Changes in Default Mode Network as
Automaticity Develops in a Categorization Task

Farzin Shamloo, Sebastien Helie *

Purdue University

* Corresponding Author. Address: Department of Psychological Sciences, Purdue University, West Lafayette, IN 47907, USA. Email address: shelie@purdue.edu.

Abstract

The default mode network (DMN) is a set of brain regions in which blood oxygen level dependent signal is suppressed during attentional focus on the external environment. Because automatic task processing requires less attention, development of automaticity in a rule-based categorization task may result in less deactivation and altered functional connectivity of the DMN when compared to the initial learning stage. We tested this hypothesis by re-analyzing functional magnetic resonance imaging data of participants trained in rule-based categorization for over 10,000 trials (Helie, Roeder, & Ashby, 2010). The results show that some DMN regions are deactivated in initial training but not after automaticity has developed. There is also a significant decrease in DMN deactivation after extensive practice. Seed-based functional connectivity analyses with the precuneus, medial prefrontal cortex (two important DMN regions) and Brodmann area 6 (an important region in automatic categorization) were also performed. The results show increased functional connectivity with both DMN and non-DMN regions after the development of automaticity, and a decrease in functional connectivity between the medial prefrontal cortex and ventromedial orbitofrontal cortex. Together, these results further support the hypothesis of a strategy shift in automatic categorization and bridge the cognitive and neuroscientific conceptions of automaticity in showing that the reduced need for cognitive resources in automatic processing is accompanied by a disinhibition of the DMN and stronger functional connectivity between DMN and task-related brain regions.

Keywords: automaticity, default mode network, categorization, functional connectivity

1. Introduction

Automatic activities are usually effortless and are done without the need for conscious monitoring (Moors & Houwer, 2006). Many daily tasks and behaviors are processed automatically. For example, for some people playing piano and riding a bicycle are done automatically. Walking is also usually done automatically. One essential skill required to function in everyday life is the ability to recognize and categorize objects (Helie & Ashby, 2012). For example, people need to be able to categorize faces and scenes accurately without expending too much effort in order to determine appropriate sets of actions. In most cases, categorization is done automatically (Helie, Waldschmidt, & Ashby, 2010).

Even though intuitively automaticity is understood easily, it's hard to rigorously define from a scientific point of view (Moors & Houwer, 2006). Helie and Cousineau (2011) proposed that automaticity can be defined by using behavioral signatures or the cognitive processes underlying the behavioral signatures. While there is no consensus on a definitive list of behavioral signatures, proposed lists usually include efficiency, inflexibility, need for extensive practice, and fast response. Some of these signatures are more intuitive (e.g. need for extensive practice), but some are more controversial (e.g. inflexibility) and there is no general agreement that all the signatures need to be present for automatic action. Furthermore, it is not clear if it is possible to define automaticity by behavioral features alone. One alternative to feature-based approaches is to use process-based explanations of automaticity. Two possible processes for explaining automaticity are strategy shift and algorithm strengthening. Strategy shift approaches claim that qualitatively different cognitive processes are responsible for automatic and non-automatic actions whereas algorithm strengthening views claim that the same algorithm is used for non-automatic and automatic behavior, the difference being that participants get better at using that algorithm after extensive training.

This article focuses on the relationship between the default mode network (DMN) and automaticity. The DMN is a network of connected regions that is active when participants are not engaged in an external task and inhibited when focusing on an attentionally demanding task (Raichle, MacLeod, Snyder, Powers, Gusnard, & Shulman, 2001; Shulman, Fiez, Corbetta, Buckner, Miezin, Raichle, & Petersen, 1997). The following brain regions are generally considered part of the DMN (Laird, Eickhoff, Li, Robin, Glahn, & Fox, 2009): Precuneus (pC),

posterior cingulate cortex (PCC), ventral anterior cingulate cortex (vACC), dorsal medial prefrontal cortex (MPFC), bilateral inferior parietal lobules (IPL), bilateral middle temporal gyri (MTG), and left middle frontal gyrus (LMFG). Although the relationship between DMN activity and automaticity has never been explored, the fact that automatic tasks require less attentional resources than controlled tasks (Shiffrin & Schneider, 1977) allows for the prediction that DMN inhibition should be reduced when performing an automatic task (compared with a controlled task).

In addition, Helie, Roeder, and Ashby (2010) showed that the brain areas involved in automatic rule-based categorization are different from those involved in initial rule-based category learning. Specifically, initial category learning is processed by a subcortical network centered around the head of the caudate nucleus but after some practice the learned categories are re-encoded in the ventrolateral prefrontal cortex. Finally after extensive practice this cortical system becomes more caudal and dorsal, centering around the premotor areas. This suggests that the cognitive task performed by participants changes with practice (Bassett et al., 2011; Helie & Cousineau, 2011; Logan, 1988). Interestingly, there is also evidence suggesting that the DMN pattern of functional connectivity changes depending on task (Spreng et al., 2010). Hence, another prediction is that functional connectivity of the DMN changes with the development of automaticity. Comparing functional connectivity at early stages of categorization and automatic stages could be interesting because at the automatic stage (unlike early stages of categorization), participants do not need to disrupt their background thinking process after stimulus presentation: Participants can continue day dreaming, and nonetheless perform the task well. This may result in a stronger coupling between DMN and task-related regions.

The goal of this study is to explore the alterations in DMN activity and functional connectivity after automaticity develops in a categorization task. We re-analyzed data first published in Helie et al. (2010a) to study changes in blood oxygen level dependent (BOLD) signals related to automatic categorization. Specifically, the focus of this article is on changes in DMN deactivation and changes in functional connectivity patterns with three seed regions: precuneus (a key DMN region), medial prefrontal cortex (another key DMN region) and Brodmann area 6 (BA6; an important region for categorization at the automatic stage; Helie et al., 2010a; Waldschmidt & Ashby, 2011). These analyses are new in that: (1) deactivation was

not explored in Helie et al. (2010a), (2) functional connectivity analyses were not included in Helie et al. (2010a), and (3) the current article focuses on the DMN, reduction in attentional demands, and the change in cognitive task accompanying the development automatic processing. Thus, this article focuses on attention in automaticity whereas Helie et al. (2010a) focused on training-related changes in brain activity in a categorization task. To anticipate, the results show that (1) DMN deactivation is reduced after the development of automaticity in a rule-based categorization task and that (2) functional connectivity with both DMN and non-DMN regions generally increases after the development of automaticity. These results are consistent with the hypotheses of a reduced need for cognitive resources and a strategy shift in automatic categorization.

2. Materials and Methods

2.1. Sample

The hypotheses were tested by re-analyzing event-related functional magnetic resonance imaging (fMRI) data of 14 participants trained for 20 sessions in a rule-based categorization task at University of California Santa Barbara (Helie et al., 2010a). Participants gave written consent to participate in the study and before each scanning session consent was reaffirmed.

2.2. Stimuli and apparatus

The stimuli were circular sine-wave gratings of constant contrast and size that could be separated into two categories using a unidimensional rule on frequency (bar width). The orientation of the bars in the stimuli also varied from trial-to-trial but was irrelevant for categorization. Participants responded using two button boxes: Button box in the left hand for category A and button box in the right hand for category B. Each stimulus was presented for 2 seconds (1 TR). Correct responses were followed by a green check mark displayed for 2 seconds (1 TR). Incorrect responses were followed by a red “X” mark displayed for 2 seconds (1 TR). More details on the stimuli and task can be found in Helie et al. (2010a).

2.3. Neuroimaging

Sessions 1, 4, 10, and 20 were conducted at University of California Santa Barbara Brain Imaging Center using a 3T Siemens TIM Trio MRI scanner with an eight-channel phased array head coil.¹ The experiment was a rapid-event related design. Before the functional runs, a localizer, a GRE field map (not used) and a T1-flash were run. The parameter values for the T1-flash were: Repetition time (TR) of 15 ms, echo time (TE) of 4.2 ms, flip angle (FA) of 90° and field of view of 192 mm. Each slice was 0.89 mm thick with 1×1 mm in-plane resolution (256×256 matrix). These scans were followed by 6 functional runs [echo planar imaging (EPI)]. The parameters for EPI were as follows: TR of 2000 ms, echo time (TE) of 30 ms, flip angle (FA) of 90° and field of view of 192 mm. Thirty-three slices were acquired in each repetition, which were parallel to the anterior commissure-posterior commissure plane. Slices were interleaved, each 3 mm thick with 0.5 mm gap between each of them and the resolution was 3×3 mm in-plane (64×64 matrix).

2.4. Data analysis

Behavioral analyses in Helie et al. (2010b) suggest that automaticity in this task developed between Session 14 and Session 20. As a result, the fMRI data from Session 1 (with no previous practice) and Session 20 (after 11,040 trials of practice) were re-analyzed to compare initial learning with automatic performance. Before comparing deactivation levels and functional connectivity between Sessions 1 and 20, preprocessing steps were done on the data through the FMRIB Software Library (FSL) (Jenkinson, Beckmann, Behrens, Woolrich & Smith, 2012). Motion correction was done using an affine transformation and blocks with more than 3 mm head motion after spatial transformation were excluded from the analysis (about 8% of the data). For spatial smoothing, a three dimensional Gaussian filter with FWHM of 5mm was used. A haemodynamic response function (HRF) modeled as a Gamma function with mean lag of 4 seconds and standard deviation of 3 seconds and its first derivative (without orthogonalization) was convolved with all of the events. Functional images of each participant were aligned to their high-resolution structural image using an affine transformation and a boundary-based registration (BBR) cost function. The resulting image was then aligned on a

¹ The other training sessions were performed outside the scanner on a regular desktop computer. For details on the training sessions outside the scanner, see Helie et al. (2010b).

standard brain image using a nonlinear transformation and a correlation ratio (CR) cost function. The MNI152 standard brain was used for higher order analyses and visualization purposes.

2.4.1. Deactivation level

We used a linear model including four different events. Crosshair (a fixation mark displayed in 48% of the trials before the stimulus) was used as a baseline, and Stimulus was used to mark TRs in which a stimulus was present. The remaining events were estimated as nuisance parameters: Blank (when the screen was blank) and Feedback (while the feedback was displayed). The contrast of interest was (Crosshair – Stimulus), which was not explored in Helie et al. (2010a). The data were individually analyzed for each block (EPI scan) after which each participant's data in each session was averaged using a fixed effect model to obtain one brain map for each session of each participant. The between-subject session data were then averaged to obtain one brain map for Session 1 and another for Session 20 using a mixed effect model. For the between-subject analysis, a z -threshold of 2.81 for voxel-wise significance was used and statistic images were assessed for cluster-wise significance using a cluster-defining threshold with a significance level of 0.01. In addition to calculating a mean between-subject brain map for each session, a repeated measure t -test was performed to compare BOLD in Sessions 1 and 20. For the within-subject analysis, we used a z -threshold of 1.96 for voxel-wise significance and a cluster-defining threshold with significance level of 0.05.

2.4.2. Functional connectivity

In deactivation level analysis, the activity of single voxels was compared without looking at the relations between them. Functional connectivity analysis aims to look at functional interactions between spatially remote neurophysiological events, so instead of looking at how the activity of one single voxel changes, the relation between them is compared. The functional connectivity analysis focuses on how the functional connectivity of three seed regions, namely precuneus, medial prefrontal cortex (two important DMN regions), and BA6 (an important region for categorization at the automatic level), changes after extensive practice (see Section 2.4.2.1 below for a justification).

The first step was to fit a model to the data that includes all systematic sources of variance (i.e., all four events in the experiment) in order to remove unwanted task-related

variance from the functional connectivity analysis. The functional connectivity analysis was performed on the residuals of that model. To reduce spectral leakage, estimates of cross-spectrum and power spectrum were used instead of the values themselves. Cross-spectrum and power spectrums for discrete time series were estimated by Welch's modified periodogram averaging method (Welch 1967) using Matlab.

In order to obtain brain maps of functional connectivity, a single value measure for the functional connectivity in each voxel is needed. To do so, we used (Andrew and Pfurtscheller 1996):

$$\widehat{coh}_{xy}(\bar{\lambda}) = \frac{|\sum_{\lambda} \widehat{f}_{xy}(\lambda)|^2}{\sum_{\lambda} \widehat{f}_{xx}(\lambda) \sum_{\lambda} \widehat{f}_{yy}(\lambda)} \quad (1)$$

where $\widehat{f}_{xy}$, $\widehat{f}_{xx}$ and $\widehat{f}_{yy}$ are estimates of the cross-spectrum of x and y and the power spectrums of x and y (respectively). Since the hemodynamic function only contains information between 0 and 0.15 Hz, the sum is over this range.

2.4.2.1. Justification for the choice of seed regions

The precuneus was selected as a seed region because there is evidence suggesting that it is the functional core of the DMN (Utevsky, Smith, & Huettel, 2014). Utevsky et al. (2014) studied brain networks to see how they interact and how behavior is orchestrated. They showed that the precuneus is the only region that increases its functional connectivity with the DMN network during rest and also increases its functional connectivity with task-dependent regions during the task. The bilateral precuneus mask was created by using voxels that have a probability of 70% or more of being part of the 'precuneus cortex' according to the Harvard-Oxford cortical structural atlas. The mean time-series of the mask was used as the seed for coherence analyses.

The medial prefrontal cortex is another important DMN region. A study by Uddin, Kelly, Biswal, Castellanos, and Milham (2009) on resting state data suggests that MPFC may have a role in modulating visual spatial and temporal attention networks. Hence, if MPFC couples more strongly with task-related regions in the present study, this may indicate that the modulatory role of MPFC discussed in Uddin et al. (2009) increases with the development of automaticity. The bilateral MPFC mask was created by using voxels that have a probability of 70% or more of

being part of the ‘frontal medial cortex’ according to the Harvard-Oxford cortical structural atlas. The mean time-series of the mask was used as the seed for coherence analyses.

Finally, BA6 was chosen since it is considered to be one of the most important regions for categorization at the automatic level (Helie et al., 2010a; Waldschmidt & Ashby, 2011). Functional connectivity analysis with BA6 as seed was conducted to test whether there is any DMN region that changes its functional connectivity pattern with BA6 at the automatic level. The bilateral mask was created by using voxels that have probability of 70% or more of being part of the ‘GM Premotor cortex BA6’ according to the Juelich histological atlas. The mean time-series of the mask was used as the seed for coherence analyses. The masks used as seed regions are shown in Figure 1.

Figure 1. Masks used as seed regions for the functional connectivity analysis ($x = 0$). Red = medial prefrontal cortex; Yellow = BA6; Blue = precuneus.

2.4.2.2. Voxel-wise analysis

The goal of this analysis is to compare Sessions 1 and 20 in order to assess whether the coherence of different brain regions with seed areas changes as automaticity develops. We ran two series of one-tail binomial tests on each voxel. First, a one-tail binomial test was performed to identify brain regions that show stronger coherence with the seed region after extensive practice. Second, another test was performed to identify regions that reduced their coherence with the seed region after extensive practice.

Success for a voxel was defined as having a stronger coherence in Session 20 compared to Session 1. The null hypothesis was no change in coherence after the development of automaticity. This was operationalized as having a probability 0.5 of success. We defined

$Coherence_i^{20}$ and $Coherence_i^1$ as the coherence of the i^{th} participant in Sessions 20 and 1 respectively. D_i was defined as the difference between coherences in Session 20 and Session 1 for the i^{th} participant. Values of $D_i > 0$ were labeled ‘success’ and $D_i \leq 0$ were labeled ‘failure’. For each voxel two binomial tests were performed. In the first, test voxels that showed 12, 13 or 14 successes were marked (i.e., voxels showed stronger coherence with the seed region after practice in 12, 13 or 14 participants). In the second, test voxels with 0, 1 or 2 successes were marked (i.e., voxels showed weaker coherence with the seed region after practice in 12, 13 or 14 participants). The probability of rejecting the null hypothesis was 0.0065 for each test, but multiple testing correction was applied resulting in an overall probability of 0.013.

2.4.2.3. Cluster size correction

When dealing with fMRI data one possible solution to address the multiple testing problem is cluster size correction. We chose a 26-connected neighboring standard to form clusters which means that a voxel is connected to another voxel if it touches one of its faces, edges or corners. Clusters were formed using voxels that were statistically significant according to the binomial testing described above. After forming clusters, we set a threshold and retained clusters that have a size bigger than the set threshold. The way to choose the threshold is by bootstrapping techniques.

The goal of bootstrapping was to obtain an estimate of the cluster size distribution to distinguish small clusters that formed due to Type I errors when marking ‘success’ voxels from clusters that were formed because of an actual change in coherence in that brain region between Sessions 1 and 20. The first step in the bootstrapping was to generate new artificial data with a realistic connectivity structure. Artificial brains were generated by re-arranging each participant’s data. This was possible because each session of each participant was composed of more than one EPI and, because the design was jittered, the order in which the events were presented in each EPI was different. Consider a session with two EPIs, EPI 1 and EPI 2. Two artificial coherence maps were generated by calculating the coherence between a mask extracted from EPI 1 and voxels in EPI 2, and vice versa. This was then repeated with EPIs 1 and 3, and 2

and 3.² This procedure was applied to Sessions 1 and 20 for each mask and each participant, which resulted in 252 artificial brains. In Step 2, we took the artificial brain maps of coherence generated using data from all fourteen participants and ran the same two binomial tests that were ran on the original data to identify ‘success’ voxels and form clusters (see Section 2.4.4.2). This resulted in 18 functional connectivity analyses (i.e., 6 for each seed region). The cluster sizes were then recorded for each seed region. This procedure resulted in about 15,600 clusters (i.e., about 5,200 clusters for each seed region). Small clusters were more likely to appear, with about 55% of the clusters being single voxel clusters and about 95% of the clusters having ten voxels or less. In step 3, we chose 0.001 as the threshold for accepting a cluster which corresponds to a cluster size of 69, 15 and 73 for precuneus, MPFC and BA6 respectively.

3. Results

3.1. Deactivation level results

Figure 2 shows the regions that were deactivated in Session 1. As can be seen, there were two clusters that were deactivated in Session 1. These clusters were located in the medial prefrontal cortex (Max. $z = 4.06$, $x = 2$, $y = 50$, $z = -6$, cluster size = 471) and left inferior parietal lobule (Max. $z = 4.55$, $x = -46$, $y = -72$, $z = 32$, cluster size = 284). Both of them are well-established DMN regions. However, no region was found to be deactivated in Session 20. These results provide initial support for the hypothesis that DMN deactivation is reduced in automatic categorization.

² The number of repetitions was limited by one participant having 3 blocks removed due to excessive head motion, and the same number of EPIs needed to be used for all participants. As a result, 3 EPIs were used for each participant.

Figure 2. DMN regions deactivated in first session: medial prefrontal cortex (Max. $z = 4.06$, $x = 2$, $y = 50$, $z = -6$, cluster size = 471), left inferior parietal lobule (Max. $z = 4.55$, $x = -46$, $y = -72$, $z = 32$, cluster size = 284).

Figure 3 shows the results of the comparison between Sessions 1 and 20. As can be seen, there was one cluster in which deactivation was lower in Session 20 compared to Session 1. Table 1 shows the peak coordinates. As can be seen, the cluster contains multiple peaks located in the precuneus and posterior cingulate cortex. Both of these are DMN regions, which confirms that deactivation is reduced between Sessions 20 and 1. No brain regions showed higher deactivation in Session 20 compared to Session 1.

Figure 3. DMN regions showing more deactivation in the first session than in the last session. There is one cluster which includes the precuneus and the posterior cingulate cortex.

Table 1. Peak activity from Figure 3.

	Z	Coordinates			Location
		x	y	z	
P1	3.21	-8	-66	32	pC
P2	3.06	-6	-70	32	pC
P3	2.97	6	-54	28	pC
P4	2.85	2	-52	16	PCC
P5	2.76	0	-64	32	pC

P6	2.69	-4	-58	12	PCC
----	------	----	-----	----	-----

Note. The cluster size was 443.

3.2. Functional connectivity results

3.2.1. Functional connectivity with precuneus

There were both DMN and non-DMN regions that showed greater coherence with precuneus after the development of automaticity. Specifically, the regions were left Middle Frontal gyrus (DMN), left Inferior Parietal lobule (DMN), right Middle Temporal gyrus (DMN), BA6 (non-DMN), anterior Prefrontal Cortex (non-DMN) and left Superior Parietal lobule (non-DMN). These regions are shown in Figure 4, and the coordinates of the maximum coherence difference of each cluster is shown in Table 2. No region was identified to have stronger coherence with precuneus in Session 1 compared to Session 20.

Figure 4. Regions having stronger coherence with precuneus in Session 20 compared to Session1.

Table 2. Maximum differences in mean coherence from Figure 4.
Clusters are ordered based on size.

	Coordinates			Location	Cluster size
	x	y	z		
Cluster 1	-48	14	42	IMFG	247
Cluster 2	0	-14	56	BA6	197
Cluster 3	-48	-68	36	IIPL	142
Cluster 4	62	-32	0	rMTG	89

Cluster 5	-2	60	32	aPFC	78
Cluster 6	-18	-46	62	ISPL	75

3.2.2. Connectivity with medial prefrontal cortex

Again, there were both DMN and non-DMN regions that showed greater coherence with MPFC after the development of automaticity. These regions are shown in Figure 5, and the coordinates of the maximum coherence difference in each cluster are shown in Table 3. Similar to the precuneus (Section 3.2.1), the left Middle Frontal gyrus (DMN), anterior Prefrontal Cortex (non-DMN), and Superior Parietal lobule (non-DMN) showed increased coherence with the MPFC after the development of automaticity. However, note that there was no overlap between the clusters that increased their coherence with MPFC and the clusters that increased coherence with the precuneus. The precuneus (DMN) and Secondary Visual Cortex (non-DMN) also increased their coherence with MPFC after the development of automaticity. There is only one cluster that showed weaker coherence with MPFC after automaticity development. This cluster contains parts of ventromedial orbitofrontal cortex.

Figure 5. Regions having stronger coherence with MPFC in Session 20 compared to Session1 (green) and region that have stronger coherence with MPFC in Session 1 compared to Session 20 (blue).

Table 3. Maximum differences in mean coherence from Figure 5.
Clusters are ordered based on size.

	Coordinates			Location	Cluster size
	x	y	z		
	Session 20 > Session 1				
Cluster 1	28	60	8	aPFC	83
Cluster 2	6	-52	34	pC	55
Cluster 3	36	-92	14	V2	53

Cluster 4	-38	8	54	IMFG	40
Cluster 5	-14	-68	48	SPL	28
Session 1 > Session 20					
Cluster 1	-22	10	-18	vmOFC	38

3.2.3. Connectivity with BA6

Figure 6 shows changes in coherence with BA6. The only region that is identified to have stronger coherence with BA6 after automaticity development is the left Inferior Parietal lobule, which is a DMN region (Max. coordinates $x = -54$, $y = -60$, $z = 26$, cluster size = 114). Note that IPL also increased its functional connectivity with the precuneus, and there is a small overlap between the IPL clusters found to increase coherence with the precuneus and BA6. No region was identified to have stronger coherence with BA6 in Session 1 compared to Session 20.

Figure 6. Left Inferior Parietal lobule (cluster size = 114) shows stronger coherence with BA6 in Session 20 compared to Session1.

4. Discussion

A deactivation level analysis and a functional connectivity analysis were done to study changes in DMN after automaticity development in rule-based categorization. The results show that the medial prefrontal cortex and left inferior parietal lobule were deactivated in Session 1 (both DMN regions), but no cluster was significantly deactivated in Session 20. Comparing deactivation levels in Sessions 1 and 20 show that the precuneus and the posterior cingulate cortex were less deactivated in Session 20 than in Session 1 (again, both DMN regions).

Analysis of the behavioral results of the same experiment (Helie et al., 2010b) suggests that participants acquired automaticity between Sessions 10 and 20, so these results suggest that the DMN is less deactivated at the automatic stage of categorization.

The second set of analyses focused on functional connectivity. Three seed-based functional connectivity analyses were performed: (1) precuneus, (2) MPFC and, (3) BA6. Both DMN and non-DMN regions increased their functional connectivity with precuneus and MPFC (two important DMN regions). Increase of functional connectivity between DMN regions at the automatic stage may be due to the fact that at the automatic stage participants tend to engage in mind wandering more often than during initial learning. During initial learning, participants need to focus on the external stimuli to learn the task. The precuneus and MPFC also increase their functional connectivity with non-DMN regions. The possible roles of these non-DMN regions in the categorization task are discussed below:

Anterior prefrontal cortex (with both precuneus and MPFC, no overlap): The function of this region of the brain is one of the least understood among all brain regions (Ramnani & Owen, 2004). Although its function is poorly understood, Koechlin and Hyafil (2007) suggest that the main function of this region is ‘cognitive branching’. Cognitive branching refers to the ability of maintaining a running task in a pending state to retrieve it after completion of another task. DMN regions are activated when people are day dreaming. The reason that this region shows stronger coherence with precuneus might be due to the fact that participants are day dreaming and each time a stimulus appears they put their day dreaming on hold and resume daydreaming after responding to the stimulus. This explanation is consistent with the gateway hypothesis (Burgess, Dumontheil, & Gilbert, 2007), which posits that an important role of rostral PFC is to serve as a ‘gateway’ between internally-driven and externally-driven cognition. As a result, Burgess et al. argue that rostral PFC should be active after extensive practice, when the task has become easy and participants can perform the task quickly before getting back to mind wandering. It is also interesting to note that Gilbert et al. (2010) found different patterns of functional connectivity for the lateral and medial parts of rostral PFC in a meta-analysis. In the present analysis, lateral and medial aPFC also showed different patterns of functional connectivity: the lateral part of rostral aPFC increased its functional connectivity with the MPFC whereas the medial part of rostral aPFC increased its functional with the precuneus.

Superior Parietal lobule (with both precuneus and MPFC, no overlap): This cluster, which also includes parts of primary somatosensory cortex, plays a role in movement-related actions. Bedard and Sanes (2009) identified SPL as one of the regions that shows finger-movement related activation. The participants in this experiment pressed buttons in response to stimuli, so stronger coherence with this region may correspond to altered functional connectivity pattern between DMN and task-related regions related to automaticity.

BA6 (with precuneus): A study by Helie et al. (2010a) on the same data suggests that a cortical system gradually replaces an initial subcortical neural system in automatic processing (also: Helie, Ell, & Ashby, 2015; Waldschmidt & Ashby, 2011). The study also suggests that after extensive practice this cortical system becomes more caudal and dorsal, and finally centers on premotor areas. The increase of functional connectivity between precuneus and BA6 may be an evidence of the DMN getting involved in the task at the automatic stage.

Secondary Visual Cortex (with MPFC): This region is one of the primary regions that responds to simple visual characteristics, among them orientation and spatial frequency (Anzai, Peng, & Van Essen, 2007, Hegde & Van Essen, 2000). These two are the features that varied between the stimuli which suggest that V2 is involved in the categorization task. Hence, in line with the explanation for BA6, this may constitute evidence of the DMN getting more involved in the task at the automatic stage.

In addition to increase in functional connectivity between two important DMN regions and task related regions, BA6 (an important region for automatic categorization) also increases its functional connectivity with left inferior parietal lobule, a DMN region. Therefore, altogether these results show that after automaticity development DMN regions and task-related regions are more strongly coupled when compared to early stages of category learning.

There is no region that reduces its functional connectivity with precuneus and BA6 after the development of automaticity. However, this is not the case for MPFC. Ventromedial orbitofrontal cortex (vmOFC) reduced its functional connectivity with MPFC after extensive practice. This region plays an important role in feedback processing (Elliot, Frith, & Dolan, 1997). It is reasonable to assume that at the automatic stage of categorization participants do not pay attention to the feedback as much as they do in the early stages of categorization because

they make very few errors.³ Since the MPFC has a modulatory role in visuospatial and temporal attention networks (Uddin et al., 2009), it is not unexpected that vmOFC reduces its functional connectivity with MPFC.

5. Conclusion

This study provides evidence for three hypotheses: (1) First, a strategy-shift happens at the automatic stage of categorization (Helie & Cousineau, 2011; Logan, 1988). In accordance with Helie et al. (2010a), the results of this study show that neural activity is different at the automatic stage, and patterns of functional connectivity between DMN and task-related regions also change with practice. (2) Second, the results presented herein largely support the hypothesis that the DMN's pattern of functional connectivity is task dependent. Other studies (e.g., Spreng et al., 2010) suggest that there is not a simple task-independent relation between DMN and the external attention system (EAS). Because there is a strategy-shift in automatic categorization, the functional connectivity of the DMN also changes. (3) Third, the result of the functional connectivity analyses is also in line with the hypothesis that at the automatic stage the task can be done without interrupting internalized thinking. This would explain the increase in coupling of DMN and task-related regions.

6. Future work

Future work should focus on the generality of these findings. For example, would DMN deactivation diminish after the development of automaticity in other tasks? Also, work should be devoted to exploring whether the changes in functional connectivity between task-related and DMN regions are specific to the regions identified with this analysis (e.g., BA6) or if other task-related regions would be functionally connected to the DMN if the participants had automatized a different task. For example, different task-related regions could couple more strongly with the DMN after the development of automaticity in, e.g., the serial reaction time task. Additionally, as in most DMN studies, not all DMN regions were found to be deactivated during initial learning (Laird et al., 2009). It would be interesting to run others studies using tasks in which these other DMN regions are found to be deactivated during initial learning (e.g., ventral ACC), and observe

³ Behavior production independent of feedback is also a criterion for habit learning (Helie & Cousineau, 2011).

how the deactivation and functional connectivity changes with the development of automaticity. More importantly, future work needs to focus on bringing together the cognitive and neuroscience literature on automaticity and habit learning to ensure that the concepts and methods used are compatible and consistent. The results in this study suggest that they are.

7. Acknowledgments

This research was supported in part by award number #1349677-BCS from the National Science Foundation.

8. References

- Andrew, C., & Pfurtscheller, G. (1996). Event-related coherence as a tool for studying dynamic interaction of brain regions. *Electroencephalography and clinical Neurophysiology*, 98, 144-148.
- Anzai, A., Peng, X., & Van Essen, D. C. (2007). Neurons in monkey visual area V2 encode combinations of orientations. *Nature Neuroscience*, 10, 1313-1321.
- Bassett, D. S., Wymbs, N. F., Porter, M. a, Mucha, P. J., Carlson, J. M., & Grafton, S. T. (2011). Dynamic reconfiguration of human brain networks during learning. *Proceedings of the National Academy of Sciences*, 108, 7641–7646.
- Bédard, P., & Sanes, J. N. (2009) Gaze and hand position effects on finger-movement related human brain activation. *Journal of Neurophysiology*, 101, 834-842.
- Burgess, P. W., Dumontheil, I., & Gilbert, S. J. (2007). The gateway hypothesis of rostral prefrontal cortex (area 10) function. *Trends in Cognitive Sciences*, 11, 290-298.
- Elliot, R., Frith, C. D., & Dolan, R. J. (1997). Differential neural response to positive and negative feedback in planning and guessing tasks. *Neuropsychologia*, 35, 1395–1404.
- Gilbert, S. J., Gonen-Yaacovi, G., Benoit, R. G., Volle, E., & Burgess, P. W. (2010). Distinct functional connectivity associated with lateral versus medial rostral prefrontal cortex: A meta-analysis. *NeuroImage*, 53, 1359-1367.
- Hegd, J., & Van Essen, D. C. (2000). Selectivity for complex shapes in primate visual area V2. *Journal of Neuroscience*, 20, 1-6.
- Helie, S. & Ashby, F. G. (2012). Learning and transfer of category knowledge in an indirect categorization task. *Psychological Research*, 76, 292-303.
- Helie, S., & Cousineau, D. (2011). The cognitive neuroscience of automaticity: Behavioral and brain signatures. *Cognitive Sciences*, 6, 25-43.

- Helie, S., Ell, S.W., & Ashby, F.G. (2015). Learning robust cortico-frontal associations with the basal ganglia: An integrative review. *Cortex*, 64, 123-135.
- Helie, S., Roeder, J. L., & Ashby, F. G. (2010a). Evidence for cortical automaticity in rule-based categorization. *Journal of Neuroscience*, 30, 14225-14234.
- Helie, S., Waldschmidt, J. G., & Ashby, F. G. (2010b). Automaticity in rule-based and information-integration categorization. *Attention Perception and Psychophysics*, 72, 1013-1031.
- Jenkinson, M., Beckmann, C. F., Behrens, T. E., Woolrich, M. W., & Smith, S. M. (2012). FSL. *NeuroImage*, 62, 782-790.
- Koechlin, E., & Hyafil, A.(2007). Anterior prefrontal function and limits of human decision-making. *Science*, 318, 594-598.
- Laird, A. R., Eickhoff, S. B., Li, K., Robin, D. A., Glahn, D. C., & Fox, P. T. (2009). Investigating the functional heterogeneity of the default mode network using coordinate-based meta-analytic modeling. *Journal of Neuroscience*, 29, 14496-14505.
- Logan, G. D. (1988). Toward an instance theory of automatization. *Psychological Review*, 95, 492-527.
- Maddox, W. T., Ashby, F. G., & Gottlob, L. R. (1998). Response time distributions in multidimensional perceptual categorization. *Perception & Psychophysics*, 60, 620-637.
- Moors, A., & Houwer, J. D. (2006). Automaticity: A theoretical and conceptual analysis. *Psychological Bulletin*, 132, 297-326.
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences*, 98, 676-682.
- Ramnani, N., & Owen, A. M. (2004). Anterior prefrontal cortex: insights into function from anatomy and neuroimaging. *Nature*, 5, 184-194.

- Shiffrin, R. M., & Schneider, W. (1977). Controlled and automatic human information processing: II. Perceptual leaning, automatic attending, and a general theory. *Psychological Review*, 84, 127-190.
- Shulman, G. L., Fiez, J. A., Corbetta, M., Buckner, R. L., Miezin, F. M., Raichle, M. E., & Petersen, S. E. (1997). Common blood flow changes across visual tasks: II. Decreases in cerebral cortex. *Journal of Cognitive Neuroscience*, 9, 648-663.
- Spreng, R. N., Stevens, W. D., Chamberlain, J. P., Gilmore, A. W., & Schacter, D. L. (2010). Default network activity coupled with frontoparietal control network, supports goal-directed cognition. *NeuroImage*, 53, 303-317.
- Uddin, L. K., Kelly, A. M., Biswal, B. B., Castellanos, F. X., & Milham, M. P. (2009). Functional connectivity of default mode network components: correlation, anticorrelation, and causality. *Human Brain Mapping*, 30, 625–637.
- Utevsky, A. V., Smith, D. V., & Huettel, S. A. (2014). Precuneus is a functional core of the default-mode network. *Journal of Neuroscience*, 34, 932-940.
- Waldschmidt, J. G., & Ashby, F. G. (2011). Cortical and striatal contributions to automaticity in information-integration categorization. *NeuroImage*, 56, 1791-1802.
- Welch, P. D. (1967). The use of fast fourier transform for the estimation of power spectra: A method based on time averaging over short, modified periodograms. *IEEE Transactions on Audio Electroacoustics* 15, 70–73.