Age-related Changes in Conflict-related Activity in the Superior Frontal Gyrus: 

Implications for Cognitive Control

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Cognitive Control (CC) is a necessary function of everyday life, used for inhibiting inherent actions to successfully accomplish tasks. The present study used a subset of the data from a larger study by Wilk & Morton (2012), with a particular focus on the SFG-complex (i.e., dorsolateral SFG [SFGdl], anteromedial SFG [SFGam], posterior SFG [SFGp]). Participants completed the Size-Congruency Task, measuring conflict adaptation, while their hemodynamic response activity was measured using functional magnetic resonance imaging (fMRI). This generated a group-contrast map of the conflict-related activity, which was then correlated with participant age, allowing for group-contrast maps of the age-related changes in conflict-related activity. Analysis of the SFG-complex revealed significant results in the SFGp, but not in the SFGdl, nor the SFGam. Future studies should expand upon these findings in the SFGp, as well as the whole SFG-complex, using different CC paradigms to investigate whether the SFG-complex has a role in CC.

Keywords: cognitive control network, size-congruency task, superior frontal gyrus, conflict adaptation, functional MRI

Over the past 30 years, neuroscientific understandings of the brain’s architecture and function have increased, improving medicine through the development of targeted treatment plans for cognitive diseases, as well as finding their underlying mechanisms. More recently, developmental cognitive neuroscience has been at the forefront of neuroscience due to advancements in imaging techniques (e.g., functional magnetic resonance imaging [fMRI], diffusion tensor imaging, electroencephalogram, etc.; Berniker & Kording, 2015). The primary focus of developmental neuroscience is to use the various functional imaging and cyto- or myelo-architecture parsing techniques (e.g., diffusion tensor tractography, histology) to identify at the microscopic level, regions of the brain responsible for computing the solution to some circumscribed problem; the search for modules (Cole & Schneider, 2007).

The search to find cognitive control’s (CC) module of computation and the constituents of Cognitive Control Networks (CCN) is still an ongoing process and is thus still at the forefront of brain imaging studies (Cole & Schneider, 2007). CC is the process by which goals or plans influence one’s behaviour by overriding automatic responses, which results in flexible adaptation to a situation and the direction of goal-oriented behaviour (Cole & Schneider, 2007). Fair and colleagues (2007) posit that the brain has several CCNs responsible for the various aspects of CC. Since the superior frontal gyrus (SFG) contains the dorsolateral prefrontal cortex (dlPFC), it is likely that the SFG is a CCN node. The SFG includes the

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dIPFC, but also two other subregions further parsed in this review. To account for these three subregions, the dorsolateral (SFGdl), posterior (SFGp), and the anteromedial (SFGam) SFG will henceforth be referred to as the SFG-complex. Past literature has found that CC development and activity are measurable and are linked to task performance (Diamond, 2002; Ezekiel, Bosma, Morton, 2013; Li et al., 2013; Morton et al., 2009; Rubia et al., 2006; Sadaghiani & D’Esposito, 2015; Wendelken et al., 2012; Wilk & Morton, 2012). Notably, the brain goes through dramatic changes in both synaptic and white matter density, which increases neuronal efficiency, resulting in more activity as the neural architecture of a certain process develops (Wilk & Morton, 2012).

The frontal cortex, the location of the SFG-complex, increases in cortical area, thickness, and synaptic density until around age 11 (Dursten & Casey, as cited in Choudhury, Charman, & Blakemore, 2008; Huttenlocher & Dabholkar, 1997). This is followed by a dramatic decline, through pruning, until the overall synaptic density of most brain regions is relatively equal in volume by adulthood (Dursten & Casey, as cited in Choudhary et al., 2008; Huttenlocher & Dabholkar, 1997). It is this reason why it has been consistently viewed and measured that there are definitive age-related changes in the frontal cortex (i.e., the PFC), and these age-related structural changes are directly linked to age-related functional (i.e., activity) changes in those same brain regions (Diamond, 2002; Ezekiel et al., 2013; Li et al., 2013; Morton et al., 2009; Rubia et al., 2006; Sadaghiani & D’Esposito, 2015; Wendelken et al., 2012; Wilk & Morton, 2012). These age-related changes in activity are viewed through the use of MRI devices.

The Necessity of fMRI

Until recently, the sheer scarcity of postmortem child and adolescent brains inhibited developmental cognitive neuroscientists’ ability to properly research the age-related changes in structure and function of the entire brain, since older methods required years to accurately measure any one brain region (Huttenlocher & Dabholkar, 1997). With the development of functional neuroimaging...
techniques, numerous brain imaging studies have provided significant amounts of data for developmental cognitive neuroscientists (Choudhary et al., 2008; Huttenlocher & Dabholkar, 1997; Wilk & Morton, 2012). Without the MRI, the study of the brain and the functional neurodevelopmental aspects known today would have taken several decades of extensive study to achieve even a small portion of what we know now.

Several fMRI studies have investigated the development of the brain’s structure during childhood and adolescence, as well as the continuing development seen throughout DT (Giedd et al., 1999; Huttenlocher & Dabholkar, 1997; Wilk & Morton, 2012). The brain regions that undergo pronounced development during adolescence are particularly those involved with cognitive control and executive functioning, with the most change occurring in the prefrontal cortex (PFC), a major functional region of the brain strongly associated with CC (Huttenlocher & Dabholkar, 1997). The PFC covers half of the structural location of the SFG-complex (see Figure 1). This paper focuses on the constituent components of the SFG: the dorsolateral (SFGdl), the posterior (SFGp), and the anteromedial (SFGam) SFG (see Figure 1).

T2*-weighted fMRI images. Understanding how the magnetic resonance imaging (MRI) machine functions is key to understanding the results of the present study that employ fMRI in its methods. The MRI machine can measure brain structure through a radio frequency excitation pulse allowing for T2-weighted contrast images (Glover, 2011). T2-weighted contrast images are generated through the measurement of how rapid protons dephase (proton spin decay from procession in the transverse plane), with differences in the speeds of this dephasing based on local magnetic inhomogeneities (Glover, 2011). This is very important to functional imaging of the brain (i.e., fMRI), since it allows for a measurement of Blood Oxygen Level Dependent (BOLD) signals. This indirect measure of neuronal activity in the brain allows for the generation of T2*-weighted contrast images. T2*-weighted contrasts rely on the dephasing associated with the blood oxygenation level in specific neurons; the [Deoxyhemoglobin:Oxyhemoglobin] ratio (Glover, 2011). There is more rapid dephasing in areas with greater deoxyhemoglobin, resulting in a weak T2* signal; with more oxyhemoglobin in a specific region, the slower the dephasing of protons, the stronger the T2* signal (Glover, 2011). Neurons that are activated during a cognitive task require more oxygen, which is carried by oxyhemoglobin, that allows them to function at a higher rate necessary to meet the cognitive demand (Glover, 2011). Thus, there is increased blood flow to these neurons. This allows for an image of the increased brain activity as a measure of more oxygenated blood (BOLD) moving to a metabolically active brain region (Glover, 2011). Essentially, the MRI machine allows for the indirect discovery of which specific neurons in a brain region are activated because of a cognitive task; a measure of brain function (Glover, 2011; see Methods).

Cognitive Control and the CC Network Studying the development of brain regions associated with CC is foundational to neurodevelopmental research because of the dynamic nature of the brain. Analyzing the normal developmental trajectories of the brain is fundamental to understanding any derivation caused by the environment, drugs, brain damage, or even illness (Diamond, 2002). The brain changes over time, and how it affects executive functioning can provide insight as to why a child might act differently than an adult in different scenarios. Rubia and colleagues (2006) posit that increased brain activation of the PFC, a critical node of the CCN, is positively correlated with age and task performance. So as a child ages, this brain region develops, resulting in increased activity; and since this region is implicated in
CC, this increased activity is indicative of improving CC. This sets the stage for the two prevailing theories of CC.

The two prevailing theories stem from two views of brain maturation: **Maturational** and **Interactive Specialization**. First, the **Maturational** view of brain, where a specific part of the brain (ex: the PFC) is encoded by a gene, that codes for a structure, which has one function; the relationship between structure and function is static (e.g., the dLPFC is solely responsible for CC). Maturationists, like Diamond (2002), assume that specific cognitive skills come “online” as the cortical structures solely responsible for that particular cognitive skill mature over DT. Diamond (2002) placed the increasing performance in CC over DT, directly to the development of the PFC; specifically, the dLPFC. Since the development of the dLPFC is protracted, the development of CC follows the same developmental pattern, and since lesions to the dLPFC result in decreased performance in CC tasks, Diamond (2002) links the two together.

The second view of brain maturation is described by Cole and Schneider (2007) and Fair and colleagues’ (2007) CCN model that follows the **Interactive-Specialization** view of the brain. This view suggests that multiple different brain regions, spatially separated or anatomically connected (via white matter tracts), are responsible for several different functions. Per this model, the development of a function, CC for example, is hinged on the development of these connections between several spatially separated brain regions, as well as the development of these brain regions themselves. Cole and Schneider (2007) and Fair and colleagues (2007) call this the **Cognitive Control Network** (CCN) model, which while being the over encompassing model, there are different networks covering different aspects of CC.

**The two major CCNs.** The two major CCNs in the current literature (Sadaghiani & D’Esposito, 2015) are the **Fronto-Parietal Network** (FPN) and the **Cingulo-Opercular/Insular Network** (CON). The FPN is composed of the dLPFC, mid cingulate precuneus, inferior parietal lobule (IPL), intraparietal sulcus (IPS), dorsal/lateral Frontal cortex (dF), and the cerebellum (Sadaghiani & D’Esposito, 2015). This network is responsible for “Adaptive Online Control”, supporting the initiation of control, adaptation to errors, and moment-to-moment adjustment of control, which, constitute conflict adaptation (Fair et al., 2007). The CON is composed of the dorsal anterior cingulate cortex (ACC), anterior insula (frontal operculum), dorsal anterior PFC, the thalamus, and right anterior inferior parietal lobe (Sadaghiani & D’Esposito, 2015). This network is responsible for stable maintenance of task control, task goals, and has a role in conflict adaptation (Fair et al., 2007; Sadaghiani & D’Esposito, 2015). However, its true responsibilities are still contested (Sadaghiani & D’Esposito, 2015). The Brodmann regions that the SFG-complex includes are associated with both CCNs, as well as several other neural networks (e.g., the Default mode Network).

**The Present Study**

**Purpose and Aims**

The aims of the present study are to measure the developmental (age-related)
changes in conflict-related BOLD activity in the SFG and its role in cognitive control, specifically with respect to conflict-adaptation across childhood, adolescence, and throughout early- to mid-adulthood.

**Location of the SFG.** The SFG-complex is located in the upper third (Brodmann areas 6, 8, 9, and 32) of the frontal lobe and has been linked to self-awareness and the sensory system (Goldberg, Harel, & Malach., 2006; Li et al., 2013). The SFG-complex consists of three constituent subregions. First, the SFGdl, that includes the cytoarchitecture of Brodmann Area (BA) 9 (e.g., the functional location of the dlPFC), as well as having an anatomical and functional connectivity to the middle and inferior frontal gyri (see Figure 1). Second, the SFGam, which includes the posterior part of BA 6, coincides with the functional region of the pre- supplementary motor area (SMA) and shows a structural connection to the anterior and medial cingulate cortices (see Figure 1). And third, the SFGp, which coincides with the functional location of the SMA proper and the premotor cortex, shows an anatomical and functional connection to the thalamus, frontal gyrus, the precentral gyrus, the medial cingulate cortex, and the caudate (see Figure 1).

The pre-SMA exerts control over voluntary actions in situations of response conflict, that allows for inhibitory control and has a role in CC (Li et al., 2013). Essentially, the SFG-complex likely has a substantial role in cognitive control due to its composition of, anatomical connection to, and functional responsibility with several CC-related brain regions.

**Potential linkage to CC as a complex.** The SFG-complex is also linked to self-awareness—in a task where it was turned “off”, participants lacked self-awareness—which is the ability to separate oneself from the environment and other individuals (Goldberg et al., 2006). Self-awareness should be considered separate from consciousness—the awareness of one’s environment and body—since self-awareness is how one consciously knows and understands their own feelings, motives, and desires (Goldberg et al., 2006). This link to self-awareness may have implications for cognitive control, since without self-awareness, one could not differentiate oneself from their “goal”, and its location and relation to the self. One would need an awareness of the self to grab an object, and this would have to be actively maintained.

In the study by Li and colleagues (2013), the SFG-complex coincides with the functional location of the SMA, which is involved in the execution of motor function within the working memory. This further lends to the plausibility that self-awareness may be linked to the SFG, since it can assist goal-directed behaviour.

In the present study, it is hypothesized that the SFG-complex, specifically, the SFGp, SFGam, and the SFGdl, will show age-related changes in conflict-related BOLD activity. The goal of this study is to explore how neural activity in the SFG-complex differs in children, adolescents, and adults during their performance in the Size-Congruency task; the BOLD brain activity of this task being a measure of conflict-adaptation and processing. The present study will extend past literature by examining the SFGdl, SFGam, and the SFGp’s roles in conflict adaptation through the conduction of region of interest analyses on the SFG-complex bilaterally. Also, since most of the previous literature relies on the Developmental Card Sort Task (DCCS) or Simon task (Diamond, 2002) as a measure of conflict adaptation, a different task (the Size-Congruency Task) will add to the body of literature in support of the SFGdl and SFGam’s roles in CC, particularly their roles in conflict adaptation throughout DT. Also, few studies have examined the age-related changes in CC-related activity in the SFG-complex as a whole. The frontal cortex is late developing (Diamond, 2002; Fair et al., 2007; Huttenlocher
& Dabholkar, 1997), so children have an undeveloped frontal cortex. Thus, the BOLD activity in this brain region will likely be much lower in children than adolescents and adults, who have a much more (or fully) developed frontal cortex. With this assumption, there will likely be age-related increases in the SFG-complex’s BOLD activity during the CC task. To examine this, a small subset of the overall data from Wilk and Morton (2012) was analyzed using neuroimaging analysis techniques, specifically using MATLAB’s spm12 package.

**Method**

The data used in the present study is a subset of data collected as a part of a larger study by Wilk and Morton (2012) that also analyzed age-related changes in brain activity associated with moment-to-moment adjustment of control (i.e., conflict adaptation). The present study seeks to validate the methods used by these authors and to expand the results to account for age-related differences in conflict-related activity in the SFG-complex. All procedures were approved by the University Research Ethics Board of the University of Western Ontario and thus agree with the required ethics rules in the context of fMRI research.

**Participants**

There were a total of 27 participants in the present study taken from Wilk and Morton’s (2012): eight children aged 9.7 to 11.6 ($M = 10.7$, $SD = 0.6$), seven adolescents aged 12.1 to 16.2 ($M = 15.1$, $SD = 1.4$), and 12 adults aged 21.0 to 32.4 ($M = 24.4$, $SD = 3.3$); as shown in Table 1. All participants were recruited from Western University. Participants younger than 18 years of age ($n = 15$) were recruited from the Child Development Participant Pool. Participants older than 18 years of age ($n = 12$) were recruited from either the Undergraduate or Graduate student populations of Western University. The broad age range was purposely selected to allow for age-related testing associated with conflict adaptation. All participants were right-handed and had normal or corrected to normal vision. Children were trained in a mock fMRI to limit movement during the fMRI scans to mitigate motion contamination. Consent and assent were provided by participants, and children under the legal age (18) had consent provided by their parents.

**Procedure**

The cognitive control paradigm. The cognitive control paradigm administered by Wilk and Morton (2012) is a modified version of the Size-Congruency Task; it is a stimulus-response compatibility task with compatible (i.e., congruent) and incompatible trials (i.e., incongruent; see Figure 2). This task allowed for CC measurements based on a measurement of the size-congruity effect; the incompatible trials require the participant to inhibit their natural tendency to select the physically larger stimuli, as the numerically larger digit, despite it being of a smaller numerical value (Henik & Tzelgov, 1982). This results in increased activity in botCCNs to process this “conflict” (i.e., instinctual “gut” response to correct response) to allow for a proper response in incompatible trials. The compatible stimuli do not break the inherent natural convention of larger numerical value with larger physical size and vice versa, thus making the compatible stimuli easier to process, which results in less BOLD activity. This difference in BOLD activity allows for the contrast maps discussed in Methods.

**Procedure.** An Event-Related study design was used, which allows for specific analysis of individual number stimuli. On each trial, participants were presented two Arabic numbers (ranging from 1 to 9) concurrently that differ in numerical and physical size, with the physically smaller number stimuli presented in 30-point font and the physically larger number stimuli presented in 60-point font (see Figure 2). Arabic numbers were presented for 1950 ms in...
white letters on a black background on a digital screen, and participants were told to press a button indicating the numerically larger digit. The incompatible stimuli differed from the compatible stimuli in that the numerically larger number was physically smaller than the numerically smaller number (see Figure 2).

The participants in the present study were presented with 75% compatible and 25% incompatible trials (4 of 16 trials are compatible, 12 of 16 are incongruent), used by Wilk and Morton (2012) in one subset of their data would not elicit the necessary hemodynamic response activity; the 25% compatible trials would result in lower conflict adaptation activity, since the brain would adapt to this “barrage” of incongruent stimuli resulting in less BOLD activity (Wilk & Morton, 2012), and so this dataset was not used.

The original Wilk and Morton (2012) study used 224 trials presented in 16 blocks for four, 7.8 min runs; however, in the present study, since only the 75% compatible condition for two runs are used, 64 trials were used. These 64 trials are comprised of 48 compatible trials and 16 incompatible trials, where 75% of the trials presented are compatible and 25% are incompatible. Jittering (i.e., random inter-trial intervals) was used between each individual trial to randomize the time in-between each trial. This interval varied between 1500 ms to 4500 ms ($M = 3000$ ms), however, the ordering of the trials was fixed for all participants. To clarify, this fixed presentation of trials means that the stimuli (trials and conditions) are presented in the same order, but the onset of each stimuli was varied for each participant. There was also 8000 ms of several breaks accounting for 12.5% of the total time spent. Participants viewed the stimuli while in the magnetic resonance imaging (MRI) machine using a mirror and indicated their answer by pressing a button. The original four runs collected in the MRI machine were T2*- weighted functional whole brain volumes, and T1-weighted anatomical whole brain volumes; only the first two runs were used.

**fMRI Data Acquisition.** A 3 Tesla Siemens Tim Trio MRI system was used to create whole brain volume images of T2*- weighted contrasts of the 58 participants for four runs. The data used in the present study is for 27 participants, each generating 234 whole brain volumes for each participant for two runs (of
four runs total) during the CC paradigm, the Size-Congruency Task. Images were taken in 2 s intervals in the Wilk and Morton (2012) study. In order to account for, and potentially mitigate, any dramatic changes in data, caused by shifting of the head, neck muscle relaxation, breathing, and swallowing motion correction was applied. Motion correction can be a significant issue with resolution and measurement of BOLD (hemodynamic response) activity for the specific brain region of interest—participants were first trained in a mock MRI, so they would be accustomed to the MRI (Wilk & Morton, 2012). Functional brain volumes consisting of 234 whole-brain volumes were each comprised of 32-slices, each having a 3mm thickness (3x3x3 mm voxel resolution), with no gaps between slices. T1-weighted anatomical whole-brain scans were also taken during the same neuroimaging session, and these consisted of 192 slices at 1mm thickness (1x1x1 mm voxel resolution) and allowed for co-registration during data preprocessing.

**Neuroimaging Analysis**

**Data preprocessing (SPM).** MATLAB’s *spm12* package was used to analyze the data provided by Wilk and Morton’s (2012). *spm12* is the Statistical Parametric Mapping package available on MATLAB that allows for the analysis of NIFTI-1 brain image files. *Spm12* was used to preprocess the data (see Figure 3). For each participant separately, the following data pre-processing was applied. First, *motion correction* was applied by comparing the 243 volumes (i.e., one scan of the brain) taken, of one participant, to the first volume as a reference, and then *realignment* the subsequent volumes (i.e., 242) to the reference, by applying transformations around six motion parameters (i.e., x-, y-, z- axes translations, and pitch, yaw, roll rotations). This is very important because motion-contamination dramatically alters the data derived from fMRI scans since it has the potential of causing an incorrect MNI (Montreal National Institute) coordinate reading; for example, voxel A at time 5 s is no longer the same MNI coordinate at time 25 s. Since, no participant deviated by 2mm (the maximum allowed deviation) either translationally or rotationally, no participant was excluded from the study due to motion-contamination.

Following realignment and motion correction, the T2*-weighted functional scans (volumes) are co-registered with a T1-weighted structural (anatomical) scan to allow for an overlay of the areas of activity identified by the functional scans onto a high-resolution anatomical scan. This allows for easy identification of areas where there is increased BOLD activity; this is nearly impossible on raw T2*-weighted functional scans (see Figure 3). Following co-registration, normalization was applied to the data, where all the participants’ T2*-weighted images were warped onto a standardized 91 x 109 x 91 stereotaxic space (i.e., the MNI 152 space). All the contrasts were standardized onto the adult stereotaxic space to allow for within-Group (inter-subject) analyses and comparison (see Figure 3). Finally, smoothing was applied to the data using an 8mm FWHM Gaussian Kernel that allows for a substantial signal-to-noise ratio boost (see Figure 3).
Analysis

First-level Analysis – Single-Subject (Within-subject)

Using MATLAB’s *spm12* package, and the *fMRI* specific package of *spm12*, the data for the 27 participants of the present study were analyzed on both the First-Level and Second-Level. First-Level Analysis, also known as single-subject analysis, models the BOLD response activity of one participant. The BOLD response activity was estimated using a General Linear Model (GLM) that generated event-related predictors for each participant individually. The design matrix of the GLM had 20 predictors, 10 predictors for each of the two runs, with the first two predictors for each run accounting for the *onset* of the compatible and incompatible trials; the third predictor explaining when an error was made by the participant; the fourth to ninth predictors accounting for the six variables of motion (x-, y-, z- axes, and pitch, yaw, roll; all addressed by *spm12* pre-processing); and the tenth predictor being a required “blank”. The first two predictors are the *Behavioural* predictors, which represent the Event-Related Design of the present study, that is characterized as a *stick function* (see Figure 4). This *stick function* does not represent the hemodynamic activity of the brain, so a *Physiological* predictor must be generated that predicts the hemodynamic activity of the brain in response to the presented stimuli (i.e., the incompatible and compatible trials; see Figure 4). This is done by convolving the *Behavioural* predictor’s *stick function* with a canonical hemodynamic response function (see Figure 4); this *Physiological* predictor was then used for model estimation. Furthermore, this allowed for the generation of parameters (β; beta-coefficient) for each of the 10 predictors for the two runs for each participant, by running their *Physiological predictor* through the GLM. A t-statistic for each voxel was then calculated using these parameters with the equation:

\[ t = \frac{\beta(\text{incompatible}) - \beta(\text{compatible})}{\text{variance}}. \]

The GLM allowed for the production of scaled images (i.e., statistical maps) for each participant that highlighted voxels where the t-statistic is not zero using different significance threshold for the two masks used in the present study; see Region of Interest Analysis using Masks. To summarize, the First-Level Analysis determined by just how much a particular voxel’s BOLD signal changed when comparing the incompatible trials to the compatible trials in the 75% compatible condition for a single participant.

![Figure 4](https://example.com/figure4.png)

*Figure 4. An event-related predictor and a canonical hemodynamic response function convolved to form the psychological predictor (Convolved time-series; Bach, Flandin, Friston, Dolan, 2009)*

Second-level Analyses – Within Group

Two separate within-group analyses were conducted using Second-level analysis: (1) A group contrast map generated from using the differences between the incongruent and congruent trials (i.e., conflict-related activity); and (2) the age-related changes in conflict-related activity between all participants. After generating First-Level Analyses for each participant, the results were used in a group
analysis to analyze the global BOLD activity across the entire sample. These contrast maps were generated using a significance threshold of $\alpha = .05$ (see Figure 5 and Table 2). The activated voxels were brain regions with a greater than zero t-statistic. Furthermore, this contrast map was then covaried with age (in months) in order to generate another contrast map of the age-related changes in conflict-related activity for the entire sample (see Figure 6 and Table 3). Lastly, exploratory analyses were conducted on the SFG-complex’s constituents, summarized in Table 3. It must be noted that no corrections for multiple comparisons were made.

**Regions of Interest (ROI) Analysis using Masks**

A *Mask* allows for the focusing of analysis on a specific subset of brain region(s), by excluding every region outside the demarcated area; this mask is applied to the dataset during *Second Level* Within-Group analysis. Two *masks* were used in the present study: (1) covers the regions within the two major CCNs that the CC paradigm activates, the FPN and CON; and (2) one that covers the regions exclusively in BA46 and BA9 (i.e., the dlPFC/ SFGdl). In essence, the CCN and BA46/BA9 *masks* reduce the number of comparisons. A threshold $\alpha = .05$ was used with the CCN *mask* and a threshold $\alpha = .1$ was used with the BA46/BA9 (i.e., dlPFC) *mask*; both $\alpha$’s are very liberal thresholds of activation.

**Results**

**First-level Analysis – Single-Subject**

A total of 27 contrast maps ($p = .05$, uncorrected) were produced from compatible and incompatible trials, generated from *First-Level analyses*. This allowed for an image of the brain regions associated with greater hemodynamic activity during the incompatible trials to be compared against the compatible trials. Using this data, the age-related differences were generated into a group contrast map.

**Second-level Analyses – Within Group**

Two group contrasts maps were generated using the Single-Subject analysis results. First, a contrast map of the BOLD

![Figure 5](image1.png)  ![Figure 6](image2.png)

*Figure 5.* spm fMRI within-group contrast map of the activation comparing incongruent and congruent trials, at $p < 0.05$, uncorrected. Red circles indicate regions within the SFG-complex.

*Figure 6.* spm fMRI contrast image of the age-related increases in conflict-related activity showing both the right and left SFG-complex, at $p < 0.05$, uncorrected. Red circles indicate regions within the SFGp.
activation in children, adolescents, and adults comparing the incompatible and compatible trials was generated. All three regions of the SFG-complex, the SFGp, SFGdl, and SFGam, show significant BOLD (i.e., conflict-related) activity, shown in Figure 5 and Table 2. The focus of the present study is on the second group contrast map, which used the first group map and covaried the age of the participants (in months) with changes in conflict-related activity, shown in Figure 6 and Table 3.

Consistent with the hypothesis, there was a significant age-related change in conflict-related activity in the right SFGp (MNI coordinates [16, -8, 66]: \( p = .018, t(25) = 2.21 \); MNI coordinates = [20, -6, 66]: \( p = .018, t(25) = 2.22 \)) and the left SFGp (MNI coordinates [-18, -2, 66]: \( p = .022, t(25) = 2.13 \)) at significance levels of \( p > 0.05 \), uncorrected. However, inconsistent with the hypothesis, only the SFGp showed significant increases, with no age-related changes in conflict-related activity in the other two subregions of the SFG (SFGdl and SFGam) at a significance threshold of \( \alpha = .05 \). But, at a significance threshold level of \( \alpha = .1 \), the left SFGdl does show age-related increases in conflict-related activity (MNI coordinates [-30, 20, 34]: \( p = .080, t(25) = 1.43 \); MNI coordinates [-38, 4, 38]: \( p = .088, t(25) = 1.35 \)); the dlPFC-specific mask was used to separately analyze the dlPFC (SFGdl). See Table 3 for a summary of all voxels that showed a significant age-related increase in conflict-related activity.

**Discussion**

The present study predicted that the SFG-complex would show age-related increases in BOLD activity bilaterally during the presentation of the CC paradigm, the Size-Congruency Task. Inconsistent with the hypothesis, the SFG-complex did not show age-related changes (increases) in conflict-related BOLD activity bilaterally. However, the right SFGp did show significantly (\( p < .05 \)) greater BOLD activation during the administration of the CC paradigm, when comparing the children, adolescents, and adults. Contrary to expectations, the key brain region responsible for CC in the two major theories of CC, the SFGdl (dlPFC), did not show any age-related changes in conflict-related activity, nor did the SFGam, both of which have been implicated in CC (Diamond, 2002; Fair et al., 2007; Li et al., 2013). Yet, looking at the first contrast map of conflict-related activity, both subregions were activated in response to conflict, reaffirming past literature. Since the SFGdl has a considerable amount of literature placing the responsibility, solely or as a part of a network, of CC over DT in this brain region, the researcher raised the significance threshold to \( \alpha = .1 \), allowing for significant findings in the SFGdl (i.e., dlPFC). If the results of the present study are contrary to not only Wilk and Morton (2012), but nearly all the past literature on age-related changes in the dlPFC, the validity of the paper should be called into question; thus, the necessity of decreasing the threshold to \( \alpha = .1 \) is clear.

Since the initial hypothesis was that the SFG-complex would show conflict-related activity significantly increasing over DT, the hypothesis cannot be accepted. This is because only the SFGp has a significant age-related increase in conflict-related activity, while the SFGdl and SFGam show no significance in age-related activity. Therefore, the SFGp potentially has some role in processing conflict (i.e., conflict adaptation) across DT, but the SFGdl and SFGam, while involved in conflict adaptation (see Figure 5 and Table 2), the present study cannot show that they process conflict across DT even with a liberal significance threshold of \( \alpha = .05 \) (see Figure 6 and Table 3).

Li and colleagues (2013) found that the SFG-complex has anatomical and functional connectivity patterns with several regions implicated in CC: the ACC, MFG, MCC, dlPFC, and the PPC. The SFG-complex’s association
with these regions strongly suggests that the SFG-complex may assist or influence decision-making, attention allocation, response and impulse inhibition (Li et al., 2013). The conflict adaptation contrast images, seen in Figure 5 and Table 2, show that these regions are activated in the conflict adaptation paradigm. The results of the conflict-related BOLD activity (Figure 5 and Table 2) coincide with the current literature (Diamond, 2002; Fair et al., 2007; Li et al., 2013; Sadaghiani & D’Esposito, 2015).

The SFGdl. The findings of this study are not consistent with the past literature with respect to age-related changes in conflict-related activity, especially in the SFGdl; BA of the dlPFC. The dlPFC has extensively and consistently been shown to have age-related increases in CC-related activity (Diamond, 2002; Ezekiel et al., 2013; Li et al., 2013; Morton et al., 2009; Rubia et al., 2006; Sadaghiani & D’Esposito, 2015; Wendelken et al., 2012) and to not see any age-related changes in CC-activity at a liberal threshold of $\alpha = .05$ is surprising. Diamond (2002) posited that because the dlPFC (SFGdl) was late developing, and the performance on CC tasks coincides with this protracted development, and since lesions in this brain region result in significant drops in performance on these tasks, the two were clearly linked. The dlPFC should be more active over DT since it is continuously developing and being relied more upon over DT; so increased activity in the dlPFC (i.e., SFGdl) over DT (Diamond, 2002) was expected. Similarly, Wendelken and colleagues (2012), using a CC task reliant on reorganization, found that the dlPFC (i.e., SFGdl) shows age-related differences in BOLD activation, specifically in the left dlPFC (i.e., SFGdl). Since the dlPFC (i.e., SFGdl) is slow developing, children will take longer to answer the reorganizing CC task compared to older participants (Wendelken et al., 2012). The literature supports the fact that children will have slower response times in CC tasks, since it requires them more time and processing, due to the underdevelopment of the connections between the CCN components, and the underdevelopment of the CCN components themselves (Diamond, 2002; Ezekiel et al., 2013; Fair et al., 2007; Waxer & Morton, 2011).

The present study did find significant conflict-related activation of the left dlPFC (see Figure 5 and Table 2), supporting the validity of the methods of Wilk and Morton (2012), and the results of the past literature, inasmuch as showing that the dlPFC is associated with CC. However, by lowering the significance threshold, a significant difference was found in the dlPFC (SFGdl) for age-related increases in conflict-related activity ($p < 0.1$, uncorrected). The results of this study are contrary to the past literature, in that there were no significant age-related changes at a higher confidence (i.e., threshold) level, and because of that, the present study cannot show that there were age-related changes in conflict-related activity in the SFGdl. However, it can be concluded the SFGdl is indeed involved in CC, per the contrast image of the incompatible and compatible trials generated in this study (see Figure 5). This discrepancy suggests additional exploratory studies to analyze the potential age-related increases in SFGdl BOLD activation using several different CC paradigms (e.g., Card Sort Tasks, Simon Task, Stroop Task; see Future Directions and Limitations).

The SFGam. The SFGam has also been strongly associated with CC due to its anatomical and functional connectivity to the ACC and MCC, and since it coincides with the functional location of the pre-SMA (Li et al., 2013). Li and colleagues (2013) show that the SFGam is linked to, and is a part, of both the CCN and the default mode network (which is the area of the brain active during periods of rest). The pre-SMA (i.e., SFGam) has been implicated in exerting control over voluntary actions in situations of response conflict, specifically
recruited during inhibition and task-switching. Furthermore, the ACC is a pivotal component of the CON, and while the ACC alone shows age-related increases in conflict-related activity (see Table 3 and Supplementary Materials), the SFGam does not. Since the SFGam is anatomically linked to the ACC, perhaps its role is that of a mediator, rather than one that directly processes conflict. Also, the conflict adaptation paradigm activates the CON, as seen in Figure 5 and Table 2, so two potential explanations can be derived from this activation profile: (1) The SFGam shows no age-related changes in CC-related activity because it acts as a mediator; (2) the Size-Congruency Task does not activate the CON to the same extent as other CC paradigms. If either explanation were to be adopted, then the SFGam cannot be ruled out of having a role in CC over DT; of course, much more research must go into this brain region involving various CC tasks in order to account for the various aspects of CC, apart from and including conflict adaptation, such as working memory and moment-to-moment of adjustment of control, or even other measures of inhibition.

The SFGp. The SFGp is a part of the motor control network (MCN) since it coincides with the functional location of the SMA proper and premotor cortex, as well as showing an anatomical, through white matter, and functional connection to the thalamus, frontal gyrus, precentral gyrus, medial cingulate cortex, and the caudate; these brain regions are all nodes of the MCN (Li et al., 2013). Essentially, the SFGp has been shown to be correlated with the sensorimotor-related brain regions. The MCN is responsible for generating temporally-dependent commands that move a person’s limbs and body (Berniker & Kording, 2015). This is important because the CC paradigm, the Size-Congruency Task, involves the movement of the hand to press one of two buttons to select the correct response in the incongruent and congruent trials (Wilk & Morton, 2012). This potentially confounds the significant results obtained in this study, because the SFGp was the only location within the SFG-complex to show significant age-related changes in activity; this “activity” is not necessarily conflict-related, rather there is the potential of this activity being motor-related (but still CC-related). The hesitation one experiences while selecting the correct answer in the incongruent trial compared to the very little to no hesitation one experiences in the congruent trial. And since this “hesitation” is mediated by motor control insofar as deciding one answer over the other, the activation profile might be very similar to that of what has been coined “conflict-related activity” (the incongruent to congruent contrasts as a result of conflict adaptation). To clarify, hesitation occurs because of the competing stimuli (i.e., numerical and physical sizes) participants are exposed to in the task; conflict-adaptation allows for one to inhibit the innate response of assuming the physically larger digit is numerically larger (e.g., in incongruent trials). This hesitation in selecting the correct answer requires a quick change in a motor command, and since over DT, the frontal cortex develops significantly, age-related changes in motor-related activity are also observable. Potential ways of mitigating this confounding responsibility of the SFGp is discussed in the proceeding section.

Future directions and limitations. With future studies, the SFGam and SFGdl could potentially also be shown to have a role in some other aspect of CC across DT; age-related changes in patterns of brain activity in the SFGdl and SFGam associated with cognitive control, but apart from conflict adaptation. The SFGdl encompasses not only the dlPFC but is also anatomically and functionally connected to the middle and inferior frontal gyri; all of which have been implicated in CC (Li et al., 2013). It is thus surprising to not see significant age-related increases in CC-related activity in any of these regions at a very liberal threshold of $\alpha = .1$,
since the literature posits otherwise (Ezekiel et al., 2013; Hu et al., 2016; Waxer and Morton, 2011). Potential reasons for this lack of significance in age-related changes in conflict-related activity hinge on the kind of CC that the Size-Congruency Task measured, particularly response inhibition and moment-to-moment control (Henik & Tzelgov, 1982). CC is not limited to only these two aspects, but has much broader responsibilities, like working memory, decision making, planning, impulse control, and organization. So, while they may not have a responsibility in these two aspects of CC over DT, both the SFGdl and SFGam have been implicated in these other aspects (Li et al., 2013; Hu, Ide, Zhang, & Chiang-shan, 2016).

There was also much more pronounced activity in the right SFGp, with analysis using spm revealing a much lower age-related increase in conflict-related activity in the left SFG (see Figure 6 and Table 3); the left SFGp showed less age-related increases in conflict-related activity than the right SFGp, in that the correlation of age and the magnitude of activation is slightly lower in the left than the right SFGp. This might point to a lateralization of the CC network involving the SFG-complex being right-lateralized in right-handed individuals. Hu and colleagues (2016) studied lateralization of the SFG, where they found that the “Right SFG” (here meaning the right anterior SFGdl) was associated with inhibitory control (i.e., conflict adaptation). However, Hu and colleagues (2016) used the Stop Signal Response Task (SSRT), which is a well-established paradigm measuring for inhibitory control. The CC paradigm of the present study also measures response inhibition, but it generates much broader activation of the FPN and CON (i.e., also measure moment-to-moment adjustment of control), whose activity is not exclusive to response inhibition. The SSRT in Hu and colleagues (2016) showed much less activity in the overall FPN or CON and was localized to the prefrontal and parietal cortices. Their finding that the “Right SFG” is associated with inhibitory control does not apply to the right SFGp, where there were age-related increases in conflict-related activity in the present study. While their results confirm the importance of the dlPFC (anterior SFGdl) in nearly all aspects of CC, their results do not account for the age-related changes in activity, due to their use of only adults in their study. Future studies must include both right- and left-handed individuals to potentially find whether the brain lateralizes conflict adaptation in the SFGp over DT. Hu and colleagues (2016) study is important to parse, because they fail to consider using a task that activates the entire SFG-complex, and opt to study only the SFGdl bilaterally, but further add to the roles of right and left SFGdl in response inhibition and working memory respectively. Future studies could use their methods and focus on the bilateral nature of the entire SFG-complex.

There were many limitations in the present study that may help in parsing why the SFGam and SFGdl resulted in data contrary to the current literature. A major limitation is the correlational nature of the study, that, while being useful for suggesting a possible causal relationship cannot establish causality. These studies essentially have poor validity because they cannot prove that variable A (e.g., conflict adaptation process) causes a change in variable B (e.g., increased/changes in BOLD activity). They only show a weak or strong relationship (covariation) between two or more variables (e.g., increases conflict-related activity over DT). Of course, if this relationship is weak (low correlation), one can assume that there is no causal relationship. It is thus crucial to also conduct longitudinal studies to measure, for example, changes in brain activity in the SFGp, SFGam, and SFGdl at various timepoints of one participant. This will allow for the establishment of a true causal relationship. Thus, it is important to account for all the limitations and
future directions provided by this paper to concretely establish the SFG-complex as a component of a CCN and its importance over DT; or perhaps develop a new CCN centered around the SFG-complex.

A second major limitation would be the lack of a behavioural task performance analyses in the present study. Increased BOLD activity over DT in the SFG-complex is not definitively indicative of the increasing responsibilities of these brain regions in CC (i.e., conflict processing). It is thus necessary to analyze behavioural data in both trials, to empirically demonstrate CC improvements; while the present study did not analyze behavioural data, the study by Wilk and Morton (2012) did, and they were able to empirically show that increased BOLD activity was indeed indicative of increasing task performances. Future studies must employ many more behavioural paradigms alongside the many CC paradigms to account for age-related changes in CC abilities.

Lastly, while it may not be a limitation, future studies should use a more specific mask that covers only the region of the SFG-complex to reduce the number of comparisons allowing for more clear contrast images and analyses of the distinct Brodmann areas.

**Implications.** As previously mentioned, the potential that the SFGam (or SFGdl) was not activated, as it should have been per the literature, might be indicative of the failure of the CC paradigm, the *Size-Congruency Task*. While it may activate both the FPN and CON, conflict adaptation is chiefly a response-inhibition form of CC. Different tasks, particularly the DCCS and Simon tasks, have found age-related changes in CC-related activity in the SFGam and SFGdl, so it is plausible that the *Size-Congruency Task* might not activate the CCN to the same extent as other tasks over DT, or, since this task primarily is a measure of response inhibition, only the appropriate regions show age-related increases, while the other subregions of the SFG are responsible for a different CC process over DT. Future studies should include as many CC paradigms as possible to account for this discrepancy between the literature and the results of the present study.

A major implication of this study is the addition of the SFGp to a CCN, since it is the only brain region of interest that resulted in significant age-related increases in CC-related activity. The SFGp should thus be the focus of more CC-related studies. The results of this study show that the SFGp has a role in response inhibition, which is one of many CC-related responsibilities of CCNs. The SFGp’s connection to the precentral gyrus, caudate, thalamus, and frontal operculum, indicate its role in the MCN, and since the SFGp coincides with the functional location of SMA proper and premotor cortex, the paradigm used might have caused increased activity here but not as a result of CC (response inhibition; conflict adaptation). The paradigm involves the clicking of a button while in the fMRI to select the correct stimuli in a trial. Thus, it is likely to show age-related BOLD activity, because of this motor-related activity, and not because of CC.

Future studies must eliminate the need to move one’s hand to select the proper stimuli in order to account for the motor control aspect of the SFGp. Perhaps, a measure relying on saccades (i.e., eye movements) to indicate selection, in order to eliminate this reliance on motor action that the SFGp has a role in; the SFGp is part of the MCN which is responsible for initiating and generating movement (e.g., moving one’s hand to press the button). The MCN role of the SFG needs to be eliminated from future studies, because of its potential of being confounding, due to the reasons outlined in the discussion. The fMRI contrast image is not showing just CC-related activity, but rather conflict-related activity, which can be both CC-related and Motor-related. Also, over DT, an individual’s motor control dramatically
increases which can explain the age-related changes in activity in the present study (Berniker and Kording, 2015; Choudhary et al., 2008; Diamond, 2002). This reiterates the necessity of eliminating motor-related activity from future studies.

**Concluding Remarks.** Brain imaging is simply a method of viewing some aspect of the brain, not an explanation of why that activity occurs or what it means. A detailed cognitive account of the underlying function, using behavioural or other psychological batteries, is required. While the cognitive adaptation task shows the ability of the brain to adapt to some cognitively challenging task, it is not a true measure of a behaviour, in that it has some failings. The results rely on correlation, so results obtained from these results do not show causality; the age-related activity seen in the SFG is not necessarily caused by age. To establish causality, a longitudinal study directly measuring the age-related changes in activity (and structure) in the SFG is required to fully confirm whether the age-related changes in the SFG truly develops over DT. Further studies should use different tasks to measure the various other aspects of CC, apart from conflict adaptation (which is a form of response inhibition), to measure whether the SFGam and SFGdl show age-related increases in CC-related activity. Establishing the SFGp as a CCN constituent or generating a new neural network with the key node being the SFG-complex is probable given its many functional and anatomical connections to CC-related brain regions and will require further research.

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Final Revision Received: 04/05/2019

**References**


Table 1
Participant ages in years.

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Table 2
Brain regions that showed significant activation comparing the incongruent trails to congruent trials.

<table>
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<th>MNI Coordinates</th>
<th>p-value</th>
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<tr>
<td></td>
<td>R</td>
<td>16 -6 66</td>
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<td>L</td>
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<td>0.022*</td>
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<tr>
<td>SFGam</td>
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<td>ACC</td>
<td>R</td>
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<td>0.005**</td>
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<td>SFGdl</td>
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<tr>
<td></td>
<td>L</td>
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Note: ** indicates significance at p < 0.01, * indicates significance at p < 0.05.

Table 3
Brain regions that showed age-related changes in conflict related activity.

<table>
<thead>
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Note: ** indicates significance at p < 0.05, * indicates significance at p < 0.01.
Supplementary Materials

*spm fMRI* contrast image of the age-related increases in conflict-related activity showing both the right and left SFG-complex, at p < 0.05, uncorrected. Red circles indicate regions within the SFGdl and ACC.
Raw Data Readouts from *spm*:

**con-age**

![SPM results](image)

**SPM results:** Analysis/Group_age
- Height threshold $T = 1.708141$ ($p < 0.05$ (unc.))
- Extent threshold $k = 0$ voxels

**Statistics: $p$-values adjusted for search volume**

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*Table shows 16 local maxima more than 4.0 mm apart*

- Height threshold: $T = 1.71$, $p = 0.049$ (1.000)
- Extent threshold: $k = 0$ voxels
- Expected voxels per cluster, $<k> = 256.940$
- Expected number of clusters, $<c> = 21.82$
- FWE: 0.049, FDR: Inf, FWEc: Inf, FDRc: Inf

**Degrees of freedom $= [1.0, 25.0]$**

**FWHM = 13.1 13.4 13.2 mm mm mm; 0.5 6.7 6.8 (voxels)**

**Volume = 117936 = 14742 voxels = 27.1 resels**

**Voxel size: 2.0 2.0 2.0 mm mm mm; (resel = 287.79 voxels)**
AGE-RELATED BOLD ACTIVATION IN THE SFG

con-age

SPM\{T_{25}\}

Those analyses Group age

Height threshold \( T = 1.316345 \) \( (p<0.1 \text{ (unc.)}) \)

Extent threshold \( k = 0 \) voxels

Statistics: \textit{p-values adjusted for search volume}

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Table shows 16 local maxima more than 4.0 mm apart

Height threshold: \( T = 1.32, p = 0.095 \) (1.000)

Extent threshold: \( k = 0 \) voxels

Expected voxels per cluster, \( <k> = 828.964 \)

Estimated number of clusters, \( <c> = 105.991 \)

Degrees of freedom = \([1.0, 25.0]\)

FWHM = 13.1 13.4 13.2 mm mm mm; 6.6 6.7 6.6 (voxels)

Volume: 117936 = 14474 voxels = 27.1 mm

Volume slice: 7 9 5 0 7 0 mm mm mm; voxel = 297.79 voxels
AGE-RELATED BOLD ACTIVATION IN THE SFG

Statistics: *p*-values adjusted for search volume

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<td>0.999</td>
<td>2.11</td>
<td>2.01</td>
<td>0.012</td>
<td>-38</td>
<td>-44</td>
</tr>
<tr>
<td>1.000</td>
<td>0.999</td>
<td>2.62</td>
<td>2.45</td>
<td>0.007</td>
<td>-24</td>
<td>58</td>
</tr>
<tr>
<td>1.000</td>
<td>0.999</td>
<td>2.45</td>
<td>2.30</td>
<td>0.011</td>
<td>30</td>
<td>58</td>
</tr>
</tbody>
</table>

Table shows 3 local maxima more than 8.0mm apart.

Degrees of freedom = [1.0, 26.0]
Expected voxels per cluster, \(<k> = 207.087\)
Voxel size: 2.0 2.0 2.0 mm mm mm; (resel = 231.20 voxels)