IT'S NOT THE RULE! RULE-DECODABILITY IS NOT LIMITED TO COGNITIVE CONTROL-RELATED FRONTOPARIETAL REGIONS

A THESIS SUBMITTED TO
THE GRADUATE SCHOOL OF ENGINEERING AND SCIENCE
OF BILKENT UNIVERSITY
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR
THE DEGREE OF
MASTER OF SCIENCE
IN
NEUROSCIENCE

By
Tamer Gezici
July 2023

It’s not the rule! Rule-decodability is not limited to cognitive control-related frontoparietal regions.

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We certify that we have read this thesis and that in our opinion it is fully adequate, in scope and in quality, as a thesis for the degree of Master of Science.

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ABSTRACT

IT'S NOT THE RULE! RULE-DECODABILITY IS NOT LIMITED TO COGNITIVE CONTROL-RELATED FRONTOPARIETAL REGIONS

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M.S in Neuroscience

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July 2023

Performing tasks require us to abide and apply the relevant rules to the task (ie., do not wash white clothes with coloured clothes). As we perform tasks, these rules are maintained through cognitive control processes. Functional magnetic resonance imaging (fMRI) studies have shown that rule representations are decodable in a set of regions called the multiple demands (MD) network. Another set of regions called the default mode network (DMN) decorrelate with task-related networks. However, recent studies show that rule representations are decodable in tasknegative networks such as DMN as well.

The present study investigated rule decodability using multivariate fMRI analysis methods. Subjects performed an event-related rule switch fMRI experiment in which there were two rules: categorizing numbers as even/odd (parity rule) or greater/smaller (value rule) than 10.

In our first analysis, these two rules were modelled based on the switch or repeat status of the specific trial. We found that on switch trials, rules were decodable across the whole brain. In contrast, on repeat trials rules could not be decoded from any

brain region. Curiously, repeat trials rule classification was significantly below chance, suggesting that training the classifier on one set of patterns made them worse than chance in classifying on the remaining set. This would happen if different instances of the same rule on repeat trials may have been accompanied by very different patterns of activity.

In our second analysis we investigated if rule-related patterns changed with the number of consecutive repetitions or the number of consecutive switches, e.g., if the activity-pattern related to the parity rule on the first instance of a repeat trial was different from the pattern when this rule repeated again. We found that this was indeed the case. While the same rule could not be classified much across two consecutive switch trials, the same rule could be classified nearly everywhere across two consecutive repeat trials.

Keywords: *Cognitive control, task-sets, rule representations, functional magnetic resonance imaging, multiple demands network, default mode network.*

ÖZET

BU BİR KURAL DEĞİL! KURALLARIN ŞİFRELEMESİ YALNIZCA BİLİŞSEL KONTROL İLE İLİŞKİLİ FRONTOPARİYETAL BÖLGELERLE SINIRLI DEĞİL.

Tamer Gezici

Yüksek Lisans, Nörobilim

Tez Danışmanı: Ausaf Ahmed Farooqui

Temmuz 2023

Görevleri yerine getirmek, göreve ilişkin kurallara uymamızı ve uygulamamızı gerektirir (örneğin, beyaz çamaşırları renkli giysilerle yıkamamak). Görevleri yerine getirirken, kurallar bilişsel kontrol süreçleri aracılığıyla sürdürülür. İşlevsel manyetik rezonans görüntüleme (fMRI) çalışmaları, çoklu talep (MD) ağı adı verilen bir dizi bölgede kural temsillerinin kodunun çözülebileceğini göstermiştir. Varsayılan mod ağı (DMN) olarak adlandırılan başka bir bölge grubu, görevle ilgili ağlarla ilişkisizdir. Fakat, son araştırmalar, kural temsillerinin DMN gibi görevlerle alakalı olmayan ağlarda da çözülebileceğini göstermektedir.

Bu çalışma, çok değişkenli fMRI analiz yöntemlerini kullanarak kural çözümlenebilirliğini araştırmıştır. Denekler, iki kuralın olduğu olayla ilgili bir kural değiştirme fMRI deneyine girdiler. Katılımcılar gördükleri sayıları: sayıları çift/tek (parite kuralı) veya 10'dan büyük/küçük (değer kuralı) olarak kategorize ettiler.

İlk analizimizde, bu iki kural belirli bir denemeden başka bir kurala geçiş veya aynı kuralın tekrar durumuna göre modellenmiştir. Geçiş denemelerinde, kuralların tüm beyinde çözülebilir olduğunu bulduk. Buna karşılık, tekrar denemelerinde kuralların kodu hiçbir beyin bölgesinden çözülemedi. İlginç bir şekilde, tekrar denemeleri kuralı sınıflandırması, şansın önemli ölçüde altındaydı; bu, sınıflandırıcıyı bir küme

üzerinde eğitmenin, onları kalan kümede sınıflandırma sınıflandırmakta daha kötü olduğunu göstermektedir. Bu da tekrar denemelerinde beyinde gerçekleşen aktivasyon örüntülerinin birbirinden farklı olabileceğini göstermiştir.

İkinci analizimizde, kuralla ilgili örüntülerin ardışık tekrarlarlanan pozisyonlar arasında değişip değişmediğini araştırdık.

Bulgularımız bunu doğrular nitelikteydi. Aynı kural iki ardışık geçiş denemesinde sınıflandırılamazken, aynı kural iki ardışık pozisyon arasında kortekste neredeyse her yerde sınıflandırılabilir olduğunu gördük.

Anahtar sözcükler: *Bilişsel kontrol, görev setleri, kural temsilleri, fonksiyonel manyetik rezonans görüntüleme, varsayılan mod ağı, çoklu talep ağları*

ACKNOWLEDGEMENTS

It has been a good and enjoyable journey so far, and this thesis is just the beginning of this journey. If I were to make a list of names that I need to acknowledge, I would run out of space or even worse, most possibly forget to mention everybody.

I would like to thank everyone who has had even the slightest contribution to this thesis work, whether it is direct, or indirect. I would like to thank my supervisor for his guidance and my lab members and my friends for their support. I would like to thank the committee members for taking their time to go through the thesis and evaluating it. I would like to thank my mother, for bringing me up to where I have come. I would like to thank my father for always reminding me the reason to go on. I would like to thank all my relatives and family members who have supported me through my education and believing in me. I would like to thank all of my teachers, instructors and professors from my kindergarten years to my university training throughout. Finally, I would like to thank UMRAM and Bilkent University community for providing an opportunity to study here.

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CHAPTER 1

INTRODUCTION

1.1 Introduction

It is a tiring day and you are back from your menial activities (work, school, or maybe both!). One can only love doing housework, and it is time for you to do some laundry. When you decide that you would like to do laundry, you start re-organizing your thoughts in your mind and lay out a plan and a series of actions which constitute the laundry task.

You may need to think of the rooms in the house which you would be more likely to find laundry. Your teenager's messy room would be a good start. You locate a few pieces and place them in your basket. You locate and pick up every piece, you fill the basket and carry the clothes towards the washing machine. You open the detergent lid and pour detergent into the correct compartment, then you pick up the fabric softener and pour it into its compartment. You then look at your basket and decide to separate the whites from the coloured clothes, we all know that we do not mix those two. You place your clothes into the machine and select the appropriate washing program for your clothes. Maybe your clothes are made of delicate fabric, so you decrease the spin cycle and adjust the water temperature. Just as you are done setting up your machine and are about to press the start button, your phone starts ringing. You reach for your phone and pick it up. It is a friend of yours. She asks you about your dinner plans. You shortly chat with her and hang up. You walk back towards the washing machine, only to find yourself thinking "What was I doing earlier?". After a short lapse, you remember where you left off and press the button to turn on the machine.

The laundry task consists of several small sub-tasks, and each sub-task consists of rules and procedures you need to follow. You pick up the clothes, not the dishes, you do not wash whites with darks, you put detergent and fabric softener in the correct compartment, you select the correct program for clothes. For each step in the task, the rule you applied changed depending on the intermediate step you were in. When your friend called, you switched to the phone call. At that moment, you recalled and quickly adopted a new task-set that was related to performing a phone call, which required you to temporarily focus on the new task and ignore your thoughts that were related to doing laundry. When the phone call was over, you returned to doing laundry, which again shifted your attention from the phone call back to laundry.

1.2 Tasks

But what is a task? We can say that a task is a process that allows the person to attain a discrete goal state and we perform tasks in a goal directed manner. For example, the goal when doing laundry could be turning the machine on. However, the goal is largely dependent on the person's construal of what constitutes the "task". For example, for doing laundry, one may construe that hanging the laundry for drying and folding them to the wardrobe as parts of the laundry task as well. In any case, we perform tasks to complete a discrete goal state.

One interesting observation related to how people attribute specific task labels to their behaviour is if people are executing easy, routinized behaviour and are prompted to label the task they are performing (ie. "What are you doing?"), individuals may refer to the label in relation to the larger context. For example, one may say they are "preparing breakfast" instead of "chopping fruit". However, if the same task becomes more challenging, ie., using a blunt and heavy knife to do the cutting, individuals are more likely to say they are "chopping fruit" (Vallacher & Wegner, 1987). This shows that we construe tasks as an extended episode, but if the task becomes more difficult, it is further divided.

The medium in which tasks occur may be dependent on the context. A task can be passive, requiring no solid or overt action and may not involve the manipulation of the environment (such as naming objects or doing arithmetic in your head). Some may require you to perform actions which are complex and consist of at least one part or step (doing laundry, preparing dinner, writing an essay). Achieving a task requires one to apply a set of mental or overt operations(s) and action(s) in response to the specific demands or state of the environment.

In our everyday life, things around our environment may have a variety of possible uses. However, the relevant or appropriate use is dependent on the context of the current task and the intended goal. In a particular situation, a rule which applies in one context may be inappropriate in another (ie. washing the dishes is not part of doing laundry). To complete an action, the mind needs to maintain the task relevant information and procedures.

The maintenance of task relevant information can occur through the adoption of what is called a schema (Monsell, 2003). A schema is a mental construct that allows the person to organize the relevant response and behaviour to exhibit and allocate the necessary mental resources and configure the procedures. The task-set links the relevant mental processes and representations in the mind relevant to the task, from a wide array of many possible components that are available. The appropriate link needs to be formed and the relevant processing modules need to be enabled, and the irrelevant modules need to be disabled. Recall the example of washing the dishes is not being part of doing laundry, which would be an example for an irrelevant module that needs to be disabled.

Once a schema is assembled and linked to an organized structure to the point that it allows the task to be executed, it becomes what is called a “task-set”. We use our executive control for the maintenance and implementation of the task-set that is appropriate for our goal. This task-set becomes a structure which contains the rules and procedures and can be stored in memory. This storage allows the easy retrieval

from the procedural memory when necessary. And is thought to occur through the adoption of task-sets and task-sets contain the rules and procedures (Monsell, 2017).

1.3 Cognitive control

As you progress in a task, the intermediate goal states change. The task relevant information needs to be updated or, reconfigured depending on the current step. This reconfiguration happens through the setup of specific elementary processes which allow the task to be executed. The maintenance of these task-sets and rules requires control over the task. Just like how we hold and control the knife firmly as we chop fruit, we also need to exert control over our cognition. Because otherwise, you would likely drift off the task and be unable to perform it. Therefore, we need to maintain an ability to direct your mental functions and behaviours in accordance with the internally represented intentions and goals. These high cognitive functions are what are referred to as "cognitive control." Without cognitive control, or due to deficits in control, one would have difficulty maintaining task-relevant information such as: the current rule to apply, orient their attention to the relevant stimuli, inhibit or suppress task-unrelated thoughts or responses.

Research in neuroscience has shown that the lateral prefrontal cortex (LPFC) is involved in tasks that require cognitive flexibility, such as decision-making (McGuire & Botvinick, 2010) and task-switching (Braver et al., 2003; Ruge et al., 2013). These prefrontal areas are known to be involved in higher cortical functioning and purposeful behaviour as well (Aleksandr Romanovich Luria, 1980). Monkey studies show the involvement of prefrontal neurons that code task-relevant information, response mappings, rules and working memory content (Duncan, 2010; Procyk & Joseph, 2001). Neurological studies also demonstrate the role of prefrontal regions. For example, executive dysfunction may happen when there is a lesion or damage to these regions (Burgess & Shallice, 1996). Executive dysfunction manifests itself in impaired performance, perseverative errors, inhibitory dysfunction. Thus, cognitive control allows the formation of necessary perceptual, motor and cognitive processes that allows them to accomplish goals and tasks.

1.4 Task-sets and cognitive control

During cognitive science studies, participants perform experimental paradigms, which require the recruitment of many different cognitive processes. These paradigms contain instructions which the participant needs to obey. After some practice, these instructions are maintained and followed throughout the experiment. The instructions become mental configurations, which constitute a particular set of rules. For example, in a perceptual categorization task, the rule may be to respond to faces and houses using different fingers. These rules are constraints that form the necessary task-related responses. It is these rules that form abstract task-sets which allow them to attain goal-directed behaviour. The adoption of a task-set allows the person to choose, connect and set-up the necessary processes to complete the task. Learned task-sets and rules are thought to be mediated through representations in fronto-parietal regions for future use (Dumontheil et al., 2011).

When we begin a task, we recruit the relevant task-sets and maintain them in our mental workspace. However, task-sets are psychological constructs which by cognitive scientists are used to explain specific processes. Like any other psychological construct, their existence is debatable. Most people will not be thinking that they are configuring a task-set or executing parts of the step in their mind as they do their day-to-day tasks.

Although, when people switch from one task to another, or complete intermediate steps of a task, continuing in the task requires the dissolution of the previous task-set, and the adoption of a new task-set. It is such that when someone needs to begin a task, we need to reconfigure ourselves to the task, just like how a runner may prepare herself for the run by getting in a running stance.

When a participant is taught a rule to follow, they form a task-set which configures their behaviour. The notion of the task-set is something that has been studied for almost 100 years. One study that is a precursor of the rule-switch paradigm made

participants perform an arithmetic task, showing the effect of task alternation and task repetition and the effect of task complexity on completion speed (Jersild, 1927). For example, if the participant is asked to give a specific response to the number they are seeing (is it even or odd?) the rule configuration allows the execution and selection of the response. These rules and configurations are mediated through cognitive control processes. A cognitive neuroscientist can use representations of rules and how they are configured in the mind to study questions related to cognitive control. As these are the analogous of the minimal "parts" of what constitutes a task.

This aspect of cognition, which relates to cognitive control, has been studied extensively by psychologists (Miller & Cohen, 2001). It is thought that the maintenance of rule-related configurations when engaged in a task is mediated through cognitive control processes. When a person is focused on the task and has configured the necessary rule(s) relevant to the current task, the information related to the rule is maintained as long as it is relevant. However, when the task changes there is a switch from one configuration to another (Kiesel et al., 2010; Vandierendonck et al., 2010). This involves the realisation of the switch and the retrieval of the new rule configuration. Therefore, rule configurations are directly related to cognitive control processes because the lack thereof, would prevent us from performing our tasks.

1.5 Rule switch paradigms

Cognitive control processes can be studied using rule switch paradigms (Monsell, 2003). In such experiments, subjects learn and perform a specific (discrete) task on each trial. For example, participants are taught a set of rules and apply those rules depending on the stimulus that is presented. The ability to switch from one rule to another occurs through the instantiation of rule related configurations and representations. Such rule related representations are thought to be mediated through cognitive control processes. On this account, cognitive control is said to be involved in the retrieval, selection, and execution of the accompanying rule related response.

One well-established finding of these types of behavioural experiments is the switch cost. Switching from one rule to the other leads to slower reaction times (RT) and higher error rates. Which happens when the rule is different from the previously executed rule. The switch cost has been attributed to goal shifting or the activation of the relevant rule (Rubinstein et al., 2001), task-set inertia (Wylie & Allport, 2000), residual switch costs (Whitson et al., 2014), N-2 repetition costs (Philipp et al., 2008). One account of the switch cost is related to the reconfiguration of cognitive resources to a new task set (Rogers & Monsell, 1995). This account suggests that the switch cost (ie., increase in RT) is due to the additional time that takes to activate is due to the reconfiguration processes. Another account suggested that this is due to task-set inertia ie., due to interferences from the previous task set to the new one (Wylie & Allport, 2000). Newer theories explain the switch costs as a mixture of both accounts (Kiesel et al., 2010; Vandierendonck et al., 2010).

In addition to the switch cost another finding is that tasks which constitute of predictable sequences made up of several steps are hierarchically organized. During the recall and execution of memorized motor sequences or task items, reaction time (RT) of the first item is generally higher, (for example, it takes longer to start speaking longer words) (Klapp et al., 1973), or when the sequence is a longer or a more complex task episode (Farooqui & Manly, 2019).

1.6 fMRI studies of cognitive control

Functional magnetic resonance imaging has allowed the detailed investigation of neural substrates of cognitive control. These studies suggested the involvement of a distributed frontoparietal cortical network, primarily the multiple demands (MD) network (Duncan, 2013). These are a set of regions known to become more active during tasks that involve a variety of executive functions. These regions have been noted as the dorsolateral prefrontal cortex (DLPFC), inferior frontal junction (IFJ), intraparietal sulcus (IPS), anterior insula and dorsal anterior cingulate, presupplementary motor area (Duncan & Owen, 2000). Other subcortical regions

such as the thalamus, cerebellum and basal ganglia also accompany these cortical regions. MD regions are known to be involved when the task requires cognitive flexibility, decision making, goal-directed behaviour and task-switching (Niendam et al., 2012). Another case where elevated MD activity has been observed is when the difficulty of a task is manipulated. One study showed the existence of an integrative frontoparietal system that is recruited during easy (Crittenden & Duncan, 2014) and difficult task demands (NYBERG et al., 2009).

Another set of regions, called the default mode network (DMN) regions are anti-correlated with MD regions (Raichle et al., 2001). DMN regions consist of the posterior cingulate cortex, anterior medial prefrontal cortex (AMPFC), medial temporal lobe (MTL). These regions are known to activate when participants are doing internally directed activities such as theory of mind, recalling autobiographical memories, prospection, navigation, self-projection, mind wandering (Buckner et al., 2008; Spreng et al., 2009). Such deactivation has been interpreted as the suppression of internally directed cognitive activities, which the DMN regions become more active when participants are engaged in such activities.

Due to this dichotomy between the DMN and MD, it has been proposed that these two networks are anticorrelated with each other. However, some critiques of this view have pointed at the involvement of DMN regions in externally directed tasks, as well (Spreng, 2012).

Functional magnetic resonance imaging studies have been useful in discovering the possible functions of specific brain regions and networks. In the first few decades of fMRI, researchers investigated differences in univariate activity; comparing modulation of activity in one condition to another condition or some explicit baseline, such as rest. Although these methods have been useful in explaining the function of some regions, univariate activity is not informative when trying to distinguish patterns of activity. Particularly univariate activity cannot explain when a region’s overall activation is the same across two conditions, but the response

patterns differ. To catch such differences in activity, multivariate pattern analysis which uses machine learning classification methods to discriminate patterns of neural activity between conditions can be used. See Norman et. al.'s paper for a review (Norman et al., 2006).

Multivariate pattern analysis (MVPA) has allowed the investigation of patterns of activity, and this method has been used to classify rule representations during fMRI tasks. MVPA is used to discriminate sipatially distributed brain activity patterns. These methods have been previously used for the decoding of task-relevant information and showed the involvement of frontoparietal regions (S. Li et al., 2007; Woolgar et al., 2011).

Previous studies have shown that patterns of activity for different rule types may differ and are discriminable in MD regions. The patterns of activity in MD and fronto-parietal regions related to rule classification have been well-established (M. L. Waskom et al., 2014; Woolgar et al., 2016). However, some studies show that such activity patterns are also decodable in DMN regions. One such study showed increased DMN activity during higher-level contextual switches (Crittenden et al., n.d.). Such studies have indicated the possibility of other regions being involved in cognitive control as well**.**

Performing any task requires access to a representation of the relevant stimuli response rule. While we are executing a task, the relevant rule representations should be in our head, thus under our cognitive control. These are instantiated through the access of the specific rule by reconfiguring the task set when the stimulus is presented.

A manuscript by Duymuş et. al. (in preparation) studied cognitive control in congenital blind or early blind participants and sighted controls. Blind participants were given tasks in tactile and auditory modalities, whereas deaf participants were given tasks in visual and tactile modalities. All tasks involved the manipulation of

easy and difficult conditions. For example, in the tactile modality, participants needed to discriminate the size difference between two shapes printed on a plexiglass using their fingers. In this task, difficulty was manipulated based on the protuberances of the shapes, making the difference between the two shapes less obvious in the difficult condition. The second task was an auditory or visual n-back depending on the subject's available modality. Here, difficulty was manipulated based on the "n" number of the n-back task (ie., 3-back vs 1-back). Manipulating difficulty showed peak activation clusters in blind participants in visual areas and these regions responded to manipulations to cognitive load. Additionally, when sighted controls and blind participants were compared, the most active region in tasks that are known to activate MD regions activated visual areas more in blind participants, whereas MD regions were active in sighted controls (Duymus H, personal communication, June, 2023)

1.7 Present study

The present study employs a rule switch task to investigate rule decodability in the brain using multivariate fMRI analysis methods. We were interested whether if rule representations were decodable in the brain and furthermore, the extent of decodability in the brain. We investigated these questions by modelling rule representations based on the repeat and switch status, as a conjunction of the specific trial's rule type.

CHAPTER 2

Investigation of differences in trial types

2.1 Funding

The study was funded by the Scientific and Technological Research Council of Turkey TÜBİTAK (grant number: 121K924).

2.2 Analysis 1 Investigation of differences in trial types

In this thesis, the work is divided into two lines of analysis, which the results will be reported separately, named as “Analysis 1” and “Analysis 2” all fMRI analysis methods for both studies will be explained in the upcoming section. The methods discussed for Analysis 1 are mostly common with Analysis 2, but the subtle differences will be mentioned when necessary.

2.3 Methods

2.3.1 Participants

Thirty (18 females), mean age 21, right-handed subjects were recruited via the university email lists, through friends or social circles. Participants were provided with MRI compatible glasses if necessary. One subject was excluded from analysis due to poor (< 60%) performance. Informed consent was taken, and subjects were reimbursed for their time either in course credit, payment (50TL), or both. Ethics approval was given by the Bilkent University Ethics Committee For Research With Human Participants. fMRI data were acquired using a Siemens 3T Tim Trio scanner in the National Magnetic Resonance Research Center (UMRAM) Ankara, Turkey.

2.3.2 MRI acquisition

All MRI scans were acquired using a 32-channel phased array head coil. Subject heads were fixed using foam cushions to minimise head movement. A sequential descending T2*-weighted gradient-echo planar imaging (EPI) acquisition sequence was used with the following parameters: acquisition time, 2000 ms; echo time, 30 ms; 32 oblique slices with slice thickness of 3 mm and a 0.75-mm interslice gap; in-plane resolution, 3.0 × 3.0 mm; phase oversampling, 20%; matrix, 64 × 64; field of view, 192 mm; flip angle, 78°, GRAPPA acceleration factor, 2. T1-weighted MP-RAGE structural images were acquired for all subjects (slice thickness, 1.0 mm; resolution, 1.0 × 1.0 × 1.0 mm isometric voxels; field of view, 256 mm; 176 slices).

2.3.3 Apparatus

Participants viewed an MR compatible stimulus screen (32-inch LCD display; 60 Hz refresh rate; 1280x768 pixels). Manufactured by TROYKA MED (Ankara, Turkey). Participant responses were collected via a fiber optic button box (Current Designs, fORP 904 fMRI trigger box and response system).

Subjects performed a single 10-minute fMRI run on a rule-switching task. Prior to this fMRI run, subjects had participated in a forty-minute fMRI experiment on a different and unrelated task. Subjects performed a 5–10-minute pre-scan practice outside of the scanner before starting the fMRI session.

2.3.4 Pre-processing

fMRI data were preprocessed and analyzed using SPM12 (Friston, 2007) (Wellcome Department of Cognitive Neurology, London, UK) using Automatic Analysis (aa) (Cusack et al., 2015) pipelines implemented in MATLAB (MathWorks).

The pre-processing pipeline was as follows: EPI volumes were first slice time corrected using the middle slice as reference and then realigned using the first volume as reference. A two-step coregisteration algorithm as implemented in aa was used: The structural T1-weighted image was coregistered to the SPM T1 template. The mean functional EPI was then coregistered to the structural image. Coregistration parameters of the mean EPI were subsequently applied to all functional images. Subjects were normalized into the Montreal Neurological Institute (MNI) space to 2x2x2mm resampled voxels. For univariate analysis, spatial smoothing was performed using an 8 mm full width at half-maximum (FWHM) Gaussian kernel. Unsmoothened data has been used for multivariate analysis.

2.3.5 Design

In an event-related design, subjects participated in a rule switch task in which they were simultaneously presented with a letter and a number in a colored rectangular margin (Figure 1). Subjects were asked to pay attention to the number and the color

of the margin (the letter was relevant to a different experiment). The color of the rectangular margin indicated pre-learned rules to apply: The blue margin (value trial) indicated categorizing the number as greater or less than 10 and the green margin (parity-trial) indicated categorizing the digit as even or odd. From now on, in the text these two rules will be referred to as "parity" and "value" rules.

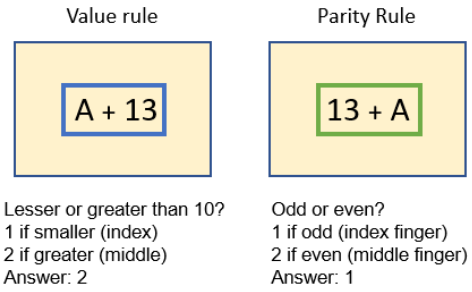

Figure 1 A sample of the two rules. The value and parity rules were presented in blue and green margins respectively. The relevant content of the rule and the key-response mappings, and the answer for the sample trial have been presented at the bottom panel of each rule. In the example above, we used the same number and letter to convey that the position of the letter and the number could occur at both sides (right or left) of the fixation.

A random number between 1 to 20 (excluding 10) was selected at random. 10 was omitted as it is unsuitable for the value-rule. Subjects were instructed to use the index (button 1) and middle fingers (button 2) for their responses. The position the number and letter were presented was selected in random (right or left side of the fixation). Key responses were mapped as odd: button 1, even: button 2; Lesser than 10: button 1, greater than 10: button 2. Stimuli remained on screen until the subject responded. See (Figure 2) for the overall flow of the experiment.

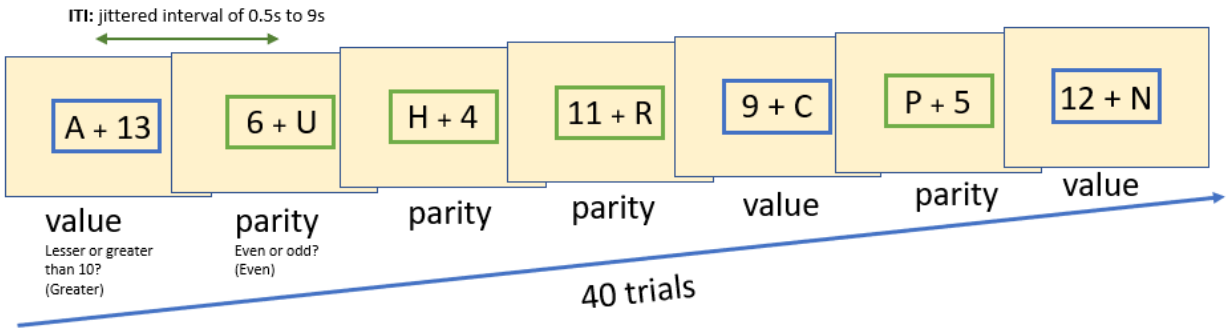

Figure 2 An example episode from the experiment. On each trial, participants viewed a letter and a number in a colored margin. The blue margin indicated the value rule (participants determined whether the number greater or smaller than 10) and the green margin conveyed the parity-rule (is the number even or odd). Between each trial, an ITI screen in the range of 0.5s to 9s was presented for feedback via a fixation cross. At the bottom of each panel, the specific rule type has been written.

Subjects received feedback on the accuracy of their response via a fixation cross which was presented for a jittered interval (range: 0.5 - 9, mean: 2.43s, std: 1.8s) which lasted from the response to the onset of the next trial. The type of rule (parity or value) on each trial was pseudo-randomised to have an equal number of repetitions of each rule type. An “episode” consisted of 40 trials. Once an episode was complete, a self-paced rest screen was presented (not shown on Figure 2).

All stimuli were presented at the center of the screen, visible from the subject’s position in the scanner via a mirror mounted onto the head coil. The outer square margins surrounding the letter and the number subtended a vertical visual angle of around 2°. The letter and number were presented in Courier New font and would appear at the middle of the screen at the right and left side of the fixation. The code running the experiment was written using PsychoPy version 2021.2.3 (Peirce et al., 2019).

2.3.6 fMRI statistical analysis

Statistical analysis was conducted using a general linear model (GLM). The time course of each voxel was high pass filtered with a cut-off period of 128s (0.0078hz). Regressors in all models were modelled as impulses of no duration (events) and were convolved with the canonical hemodynamic response function. Incorrect responses were modelled as one regressor and were not used for any analysis. Movement parameters and run means were added to the model as covariates of no interest. Parameter estimates for each regressor were calculated from the least-squares fit of the model to the data. For multivariate pattern analysis, modelling was done using normalized unsmoothed data. For univariate analysis, normalized and smoothed data were used. Event (regressor) files for all analysis were prepared using the Pandas library (McKinney, 2010).

2.3.7 General Linear Modelling

In this analysis, we investigated the multivariate decodability of trial types when the specific rule and switch/repeat status is accounted for different rules. The trial type was determined depending on the specific features of the trial. The first feature of a trial was the rule: parity or value. Recall that for parity, the rule was to determine whether the number was even or odd. For value, the rule was to determine whether the number was lesser or greater than 10. In addition to these two rules, the other feature which determined the trial type was whether the trial was a switch or a repeat. If the rule on the current trial was different than the previous trial, the trial was marked as a "switch" and if the rule was same as the previous, the trial was marked as a "repeat". The trial type was determined based on the conjunction of these two features, which yielded 4 different trial types (Figure 3). For example, if the current trial is parity and the rule changed (ie., a switch trial in which the previous trial was value) the trial type would be marked as "SWITCH_PARITY". The other three trial types were "SWITCH_VALUE", "REPEAT_PARITY" and "REPEAT_VALUE" which correspond to switching or repeating on each rule type. The first trial in a 40-trial long episode can be neither a switch nor a repeat, therefore we did not use them for analysis.

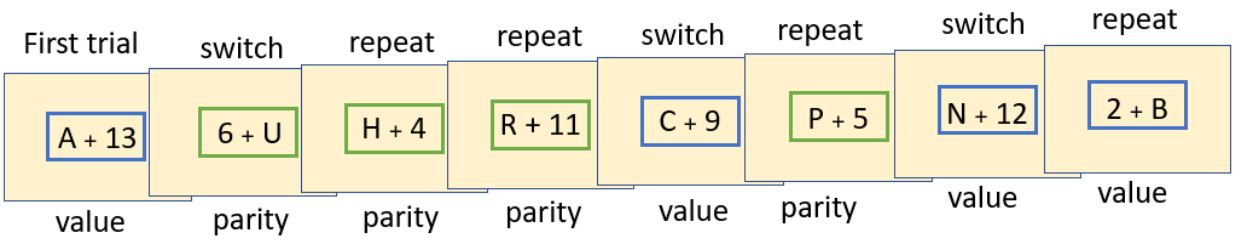

Figure 3 For the reader, the rule types (parity or switch) are written at the bottom of each trial. At the top of each trial, the switch or repeat status of the trial is written. If the rule is same as the rule of the previous trial, it is marked as a repeat. If the rule is different than the previous trial, it is marked as a switch trial. We modelled trials depending on the rule type and the switch or repeat status. The second trial is a "SWITCH" on a "PARITY" trial. Therefore, it is marked as "SWITCH_PARITY". The very first trial of an episode is neither a switch nor a repeat, therefore is negated on the figure (marked as "First trial).

For multivariate analysis, these 4 trial types were modelled as separate regressors and were chunked to 4 for cross validation. In this analysis, we were interested in classifying patterns of activity between: SWITCH_PARITY versus SWITCH_VALUE trials and REPEAT_PARITY versus REPEAT_VALUE trials.

2.3.8 Behavioural analysis

Reaction times have been plotted for each trial type using the matplotlib and seaborn graphing libraries.

2.3.9 Univariate analysis

We did a whole brain univariate analysis using the same models described above with the only the difference being the use of smoothened data. Beta estimates for each regressor from GLM model of Analysis 1 were used to estimate linear contrasts for our classification pairs: SWITCH_PARITY > SWITCH_VALUE, REPEAT_PARITY > REPEAT_VALUE. Each regressor was weighted equally in the contrast vector. We also did a whole brain univariate switch > repeat contrast and presented the F-contrast results.

2.3.10 ROI selection for multivariate analysis

Prior studies have shown decodability of task-specific features in MD and DMN regions. Therefore, we used ROIs which corresponded to these regions taken from Andrews-Hanna et. al (2010), Dosenbach et. al (2006) and Fedorenko et. al (2013). In addition to these ROIs, “unrelated” ROIs for motor, auditory and language regions which corresponded to neither DMN nor MD regions were generated via the SPM anatomy toolbox (Eickhoff et al., 2005). All ROIs were standardized into the MNI152 space with the size of a sphere of 10-mm radius.

2.3.11 ROI based multivariate classification.

For multivariate analysis (MVPA and RSA) the same GLM using the same regressors mentioned in section 2.3.7 was estimated on unsmoothed data. Beta estimates generated from the model were used for region of interest (ROI) based MVPA analysis. Multivariate pattern analysis was conducted using an in-house written script which utilizes the LIBSVM MATLAB toolbox (http://www.csie.ntu.edu.tw/~cjlin/libsvm) (Chang & Lin, 2011). We used a linear support vector machine (SVM), with default parameters (nu-SVC, linear kernel, hyperparameter C = 1) following a leave-one-out cross-validation scheme. In brief, in this scheme the classifier is trained on data from all chunks but one in which the left-out chunk is used for testing. This process is repeated iteratively until each chunk is used for testing. Results generated from each iteration are averaged, yielding a single classification accuracy. Classification accuracies (CA) minus chance (50%) were generated for each classification pair, ROI and subject and then averaged across all subjects. These classification accuracies were tested for significance using a one-sample t-test. ROI based MVPA result figures have been plotted using Pandas and Matplotlib (Hunter, 2007) libraries.

2.3.12 Searchlight based decoding.

The Decoding Toolbox (TDT – version 3.999F) (Hebart et al., 2015) was used to implement a searchlight (Kriegeskorte et al., 2006; Norman et al., 2006) based support vector machine classification. The default parameters of TDT were used (c-SVC, linear kernel, hyperparameter C = 1) with a spherical searchlight of radius 3 voxels (~9mm). Searchlight decoding procedure takes each voxel in the volume and applies a classifier to distinguish multivariate patterns of local and spatially present activity between two classes. This multivariate classification occurs within a small spherical cluster that surrounds the selected volume and is iteratively selected for each volume in the brain. For each voxel, an accuracy value is calculated and assigned. The resulting accuracies are tested via a one-sample t-test which generate an spmT map which represents voxels that contain decoding accuracies related to the classification pairs.

Classification was carried on in an identical way to the ROI based analysis using the same model described previously in Analysis 1. Similar to the ROI analysis, a leave-one-out cross validation scheme was applied. First level searchlight results (spmTs) were spatially smoothed using an 8mm FWHM Gaussian Kernel for group level analysis. Results were corrected for multiple comparisons using an FDR threshold of (p<0.05) an explicit gray matter mask was used to exclude out-of-brain activations that are generated due to the inherit nature of the searchlight algorithm. Searchlight (whole brain) renders have been generated using MRIcroGL (X. Li et al., 2016) on the MNI152 template.

2.3.13 Representational similarity analysis

Representational similarity analysis (RSA) is a method to investigate the representational content of brain activity patterns (Kriegeskorte, 2008). It is based on the calculation of correlations between the activity patterns across conditions. These correlations can be converted to dissimilarity values to investigate how stimuli or conditions are represented in the brain in relation to each other. In this type of analysis, a dissimilarity value between every pair of condition is generated. This generates what is called a representational dissimilarity matrix (RDM). An RDM is a NxN matrix, where N is the number of conditions and each conjunction of row and column represent the dissimilarity value paired for each condition. In the RDMs, the dissimilarity value for each beta estimate associated with each pair of regressor are represented as a single cell. Diagonal cells in each RDM indicates the dissimilarity value of each regressor against itself, which naturally would correspond to the minimum amount of dissimilarity (zero) and hence, the highest level of similarity.

The same ROIs used in previously described analysis were used for representational similarity analysis using the RSA toolbox (Nili et al., 2014). Beta estimates from the GLMs used in MVPA analysis were used to determine dissimilarity measures of

every regressor pairs' beta estimate against each other, generating a representational dissimilarity matrix (RDM) for each ROI. Response patterns elicited by condition pairs in each region is expressed by spearman correlation distances (1-r).

We used the same beta estimates that were used in MVPA analysis for our RSA analysis to see the dissimilarity between chunks and trial types (ie. Repeat parity chunk 1 compared with Repeat parity chunk 2). The distance measures for each trial type and each ROI were first estimated for each subject individually, and then averaged for all subjects. Group-level representational dissimilarity matrices generated by the RSA toolbox were first group averaged and then rank transformed and scaled to [0,1] using in-house Python code. Dissimilarity matrices for each ROI were then plotted using the seaborn graphing library (M. Waskom, 2021).

We also were interested in the dissimilarities between chunk pairs within the repeat and switch trials. The dissimilarity values between each possible chunk pair have been extracted from the RDMs and plotted.

2.4 Analysis 1: Results

2.4.1 Behavioural results

Overall, our participants performed very well, the mean accuracy was 96.69%, the overall RT was 1.35s (88.8 – 100%, SD=0.788). Reaction times for each trial type are shown in Figure 4. Switching between rules led to higher reaction times, showing a prominent switch cost. A repeated measures ANOVA was conducted using trial types and switch/repeat as factors. The difference between switches and repeats was significant ($F_{1,28} = 36.62$, $p < 0.001$). The difference between overall trial types

(parity versus value) was also significant ($F_{1,28} = 6.64$, $p < 0.05$), however there was no significant interaction between switch/repeat and trial types.

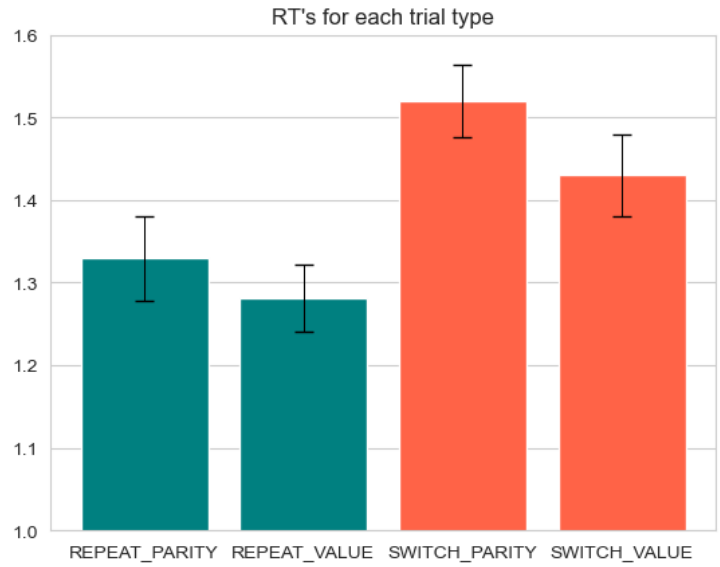

Figure 4 Reaction times for each trial type. Confidence intervals indicate 95% confidence intervals corrected for within-subject comparisons.

2.4.2 Univariate analysis results

We estimated linear contrasts for our classification pairs: SWITCH_PARITY > SWITCH_VALUE and REPEAT_PARITY > REPEAT_VALUE. Each regressor was weighted equally in the contrast vector. Both whole brain t-contrasts did not reach statistical significance when corrected for multiple comparisons (p<0.05, FDR corrected). Switch > repeat results have been presented as an f-contrast (Figure 5).

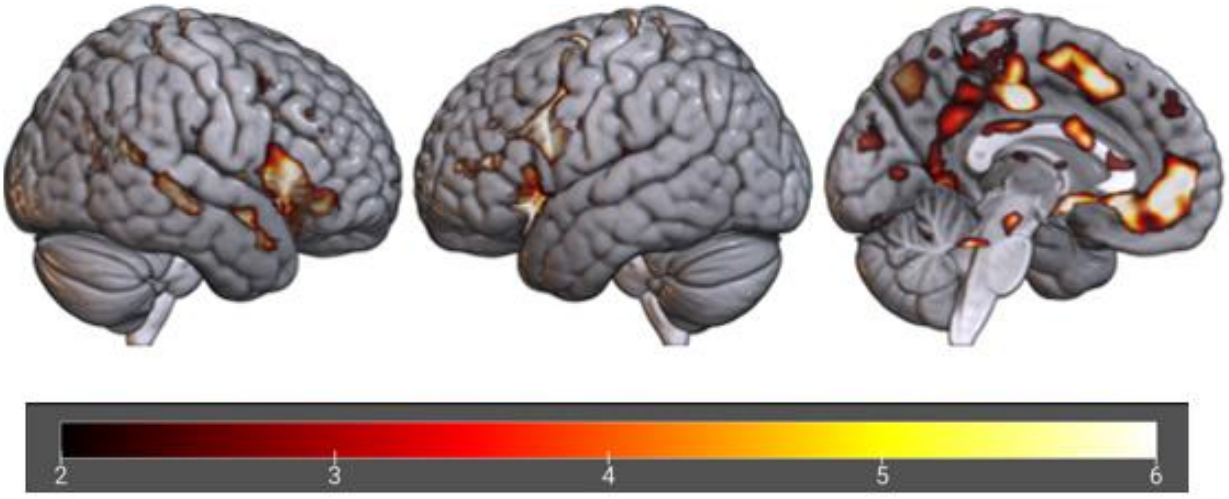

Figure 5 Univariate F-contrast results for switch > repeat.

2.4.3 ROI based multivariate classification.

In the upcoming figures, results in which classification accuracies were positive have been color-coded as red and below chance classifications have been color-coded as blue for both ROI and searchlight-based analysis.

In our first model, we were interested in classifying patterns that discriminated the two rules on switch and repeat trials. Recall from Figure 3 that a trial could be either the parity-rule or the value-rule, and a trial can either be a switch or a repeat. For example, if the subject performed a rule repeat (if the rule is same as the previous rule) and the current rule is value then the trial would be marked as "REPEAT_VALUE" (Figure 3).

The first classification pair that was tested is: SWITCH_PARITY (switch trial where the rule was parity) versus SWITCH_VALUE (switch trial where the rule was value). Results showed strong decoding accuracies that were significantly higher than chance for trial types in the whole brain for almost all ROIs following a one-sample t-test (Figure 6).

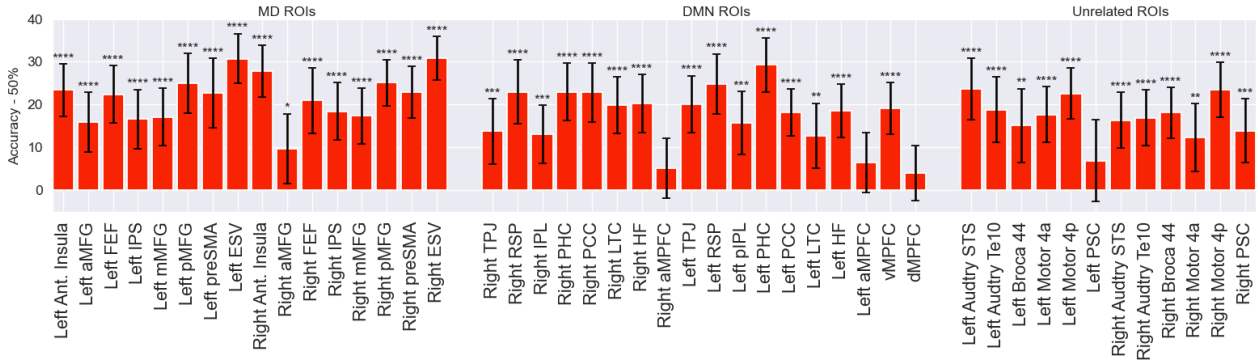

Figure 6 ROI-based MVPA results for SWITCH_PARITY versus SWITCH_VALUE trial types. Confidence intervals show 95% CI from the one-sample t-test results. Significance codes: * < 0.05, ** < 0.01, *** < 0.001, **** < 0.0001

Next, we classified REPEAT_PARITY trials (repeat trial where the rule was parity) versus REPEAT_VALUE trials (repeat trials where the rule was value). Interestingly, the classification accuracies that were calculated from this analysis were significantly below chance (Figure 7). In brief, if the cross-validation chunks used for classification are accompanied by very different patterns of activity, leading to a heterogenous chunk that the classifier can not find common patterns across, the classifier performs worse than chance. See Section 2.5 titled “Interim Discussion” for a detailed explanation on negative classification accuracies.

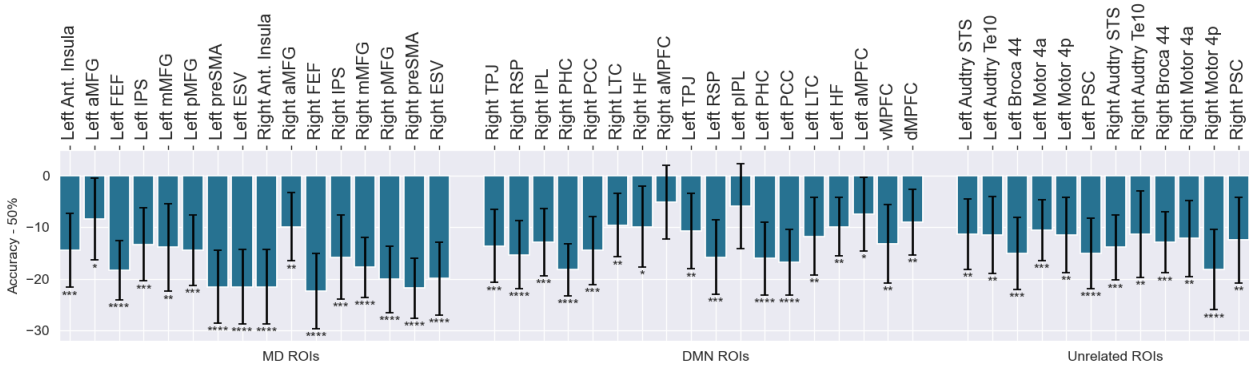

Figure 7 ROI-based MVPA results for REPEAT_PARITY versus REPEAT_VALUE trial types. Confidence intervals show 95% CI from the one-sample t-test results. Significance codes: * < 0.05, ** < 0.01, *** < 0.001, **** < 0.0001

2.4.4 Searchlight based decoding results.

To identify regions which could discriminate SWITCH_PARITY and SWITCH_VALUE trial types, a searchlight-based MVPA was conducted.

Results show wide-spread and high, positive classification accuracies at the whole brain for switch parity and switch value trial types. Rule-related patterns of activity were discriminable in nearly all regions of the brain which was consistent with the ROI based analysis results (Figure 8). Left Inferior parietal lobule (-36 -32 36, t = 15.97), left mid cingulum (-12 12 38, t = 15.24) right precentral gyrus (26 -8 44, t = 14.79) ($p < 0.05$, FDR corrected).

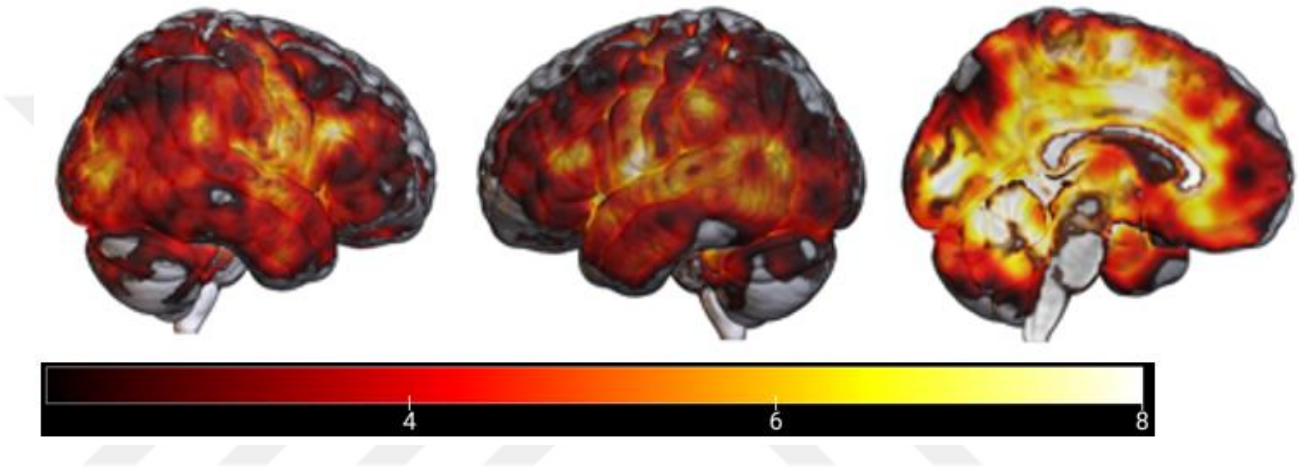

Figure 8 Searchlight MVPA results for SWITCH_PARITY versus SWITCH_VALUE trials. Colorbar below indicates t-values between 2.3 to 8 after ($p < 0.05$) FDR correction. Each voxel corresponds to the positive decoding accuracy generated from the searchlight.

Our second classification pair was REPEAT_PARITY versus REPEAT_VALUE. In this analysis, we were interested in identifying regions which could discriminate these trial types. Consistent with the ROI-based MVPA analysis, results showed significantly below chance classification accuracies at the whole brain for these two trial types. The top three peak clusters were at right anterior insula (-28 18 12, t = 12.99) right fusiform (36 -42 -8, t = 12.01) right mid cingulum (0 4 34 t = 11.68) ($p <$ 0.05, FDR corrected).

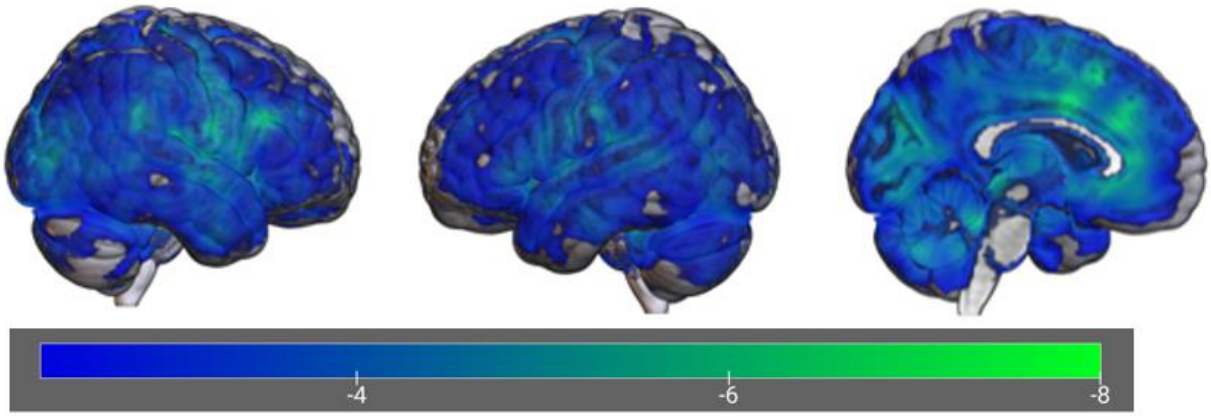

Figure 9 Searchlight MVPA results for REPEAT_PARITY versus REPEAT_VALUE trials. Colorbar below indicates t-values between -2.3 to -8 ($p < 0.05$, FDR corrected). Each voxel corresponds to the negative decoding accuracy generated by the searchlight.

2.4.5 ROI based RSA analysis

We used representational similarity analysis to investigate the dissimilarity between different trial types and chunks. This is because we were particularly interested in the differences between chunks of the same trial type. Recall that chunks correspond to a single beta estimate which represents an estimate of several instances accompanied by a particular trial type (ie., 10 instances of REPEAT_PARITY trials). For example, here, "REPEAT_PARITY_CH1" corresponds to the first chunk of the several instances of repeat parity trials. Because we were particularly interested in the differences between chunks, we used the same GLM model results used in our MVPA analysis. This way, we would be able to investigate the dissimilarity between different samples of trial types. In Figure 10, the individual dissimilarity values for each chunk against each other has been plotted for three representative ROIs, from MD, DMN and an unrelated region respectively. Results show that the dissimilarity values between repeat chunk pairs are higher compared to switch chunks pairs. To avoid clutter, we select 3 representative ROIs from MD, DMN and unrelated regions. Results show that chunks of repeat trials are vastly dissimilar to each other, whereas switch trials are similar to each other.

Figure 10 Correlation (dissimilarity values) for each pair of trial type and their corresponding chunks (ie. Repeat parity Ch1-Ch2 indicates dissimilarity between Chunk 1 and Chunk 2.

We conducted an ANOVA to see the difference between switch repeats, using subject and switch/repeat as factors, the results from the significant ROIs have been presented on Table 1.

ROI	F	p value
Left Ant. Insula	14.528	0.001
Left FEF	4.837	0.037
Left aMFG	4.56	0.042
Left Auditory STS	10.267	0.004
Left Auditory Te11	5.131	0.032
Left Broca 45	5.391	0.028
Left Motor 4a	5.275	0.03
Left PSC 3a	13.653	0.001
Right Ant. Insula	8.076	0.009
Right ESV	5.804	0.023
Right LTC	6.887	0.014
Right PHC	9.449	0.005
Right RSP	4.813	0.037
Right TPJ	13.37	0.001
Right Auditory Te10	4.858	0.037
Right Auditory Te11	6.717	0.015
Right Broca 44	4.92	0.035
Right Motor 4a	9.573	0.005
Right Motor 4p	8.305	0.008
Right PSC	9.906	0.004
Right PSC 3a	8.819	0.006
Right PSC 3b	10.667	0.003

Table 1 ANOVA results for the overall difference between switch and repeat trials, Degrees of freedom =1,27. Only ROIs that are below a significance level of 0.05 are presented.

Dissimilarity values were rank-transformed and scaled to [0,1] and have been plotted as a heatmap. The upper triangle of the RDMs have been masked for better visualization (Figure 11).

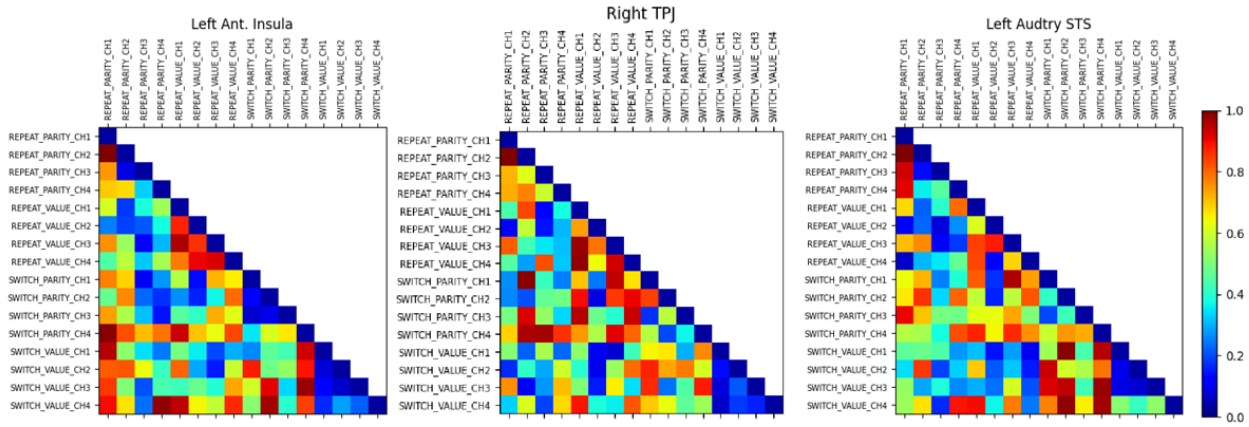

Figure 11 Three representative ROIs from MD, DMN and unrelated regions respectively. Colorbar indicates rank-transformed dissimilarity values, where 0 indicates minimum dissimilarity and 1 indicates maximum dissimilarity.

2.5 Interim discussion

In Analysis 1, we attempted to classify SWITCH_PARITY versus SWITCH_VALUE trials and REPEAT_PARITY versus REPEAT_VALUE trials. Using RSA and MVPA, we discovered that rule-representations on switch-trials were discriminable across the whole brain.

Interestingly, for repeat trials, we found that rule classification was not present anywhere in the brain and the classification accuracies were significantly below chance. This suggested that training the classifier on one set of patterns made them worse than chance in classifying on the remaining set. In other words, patterns of activity within chunks which the classifier was trained mut have differed within and across the cross-validation chunks. When activity between chunks differ, chunks that were used for training would lead to the classifier being unable to successfully identify patterns common across them and lead to a failure to classify. This can happen if patterns of activity between individual chunks are not common or heterogenous (Figure 12-b).

This finding is counter-intuitive, considering whatever activity pattern that gives rise in response to a repeat trial, should theoretically be consistent. However, one possible explanation for how specific instances of repeat trials could be vastly different from each other is if repeats that occur consecutively lead to different activity patterns (Figure 12-a). In our second analysis, we investigated this issue by comparing consecutively occurring switch and repeat positions.

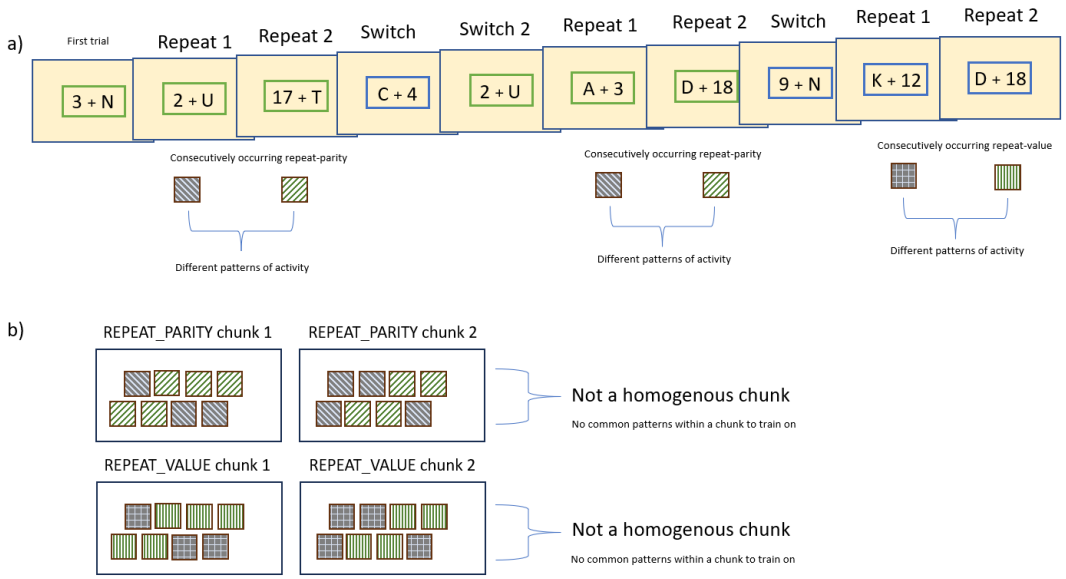

Figure 12 a) If consecutively occurring repeat trials lead to different activity patterns, instances of repeat trials within a chunk will be different from each other. b) This will lead to heterogenous training chunks, containing instances of repeat trials with vastly different activity patterns. Heterogenous training chunks will lead to the failure of finding common patterns within a chunk, yielding negative classification accuracies.

CHAPTER 3

Investigation of consecutive repeats and switches.

3.1 Analysis 2

For brevity, methods that are common across Analysis 1 and Analysis 2 will not be explicitly mentioned. The major difference in these two analyses is the GLM models and regressor layouts that have been used. In Analysis 2, one subject that has been excluded due to the lack of sufficient samples for a specific regressor type, therefore leaving 28 subjects in total for analysis. Please refer to the Methods section of Analysis 1 for the specific details on fMRI analysis.

3.2 Methods

In this analysis, we were interested in the classifying patterns elicited by a given trial type when the same rule had repeated or switched over the preceding trials. This is because in our previous analysis in which we tried classifying repeat trial types, we observed classification accuracies significantly below chance. See the section "Interim Summary" for our reasoning behind this model.

In this model the trial type was determined based on the number of local occurrences of switches and repeats until the present trial. Like Analysis 1, we first determined trial types based on the switch/repeat status and the rule type (parity/value).

For example, assume a 7-trial long sequence of trials: “value-parity-parity-value-parity-parity-parity”. Denoted by the switch (S) or repeat (R) status and the rules parity (P) or value (V). Thus, a switch and parity trial correspond to “SP”. For the trial sequence mentioned written above, symbolizing the trial types using the first letters to indicate switch/repeat and parity/value yields a sequence: “firstTrial-SP-RP-SV-SP-RP-RP”. Do note that the very first trial (value) is neither a switch nor a repeat, so the switch from value to parity; “SP” is the first element in the sequence. In this sequence, we can count and denote the switches or repeats which preceded each trial with position numbers of switches and repeats. For example, if two switches occur consecutively, the first switch is denoted as S1 and the second is denoted as S2.

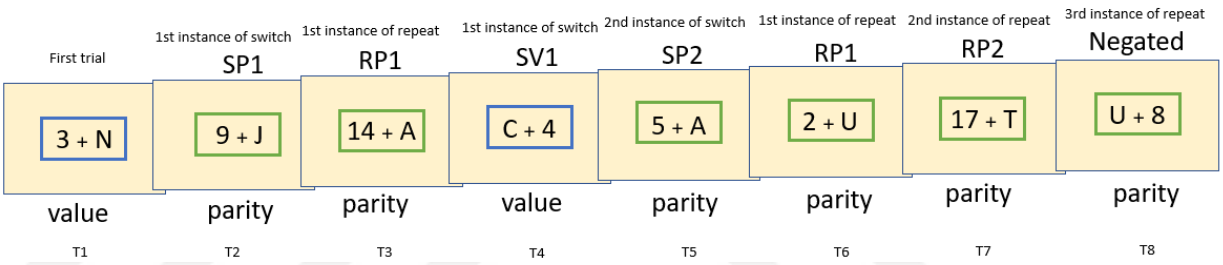

Figure 13 Local switches and repeats were determined based on the local occurrences of switches and repeats until that trial. Each trial is marked based on what happened in the preceding one or two trials. For example, when the switch and repeat status of the current trial changes, the occurrence number also changes.

The reader can make use of Figure 12 for a visual demonstration. Trial 2 (T2, bottom part) is the first instance of switching. Therefore, it is marked as S(witch)P(arity)1 “SP1”. T3 is a rule repeat and is the first instance of repeating hence it is marked as R(epeat)P(arity)1 “RP1”. T4 is a switch, therefore is marked as S(witch)V(alue)1 “SV1”. At T5, there is a rule switch again, and it is the second instance of switching hence it is S(witch)P(arity)2 “SP2”. Expanding the sequence mentioned above to account for position numbers yields a sequence such that: “firstTrial-SP1-RP1-SV1-SP2-RP1-RP2”.

Each trial type was modelled as a regressor based on its position number and the rule type. In this model there were 8 different types of regressors: SP1, SP2, SV1, SV2, RP1, RP2, RV1, RV2. Regressors were chunked to 2 for cross validation. Repeats or

switches with a position number larger than 2 (i.e., SP3, RV3, SV4, RP4 …) were modelled as a single, seperate regressor and were not used for MVPA analysis (shown as “negated” for T8 on Figure 13)

In this analysis, MVPA classification was conducted using 2 chunks per regressor. Therefore, a half-half cross validation scheme was followed. Four different binary classifications were conducted to discriminate multivariate activity patterns between: “RP1 versus RP2”; “RV1 versus RV2”; “SP1 versus SP2”; “SV1 versus SV2”.

3.3 Multivariate classification

While reporting our results, accuracy values for repeat trials have been averaged based on the trial type. For example, “RP1 versus RP2” and “RV1 versus RV2” were averaged, yielding a single result for repeat at position 1 (R1) versus repeat at position 2 (R2).

Similarly, switch trials were averaged based on trial type as “SP1 versus SP2” and “SV1 versus SV2” yielding results for switching at position 1 (S1) versus switching at position 2 (S2). Therefore, the results will be reported as if we had two classification pairs: R1 versus R2 and S1 versus S2.

3.4 Representational similarity analysis

When reporting our RSA results, the RDMs will be presented with all the regressors and their corresponding dissimilarity values against each other. When we are reporting dissimilarities between positions (i.e., R1 versus R2) we will present them by averaging all repeat position 1 trials against all repeat position 2 trials, disregarding the individual values of the trial type (parity/value) and their chunks (chunk 1 and 2) and instead averaging them. This approach yields a single dissimilarity value for R1 versus R2 trials. The same approach has been taken for switch positions as well.

3.5 Results

In our second model, we were interested in classifying patterns for switch and repeat trials depending on the number of local instances of repeats and switches that occurred in the preceding two trials (see above for a detailed explanation). For example, if two repeats occurred consecutively, the first repeat was marked as R1, and the second repeat was marked as R2. Similarly, consecutive switches were marked depending on the number of switches preceding the trial, such as: S1 and S2.

3.5.1 Behavioural results

We plotted the RTs for each trial type based on the position (Figure 14). A repeated measures ANOVA was conducted using consecutive positions and switch/repeat as factors. The difference between switches and repeats was significant ($F_{1,27} = 12.0$, $p < 0.001$). The difference between positions was also significant ($F_{1,27} = 7.38$, $p < 0.05$). However, there was no significant interaction between switch/repeat and positions.

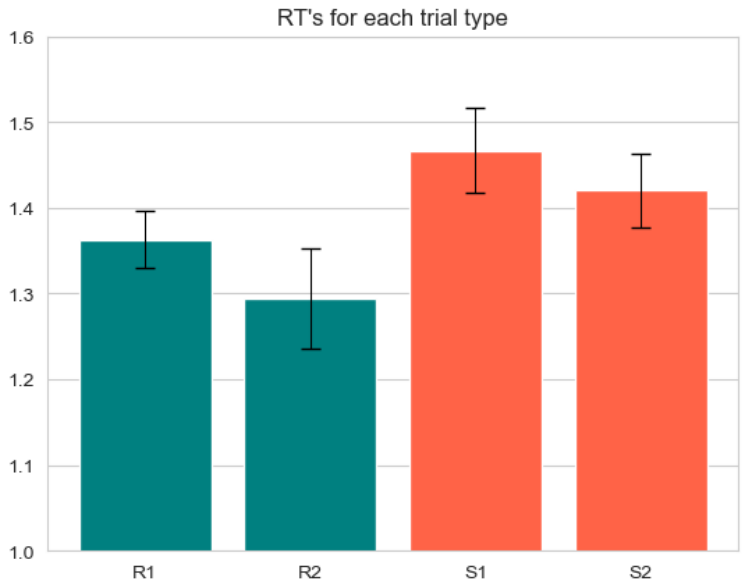

Figure 14 RTs for each repeat and switch positions. Confidence intervals show the 95% confidence interval corrected for within subject comparisons.

3.5.2 Univariate analysis results

As done with Analysis 1, for Analysis 2, linear contrasts were used to see differences in activity between trial types. The contrasts which combined RP2+RV2 > RP1+RV2 and SP2+SV2 > SP1+SV1 and were generated using the GLM explained above. The estimated GLM was used for group-level contrasts, yielding T-maps. None of the whole brain results reached statistical significance when corrected for multiple comparisons (p<0.05, FDR corrected).

3.5.3 ROI based MVPA results

Our MVPA results identified many regions in the brain that could discriminate patterns of activity R1 and R2 trials. Our analysis showed strong decoding accuracies that were significantly above chance for repeat positions in the whole brain for almost all ROIs (Figure 15).

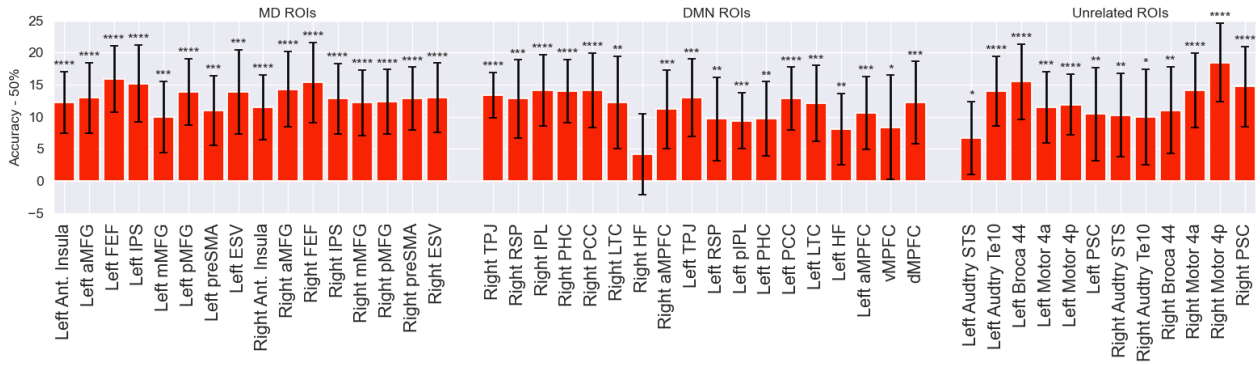

Figure 15 ROI-based MVPA results for R1 versus R2 trial types. Confidence intervals show 95% CI from the one-sample t-test results. Significance codes: * < 0.05, ** < 0.01, *** < 0.001, **** < 0.0001

Classifying patterns between consecutively occurring switch positions (S1 versus S2) did not yield a wide-spread decodability (Figure 16), contrary to Analysis 1.

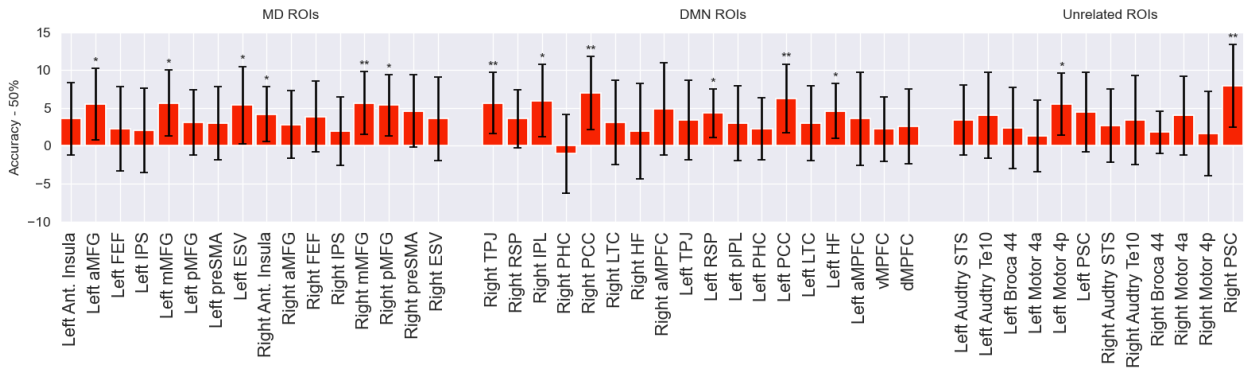

Figure 16 ROI-based MVPA results for S1 versus S2 trial types. Confidence intervals show 95% CI from the one-sample t-test results. Significance codes: * < 0.05, ** < 0.01, *** < 0.001, **** < 0.0001

3.5.4 Difference of decodability between switch and repeat trials in ROIs

The results showed that S1 versus S2 classification was less and not widespread compared to R1 versus R2 classification in the ROI results. We were interested in knowing the significance of this difference between decoding accuracies shown in Figure 14 and Figure 15. An ANOVA comparing these two ROI results as subject, ROI and switch/repeat as factors was conducted. There was a significant difference in switches and repeats on decoding accuracies ($F_{1,27} = 9.9$, $p < 0.005$). Other factors and their interactions were not significant.

3.5.5 Searchlight based MVPA.

Classifying repeat positions against each other yielded wide-spread and high, positive classification accuracies at the whole brain (Figure 18). Recall from Analysis 1 that classifying repeat trial types yielded classification accuracies that were significantly below chance. Which was indicative that instances of repeats were giving rise to different activity patterns in the brain. Being able to decode R1 versus R2 shows that repeat positions are treated in the brain differently.

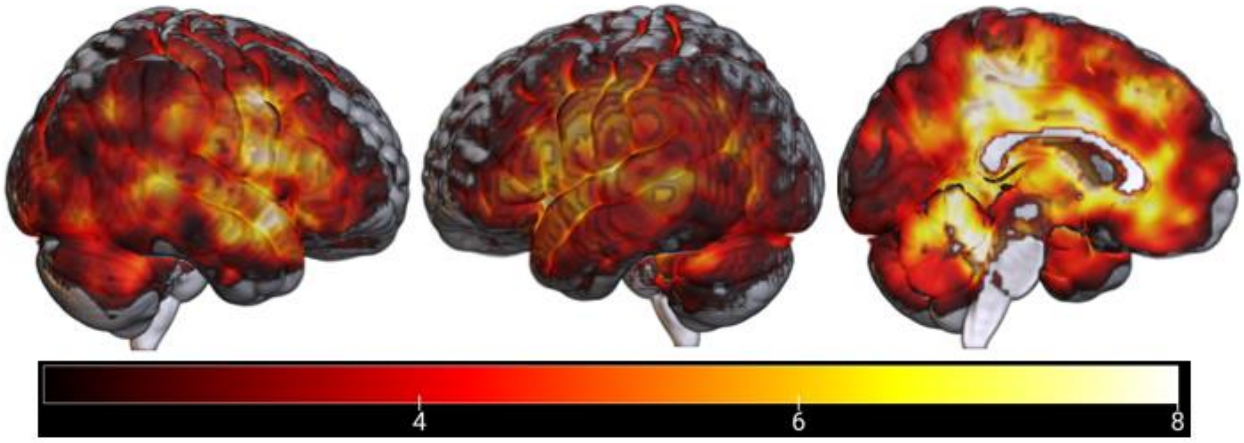

Figure 17 Searchlight MVPA results for R1 versus R2 trials. Colorbar at the bottom panel indicates t-values between 2.3 to 8 after ($p < 0.05$) FDR correction. Each voxel corresponds to the positive decoding accuracy generated from the searchlight.

Switch related activity when trained to discriminate consecutively occurring switch positions (S1 vs S2) showed that the patterns were discriminable in a few select regions. The most significant cluster was at the left posterior cingulate cortex (t = 8.09, -8 -64 -24). A few patchy clusters were also present at the temporal lobe and the pre-central gyrus.

In Analysis 1, we found that switch related activity patterns were discriminable everywhere in the brain. When we tried classifying consecutive switch positions, we found that most regions did not classify positions. This indicates that patterns of activity across specific consecutively occurring switch positions gave raise to similar activity (Figure 17).

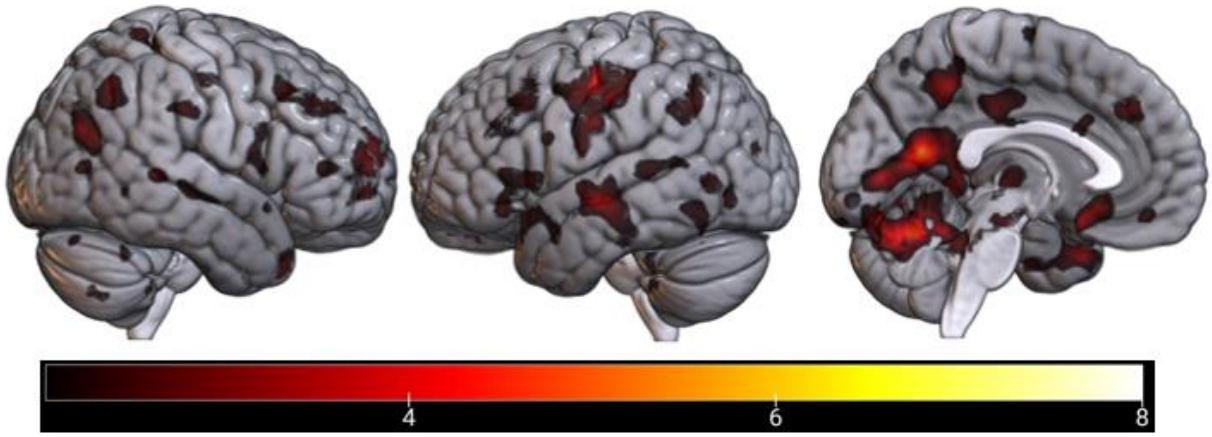

Figure 18 Searchlight MVPA results for S1 versus S2 trials. Colorbar below indicates t-values between 2.3 to 8 after ($p < 0.05$) FDR correction. Each voxel corresponds to the positive decoding accuracy generated from the searchlight.

3.5.6 ROI based RSA analysis

We used RSA to investigate the dissimilarity between consecutive repeats and switches. In Figure 19 we present the average dissimilarity between repeat 1 (R1) and repeat 2 (R2) trials for all trial types and all possible chunk pairs.

We show that the overall dissimilarity between repeat positions (R1 and R2) was higher compared to switch (S1 and S2) positions. An ANOVA was conducted using switch/repeat as a factor. There was a significant difference in the dissimilarity between switch and repeat trials in many of the ROIs (Table 2).

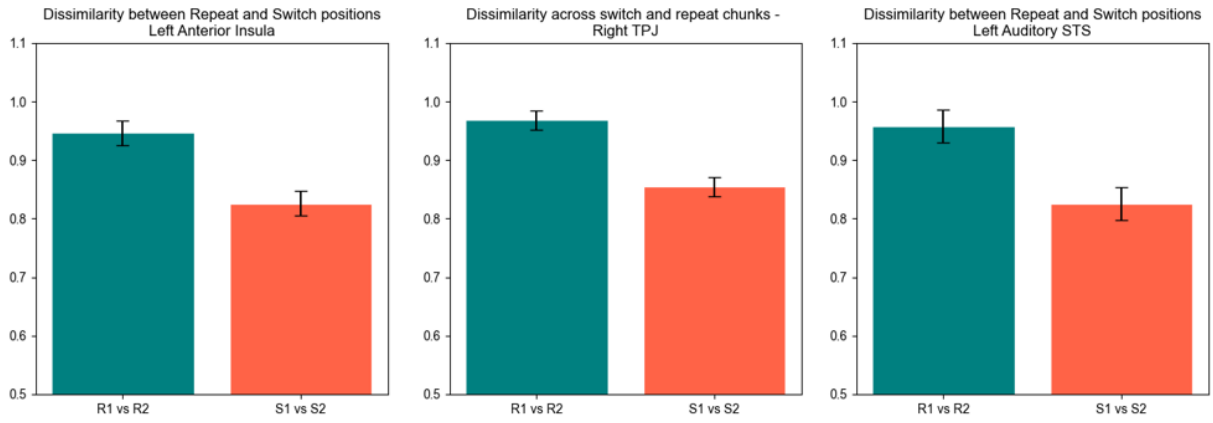

Figure 19 The overall average correlation (dissimilarity) values for R1 versus R2 combined chunks and S1 versus S2 combined chunks have been plotted.

ROI	F	p value		ROI	F	P value
Auditory Cortex	35.097	p < 0.001		Right Ant. Insula	47.503	p < 0.001
Left Ant. Insula	34.991	p < 0.001		Right ESV	48.958	p < 0.001
Left ESV	37.445	p < 0.001		Right FEF	42.684	p < 0.001
Left FEF	48.285	p < 0.001		Right HF	18.017	p < 0.001
Left HF	6.604	0.016		Right IPS	70.139	p < 0.001
Left IPS	64.621	p < 0.001		Right LTC	32.877	p < 0.001
Left LTC	21.48	p < 0.001		Right PCC	41.808	p < 0.001
Left PCC	26.097	p < 0.001		Right PHC	15.647	p < 0.001
Left PHC	10.056	0.004		Right RSP	28.468	p < 0.001
Left RSP	34.031	p < 0.001		Right TPJ	50.323	p < 0.001
Left TPJ	24.841	p < 0.001		Right aMFG	49.293	p < 0.001
Left aMFG	39.298	p < 0.001		Right aMPFC	19.681	p < 0.001
Left aMPFC	31.676	p < 0.001		Right mMFG	30.81	p < 0.001
Left mMFG	51.392	p < 0.001		Right IPL	61.809	p < 0.001
Left pIPL	42.479	p < 0.001		Right pMFG	42.423	p < 0.001
Left pMFG	61.659	p < 0.001		Right preSMA	54.313	p < 0.001
Left preSMA	53.759	p < 0.001		Right Auditory STS	20.983	p < 0.001
Left Auditory STS	23.55	p < 0.001		Right Auditory Te10	19.177	p < 0.001
Left Auditory Te10	34.313	p < 0.001		Right Auditory Te11	39.274	p < 0.001
Left Auditory Te11	37.285	p < 0.001		Right Auditory Te12	23.619	p < 0.001
Left Auditory 12	15.089	p < 0.001		Right Broca 44	47.016	p < 0.001
Left Broca 44	64.019	p < 0.001		Right Broca 45	25.696	p < 0.001
Left Broca 45	28.778	p < 0.001		Right Motor 4a	32.419	p < 0.001
Left Motor 4a	84.137	p < 0.001		Right Motor 4p	47.906	p < 0.001
Left Motor 4p	43.568	p < 0.001		Right PSC	49.292	p < 0.001
Left PSC	40.912	p < 0.001		Right PSC 3a	38.793	p < 0.001
Left PSC 3a	36.33	p < 0.001		Right PSC 3b	49.183	p < 0.001
Left PSC 3b	50.712	p < 0.001		dMPFC	48.045	p < 0.001
				vMPFC	23.467	p < 0.001

Table 2 ANOVA results for the overall difference between S1 + S2 and R1 + R2 trials, Degrees of freedom =1,26. Only ROIs that are below a significance level of 0.05 are presented.

The RDMs in Figure 20 show that dissimilarities between repeat position 1 (R1) trials and repeat position 2 (R2) trials are more dissimilar to each other compared to switch position 1 (S1) versus switch position 2 (S2) trials.

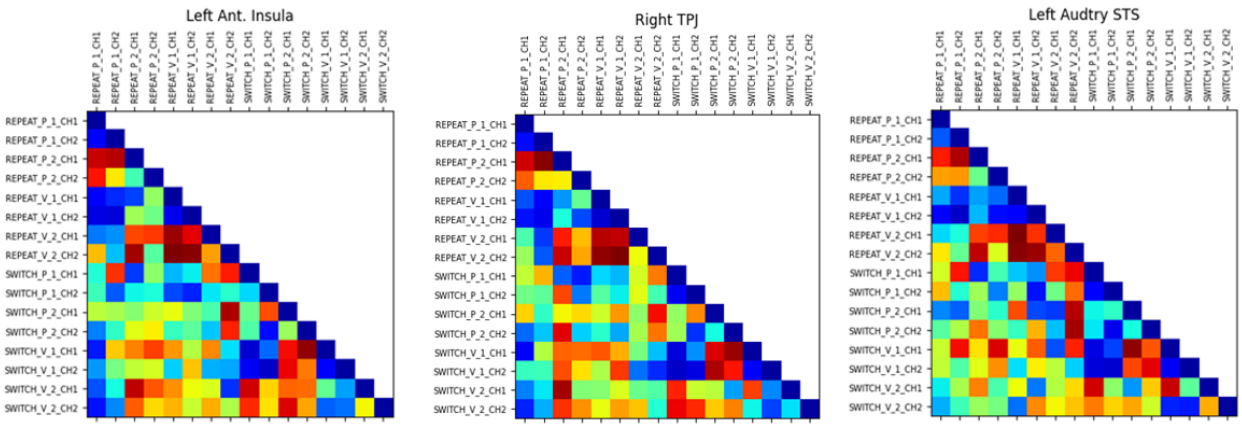

Figure 20 Three representative ROIs from MD, DMN and unrelated regions respectively. Colorbar indicates rank-transformed dissimilarity values, where 0 indicates minimum dissimilarity and 1 indicates maximum dissimilarity.

CHAPTER 4

DISCUSSION

4.1 Discussion

Studies of cognitive control have shown the presence of rule-related activity in the fronto-parietal networks. While we do tasks, we need to follow specific rules and maintain these rules or reconfigure them as the goal states change. The rules we follow as we perform tasks are governed by cognitive control processes, therefore being able to decode rule representations allows us to investigate cognitive control. Previous studies have shown that rule-related representations are decodable in frontal and parietal regions and the multiple demands network (MD) (M. L. Waskom et al., 2014; Wisniewski et al., 2015; Woolgar et al., 2011). Therefore, MD regions have been thought to be related to cognitive control processes. However, another study showed that DMN regions can also be active during task-switches if switching between larger contexts (Crittenden et al., n.d.). Another paper explored the possibility that the DMN might be actively involved in fulfilling cognitive demands (Vatansever et al., 2015). The authors tested this hypothesis using a finger opposition paradigm. The experiment consisted of two blocks with task and fixation periods. The authors show task-specific changes in the DMN topography, with increased connectivity of the posterior cingulate cortex with the left superior frontal gyrus. Furthermore, the study found an interactive and dynamic reconfiguration of the DMN regions' functional connections, suggesting their involvement with the task at hand. The DMN showed higher-level global parallel processing power yet preserved small-world architecture in comparison with rest. These findings suggest that the DMN does not disengage during this paradigm, but instead may be involved in task-

relevant processing. Overall, these studies show that the involvement of tasks may not be limited to internal or external mentation.

We used multivariate fMRI analysis methods to investigate rule representations in the brain by employing a rule-switch paradigm. In Analysis 1, our MVPA results showed that switch rule representations were classifiable above chance in the whole brain in both searchlight based and ROI based analysis. For repeat trials, we found that rule representations were not present anywhere in the brain, and the classification accuracies were significantly below chance. This was indicative that instances of repeats within a cross-validation chunk led to different types of activity. In other words, instances of repeat trials were very different from each other. Thus, we used RSA to see the dissimilarity between repeat and switch chunks the results from this analysis was consistent with our hypothesis. We found that dissimilarity within repeat chunk pairs was higher compared to switches.

We hypothesized that the high dissimilarity between repeat chunks could be due to consecutive repeating. We modelled trials based on the consecutiveness (ie. repeating once or twice in a row). Our results showed that consecutively occurring positions ie., repeat 1 versus repeat 2, were discriminable in nearly the whole brain. On the other hand, consecutively occurring switches (switch 1 versus switch 2) yielded positive classifications in some ROIs and patchy results in searchlight analysis. However, the activity was not as widespread as repeats.

Univariate analysis was also conducted for the classification pairs mentioned above; however, these did not yield any significant results after corrections for multiple comparisons. It is known that multivariate analyses are better to catch differences in patterns of activity. For example, when the net BOLD activity between two conditions does not differ but the patterns within voxels do.

One review paper investigated papers which used multivariate pattern analysis methods to decode perceptual, response or value related representations (Bhandari et al., 2018). They found that the overall decodability of prefrontal regions (55.4%) for these categories was lower compared to occipital visual areas (66.6%) and temporal areas (71.0%). The results of our analysis show much higher decoding accuracies compared to the overall decodability of these studies. One possible reason for this decodability difference could be that in our experiment we did our MVPA within a

single run, it could be that the generalizability of samples becomes better when more runs are utilized. Another possibility is that the involvement of frontal regions changes as people progress within the fMRI session (ie., stay more in the scanner), thus the overall decoding may decrease with practice or exposure to the task.

We found one study in which participants participated in a rule switch experiment in which they needed to categorize houses from faces and the rules were modelled based on the switch or repeat status (ie., HouseSwitch, FaceRepeat) (Qiao et al., 2017). In this study, the authors found that switch trials were less stable to decode and repeat trials were more decodable. They interpreted that task-set (rule) related representations would be less stable when switching, and this process was suggestive of the task-set inertia hypothesis (Wylie & Allport, 2000). Leading to accuracy and lower stability in decoding. One major difference that distinguishes our study from theirs is that in their study, the cue that indicates the rule to apply in the upcoming trial is presented before the trial is initialized. This indicates that rule and task-set related representations are most likely initialized at a temporally earlier stage than the actual response stage. Whereas in our study, the stimuli to respond and the rule to apply are presented simultaneously.

DMN regions are known to deactivate during external tasks, because they are thought to be specialized for activities that require internal mentation. Tasks that we execute have a hierarchical structure, constituting of several steps. However, an entire episode related to a task is hierarchically executed as one unit (Farooqui & Manly, 2019). When we begin a task, the programs that are related to the task are assembled, causing maximal deactivation in DMN regions. As we progress in the task, the sub-steps within the task episode start dismantling as we start approaching completion. One study utilized a design where they organized sequences of task events identical in their attentional and control demands into larger task episodes (Farooqui & Manly, 2018). They found that DMN deactivation across such sequential events was never constant, but was maximum at the beginning of the episode, then decreased gradually across the episode, reaching baseline towards episode completion, with the final event of the episode eliciting an activation. Interestingly, this pattern of activity was not limited to a fixed set of DMN regions but, across experiments, was shown by a variable set of regions expected to be uninvolved in processing the ongoing task. The study suggests that cognitive entities

that enable such hierarchical execution of goal-directed behavior may cause the ubiquitously seen deactivation during external task execution. Further, while this deactivation has previously been associated with a defined set of the so-called default mode regions, current study demonstrates that deactivation is shown by any region not currently involved in task execution, and in certain task episodes can even include attention related fronto-parietal regions as well as primary sensory and motor regions. Knowing that in our study switch related activity leads to wide-spread activity in the whole brain, and the study mentioned earlier also shows a similar result. We argue that while we execute tasks, the way the mind constructs trials are dependent on the place where the boundaries of one task ends, and another starts. For example, imagine you are executing the task in the present study and the trials you were executing are as follows: parity-parity-parity-value-value-parity. The parts in which the rule switches, corresponds to a re-configuration process. This re-configuration point also would correspond to a part whereby one episode ends (ie. a parity episode) and a new one starts (value episode). If you were asked to show the boundaries of possible episodes, you would mark trial 4 as a part whereby the episode ends, and another starts. This trial 4 also happens to correspond to a switch, and hence, the end of an episode. We propose that these parts in which an episode ends correspond to parts where the brain re-configures itself. Therefore, the switch-related activity we see could be a reconfiguration process.

4.2 Conclusion

This study shows that rule representations are present (decodable) in the whole brain for switch trials. On the other hand, repeat trials are present only when consecutive positions are classified against each other.

The ability to decode rule representations in all brain regions, including ROI's that are seemingly unrelated to the task (such as Auditory STS), indicates that when we begin a task (ie., switch from our current task to the other) our mind reconfigures things in such a way that whatever this effect is, it leads to a reconfiguration that is globally present in the brain.

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