Research report

A structural equation modeling analysis of attentional control: an event-related fMRI study [☆]

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Abstract

We report here the first investigation of the effective connectivity between neural structures supporting attentional control using structural equation modeling and functional magnetic resonance imaging (fMRI). Attentional control was examined by employing a modified version of the flanker task. We found that the inconsistent condition elicited a significantly greater number of path coefficients than the consistent condition. In addition, we report that the strength of the prefrontal paths common to both conditions were not different, but that the remaining six paths were different between conditions. Importantly, these results suggest that the *relationship* between regions supporting attentional control differ between task conditions but the strength of the relationship between some prefrontal regions is invariant between task conditions. Additionally, we found that the paths were significantly lateralized to the right hemisphere. These results are discussed in relation to theories of the function of each region in attentional control.
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1. Introduction

Over the past decade, functional neuroimaging studies have identified brain regions associated with the performance of cognitive and perceptual tasks. These data have proven invaluable in establishing the cartographies of cortical loci that support cognitive processing. However, as the cognitive neurosciences mature, it has become increasingly important to more formally investigate how these regions dynamically influence one another to support cognition.

Neuroimaging research typically employs a general linear model (GLM) approach to investigate brain activation patterns [13]. Although this type of statistical analysis has proven fruitful in determining how brain regions react during certain cognitive tasks, the analyses are often limited to examining the magnitude and extent of neural activation.

Structural equation modeling (SEM) is one statistical method that can be applied to neuroimaging data to investigate the way a network of brain regions influence one another when performing a given task. By computing the interregional covariances and specifying a model of predicted relationships among brain regions, path coefficients can be derived to represent the strength and direction of the effect that one region exerts on another. This approach has been applied to visual perception in spatial and object identification [20], working memory [21], attentional modulation of visual processing [6], episodic memory [17], nondeclarative long term memory [22] and age-related changes in encoding and recall [8]. Although one study employed SEM to assess top down attentional modulation

of visual processing [6], SEM has not been used to investigate the relationship among neural systems underlying attentional control in a response conflict paradigm, that is, in a paradigm in which subjects are instructed to selectively attend to a subset of the available information and ignore potentially conflicting distractors.

In the current study, we employed SEM to assess the relationship among brain regions supporting attentional control in response conflict. We used a version of the flanker task designed by Botvinick et al. [4]. In this task, participants are presented with a series of five arrows and asked to respond with a button press to the direction of the center arrow. The center arrow could point to the left or right while the flanking arrows point in the same (consistent: <<<<<) or opposite (inconsistent: <<><<) direction.

There were two motivating factors for the current study. First, the relationship between regions involved in attentional control has not been studied using this type of statistical analysis. However, relatively precise hypotheses regarding which brain regions interact and under what conditions they interact, have been systematically examined with animal research [9,10], lesion data [14] and cognitive task manipulations in humans [1,2,4,11–19,23,24]. (Note that the term 'interact' can have multiple meanings; the current paper uses the word in a relational sense and not in a statistical sense.) By utilizing this information, and formulating a model of predicted relationships among brain regions in an SEM approach, we were able to examine current theories of regional interactions that support attentional control.

Second, typical studies utilizing flanker or Stroop tasks often examine how the inconsistent condition invokes the attentional network to a greater *degree* than the consistent or neutral condition. The results from these studies suggest that the attentional network is at least partially recruited in non-conflict conditions (e.g., consistent, neutral), but to a lesser *degree* than in the inconsistent condition [19,23,24]. So, the degree of activity within the attentional network fluctuates according to task demands. However, whether the *interactions* between regions also vary according to task demands has not been examined. There are two possibilities, either the interactions between regions remain constant while the degree of activity in each of the regions varies, or the interactions between regions also vary by task demands. For example, if according to an SEM framework, a relationship exists between the inferior parietal lobule and inferior frontal gyrus for one condition, we could ask whether that relationship remains static, or varies, across other conditions.

In addition, the power of SEM lies in its ability to determine whether two regions are related, and also to determine the strength and direction of the relationship. If the relationship between brain regions remains constant but the degree to which the attentional system is invoked varies, then the number and direction of paths in the SEM should be the same for both conditions, while the strength of the path coefficients should be larger for the inconsistent condition. However, if the relationship between regions

differs for each condition of the flanker task, then the direction or number of paths should be different across conditions. If this latter result is found, then it would suggest that the *relationship* between regions within the attentional network is different between the two conditions of the flanker task.

In summary, we employed SEM to assess the relationships between brain regions involved in attentional control. This analysis not only provides the first examination of the effective connectivity among brain regions involved in the attentional network, but illuminates current theories of the relationship among brain regions. In addition, our analyses provides important information regarding whether the relationship between regions in both conditions of the flanker task are directionally equivalent. This particular analysis compliments and adds to common GLM analyses of neuroimaging data that are typically limited to investigating the magnitude and extent of neural activation.

2. Materials and methods

2.1. Participants

Twenty (10 female) right-handed individuals ranging in age from 21 to 27 participated in the experiment. All participants were screened for a history of neurological insult and disease and provided an informed consent prior to participation. All participants had normal or corrected to normal visual acuity. The study was approved by the University of Illinois Institutional Review Board.

2.2. Stimuli and design

Two trial types were included: (1) *inconsistent trials* in which the flanking arrows provided conflicting information to that of the center arrow and (2) *consistent trials* in which the flanking items cued the same response as the center arrow. A two-button manual response box was used with the left most button corresponding to a left pointing center arrow and the right most button corresponding to a right pointing center arrow. Participants were told to respond to the direction of the center arrow as quickly and as accurately as possible, using their left and right index fingers.

We used a first-order counterbalanced randomized design, in which each trial consisted of a fixation stimulus (+) lasting 13.5 seconds followed by a 1 s cue (——) informing the participant of an oncoming trial followed by a 1.5-s presentation of the imperative stimulus (e.g., <<><<). Each participant completed six runs of 17 trials each, preceded by a single practice block with feedback.

2.3. Formulation of the SEM

Previous neuroimaging studies have reported a number of brain structures consistently implicated in attentional

control paradigms such as task switching [16], flanker [4] and Stroop [1,2,19,23,24]. The regions of interest (ROIs) in the current study were defined on the basis of this body of research and included the inferior frontal gyrus (IFG), middle frontal gyrus (MFG), inferior parietal cortex (IPC), superior parietal cortex (SPC), thalamus (TH) and anterior cingulate cortex (ACC). Although not an exhaustive list of ROIs, these regions are some of the more commonly investigated and discussed in relation to attentional control and response conflict processes. Therefore, our preliminary model (Fig. 1A) was created from known neuroanatomical paths as well as theories regarding the function of each region in attentional control.

The exact role of ACC in attentional control and executive processes has been a dominant source of debate in cognitive neuroscience [7]. Similarly, the precise relationship that the ACC has with other regions is also controversial [1,2,11,19,23]. Although all current theories propose some relationship between prefrontal regions and ACC, the direction of the relationship is a current source of investigation [19,23]. Therefore, since the direction of this relationship remains under scrutiny, we proposed a reciprocal relationship between ACC and MFG, thereby allowing all current theories of ACC/DLPFC relationships to be modeled.

The second modeled relationship in prefrontal cortex was a reciprocal path between the MFG and IFG. Some theories propose that certain subregions of IFG influence the activity in MFG, which is thought to be involved in among other things, working memory processes and the maintenance and execution of an attentional set [1,11,19,23,24]. Although these regions are known to be anatomically and functionally related, the direction of the relationship in attentional control is currently unknown, therefore, both directions between IFG and MFG were modeled in the current design.

In addition, we hypothesized that both the IPC and SPC were reciprocally related with MFG and IFG. These regions have been established in non-human primates and humans
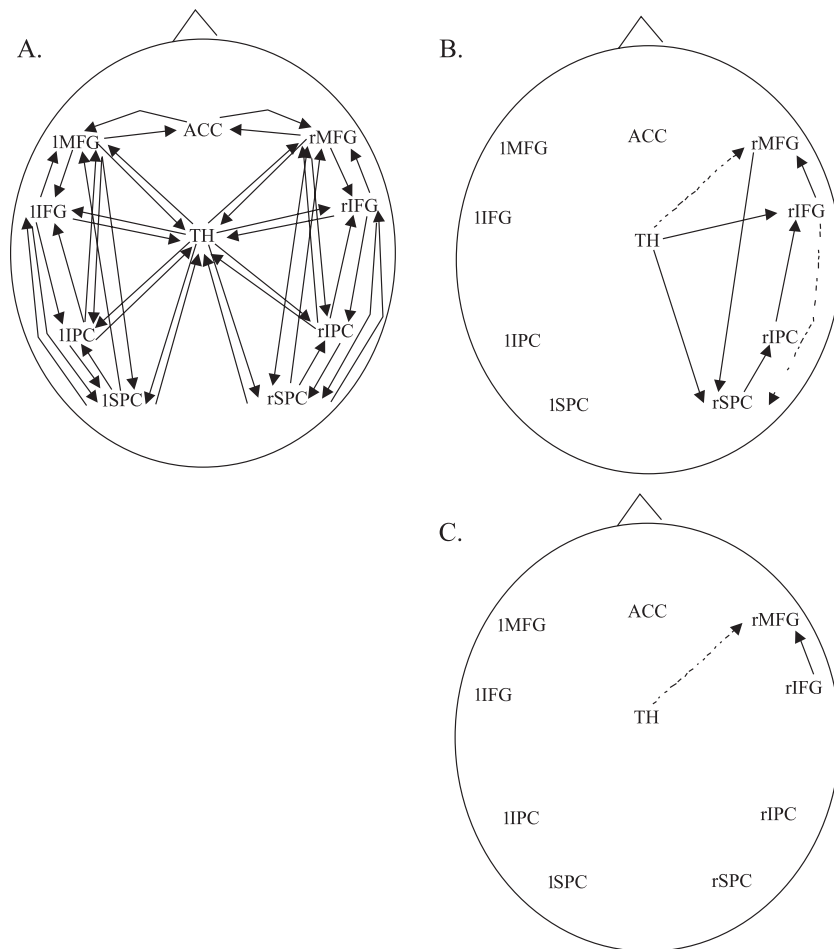

Fig. 1. (A) A schematic display of the proposed original model. (B) The simplified model obtained by retaining the significant paths from the proposed model. These are also the significant paths for the inconsistent versus baseline comparison (positive coefficients shown in bold faced lines; negative coefficients shown in dashed lines). (C) The paths for the consistent versus baseline comparison (positive coefficients shown in bold faced and negative coefficients shown in dashed lines). ACC=anterior cingulate cortex, rMFG=right middle frontal gyrus, lMFG=left middle frontal gyrus, rIFG=right inferior frontal gyrus, lIFG=left inferior frontal gyrus, TH=thalamus, rIPC=right inferior parietal cortex, lIPC=left inferior parietal cortex, rSPC=right superior parietal cortex, lSPC=left superior parietal cortex.

to be functionally and anatomically connected to prefrontal regions [9,10]. The parietal regions have been implicated in a variety of cognitive processes such as working memory [30] and attentional and inhibitory control [2]. Therefore, two different parietal regions were included in the model because of their consistent involvement in attentional control tasks [2]. Furthermore, we predicted that there would exist a relationship between the SPC and IPC based on reported correlations between these regions [24]. Since posterior regions influence prefrontal regions [8,23] and, similarly, prefrontal regions influence posterior regions [12,23,24], we felt it prudent to model reciprocal relationships between prefrontal and posterior regions to accommodate these relationships.

Finally, the TH is a subcortical structure known to be involved in a number of facets of attentional control [18]. Based on LaBerge's model of the pulvinar's involvement in attention and well-established anatomical relationships between the TH and parietal and prefrontal regions [29], we hypothesized reciprocal paths from the TH to the MFG, IFG, IPC and SPC.

2.4. Procedure and image processing

Participants were placed in a 1.5-T GE Signa scanner equipped for echo-planar imaging (EPI). Head position was stabilized using a bite-bar attached to the head coil to minimize motion during the session. A total of 810 T2* weighted echo-planar images were acquired for each participant (TR=2017 ms, TE=40 ms, flip angle=90°) each consisting of 20 contiguous slices (3.75×3.75×5.0 mm) parallel to the AC-PC line.

The first four volumes of each run were discarded to allow the MR signal to reach steady state. Functional data for each participant were slice time corrected, motion corrected, spatially registered to stereotaxic space and spatially smoothed using a 3D Gaussian kernel (FWHM=8×8×8 mm). A high pass temporal filter was then applied at 100 seconds, as was a 4-s Gaussian lowpass filter. SPM99 was used for image processing and statistical analysis [13].

2.5. Statistical analysis

The GLM was applied at each voxel in the predefined ROIs for all participants, using an empirically derived model of the hemodynamic response function (SPM99). Both conditions (inconsistent and consistent) were modeled separately and compared to a 13.5-s baseline immediately preceding the onset of the stimulus. Therefore, for each condition, the resulting beta weights provide a test of significant deviation from zero. The comparison of each condition to baseline was preferred over a direct comparison of the conditions so that regions associated with the attentional network could be examined regardless of the level of conflict. Modeling the results from the direct comparison would only have provided the relationship among regions associated with conflict and not attentional control more globally. We directly examined whether the inconsistent condition relied on the proposed model to a greater degree than the consistent condition by testing for equality of the path coefficients in the models (see SEM section below).

The beta maps consisted of a parameter estimate at each voxel for all participants. The peak beta values were extracted from a 27-cubic voxel area (each voxel was 2×2×2 mm) in each of the 10 predefined ROIs for all participants. Since all subjects were preregistered to a standardized space the 27-voxel cube was positioned in the same region for all participants, thereby reducing any variation associated with brain or ROI volume. The covariance matrix was derived using these beta values at each of the ROIs. SEM was carried out using M-Plus software [25].

2.6. Structural equation modeling

SEM can be viewed as a combination of factor analysis and regression, and provides a general framework for statistical analysis that includes many traditional multivariate procedures as special cases (e.g., factor analysis, regression analysis and canonical correlation). Applications of SEM to investigate connectivity between brain areas in functional magnetic resonance imaging (fMRI) data have become more popular in recent years (e.g., Refs. [20–22]).

In the SEM literature, goodness-of-fit (GOF) of the model is usually evaluated by a chi-square test and goodness-of-fit indices such as standardized root mean square residual (SRMR) [3], and comparative fit index (CFI) [3]. However, the conventional chi-square test may not be well behaved if the normality assumption is violated. Instead, Satorra and Bentler [27] proposed an adjustment on the original chi-square, which is robust against non-normality (S–B χ^2).

In addition, simulation studies suggest the following fit index cut off value guide for good models with continuous outcome variables: CFI>0.95 in combination with SRMR< 0.08, which can retain acceptable proportions of simple and complex true-population models and reject reasonable proportions of various types of misspecified models [15]. Maximum likelihood estimation is used to fit all the models in this study, the GOF of the models are evaluated by the Satorra–Bentler χ^2 supplemented with CFI and SRMR.

2.7. Direct comparisons

It is common for researchers using SEM to face the problem of choosing from among two or more competing models. As with the general problem of model selection in statistics, the choice of which procedure to use depends on whether or not the competing models are "nested" within one another. In a loose sense, we can say that model A is

nested within model B if model A is a special case of model B. For example, we can assume that Fig. 1A (as model A) has been fit simultaneously to both inconsistent and consistent conditions but allowing all the paths to have different magnitudes for the two conditions. Model B is a special case of model A if some or all of the paths are constrained to be the same across the two conditions. For example, in this study our modified models (Fig. 1B and C) can be considered nested models within the original model (Fig. 1A). We use the maximum likelihood method to fit all of these models and we can obtain Satorra–Bentler χ^2 test statistics for each of them.

When two models are nested, the Satorra–Bentler χ^2 test statistics from each of these models can be compared against each other. The detailed procedure for how to perform this test is described in Satorra and Bentler [27]. We used this method to test whether a path is equally strong in magnitude between the inconsistent and consistent models.

We first simultaneously tested whether all of the eight paths in Fig. 1B were the same between the inconsistent and consistent conditions. To do this, we fit two models, one with all eight constraints imposed simultaneously between the two conditions and one without any constraints. This step produces a result that signifies whether any of the paths between the two models are significantly different without specification of which paths were significantly different.

Next, in order to evaluate each path individually, we performed eight model comparison tests to check which path(s) differ significantly between the two conditions. The procedure was done as follows: we fit a model with a constraint on one of the paths (e.g., from Th to rMFG) to be the same between the two conditions while the others remain unconstrained (i.e., the other seven paths are allowed to be different between the two conditions). This (nested) model is compared with the model without any constraints (i.e., all eight paths can take different values in the two conditions) by the S–B χ^2 difference test [28]. The result of this step is a test statistic representing the probability that the two paths are of equal strength. In other words, the test provides a direct comparison between a path from one model (e.g., consistent) with the same path from the other model (e.g., inconsistent).

A similar analysis was conducted to test for laterality differences between the paths in the right hemisphere with the paths in the left hemisphere. For the inconsistent condition, we first used the model in Fig. 1B and simultaneously added the same paths in the left hemisphere while keeping all paths unconstrained. Then, we fit this same model with constraints imposed so that the paths in both hemispheres were of equal magnitude. The constrained model was then tested against the unconstrained model by the S–B χ^2 difference test as explained in the comparison between the inconsistent and consistent conditions. Finally, we fit eight models, each model with one constraint imposed across the corresponding path in the left and right hemispheres of the brain while the remaining seven were

left unconstrained. The constrained model is then compared with the model without any constraints by the S–B χ^2 difference test. This analysis results in a direct comparison between a path in the right hemisphere with the same path in the left hemisphere.

The same method was conducted to test for laterality effects in the consistent condition with the exception that all eight paths in the inconsistent condition were also tested for laterality differences in the consistent condition.

3. Results and discussion

Participants were reliably slower to respond to inconsistent ($M=620$ ms) compared to consistent ($M=530$ ms) trials ($t(19)=13.9$, $p<0.0001$). The average error rates were less than 2% and did not systematically vary as a function of time spent performing the task.

For both inconsistent and consistent conditions the S–B chi-squared statistics are rejected at the $p<0.05$ level, and both CFI and SRMR are smaller than the recommended cutoff for the model in Fig. 1A (inconsistent: S–B $\chi^2=15.27$, $df=7$, $p<0.0326$, CFI=0.86, SRMR=0.084; consistent: S–B $\chi^2=16.56$, $df=7$, $p<0.021$, CFI=0.862, SRMR=0.094). Therefore, we refined and simplified our model by including only the significant paths from the original model and reran the analysis. The simplified model fit the data well for both the inconsistent versus baseline (S–B $\chi^2=2.23$, $df=2$, $p=0.32$, CFI=0.99, SRMR=0.06) and the consistent versus baseline comparisons (S–B $\chi^2=2.67$, $df=2$, $p=0.26$, CFI=0.96, SRMR=0.06). The simplified models for the inconsistent and consistent conditions are presented in Fig. 1B and C, respectively. The standardized path coefficients for the simplified models are presented in Table 1.

Table 1
Entries in the table are the path coefficients from the row variable to the column variable

	rMFG	rIFG	rSPC	rIPC
Inconsistent >base				
TH	**−0.609**	**0.430**	**0.881**	
rMFG			**0.758**	
rIFG	**0.617**		**−0.886**	
rSPC				**0.354**
rIPC		**0.461**		
Consistent >base				
TH	**−0.513**	0.324	−0.130	
rMFG			−0.160	
rIFG	**0.711**		0.304	
rSPC				0.164
rIPC		0.044		

Values are the standardized path coefficients corresponding to the inconsistent versus baseline comparison and consistent versus baseline comparison. All bold-faced path coefficients are significant at 0.05. rMFG=right middle frontal gyrus, rIFG=right inferior frontal gyrus, TH=thalamus, rIPC=right inferior parietal cortex, rSPC=right superior parietal cortex.

The simplified model fit equally well for both inconsistent and consistent conditions. However, the patterns of the path coefficients were different between the two conditions. All path coefficients were significant in the inconsistent condition whereas only two paths (Th to rMFG and rIFG to rMFG) were significant for the consistent condition.

To address whether the strength of the paths in the inconsistent condition were significantly different from the strength of the paths in the consistent condition we directly compared the models and the paths between each of the models. To do this, we performed two sets of tests (see Section 2 for details). The first test revealed that the magnitude of at least one of the eight paths in Fig. 1B for the inconsistent condition was significantly different than one of the paths for the consistent condition (Fig. 1C) by the S–B χ^2 difference test (S–B χ^2=19.36, df=8, p=0.026).

Following this result, we performed eight model comparison tests to evaluate each path individually to check which path(s) differ significantly between the two conditions. Among these eight paths, six of them were found to be significantly different between the two conditions. The two paths that did not differ between the two conditions were from Th to rMFG (S–B χ^2=0.01, df=1, p=0.92) and from rIFG to rMFG (S–B χ^2=0.08, df=1, p=0.78). This means these two paths are equally strong in both inconsistent and consistent conditions, while the remaining six paths were different. These six paths were significant in the inconsistent condition but not in the consistent condition (see Table 1). Because the majority of these paths are significantly different from each other, the result supports the claim that response conflict in the flanker task affects the *relationship* between regions in the attentional network. In addition, the results suggest that even though the degree of prefrontal activity typically increases for the inconsistent condition [1,2,19,23,24], the strength of the relationship between some of the prefrontal regions does not increase for the inconsistent relative to the consistent condition.

This result may make sense within the context of theory about the role the prefrontal regions play in maintaining and controlling an attentional set during Stroop and flanker tasks (e.g., Ref. [1]). First, it is possible that an attentional set is not maintained by any one particular prefrontal region, but rather by the relationship between the Th, MFG and IFG; each region playing a separate but necessary role in the maintenance of the set. If one assumes that the maintenance of an attentional set is necessary in both conditions (e.g., "respond to the direction of the center arrow" is common to both conditions), then the prefrontal paths that are of equivalent strength between the two conditions may be related to the maintenance of the set while the paths that are different between conditions is related to a process specific to the inconsistent condition (e.g., resolving conflict). And as was stated previously, the equivalent paths between the prefrontal regions does not imply that the magnitude of activation in each of these regions is also equivalent between the conditions. In fact, our finding suggests that

although previous studies find differences in the magnitude of activation between conditions in these same prefrontal regions, the relationship between these regions does not differ.

Although our results make sense within an attentional set theory, there are other reasons that could also explain the equivalent prefrontal paths. For example, another cognitive process common to both the consistent and inconsistent condition is the need to make a single response among a competing alternative response. Although on some level this process must be related to an attentional set mechanism, the relationship between the prefrontal paths may be related to response generation and response conflict inherent in any choice RT task. Importantly, this idea is also supported by research suggesting a role of the right prefrontal regions in response conflict and response generation processes [23].

There are also paths among the parietal, prefrontal, and thalamus regions for inconsistent trials that are not present for consistent trials. Since both prefrontal and parietal regions are involved in executive processes [1,2,10,23,24], the prefrontal cortex may need to recruit additional resources (e.g., IPC and SPC) to accomplish task demands for the resolution of response conflict in the inconsistent condition. Another not mutually exclusive possibility is that the parietal regions are necessary for processing the inconsistent spatial information provided by the flanking arrows while the prefrontal and thalamus regions are involved in inhibiting the flanking items (regardless of consistency). The consistent trials, which do not require the degree of spatial processing in order to produce a correct response, may not need the relationship between the parietal and prefrontal brain areas for accomplishing task demands. In order to test whether this relationship is specific to the spatial demands of the flanker task a complimentary non-spatial attentional control task (e.g., Stroop) could be employed in order to test whether these same relationships between regions remain.

Another option, however, is that these parietal regions are specifically involved in either the perception of the conflict or the resolution of the conflict regardless of whether the source of the conflict is spatial or non-spatial in nature. If this be the case, then a Stroop test should show the same relationship between the prefrontal and parietal regions as found in this study.

We found a significant path coefficient between the right IFG and the right MFG for both conditions. The MFG has been implicated in working memory processes, episodic memory processes, inhibitory control, and maintenance of an attentional set [1,5], whereas the IFG is thought to be involved in the selection of information among competing alternatives, semantic and/or phonological processing, and working memory (e.g., Ref. [32]). A positive unidirectional path coefficient between these two regions suggests that the IFG is influencing the MFG, but the MFG only indirectly affects the IFG through some other region. Consistent with this, Owen et al. [26] have argued for a two-stage model of

working memory by which sensory and stimuli information from posterior regions feed first into the inferior frontal sulcal regions and when monitoring or manipulation of the information in working memory is required, the information is fed from inferior frontal regions into dorsal frontal regions where that type of processing can be conducted. Our SEM results provide evidence in support of a claim for a unidirectional relationship between the ventral and dorsal regions of prefrontal cortex.

Although the right IFG was positively affecting the right MFG, it was negatively affecting the activity in the right SPC, but only for the inconsistent condition. Some studies have suggested that the right SPC could be conceptualized as the locus of a visuo-spatial sketch pad in working memory [30]. If this is the case, then it is possible that the right IFG is selecting a response from competing alternatives within spatial working memory and inhibiting the alternative responses. The inconsistent condition may require more control and greater selection in working memory because of the conflicting information. Although speculative, the inhibition of alternative responses based on information being held on-line within spatial working memory may be producing the negative relationship between the right IFG and the right SPC.

Importantly, our result cannot argue that the *magnitude* of the activation in any of the given regions is different between conditions. Instead our results suggest that the two conditions recruit some similar paths in the attentional network (MFG, IFG, Th), but that the inconsistent condition recruits additional paths not evident in the consistent condition (Th, IPC, SPC, IFG). Furthermore, our results suggest that the two prefrontal paths recruited for both conditions are recruited equally as much in the inconsistent condition as in the consistent condition. Therefore, it is apparent that the relationship between some of the regions involved in attentional control for this task are different for the inconsistent condition than the consistent condition, yet some of the paths in the prefrontal regions are the same.

It is notable that all significant path coefficients were lateralized to the right hemisphere. In order to test whether the paths in the right hemisphere were significantly different than the paths in the left hemisphere, we conducted a similar analysis as that described for the comparison of the paths between the incongruent and congruent conditions (described in Section 2). The results from the first analysis revealed a significant difference between the constrained and unconstrained models (S–B χ^2=73.55, df=8, p<0.001), thus indicating that at least one of the paths was significantly different between the hemispheres for the inconsistent condition. The result from the comparison of the eight individual models found that all eight paths were significantly different between the hemispheres (at p<0.05). Notably, all of the paths in the right hemisphere were significant, but those on the left were not. This result argues that the relationship between regions quantitatively differs between hemispheres for this condition.

Similarly, we did the same laterality comparison for the consistent condition and found from the first test that at least one of the paths was significantly different in magnitude between the hemispheres (S–B χ^2=17.47, df=8, p=0.025). From the second analysis, we found that only two of the paths were significantly different between the hemispheres (Th to rMFG and rSPC to rMFG—the two significant paths in Table 1 and Fig. 1C). The other six paths were not significantly different between the left and right hemispheres for the consistent condition. In addition, these non-significant paths were also not significantly different from zero (i.e., the six paths were not significant in either the left or right side of the brain).

In short, we found that each path that was tested in the right hemisphere was significantly greater in strength than that same path in the left hemisphere for both the consistent and inconsistent conditions. This result supports the claim that the results from our SEM were significantly lateralized to the right hemisphere.

There are a few possibilities for this lateralization. First, this version of the flanker task relies on spatial processing strategies, which tend to tax the right hemisphere to a greater extent than the left [31]. However, it is also possible that the laterality effect signifies the importance of the right hemisphere in attentional control and response conflict. Future studies could investigate whether the right lateralized effects seen in the current results are due to spatial processing strategies or a general role of the right hemisphere in response conflict by employing a largely verbal task to observe the effective connectivity among regions in the left hemisphere.

It is also notable that the paths associated with the ACC were not significant. In the simplified model, when we included the paths to and from the ACC, the goodness of fit fell well below our criterion. This null effect is interesting considering that the ACC has been implicated in this task [4]. However, in the first study employing these stimuli [4], ACC activity was only reported in an ROI analysis when an inconsistent followed a consistent stimulus. Because of a small number of trials in the current design, we were unable to investigate the relationship of ACC with other regions when an inconsistent stimulus followed a consistent stimulus.

Importantly, our results suggest a quantitatively different relationship among brain regions in the two conditions of this task. Some potential explanations for the direction and strength of the paths have been explicated here; however, more theory and empirical work should help extend and validate these claims. Furthermore, only unidirectional paths survived within our model, suggesting that feedback mechanisms may exist only within the larger circuit of regions involved in attentional control. Future studies of attentional control and working memory that employ connectivity methods such as SEM may provide more information regarding whether the unidirectional paths found in the current study are ever, and if so, under what conditions, susceptible to bidirectionality.

In conclusion, we report the first application of SEM to examine the relationship among brain regions involved in attentional control. First, our results demonstrate the importance of the hypothesized regions and networks in attentional control. Furthermore, our results have shown that the inconsistent and consistent conditions recruit some of the same network, but that the inconsistent condition recruits additional paths to support task demands. Importantly, this result suggests that both the *degree* of activity and the *relationship* between regions differs between task conditions. Additionally, the strength of the paths common to both conditions also differs between conditions. Our results also suggest that the paths between neural loci supporting attentional control in the flanker task are largely lateralized to the right hemisphere suggesting a process-specific lateralization of spatial inhibitory processing, and/or a specificity of the right hemisphere in attentional control. These results both confirm and constrain existing models of the role that these regions might play in attentional allocation in this task, as well as in attentional allocation and inhibitory processing more generally, in a way that is not possible using more traditional analytic techniques.

The remarkably good fit between the theoretical accounts in the extant literature on attentional control and our empirical findings are quite encouraging, and represent converging support for both the theoretical accounts and the SEM approach in this domain. Future research using SEM in functional neuroimaging is likely to contribute greatly to our understanding of the dynamics of neurocognitive processes. It will be important for future studies to determine the validity of the model, results and theoretical implications, by extending this statistical method to other paradigms investigating attentional control as well as subject populations that have a deficit in attentional processing.

Acknowledgments

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