11	14.00	-36	62	1							
	L Sup Frontal	10		13.60	-42	56	10							
	Inf Brainstem	N/A	38	12.67	-6	-13	-32							
	R Uncus	34		9.33	12	-4	-29							
	Inf Brainstem	N/A		8.94	6	-22	-32							
	R Med Frontal	6	65	11.32	15	11	64							
	R Sup Frontal	6		9.09	12	20	61							
	R Sup Frontal	6		8.17	24	-7	70							
	R Sup Parietal Lob	7	15	10.07	27	-55	73							
	R Sup Parietal Lob	7		8.12	33	-49	73							
	L Med Frontal	6	28	9.48	-9	11	61							
	L Sup Frontal	6		8.22	-15	-1	67							
	R Lingual	17	31	9.36	15	-103	-14							
	R Cerebellum (declive)	N/A		7.01	15	-94	-17							
	R Cuneus	18		6.61	12	-106	7							
	R Precentral	4	26	8.50	42	-10	58							
	R Mid Frontal	6		7.41	39	2	58							
	L Ant Cingulate	24	15	6.56	-3	26	19							

Table 4a. RSNs areas of significant activation and deactivation in the speech condition. Activation is significant with $p < 0.05$ FWE and a cluster threshold of 10. BA, Brodmann Area; R, Right; L, Left; Sup, Superior; Mid, Middle; Inf, Inferior; Med, Medial; Lob, Lobule; Ant, Anterior; Pos, Posterior.

Network	Activation							Deactivation						
	Region	BA	Cluster size (Voxels)	Peak *t* score	Coordinates			Region	BA	Cluster size (Voxels)	Peak *t* score	Coordinates		
Auditory	R Transverse Temporal	42	6219	20.59	63	-10	7	R Ant Cingulate	32	941	10.87	21	35	-2
	R Transverse Temporal	41		20.00	42	-28	10	L Caudate Body	N/A		9.65	-18	14	19
	L Transverse Temporal	42		19.50	-63	-10	7	L Ant Cingulate	32		9.52	-18	41	1
	L Med Frontal	6	390	9.78	0	-1	55	L Pos Cingulate	30	598	9.77	-21	-49	16
	L Cingulate	24		8.39	-6	-7	34	L Supramarginal	40		9.65	-39	-43	31
	R Cingulare	24		7.87	3	-13	43	L Sup Temporal	22		9.48	-33	-52	10
	L Mid Occipital	18	22	7.89	-39	-91	4	R Parahippocampus	18	226	8.80	30	-61	10
	R Sup Frontal	9	83	7.73	12	62	22	R Cingulate	31		7.73	24	-43	22
	R Sup Frontal	10		7.51	6	65	16	R Lingual	19		7.56	30	-70	4
	L Med Frontal	10		7.17	0	65	10							
	R Sup Frontal	10	34	7.67	30	59	-5							
	R Sup Frontal	10		7.06	30	59	4							
	R Sup Frontal	10		6.05	21	68	4							
	L Mid Temporal	37	10	7.43	-45	-73	13							
	L Precuneus	19	24	7.38	-9	-79	49							
	L Precuneus	19		6.49	-18	-79	49							
	L Mid Occipital	19	58	7.13	-51	-82	-8							
	L Cerebellum (declive)	N/A		6.44	-45	-70	-20							
	R Postcentral	3	32	6.63	30	-31	64							
	R Sup Frontal	10	11	6.44	21	59	16							
	R Cerebellum (declive)	N/A	18	6.32	48	-70	-17							
Sensorimotor	L Inf Parietal Lob	40	7302	25.23	-42	-34	61	R Precentral	6	405	9.80	42	5	22
	R Postcentral	40		23.56	45	-31	61	R Mid Frontal	9		9.00	42	14	25
	L Postcentral	5		22.89	-27	-34	64	R Claustrum	N/A		8.59	30	-1	19
	L Med Frontal	9	288	10.14	-3	59	10	L Mid Frontal	9	146	7.90	-33	17	28
	L Med Frontal	10		9.73	-6	50	4	L Mid Frontal	9		7.42	-42	26	28
	L Sup Frontal	9		6.72	0	56	22	L Mid Frontal	9		7.40	-51	23	28
	L Sup Temporal	38	15	7.88	-33	11	-26	R Thalamus	N/A	22	7.62	3	-7	19
								L Caudate Body	N/A	20	7.58	-21	5	25
								L Cuneus	19	27	7.37	-3	-91	34
								L Precuneus	7		7.04	0	-70	46
								L Cingulate	24	10	6.61	-12	17	31

Table 4b. RSNs areas of significant activation and deactivation in the speech condition. Activation is significant with $p < 0.05$ FWE and a cluster threshold of 10. BA, Brodmann Area; R, Right; L, Left; Sup, Superior; Mid, Middle; Inf, Inferior; Med, Medial; Lob, Lobule; Ant, Anterior; Pos, Posterior; --, Not available.

Network	Activation							Deactivation						
	Region	BA	Cluster size (Voxels)	Peak *t* score	Coordinates			Region	BA	Cluster size (Voxels)	Peak *t* score	Coordinates		
Dorsal DMN	R Mid Temporal	39	5407	24.86	48	-64	22	R Inf Frontal	45	820	10.89	51	17	-2
	L Pos Cingulate	30		24.15	-6	-58	13	R Mid Frontal	46		10.16	45	38	19
	L Mid Temporal	19		21.88	-51	-64	22	R Mid Frontal	10		8.49	33	50	4
	L Med Frontal	11	726	12.11	0	47	-20	R Sup Parietal Lob	7	348	9.85	33	-58	61
	L Med Frontal	10		11.95	0	53	-14	R Inf Parietal Lob	40		8.73	48	-40	49
	L Ant Cingulate	32		11.51	-3	35	-17	R Inf Parietal Lob	40		7.60	36	-43	46
	L Sup Frontal	8	109	9.23	-24	32	52	R Cingulate	32	112	9.31	6	23	40
	L Sup Frontal	8		7.93	-15	38	52	R Cingulate	32		8.68	6	29	34
	L Sup Frontal	8		6.63	-18	41	43	R Sup Frontal	6		6.35	3	14	49
	L Mid Temporal	21	53	6.99	-63	-4	-26	L Inf Frontal	--	86	8.27	-36	44	-5
	L Inf Temporal	21		6.27	-63	-10	-17	L Mid Frontal	10		6.48	-27	44	4
								R Sup Temporal	13	31	6.91	42	-28	4
								R Insula	13		6.15	45	-22	-5
								L Globus Pallidus	N/A	13	6.69	-18	-16	-5
Ventral DMN	R Angular	39	5881	24.75	51	-64	40	L Sup Parietal Lob	7	36	9.86	-6	-64	67
	L Precuneus	19		23.84	-42	-70	46	L Precuneus	7		8.07	-6	-55	70
	L Precuneus	19		23.15	-30	-67	43	L Mid Occipital	37	234	9.73	-57	-76	10
	R Mid Temporal	21	372	11.79	66	-31	-8	L Fusiform	19		9.35	-57	-70	-11
	R Sub-gyral	--		9.06	45	-31	-2	L Mid Temporal	37		8.77	-51	-64	4
	R Sup Temporal	22		7.86	54	-16	-8	L Sup Temporal	42	35	7.84	-63	-28	16
	R Precentral	9	246	9.38	48	26	34	R Inf Temporal	19	16	6.30	60	-67	1
	R Mid Frontal	9		8.91	45	14	40	R Mid Temporal	37		5.65	51	-64	7
	R Mid Frontal	6		7.44	39	11	52	R Fusiform	37		5.64	57	-67	-11
	L Lingual	17	111	8.67	-15	-103	-8							
	L Inf Occipital	18		7.82	-30	-94	-5							
	L Lingual	18		7.18	-9	-94	-11							
	R Sup Frontal	10	67	8.40	30	59	-5							
	R Mid Frontal	10		6.11	39	56	4							
	R Lingual	18	185	8.21	27	-76	-8							
	R Cerebellum (declive)	N/A		7.92	27	-82	-14							
	R Cerebellum (declive)	N/A		7.68	18	-82	-11							
	R Med Frontal	8	131	8.16	6	32	37							
	R Sup Frontal	8		6.77	3	26	49							
	R Sup Frontal	8		6.42	9	47	40							
	L Mid Frontal	6	113	7.86	-42	11	49							
	L Precentral	9		7.30	-42	11	40							
	L Mid Frontal	9		6.75	-51	17	34							
	R Sub-lobar (extra-nuclear)	13	26	7.67	33	17	-14							
	R Parahippocampus	35	11	7.44	21	-37	-8							
	L Mid Frontal	10	22	6.79	-36	56	-5							
	L Mid Temporal	21	12	6.77	-66	-16	-11							
	L Mid Temporal	21		5.66	-69	-34	-14							
	R Sup Frontal	8	33	6.47	24	32	46							
	R Sup Frontal	6		6.39	21	26	52							
	L Cerebellum (declive)	N/A	10	6.23	-24	-73	-14							

Table 5. Speech network areas of significant activation and deactivation in the speech condition. Activation is significant with $p < 0.05$ FWE and a cluster threshold of 10. BA, Brodmann Area; R, Right; L, Left; Sup, Superior; Mid, Middle; Inf, Inferior; Med, Medial; Ant, Anterior; Pos, Posterior.

Network	Activation							Deactivation						
	Region	**BA**	**Cluster size (Voxels)**	**Peak *t* score**	**Coordinates**			**Region**	**BA**	**Cluster size (Voxels)**	**Peak *t* score**	**Coordinates**		
Speech	L Sup Temporal	22	6226	23.86	-54	5	-2	R Insula	13	2795	11.94	42	-1	13
	L Insula	13		20.78	-36	14	-8	R Caudate Body	N/A		11.65	24	11	22
	L Inf Frontal	46		18.26	-45	44	4	R Claustrum	N/A		10.86	27	14	13
	L Cingulate	32	127	11.40	0	11	40	L Mid Occipital	18	36	9.99	-51	-85	-8
	L Cingulate	24		10.51	-3	14	31	L Mid Occipital	19		7.87	-57	-79	1
	L Thalamus	N/A	30	7.51	-9	-13	4	L Mid Occipital	19		6.16	-57	-76	-8
	R Cerebellum (declive)	N/A	46	7.19	36	-67	-20	R Parahippocampus	36	356	9.58	39	-28	-20
	R Cerebellum (uvula)	N/A		5.89	39	-73	-26	R Fusiform	20		9.47	39	-37	-17
	R Fusiform	19		5.70	39	-70	-5	R Sub-gyral	20		8.93	48	-16	-20
	L Ant Cingulate	32	11	6.66	-3	38	13	L Mid Occipital	19	47	9.13	-42	-88	25
	R Inf Occipital	18	16	6.34	36	-82	-2	L Sup Occipital	19		8.43	-36	-85	37
								L Mid Occipital	18		7.97	-36	-94	19
								R Med Frontal	10	79	8.67	15	62	-11
								R Med Frontal	10		5.84	12	68	-2
								L Lingual	19	62	7.96	-30	-70	7
								L Pos Cingulate	30		7.40	-27	-64	13
								R Ant Cingulate	32	13	6.02	24	35	-5
								R Ant Cingulate	32		5.67	18	44	-5

Table 6. Speech network areas of significant activation in the Rest-Pre condition compared to the speech condition. Activation is significant with *p* < 0.05 FWE and a cluster threshold of 10. BA, Brodmann Area; R, Right; L, Left; Sup, Superior; Mid, Middle; Inf, Inferior; Med, Medial; Lob, Lobule; Pos, Posterior.

Network	Rest-Pre > speech							speech > Rest-Pre						
	Region	**BA**	**Cluster size (Voxels)**	**Peak *t* score**	**Coordinates**			**Region**	**BA**	**Cluster size (Voxels)**	**Peak *t* score**	**Coordinates**		
Speech	L Mid Temporal	39	481	18.02	-63	-61	16	R Inf Temporal	20	11	15.84	57	-7	-41
	L Mid Temporal	21		11.94	-66	-61	7	L Lingual	18	14	13.52	0	-97	-14
	L Sup Temporal	22		10.55	-69	-49	16	L Lingual	17		8.95	-6	-106	-11
	R Mid Temporal	21	1239	13.30	60	5	-23	L Med Frontal	25	13	11.47	-9	14	-20
	R Mid Temporal	21		12.21	66	-58	7	L Med Frontal	25		11.28	-6	23	-23
	R Mid Temporal	21		12.16	72	-34	-5	R Mid Temporal	21	20	11.05	42	2	-38
	R Med Frontal	6	19	10.29	18	11	64	R Sup Temporal	38		8.18	36	8	-38
	R Sup Frontal	6		7.18	18	2	70	R Uncus	28	43	10.84	15	-10	-35
	R Sup Frontal	10	29	9.45	27	59	22	Inf Brainstem	N/A		7.61	12	-25	-32
	R Sup Frontal	10		7.47	33	53	22	R Uncus	36		6.79	27	-10	-38
	L Cerebellum (uvula)	N/A	11	8.89	-12	-88	-32	R Inf Frontal	11	40	10.18	15	38	-26
	L Cerebellum (pyramis)	N/A		7.60	-21	-85	-32	R Sup Frontal	11		9.52	15	50	-23
	L Mid Temporal	21	16	8.58	-72	-25	-2	L Med Frontal	11		9.21	0	44	-26
	L Mid Temporal	21		6.63	-72	-37	-8	L Insula	13	1393	9.00	-36	14	-8
	L Mid Temporal	21		5.79	-72	-22	-11	L Insula	13		8.97	-39	-7	1
	R Sup Frontal	9	10	8.30	45	41	25	L Putamen	N/A		8.85	-27	2	-2
	R Pos Cingulate	23	24	7.67	9	-46	28	L Med Frontal	10	10	8.25	0	62	-17
	R Precentral	4	25	7.24	48	-10	52	L Precentral	4	16	6.38	-57	-13	25
	R Precentral	6		5.87	42	-1	58							
	R Mid Frontal	6		5.83	48	5	52							
	R Cerebellum (culmen)	N/A	44	7.15	3	-40	-11							
	R Cerebellum (culmen)	N/A		6.79	15	-37	-11							
	R Cerebellum (culmen)	N/A		5.86	3	-46	-20							
	R Paracentral Lob	5	31	6.65	27	-37	52							
	R Postcentral	3		5.67	30	-28	55							
	R Mid Frontal	8	31	6.64	42	23	43							
	R Mid Frontal	8		6.29	36	23	37							
	R Mid Frontal	8		6.00	42	29	37							
	R Insula	13	13	6.48	51	-37	28							
	R Inf Parietal Lob	40	11	6.35	57	-49	40							
	L Precuneus	31	13	6.08	-6	-46	31							
	R Precuneus	31		5.70	3	-46	37							