A COMPUTATIONAL MODEL OF PREFRONTAL AND STRIATAL INTERACTIONS IN PERCEPTUAL CATEGORY LEARNING

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Abstract

Work on multiple-system theories of cognition mostly focused on the systems themselves, while limited work has been devoted to understanding the interactions between systems. Generally, multiple-system theories include a model-based decision system supported by the prefrontal cortex and a model-free decision system supported by the striatum. Here we propose a neurobiological model to describe the interactions between model-based and model-free decision systems in category learning. The proposed model used spiking neurons to simulate activity of the hyperdirect pathway of the basal ganglia. The hyperdirect pathway acts as a gate for the response signal from the model-free system located in the striatum. We propose that the model-free system's response is inhibited when the model-based system is in control of the response. The new model was used to simulate published data from young adults, people with Parkinson's disease, and aged-matched older adults. The simulation results further suggest that system-switching ability may be related to individual differences in executive function. A new behavioral experiment tested this model prediction. The results show that an updating score predicts the ability to switch system in a categorization task. The article concludes with new model predictions and implications of the results for research on system interactions.

Keywords: computational modeling, cognitive neuroscience, system interactions, perceptual categorization, executive functions

1 Introduction

The last 25 years have shown an increased interest in multiple-system theories of cognition (Ashby et al., 1998; Hélie et al., 2011; Kahneman, 2012; Sloman, 1996; Sun, 2002), and recent advances in cognitive neuroscience showing complementary roles of brain circuits has produced a surge in such interest (Eichenbaum & Cohen, 2001; Schacter et al., 2000; Squire, 2004). From a cognitive perspective, Sloman (1996) proposed that complementary associative and rule systems are used in reasoning and reviewed much evidence for it. Likewise, Kahneman and Frederick (2002) proposed a model of two cognitive systems, where *System 1* is fast and automatic (e.g., associative) while *System 2* is slow, effortful, and logical (e.g., rule-based). These ideas have been examined by using computational modeling techniques and progress has been made in various domains by generating quantitative predictions. COVIS (Ashby et al., 1998), CLARION (Sun, 2002), the Explicit-Implicit Interaction (EII) theory (Hélie & Sun, 2010), and TELECAST (Hélie et al., 2011) are all examples of computational models implementing such ideas.

The work on multiple systems in cognitive neuroscience has been twofold. First, some of the work has been devoted to locating the neural substrate of existing cognitive theories of multiple systems. For example, separable and distinct neural mechanisms have been found to facilitate explicit (e.g., rule-based) and implicit (e.g., associative) learning. Specifically, the hippocampus and temporal-parietal cortex have been shown to support explicit rule-based learning and knowledge representation (Cohen et al., 1985; Eichenbaum, 1999; Hélie et al., 2010; Hélie et al., 2021). In contrast, the implicit associative learning circuit is believed to be mediated by a cortical-subcortical circuit with a prominent role for the striatum (Heindel et al., 1989; Knowlton, 2002;

Reber & Squire, 1994; Waldschmidt & Ashby, 2011). Of particular interest, the medial temporal lobe and the basal ganglia are found to be differentially involved in explicit and implicit systems.

Second, much effort has been devoted to work related to model-based (MB) and model-free (MF) reinforcement learning (RL) (e.g., O'Doherty et al., 2017; Otto et al., 2013; Russek et al., 2017). Reinforcement learning (Sutton & Barto, 1998) is a class of learning algorithms inspired by early work in psychology showing that behavior is shaped by reinforcement using operant conditioning (Skinner, 1948; Thorndike, 1898). Specifically, a reward following an action increases the likelihood of that action in the future, while punishment reduces the frequency of that action in the future. The scenario where the agent directly associates the stimuli with a response is called *model free reinforcement learning (MF-RL)* (Rescorla & Wagner, 1972). However, while behaviorists were working on instrumental conditioning, Tolman (1948) provided evidence that animals do not just learn *Stimulus* → *Response* associations, but also build cognitive maps representing transition probabilities between different states of the world. This type of learning is referred to as *model-based reinforcement learning (MB-RL)* (Russek et al., 2017). Because the knowledge learned is the basis for choice and decision-making, the model-based and model-free labels have often been used to qualify decision-making processes.

It should be noted that model-based and model-free do not refer to specific processes, but to classes of processes. The criteria to classify a process as MB or MF are related to *what* knowledge is involved (e.g., a cognitive map vs. direct *Stimulus* → *Response* associations) – not *how* it was learned or used. As a result, model-based and model-free processes have often been used to describe the distinction between controlled (MB) and habitual/automatic (MF) behaviors (O'Doherty et al., 2017), and most of the dual-system theories described above include one system from each of these classes of algorithms. For example, the hypothesis-testing system in COVIS (Ashby et al., 1998) is a MB system. It learns to adjust rules that can dictate how to interact with the environment. In contrast, the procedural learning system in COVIS is an example MF system. It learns to associate regions of perceptual space with motor plans. A similar argument can be made for Kahneman and Frederickson’s (2002) theory, with System 1 being MF and System 2 being MB.

Table 1 summarizes many of the system dichotomies that have been used in different domains. Each row is a different way to describe the systems dichotomy and the columns show overlap between the vocabulary used to describe different types of systems. This table needs to be read with two important caveats in mind. First, the list is incomplete. Many dual-system theories have been proposed that have not been reviewed in this article. Here we focused on the most relevant dichotomies for the current work. Second, the overlap between systems vocabulary in various domains is only partial and imperfect. For example, non-declarative memory is often described as implicit while declarative memory is often described as explicit. However, this should not be interpreted as the terms being interchangeable. These terms describe different aspects of the systems and do not have to co-occur. As a result, Table 1 should be interpreted as a heuristic and a rough map of how the various domain dichotomies overlap. In the present work, we use the terms ‘model-based’ (right column) and ‘model-free’ (left column) to refer to these dichotomies.

Table 1. Summary taxonomy of the different dichotomies reviewed

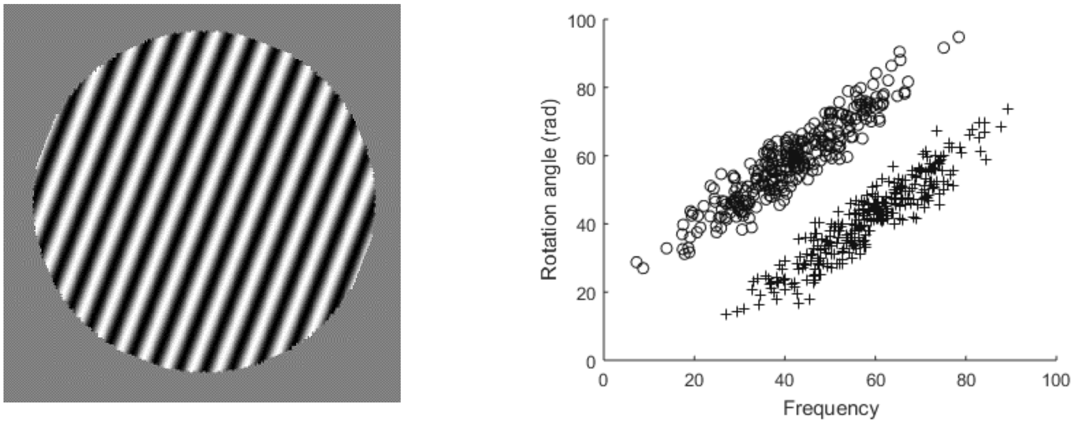
Area of Research	Dichotomies	
Cognitive psychology		
Process	Associative	Rule-based
Awareness	Implicit	Explicit
Memory	Non-declarative	Declarative
Kahneman & Frederic (2002)	System 1	System 2
COVIS (Ashby et al., 1998)	Procedural learning system	Hypothesis-testing system
Categorization task	Information-integration	Rule-based
Cognitive neuroscience		
Reinforcement learning / decision-making	Model-free	Model-based
Brain circuits	Basal ganglia	Prefrontal cortex

Note. The connections between the vocabulary used in different domains is imperfect and only approximate.

1.1 Multiple Systems Theories and Category Learning

Regardless of which model is used to implement the two systems, one common theme among multiple-system theories is that switching between systems is assumed to be easy, sometimes even seamless. However, up until recently this was an untested assumption, and evidence using perceptual category learning suggests that system-switching might be more difficult than initially thought. For example, decades of research on information-integration (II) category learning suggests that many people have difficulties switching from a model-based system (suboptimal in this task) to a model-free (optimal in this task) system.

In II categorization tasks, participants must integrate information from more than one dimension in a pre-decisional stage to maximize accuracy (Ashby et al., 1998). For example, sine-wave gratings could be used as stimuli in an II perceptual categorization task (Figure 1A), where category membership is determined by two dimensions including the frequency of the sine-wave (bar width) as well as the rotation angle (bar angle). Each stimulus can be represented as a point in a two-dimensional space, with its coordinates defining a specific frequency and rotation angle that can be used to draw a stimulus. Categories can then be defined in this two-dimensional plane. With this representation, example II category structures are shown in Figure 1B. In this figure, each symbol represents the coordinates of a stimulus in perceptual space and specifies one specific rotation angle and frequency that allows for the drawing of a unique sine wave grating. In this example, participants need to learn to categorize the ‘o’ and ‘+’ stimuli into separate categories. The optimal decision bound separating the categories can be described by drawing a diagonal line dividing the categories in Figure 1B, but notice that the line would not correspond to a meaningful verbal description. The verbal description would be: ‘o’ are stimuli where the rotation angle is larger than the frequency, which is not meaningful given that rotation angle and frequency are not commensurable. Thus, II categories are thought to be learned with MF-RL since there is no verbalizable, explicit rule to explain how categories are distinguished.



A **B**

Figure 1: (A) Example sine-wave stimulus shown in a perceptual categorization task, (B) Example II category structures. Category "o" stimuli were generated using a multivariate normal distribution with the following parameters: $\mu_o = \{38, 50\}$; $\Sigma_o = \{10, 0; 0, 280\}$. The same sampling method was used to generate category "+" stimuli: $\mu_+ = \{62, 50\}$; $\Sigma_+ = \Sigma_o$. The II stimuli were then rotated 45 degrees counterclockwise around the center of the stimulus space {50, 50}.

Decision bound models (DBM) (Hélie et al., 2017; Maddox & Ashby, 1993) can be used to identify the response pattern that participants are producing based on their response to each individual stimulus. Specifically, a representation of each participant's response is drawn in stimulus space. This representation is similar to Figure 1B, except that each stimulus is labeled using the participant's categorization response instead of the desired category label. Next, a number of DBM are fit to the participant's responses. Typically, the DBMs are linear planes that attempt to separate the participant's responses. Models with planes that are perpendicular to the axes allow for a meaningful verbal description and are considered MB. The optimal MB DBM (a vertical line located at 50 in Figure 1B) would yield about 75% response accuracy. In contrast, DBM models that allow the plane to have a slope do not yield a meaningful verbal description and are considered MF. The optimal MF DBM in Figure 1B is a diagonal line that perfectly separates the category and yields a response accuracy of 100%. Lastly, DBMs also include guessing models, where participants respond randomly without considering the information on the screen. These models are considered MB because not engaging with the task is an explicit volitional choice.

Participants typically begin learning II tasks by trying to use the suboptimal MB system (for a recent review, see Ashby & Valentin, 2017). In an II categorization task like the one presented in Figure 1, the most accurate verbal rules (e.g., stimuli with thin bars are in one category while stimuli with thick bars are in the other) can produce an accuracy of about 75%. To perform optimally, participants need to abandon such rules and rely on the MF system. Going back to Table 1, this means that participants begin learning the task using MB-RL, and need to switch to MF-RL. From a neuroscience perspective, this means switching from a learning circuit centered around the prefrontal cortex (PFC) to a learning circuit centered in the striatum.

1.2 Trial-by-trial system-switching

In the previous example, one must abandon MB-RF (based on a prefrontal circuit) and switch to MF-RL (based on a striatal circuit) in order to perform optimally. Note that this switch is self-initiated, in that there is no instruction provided to the participant informing them which system they should use, or even that they should switch systems. In past decades, research has also shown that trial-by-trial cue-based switching is extremely difficult. For example, Erickson (2008) asked participants to categorize “space shuttle” schematics (i.e., rectangles with internal line segments) into one of four categories. Two of the categories could be distinguished using a simple verbal rule [i.e., rule-based (RB) categories] while the other two categories could not be distinguished by a verbal rule (i.e., II categories). While performing the task, each category was associated with a different response button, and categories (RB or II) were cued using differing background colors. Decision-bound models were individually fit to the RB and II trials to identify “switchers” and “non-switchers.” Switchers were participants whose RB and II trial data were best fit by optimal DBM models. All other participants were labeled as non-switchers. Only 37% of the participants optimally switched between systems on a trial-by-trial basis. A more recent cue-based switching experiment by Crossley and colleagues (2018) used sine-wave gratings (as in Figure 1A) and reported a switching rate of about 40% using a similar design.

Another contribution of the Crossley et al. (2018) study was that it made a connection between system-switching in categorization and task-switching (Kiesel et al., 2010; Vandierendonck et al., 2010). In task-switching, participants are typically asked to perform one of two tasks, cued on a trial-by-trial basis. Trials where participants need to switch from one task to another suffer from a switch cost [i.e., lower accuracy and longer response time (RT)] when compared to consecutive trials of the same task. System-switching could be a special case of task-switching in which each task relies on a different categorization system. Crossley et al. (2018) examined this possibility by comparing the switch cost when participants needed to switch between two RB categorization tasks (both optimally relying on MB-RL / a prefrontal circuit) to the switch cost when participants needed to switch between a II (optimally relying on MF-RL / a striatal circuit) and a RB categorization task. They found that the switch cost was smaller when switching between two tasks relying on the same learning system compared to switching between two tasks relying on different learning systems.

The similarities between task- and system-switching noted by Crossley et al. (2018) led to further research on the effects of factors that facilitate task-switching on system-switching. For example, Hélie (2017) explored the effects of additional task training and preparation time (i.e., a delay between the switch cue and the task stimulus) on system-switching. The highest proportion of successful trial-by-trial system-switchers in that study was 65.7% of the sample. This high proportion of switchers was achieved by implementing a second session of training on II and RB category structures, and by allowing participants to have time to prepare to switch system by providing a cue before the categorization stimulus was presented. Aging research provides additional evidence that system-switching is a special case of task-switching, as aging has been shown to affect both cue-based system-switching (Hélie & Fansher, 2018), and task switching (Kray & Lindenberger, 2000).

1.3 Why is switching difficult?

The previous subsections suggest important individual differences in switching ability, with almost half of participants relying on suboptimal systems in both self-initiated and cue-based system-switching categorization experiments. Lim and Hélie (2019) simulated published II data from Hélie & Cousineau (2015) using the COVIS model of category learning (Ashby et al., 1998; Hélie et al., 2012). In this simulation, data from participants who switched to the correct striatal system (MF-RL) were fitted separately from the data of participants who failed to switch and kept relying a suboptimal system (MB-RL). By exploring the obtained model parameter values, they observed that simulated optimal participants (who switched to a striatal circuit) were more sensitive to negative feedback, while simulated suboptimal participants (who continued relying on a prefrontal circuit) were more sensitive to positive feedback. As a result, they hypothesized that optimal participants in II categorization tasks may be more sensitive to negative feedback than participants who perseverate with MB-RL. Intuitively, it makes sense that participants who are less sensitive to negative feedback may focus less on their 25%-30% error rate from using a suboptimal system, and instead focus more on the other trials where they receive positive feedback (about 70% of the trials).

To test this hypothesis, Lim and Hélie (2019) asked participants to complete both the Iowa gambling task to estimate reward sensitivity and an II categorization task to determine if the participants could switch to an optimal striatal circuit. The results supported their hypothesis. As predicted by the COVIS simulation, participants that used an optimal learning system in II categorization had lower reward sensitivity compared to participants that used a suboptimal learning system. They also had higher sensitivity to punishment than participants who used a suboptimal system. Lim and Hélie also used the Iowa gambling task data to quantify the participants' tendencies to explore the different deck options. Generally, exploration was related to the switch to MF-RL in II categorization. Sensitivity to punishment was also related to propensity to explore. These results were used to inform a new neurobiological model of system-switching described in the next section.

1.4 The present work

The goal of this article is to propose a new neurobiological theory and computational model of system-switching. The article is organized as follows. Section 2 presents a new neurobiological model of the interactions of two category learning systems supported by the prefrontal cortex and the striatum (respectively). In the proposed model, system-switching is based on the hyperdirect pathway of the basal ganglia (BG). Specifically, the hyperdirect pathway either inhibits or allows

BG activity to reach premotor areas and control behavior. This gating represents system-switching. Next, Section 3 uses the model to simulate published self-initiated system-switching data in an II categorization task. This simulation is followed by a simulation of the effects of aging on cue-based trial-by-trial switching in Section 4. Results from these simulations suggest that individual differences in executive functions (EF) may be an important predictor of cue-based trial-by-trial system-switching ability. This prediction was tested in Section 5 using a new behavioral experiment to investigate whether common measures of EF would predict whether participants could switch on a trial-by-trial basis in a categorization task. Section 6 concludes with a general discussion of possible extensions and implications of the proposed model.

2 A neurobiological theory of system-switching

The work reviewed in Section 1 suggests that system-switching is related to reward processing, and that in most multiple-system theories the decision points of the systems are in the prefrontal cortex (MB) and the striatum (MF). Together, these results allow for the proposal of a new neurobiological theory of system-switching. Previous work on the computational models of multiple systems has focused on the learning systems themselves – not the switching mechanism. The interaction between systems, particularly the neurobiological basis of the switching interaction, has rarely been discussed or systematically studied. We aim to build a neurobiological computational model to show how different brain areas can be connected to support the system-switching mechanism.

The proposed model is designed to show the neural circuit underlying the switching mechanism between the learning systems. Because the model is focused on the switching mechanism, the MB and MF modules are included as black boxes. This choice was made to increase generality of the proposed switching and minimize the number of assumptions: The only assumptions are based on circuit connectivity, so the MB system is assumed to select its response in the prefrontal cortex, and the MF system is assumed to select its response in the striatum. Importantly, both systems are circuits and can include other supporting brain areas. Aside from the basic assumptions above, here we do not make any additional assumptions about the learning and decision systems. In the next subsection we discuss some empirical results on the neural circuit underlying system interactions.

2.1 Neurobiological interactions and system-switching

Neuroimaging and behavioral evidence suggest an antagonistic relationship between explicit and implicit memories (Ashby & Crossley, 2010; Poldrack & Packard, 2003; Schroeder et al., 2002). However, Foerde et al. (2006) observed a persistent striatal activation even during explicit tasks. As a result, Crossley and Ashby (2015) proposed that the inhibition between explicit and implicit systems does not operate at the level of learning, but instead occurs at the level of expression. In most theories, MF-RL is mediated by dorsolateral striatum, while MB-RL is mediated by the PFC and medial temporal lobes (Ashby & Ennis, 2006; Fletcher et al., 1998; Mishkin et al., 1984; Tulving & Markowitsch, 1998). Many possible anatomical circuits may serve to mediate the interaction between these two learning systems. One of these possibilities is through the hyperdirect pathway of the basal ganglia, as suggested by Ashby and Crossley (2010).

To adapt to the changing environment, processes that interrupt irrelevant or unsuitable behaviors are important to achieve goal-directed behavior (Kenner et al., 2010). Such processes may act like an “emergency brake” that provides nonselective inhibition to suppress all responses (Kenner et al., 2010). In the proposed model, all responses from the striatal MF system are initially inhibited. This is consistent with existing studies showing evidence of the involvement of the hyperdirect pathway regions in response to stopping and switching situations through nonselective inhibition (Kenner et al., 2010).

The hyperdirect pathway is shown in Figure 2. This circuit acts to either allow or inhibit signals from the striatum to the cortex. The hyperdirect pathway starts with direct excitatory glutamate projections from the frontal cortex to the subthalamic nucleus (STN). Through excitatory glutamate projections, the connection from the STN is directed to the internal segment of the globus pallidus (GPi) (Joel & Weiner, 1997; Parent & Hazrati, 1995). This excitatory input offsets the inhibitory input from the striatum to the GPi, which reduces the influence of the striatum on the cortex (through the thalamus).

By reducing subthalamic activity, the hyperdirect pathway allows signals from the striatum to reach the cortex; by increasing the subthalamic activity, subcortical influence is reduced. Thus, through the hyperdirect pathway, the influence of the MF system to motor outputs in the cortex can be prevented, without having a direct interaction with the striatum itself. Because the striatum is presumably the learning site of MF-RL, MF-RL could still take place while the MB-RL system dominates responding (Crossley & Ashby, 2015). In the hyperdirect pathway, the computational function of the STN is to generate pauses for stopping and conflict processing. These pauses allow time for the accumulation of evidence to select the appropriate actions (Aron et al., 2016).

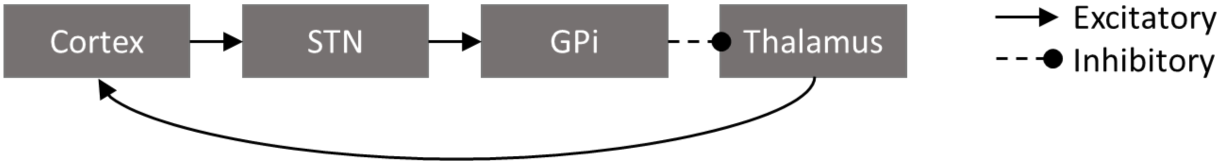


Figure 2. The hyperdirect pathway of the cortico-basal ganglia network.

2.2 Model overview

Ashby and Crossley (2010) suggested that learning system interactions are controlled by the frontal cortex and the STN through the hyperdirect pathway in the BG. The hyperdirect pathway starts with excitatory glutamate projections from the frontal cortex, through the pre-supplementary motor area (preSMA), to the STN (Paul & Ashby, 2013). The preSMA plays a role in facilitating the switch between learning systems' responding by inhibiting competing motor plans when a response conflict occurs (Hikosaka & Isoda, 2010; Nachev et al., 2007; Paul & Ashby, 2013). The preSMA sends the switch-related signals to the STN, leading the STN to suppress ongoing behavior that is no longer relevant to promote the execution of the new behavior (Hikosaka & Isoda, 2010).[1]

To suppress the response of the MF-RL system, the STN increases activation in the GPi (i.e., a main output of the BG), thus strengthening the inhibition of the thalamus. In the proposed model, the output from the thalamus is considered as the response of the MF-RL system. Inhibition of the thalamus' output represents the inhibition of the MF system output with increased STN activity. Responses from the MF-RL system converges with responses from the MB-RL system in the dorsal premotor cortex (PMd) to allow planning and preparation for an appropriate movement.

Given these considerations, the new model simulated neurons from three areas of the brain: the preSMA, the STN, and the PMd. Individual neurons were simulated using the Izhikevich (2007) firing model. Example simulated spike trains from each region are shown in Figure 3. The simulations focused on perceptual category learning, where in each trial of the simulation the

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[1] The preSMA is part of the medial PFC in primates. Interestingly, Powell & Redish (2016) showed evidence for a similar role of the medial PFC in rodents. However, the proposed theory and model is focused on primate circuits.

model had to assign a given 'stimulus' to one of the available categories. For instance, the stimulus may be a circular sine-wave grating, as shown in Figure 1, which varies from trial-to-trial in terms of orientation and bar width. However, the perceptual categorization process was not simulated, so all that was needed was a response generation process for each system. Both the MB and MF systems generated their response, and the overall output for each trial was selected at the PMd unit-level (where the two systems are competing for control). Note that because the MB and MF systems were modeled as black boxes, the proposed model is general and could be used with other stimuli or for other tasks as long as the responses are determined in the prefrontal cortex and striatum.

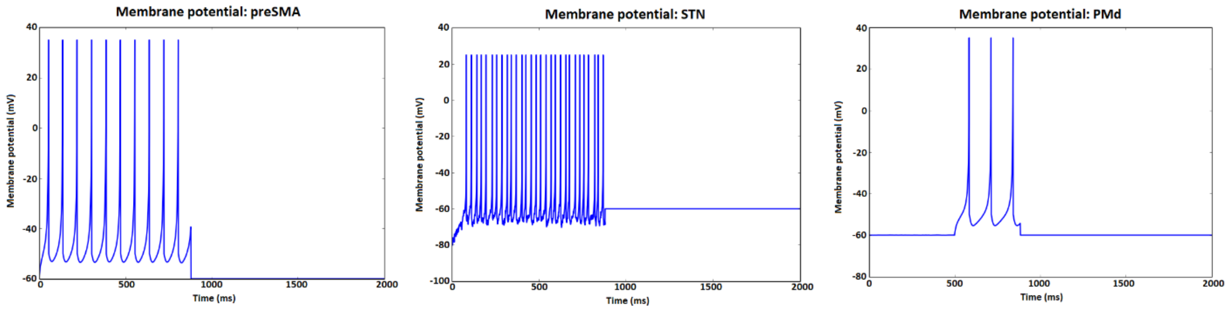


Figure 3. Example firing patterns of preSMA (left), STN (middle), and PMd (right) cells. The firing patterns were generated based on the specification stated in Eqs. A1 (preSMA and PMd) and A2 (STN).

In each trial, each system outputted a categorical decision. The system responses converged in the PMd so that the PMd units became activated accordingly. For instance, in a two-choice categorization task that requires sorting stimuli into category 'A' or 'B', if the MB system chose

‘A’ as the categorical decision, the PMd unit that signals the pressing of the button ‘A’ became activated. Initially, the PMd units should only receive input from the MB system, in line with earlier work suggesting that primates respond using MB-RL at the beginning of learning (Ashby et al., 1998; Smith et al., 2012). Thus, responses from the MF system were inhibited from reaching the PMd units. Switching is implemented as a feedback-driven reduction in inhibition of the response from the MF system to the PMd units, until a point where the activity in the PMd units is driven more by the MF system then the MB system. Spiking models were incorporated to show the dynamic process of inhibition (or reduction in inhibition) of the response of the MF system. At the end of each trial, the model output was a categorical decision (from the PMd), either pressing the button corresponding category A or B. The model learned using accuracy feedback after each choice. Figure 4 shows the flow of the circuit of the model. All computational details are included in the Appendix.

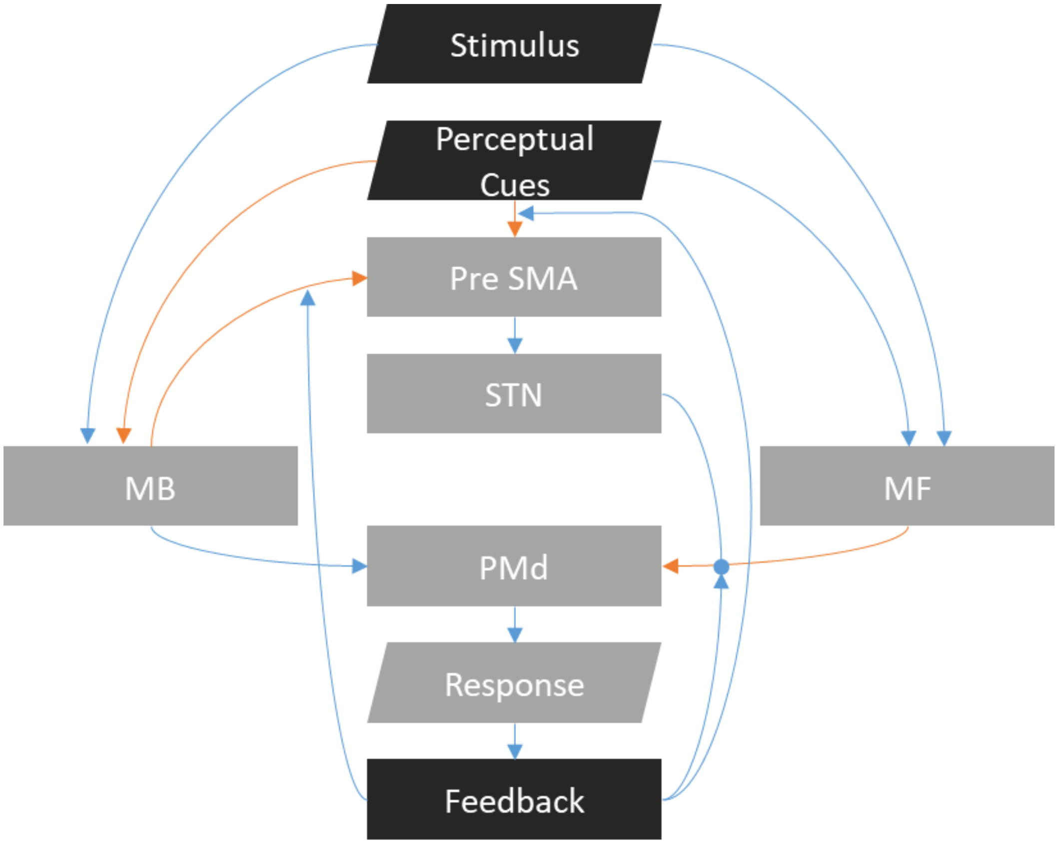


Figure 4. Block diagram representing the proposed model of system-switching. Orange lines indicate a plastic connection, while blue lines indicate a fixed connection. Arrow ends indicate activation while dot ends indicate inhibition. Grey boxes indicate processes within the agent while black boxes are outside the agent.

In an experiment that involves more than one category learning task, the perceptual stimulus may be preceded by a perceptual cue to indicate which task is to be done in the current trial, making participants aware of any change in task. For example, a stimulus can be preceded by a colored background to indicate when the task is changing. Different colored backgrounds may be used as perceptual cues for different tasks. For example, a blue background may indicate that subjects are performing an RB categorization task, while a green background may indicate an II task. As a result, trials with the same perceptual cue should be categorized with the same responding system. A change in the perceptual cue from one to another means a change in the responding system is required to categorize the stimulus shown. To account for this possibility, perceptual cues were added to the model to simulate categorization tasks that require a trial-by-trial switch between categorization learning systems. As can be seen in Figure 4, perceptual cues can affect activity in the preSMA, as well as each system's accuracy (because of switch cost).

2.3 Learning to switch

As described in the previous subsection, the proposed new model assumes that at the start of a categorization task, the MF response is inhibited so that the overall model output is MB. However, as the model receives performance feedback at the end of each trial, confidence in the MB and MF systems is adjusted. Specifically, a correct response from one of the systems increases confidence in that system, while an incorrect response from the MB system decreases confidence in that system. This captures the effect of feedback sensitivity observed in Lim & Hélie (2019). For example, higher sensitivity to negative feedback reduces confidence in the MB system more quickly, which increases the likelihood of switching to MF responding. However, if sensitivity to positive feedback is higher, then correct responses increase the confidence in the MB system and reduce the likelihood of a system switch. A similar process is used to learn the associations between cue values and systems. The equations and parameters controlling learning are detailed in the Appendix.

3 Accounting for system-switching in an information-integration categorization task

As a first test of the new model, we fit the behavioral data in the perceptual categorization task of Lim & Hélie (2019). As a reminder, participants in an II task initially use a MB (prefrontal) system, with some participants eventually abandoning the MB system in favor of a MF (striatal) system. As a result, optimal participants using a MF system were labelled as ‘switchers’. All other participants were labelled as ‘non-switchers’. To identify the participants’ responding system, DBMs were individually fit to each block of 100 trials of each participant. Participants whose last block of 100 trials was best fit by a diagonal line were optimal and assumed to use the MF system. The accuracy learning curves are shown in Figure 5 (full lines). Overall, 39 participants were labelled as switchers and 11 participants were labelled as non-switchers. As can be seen, switchers performed well throughout the experiment, whereas non-switchers performed close to chance throughout.

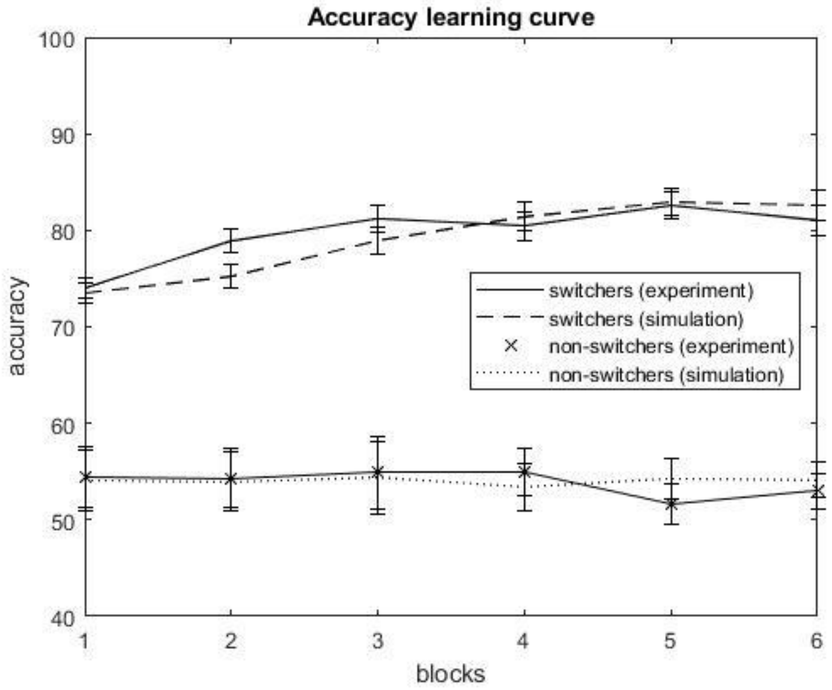


Figure 5. Average accuracy per block from Lim & Hélie (2019) and model simulation results for each block of 100 trials. Solid and dashed lines show data for participants who responded using an optimal system (switchers), whereas solid (with 'x' markers) and dotted lines indicate participants who responded using a suboptimal system (non-switchers). Error bars for experimental data are the standard error of the mean, while error bars for simulation data are the standard deviation.

3.1 Simulation

We ran 100 simulations with the model, representing 100 'participants'. The input to the model was the correct category of each stimulus shown to the participant in Lim & Hélie (2019), which was given as either "A" or "B". Each simulation consisted of 6 blocks of 100 trials (same as the behavioral experiment). Throughout the task, there was no perceptual cue for the use of a particular category learning system, thus the perceptual cues were set to 0.

During each trial, the MB and MF systems in the model generated a response according to the actual category of the stimulus and the system's accuracy probability. Because there were two categories (A and B) in the experiment, the responses of the MB and MF systems served as the inputs for the PMd units corresponding to Category A or B. The responses from the two systems were fed into the neuron-based circuit described in the Appendix. The circuit was modeled as a small-scale representation of the respective brain areas to hold a unit of STN cell, a unit of preSMA cell, and two units of PMd cells. Parameter values common to the simulations of both switchers and non-switchers are shown in Table 2.

The two PMd units were included to represent category selection, one to account for pressing the button corresponding to Category A, and the other for Category B. The PMd units were activated by the output of the MB and MF systems. Because the PMd units incorporate lateral inhibition, PMd units A and B inhibited each other.

Table 2. Parameter values used in the simulation of Lim & Hélie (2019) that were common for both switchers and non-switchers

Model-level	Parameter	Value
MF's response generation	Acc_{MF} (Eq. A5)	0.84
Perceptual cues	vc (Eqs. A6, A7, A12)	0 for all trials
$MB_{confidence}$ learning	γ_{MB} (Eq. A13)	0.008
	${MF_{confidence}}_{max}$ (Eq. A14)	5.1
Category selection	PMd integrated α-activity threshold	1.33

Note. These parameters were found using a rough grid search.

For each trial, when the output of PMd units (in the form of integrated α-activity) reached the threshold, the PMd unit that reached the threshold first was the winner. The category it represented was selected as the overall outcome of the model for that trial. If none of the α-activity of the two PMd units reached the threshold in the given time of 2000 ms, the PMd unit that had a higher α-activity at time = 2000 ms was selected as the winner. This latter case happened in about 3% of the simulated trials.

3.1.1 Accuracy Learning Curve

One category outcome, either Category A or B was chosen in each trial. For each trial, if the suggested category outcome from the model matched with the actual category of the stimulus, the model received feedback with the value 1, and 0 if the two categories did not match. For each simulation, the categorization accuracy for each block of 100 trials. The resulting simulated accuracy learning curves are shown in Figure 5 (dashed lines).

The goal of the simulation was to fit the data according to the two groups of participants, namely switchers and non-switchers. The changes in parameters that resulted in the difference between switchers and non-switchers are shown in Table 3. As can be seen, only 2 free parameters were needed to account for group differences. From Figure 5, the accuracy performance of the two groups was simulated with a RMSD of 1.69%.

Table 3. The difference in parameter values of the model to separate switchers from non-switchers

	Value

Parameters	Switchers	Non-switchers
Acc_{MB} (Eq. A4)	0.745	0.54
γ_{MF} (Eq. A14)	0.07	0.003

First, the accuracy of the MB system was set higher for switchers than non-switchers. Acc_{MB} specified how likely it was for the MB system to produce an accurate response in each trial. If participants selected the best possible response from the MB system to categorize the stimuli, a one-dimensional rule would give an accuracy of about 76%. If participants used a conjunction rule that takes into consideration both the varying stimulus dimensions, the accuracy would rise to about 91%, assuming that the best rule is used. However, it is highly unlikely that participants used a conjunction rule in such categorization tasks (Hélie et al., 2012). Conjunction rules are difficult to learn, and as a result they tend to have low salience and are rarely explored (Ashby et al., 1998). For these reasons, Acc_{MB} in both switchers and non-switchers was constrained to be lower than an accuracy of 0.76.

Second, the γ_{MF} of switchers was higher than that of non-switchers. Higher γ_{MF} signified a higher learning rate for the MF system's confidence for each update. If the MF produced a correct response, the increment for the learning update was higher. Hence, the model simulation suggests that switchers had better categorization rules in their MB system, but also learned about the efficiency of the MF system more quickly when compared to non-switchers.

3.1.2 Switchers

With an increase in MB accuracy and learning rate of confidence in the MF system, the model was able to distinguish switchers from non-switchers. With higher Acc_{MB}, a switcher participant's initial MB accuracy was higher than that of the non-switchers. Thus, high Acc_{MB} might render switching harder, but this difficulty was overcome by having higher γ_{MF} to increase the MF system's confidence at a higher rate. Thus, even if the confidence in the MB system was high, high confidence in the MF system allowed system-switching in a categorization task when more trials were carried out.

Figure 6 shows the ratio of activity in the MF system to that of the MB system for switchers. In the beginning, the ratio was 0, since the response from the MF system was not fed into PMd units (due to the inhibition from STN). As the MF system gained more confidence by producing correct responses, the ratio increased. When the ratio was below 1, if the two systems' responses conflicted, the overall response of the model followed the response from the MB system. When the ratio was around 1, the competition between the systems was higher, and the model's overall response could follow either one of the systems (or both when the suggested responses from both systems were the same). When the ratio was much greater than 1, the overall response of the model followed the response of the MF system when the two systems' responses differed. Thus, Figure 6 shows that the switch from the MB system to the MF system occurred after approximately 200 trials in this task. According to the DBM analyses in Lim & Hélie (2019)'s experiment, 31 out of 39 switchers relied on the MF system by the second block of the task (trial = 200).

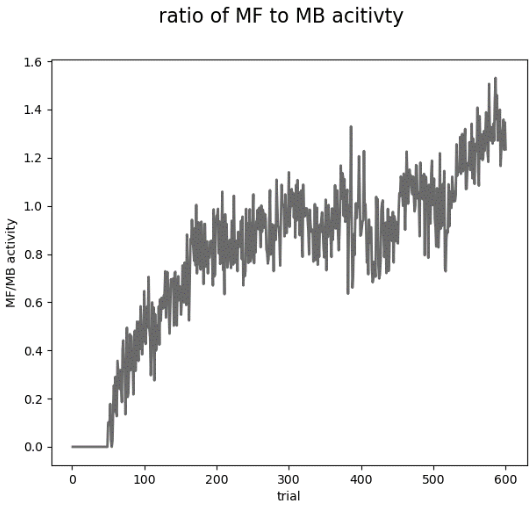


Figure 6. The ratio of activity of the MF to MB system for every trial for switchers.

3.1.3 Non-switchers

Non-switchers had lower MB accuracy and a slower learning rate for confidence in the MF system. It is important to note that non-switchers included all participants who only relied on the MB system throughout the task. Some of these participants were using suboptimal categorization rules, while others were guessing or refusing to engage with the task. This interpretation is supported by Rabi and Minda (2014), who argued that participants who were best fit by guessing DBMs struggled with identifying the correct rule or did not apply a rule consistently. As a result, the non-switchers group is not as homogenous as the switchers group and the modeling results for non-switchers should be interpreted with care.

In the proposed model, switching occurs when the MB system fails to give accurate responses over time or when the MF system gains enough confidence. In Lim & Hélie (2019)'s experiment, the average accuracy of non-switching participants was generally lower than that of switchers, even in the first block where switchers still relied on the MB system. Thus, the Acc_{MB} for non-switchers was lower than that of the switchers. As a result, the MB system's consistent failure to output a correct response should, in time, decrease the STN activity to suppress the MF system's output from reaching the PMd. However, even with sufficiently low STN activity, the weight of the MF system's response should still be lower than the weight of the STN activity to suppress switching. Thus, γ_{MF} was set low enough to slow the confidence gaining process of the MF system. This led to a failure to switch from the MB to MF system, and the continued reliance on the MB system.

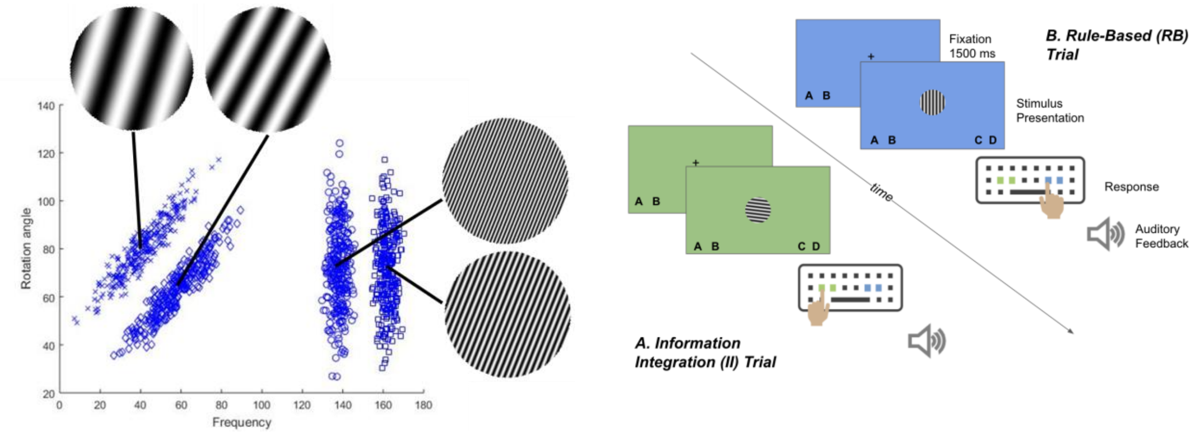
3.2 Discussion

The ability to evaluate the effectiveness of the different learning systems drives the switching capabilities of switchers and non-switchers. At the beginning of the task, even when responding using the MB system, switchers can categorize the stimulus better than the non-switchers. This could indicate that it is more difficult for non-switchers to find a good rule to implement in the MB system for the task, and that some of the non-switchers may revert to guessing. Switchers can tackle the task with more appropriate rules in the MB system and eventually learn about the efficiency of the MF system more quickly. This difference in the learning rate of system confidence is consistent with the hypothesis generated by the COVIS simulation reviewed in Section 1.3, which suggested that feedback sensitivity to update system confidence was a critical difference between switchers and non-switchers.

4 Accounting for trial-by-trial system-switching deficits in typical aging and Parkinson's disease

In this section we describe simulations of categorization system-switching comparing participants from different age groups and those with Parkinson's disease from Hélie & Fansher (2018). Past research had shown an association between aging and cognitive flexibility, where older adults are often worse at adapting to shifting situational demands when compared to younger adults (Wilson et al., 2018). Instead of examining whether participants would switch from a MB system to a MF system in II category learning, the work from Hélie and Fansher explored whether participants from different age groups could switch between categorization tasks requiring either MB-RL or MF-RL flexibly on a trial-by-trial basis. Specifically, the research explored the deficits in categorization system-switching in older adults and people with Parkinson's disease.

The experiment involved two types of category learning tasks: an RB categorization task and an II categorization task. Throughout the experiment, participants were asked to categorize circular sine-wave gratings. The category structures used in the RB and II tasks are shown in Figure 7A. Young adults, older adults, and people with Parkinson's disease were first trained in an RB categorization task for 100 trials (Block 1), followed by 400 trials of training in an II categorization task (Blocks 2-5). During the training phase, the two tasks were done separately. Background color cues indicated the type of task for the particular trial (blue for RB or green for II). Figure 7B shows example trials. After the training phase, participants went through the testing phase (Block 6). In the testing phase, a block of 100 trials requiring trial-by-trial switching between learning systems was presented, where RB and II categorization trials were randomly intermixed.[2] The data from the testing phase were used to compute the accuracy switch cost (i.e., mean accuracy in trials preceded by a trial with the same background color minus accuracy in trials preceded by a trial with a different background color). The testing phase was also used to identify successful switchers. Data from RB and II trials were separated for the test phase and DBM models were fit separately to the RB and II data. Switchers were participants whose RB data was best fit by a DBM model from the MB system and II data was best fit by a DBM model from the MF system. All other participants were labelled as non-switchers. Note that Hélie and Fansher (2018) used the same labeling methodology as Erickson (2008).



(A) (B)

Figure 7. (A) Category structures used in the RB and II tasks. ‘x’ denotes members of category “A”, “◊” denotes members of category “B”, “○” denotes members of category “C”, “□” denotes members of category “D”. “A” and “B” are II categories, while “C” and “D” are RB categories.

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[2] Hélie & Fansher (2018) also included a second test block where the location of the response buttons was changed. Because the proposed model does not include a motor component, this additional testing block is not simulated or discussed any further.

Frequency is inversely related to bar width. Rotation angle indicates the orientation of the stimulus and was calculated as the counterclockwise rotation from horizontal. (B) Example II (left) and RB (right) trials of the categorization task. Note that older adults and people with Parkinson’s disease used a response box with large buttons instead of the illustrated regular keyboard.

The study’s hypothesis was that reductions in dopamine would be related to diminished cognitive flexibility and system-switching ability (Hélie & Fansher, 2018). As a result, older participants would show impaired system-switching, and this impairment would be worse for people with Parkinson’s disease when compared to age-matched controls. Operationally, aging and Parkinson’s disease would result in a higher accuracy switch cost when compared to young adults, which would reduce the proportion of participants that could switch on a trial-by-trial basis as well as overall accuracy in the intermixed testing phase.

The results showed that participants in all groups performed well in the training phase, but group differences were present in the intermixed testing phase. The young adult group had higher accuracy in categorization compared to participants with Parkinson’s disease (Figure 8, panels A and C, respectively). However, the difference between the older adult group and people with Parkinson’s disease was not significant (Figure 8, Panels B and C). The proportion of switchers in the young adult group was greater than that in the older adult group and people with Parkinson’s disease (Figure 9). The accuracy switch cost was statistically significant for the young adult switchers and non-switchers (Figure 10a). For older adults, the accuracy switch cost was statistically significant for the switchers and trending for non-switchers. For people with Parkinson’s disease, the accuracy switch cost was not statistically significant for switchers but was statistically significant for non-switchers. Overall, the results suggest that aging decreases the ability to switch between systems.

4.1 Simulation

For each group of participants, we ran 100 simulations with the proposed model, representing 100 ‘participants’. The model received as input the desired category of each stimulus shown to the participant in the Hélie & Fansher (2018) categorization task, which was given as either “A”, “B”, “C” or “D”. Each simulation consisted of 6 blocks of 100 trials of categorization. The task flow of the simulation experiment was:

100 RB training trials → 400 II training trials →100 intermixed RB and II trials

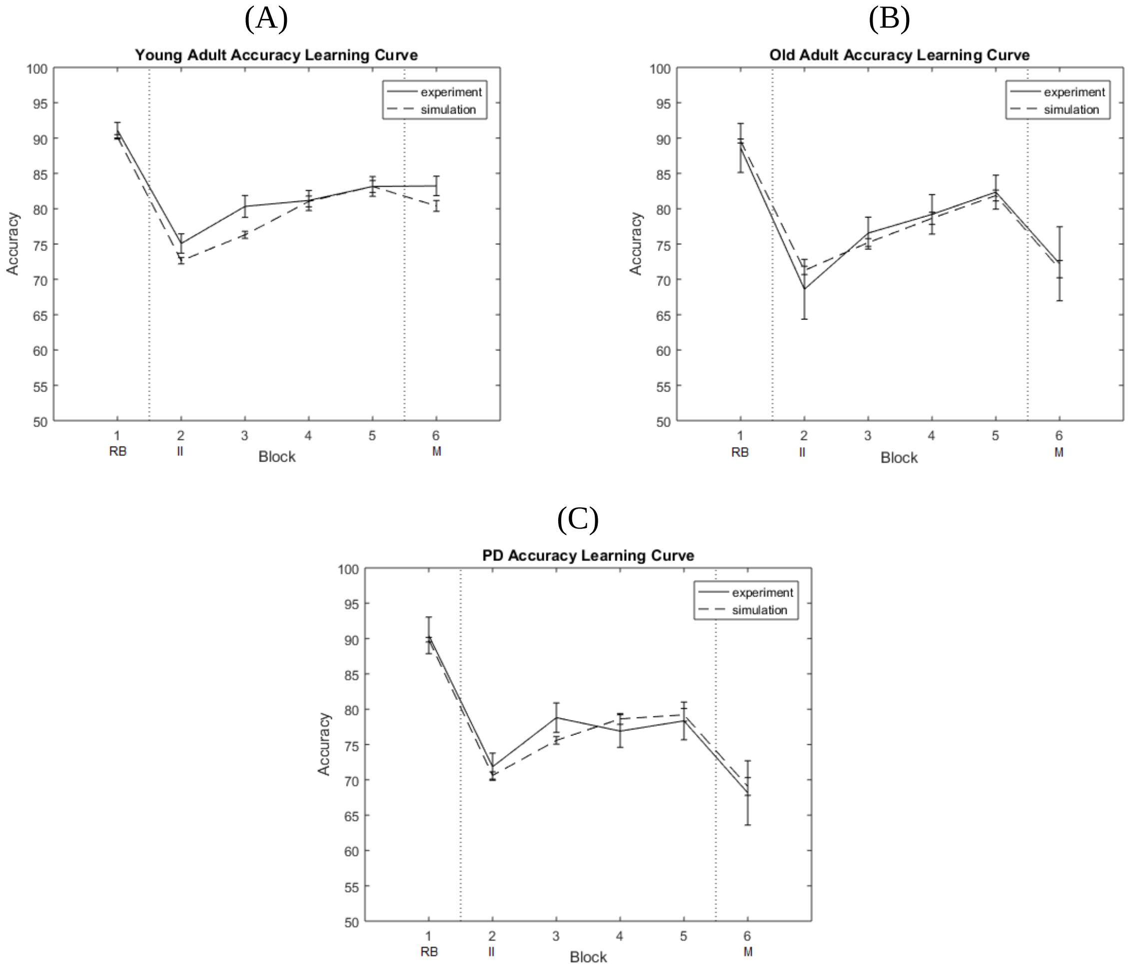

Figure 8. Mean accuracy per block in the experiment for (A) young adults, (B) older adults, and (C) people with Parkinson’s disease. Vertical dashed lines denote a change in task, and the letters over block numbers indicate the task being performed from that block until the next vertical dashed line (M = mixed). The dashed line in each panel indicates data obtained from the simulation while the solid line indicates data from the behavioral experiment conducted by Hélie and Fansher (2018). Error bars are the between-subject standard error of the mean.

In this experiment, perceptual cues were given to the participants along with the stimulus: a blue background indicated an RB trial and green background indicated an II trial. In the model, both perceptual cue parameters vc_{MB} and vc_{MF} produced a binary output (0 or 1). During an RB trial, vc_{MB} was set to 1 while vc_{MF} was set to 0, and the reverse was true for II trials. Given the relationship between RB category structures and MB systems, and II category structures and MF systems, the presence of vc_{MB} increased activation to the preSMA cell, thus inhibiting the MF system's responses from reaching the PMd cells, whereas the presence of vc_{MF} should decrease such activation to preSMA and release the inhibition of the MF system's response. However, vc_{MF} should have less of an effect on the preSMA units at the beginning of the trials and should only begin influencing responses after undergoing more training trials (i.e., the association needs to be learned). It took longer to train the MF system as compared to the MB system (Hélie & Fansher, 2018). This was achieved by setting the learning rate of vc_{MF} association to a lower value as compared to that of vc_{MB}.

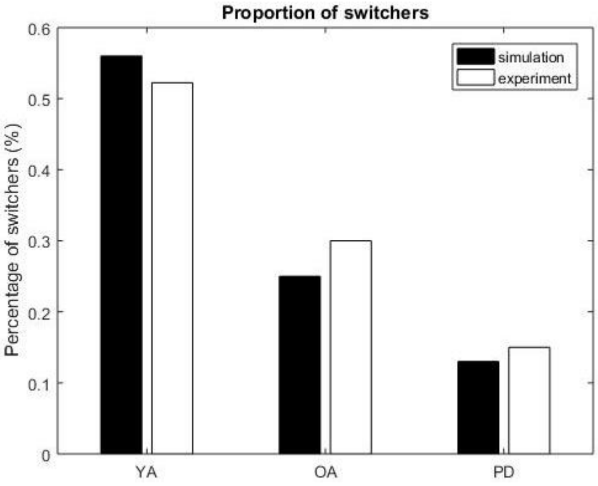

Figure 9. The proportion of switchers in each condition. Black bars indicated data from simulation while white bars indicated data from the behavioral experiment conducted by Hélie and Fansher (2018).

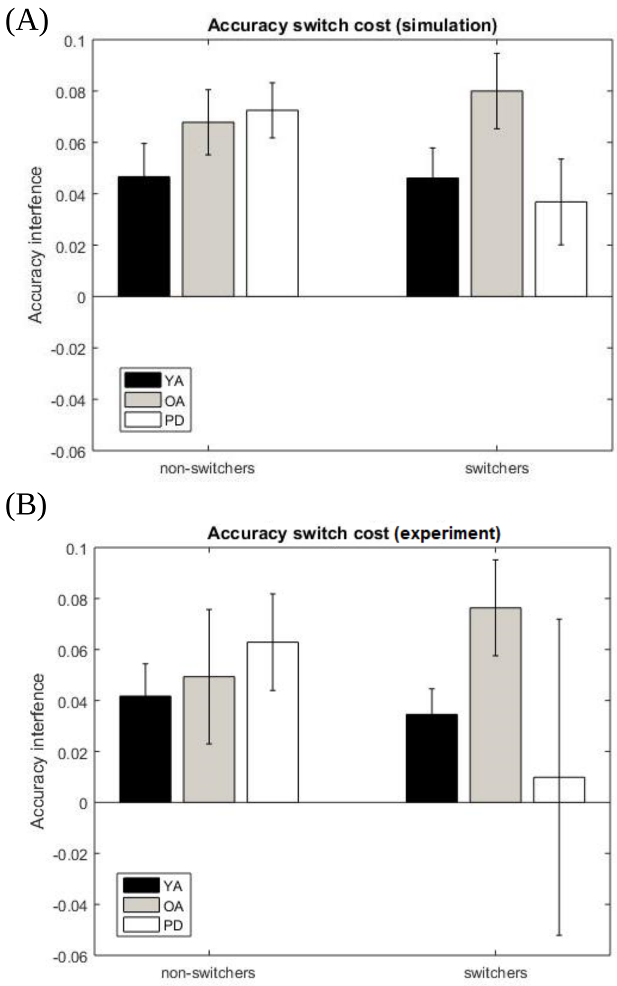

Figure 10. Accuracy switch cost for switchers and non–switchers in each group for (A) data obtained from simulation and (B) data obtained from the behavioral experiment conducted by Hélie and Fansher (2018). Black bars indicate switch cost for young adults, grey bars indicate switch cost for older adults, and white bars indicate switch cost for people with Parkinson's disease. Error bars are the between-subject standard error of the mean.

With two different tasks (RB and II) simulated, the accuracy probabilities of the MB and MF systems were task dependent. The accuracy probabilities of the MB and MF systems for RB and II tasks are shown in Table 4. The MB system allows for optimal performance in the RB task, while a MF system is optimal for an II task. In the model, the change in the task was hinted with the change in the perceptual cues. In an RB task, the MB system generates an accurate response with the probability accuracy of $ACC_{MB_{RB}}$, whereas the MF system generates an accurate response with the probability accuracy of $ACC_{MF_{RB}}$. Similarly, in an II task, the MB system generates an accurate response with the probability accuracy of $ACC_{MB_{II}}$, whereas the MF system generates an accurate response with the probability accuracy of $ACC_{MF_{II}}$. Upon switching from one task to another, the accuracy of the MB system response is affected by proactive interference, which may cause a decrease in performance shortly after a switch. Proactive interference was modeled as an exponential decay and was dependent on the previous task type (RB or II).

Table 4. Accuracy probability of MB and MF systems for RB and II tasks

Accuracy probability	Value
$ACC_{MB_{RB}}$ (Eq. 1)	0.90
$ACC_{MB_{II}}$ (Eq. 1)	0.78
$ACC_{MF_{RB}}$ (Eq. 2)	0.73
$ACC_{MF_{II}}$ (Eq. 2)	0.88

$$ACC_{MB} = \left(vc_{MB} \times ACC_{MB_{RB}}\right) + \left(vc_{MF} \times ACC_{MB_{II}}\right) - \left[R_{MB_{RB}}(vc_{MB}) + R_{MB_{II}}(vc_{MF})\right](1 - D)^{N} \tag{1}$$

$$ACC_{MF} = \left(vc_{MB} \times ACC_{MF_{RB}}\right) + \left(vc_{MF} \times ACC_{MF_{II}}\right) \tag{2}$$

The MB and MF systems generated category responses based on their accuracy probability independently. With two tasks modeled, two sets of category options were provided: C-D (RB task) and A-B (II task). In each task, the model can only choose from the two options (A and B, or C and D) depending on the cue. Both the MB and MF systems held four units of responses each, representing categorical choices of A, B, C, and D. The response from each system was fed into the PMd units (depending on the inhibition for the MF system's response).

Similar to the previous simulation, the circuit was modeled as a small-scale representation of the respective brain areas to hold a unit of STN cell and a unit of preSMA cell. With four options altogether, the model had four PMd units, one for each category option (A, B, C, and D). Each unit of cells represented the activity of the respective cell group.

The model was adjusted to accommodate the trial-by-trial switching task for three groups of participants: young adults, older adults, and people with Parkinson's disease. Importantly, switchers and non-switchers were not separately simulated as in Section 3. This is because Hélie & Fansher (2018) showed that this was an important outcome variable that differed across age groups. Hence, the three groups were simulated with mixed switchers and non-switchers where the proportion of switchers to non-switchers was a model outcome (i.e., dependent variable) based on the manipulation of parameters to achieve the simulation of the specific participant group. To include both switchers and non-switchers in a group, the model was built so that the parameters

γ_{MF} and D varied between participants, while all other parameters were fixed for simulations in the same group. The 'participants' were normally distributed and the parameters γ_{MF} and D were computed using a logistic function. Because both parameters should be modeled independently, the 'participant's' distribution was obtained twice, once for each parameter. The parameters used in the simulation of the experiment that were common for all three groups of participants were as shown in Table 5.

$$\gamma_{MF} = 0.05 \times f(x), \qquad x \sim N(\mu_{\gamma MF}, 3) \tag{3}$$

$$D = 0.99 \times f(x), \qquad x \sim N(\mu_D, 2.475) \tag{4}$$

where *f(x)* is the usual logistic function, $f(x) = \frac{1}{1+e^{-x}}$, $\mu_{\gamma MF}$ is the mean used to define the distribution of γ_{MF} for different participants, and μ_D is the mean used to define the distribution of D for different participants. γ_{MF} ranged from 0 to 0.05, while D ranged from 0 to 0.99.

Table 5. Parameter values used in the simulation of trial-by-trial categorization that were common for all three groups of participants.

Model-level	Parameter	Value
MB and MF	$R_{MB_{RB}}$ (Eq. 1)	0.42
	$R_{MB_{II}}$ (Eq. 1)	0.2
Perceptual cues	γ_S for MB strategy (Eq. A12)	0.1
	γ_S for MF (Eq. A12)	0.006
	S_{max} for MB strategy (Eq. A12)	0.3

S_{max} for MF strategy (Eq. A12)	0.03

Note. Parameters not included share the same values from the previous simulation (see Tables 2-3).

The goal of the simulation was to fit the data according to the three groups of participants. We fitted the model to find the parameters that govern switching between the systems that are affected by the change in aging. The changes in such parameters were reflected in the differences in the accuracy learning curve, accuracy switch cost, and switching proportions in the three groups of participants.

4.1.1 Modeling group differences

The three groups of participants were differentiated by adjusting the value of $\mu_{\gamma MF}$, μ_D, and R_S (working memory's proactive interference). The value of the three parameters that set apart the three groups are tabulated in Table 6. Generally, the combination of higher $\mu_{\gamma MF}$ and μ_D values, and a lower R_S, value facilitated the switching capabilities.

Table 6. The difference in parameter values of the model to simulate the three groups of participants

	Value		
Parameters	Young Adults	Older Adults	People with Parkinson's Disease
$\mu_{\gamma MF}$ (Eq. 3)	0.08	-0.21	-0.35
μ_D (Eq. 4)	1.5675	0.3795	0.1980
R_S (Eq. A6)	0.4	0.7	1.2

$\mu_{\gamma MF}$ is the mean of the normal distribution of 'participants' in a given group. From the simulation, $\mu_{\gamma MF}$ for young adults is the highest, followed by older adults and people with Parkinson's disease. A higher $\mu_{\gamma MF}$ leads to a higher range of γ_{MF} for the given group. Both μ_D and R_S are related to the resistance to proactive interference, which is known to be affected by aging (Lustig et al., 2001). Similar to $\mu_{\gamma MF}$, μ_D is the mean of the normal distribution of participants in a group used to derive the exponential decay rate for proactive interference, D. A lower μ_D in the given group led to a fixed range of D with lower values. This implies that more participants in the group have a lower decay of proactive interference.

4.1.2 Accuracy Learning Curve

One category outcome, either category A, B, C, or D was chosen for each trial. If the suggested category outcome from the model matched the actual category of the stimulus, the model received feedback with the value 1, and 0 otherwise. The model only simulated the choice option of A and B for RB tasks and C and D for II tasks. The simulation did not support the cross selection of choice in different tasks (i.e., choosing option C or D in an RB task, or choosing option A or B in an II task). For each simulation, the categorization accuracy for each block of 100 trials was computed. The accuracy learning curves are shown in Figure 8. The RMSD was approximately 1.8%.

4.1.3 Proportion of Switchers

Unlike the previous task simulation where switchers and non-switchers were simulated separately, the simulation of the trial-by-trial task switch experiment required simulation of mixed switchers and non-switchers in a group of participants. The proportion of switchers reflects the property of the participant group as the model's output by varying parameters. To compute the proportion of switchers, only the last block of the experiment (the intermixed trials) was considered. We were interested in investigating the causal mechanism that determined whether all three groups of participants were able to switch between systems.

Switchers were identified as 'participants' that could switch between the learning systems in the switching task. Note that, similar to Section 3, there are many ways that a participant could be classified as a non-switcher. For example, one may have learned correctly in the RB and II phases but not flexibly switch system during the mixed block. Alternatively, one may have failed to learn either the RB or II categories. As a result, the non-switchers group is again more heterogeneous then the switchers group, and results from non-switchers should be interpreted carefully.

In the model, the switching task was associated with different learning systems in obtaining the optimum performance (MB for RB task and MF for II task). Thus, we compared the overall output response of the model and the responses of the learning systems for each trial in the last block of the experiment. In the II task, the majority of the overall response of the switchers should follow the response of the MF system. In the RB task, the majority of the overall response of the switchers should follow the response of the MB system. If the 'participant' failed to do so, they were labeled as non-switcher. The proportion of switchers for the three groups is shown in Figure 9. The RMSD was 0.038.

4.1.4 Accuracy Switch Cost

Accuracy switch cost was also computed based on the last block of the experiment: the intermixed RB and II trials. Because this involves task switching, the first trial after a task switch was labeled a “switch” trial, while the remaining trials were labeled “stay” trials. The overall response of the trials was compared to the corresponding actual category of the stimulus for the same trials. Mean accuracy for switch and stay trials were computed separately. The accuracy switch cost was obtained by subtracting the mean accuracy of the switch trials from the mean accuracy of the stay trials. The accuracy switch costs for switchers and non-switchers for all three groups of participants are shown in Figure 10. The RMSD was 0.015.

In the simulation, when compared to the experiment from Hélie and Fansher (2018), a similar trend for accuracy switch cost for all three groups was observed. In young adults, the accuracy switch costs for switchers and non-switchers were about the same. Older adults had higher accuracy switch costs when compared to young adults for both switchers and non-switchers. Older adult switchers had higher accuracy switch cost when compared to the non-switchers of the same group. The accuracy switch cost of people with Parkinson’s disease was the highest among non-switchers, however, the accuracy switch cost of people with Parkinson’s disease was the lowest among switchers. The same reversal effect was observed in the experimental data from Hélie and Fansher (2018). This was likely caused by the small number of switchers in the Parkinson’s group.

4.2 Discussion

The previous simulation results suggest an important role for system confidence and proactive inhibition in system-switching. Both of these cognitive capacities (i.e., updating and inhibition) are executive functions (EF) (see Miyake et al., 2000). Interestingly, evidence suggests that the prefrontal cortex plays an important role in supporting EF (Fuster, 2008), which overlaps with the proposed new switching mechanism. It is also worth reminding the reader here that even among young adults, about half of the participants fail to switch systems in this task (Hélie, 2017). It is thus possible that individual differences in EF in this population contributes to one's ability to switch between systems. The remainder of Section 4.2 discusses how these model components differed between groups. In Section 5 we present a new behavioral experiment that directly tests the novel model prediction that individual differences in EF can account for individual differences in system-switching in young adults.

Higher γ_{MF} accounts for faster confidence learning in the MF system when receiving positive reinforcement. The majority of young adults had a faster learning rate of the MF system confidence. This allowed for system-switching at a higher pace. As a result, groups with higher γ_{MF} generally had a greater proportion of switchers as shown in Figure 9. The effect of higher γ_{MF} was also reflected in the steeper increase in accuracy in the II training blocks in Figure 8. Because most young adults had a higher γ_{MF}, they were faster to pick up the optimal strategy (i.e., switch to the MF system) compared to the other older age groups. This suggests that better updating system confidence based on one's performance may increase the probability of being able to switch systems when appropriate.

In addition to differences in system confidence, the simulations also used higher values of μ_D for young adults, followed by older adults and people with Parkinson's disease. This indicates that young adults generally had faster exponential decay for proactive interference after a switch (parameter D). Thus, interference from previously relevant information or rules was reduced at a higher rate. In contrast, older adults and people with Parkinson's disease generally had a lower decay rate which indicated increased resistance to deactivating previously relevant information (i.e., perseveration). As a result, the two groups had a harder time switching to a 'new' system that is more appropriate for the current task.

On the other hand, a reverse trend was observed for R_S, whereby the R_S of young adults was generally lower than for the older groups and people with Parkinson's disease. With R_S being the effect of the perceptual cue's decay on the preSMA input, higher R_S indicated greater proactive interference effects in the case of task switching to the preSMA cells. In the intermixed trials, task switching was frequent (a switch happened every few trials), and rapidly abandoning a strategy from one trial to another was required for optimal performance. The combination of lower D and higher R_S made switching from the MB to MF system harder. The previously relevant information was harder to be suppressed in the 'new' task that required relying on a different system for optimal performance. Thus, the accuracy performance shown in block 6 of Figure 8 was lower. The number of switchers in such groups was lower compared to the groups with higher μ_D and lower R_S (Figure 9). This suggests that better inhibitory processes can reduce switch cost and lead to faster switching.

5 Can individual differences in executive function account for trial-by-trial system-switching performance?

Given the results obtained by Hélie and Fansher (2018), and the simulation results presented in Sections 3 and 4, it is possible that individual ability in system-switching could be related to individual differences in EF. That is, even among healthy, young adults, there is variation in performance, in terms of which individuals are classified as switchers and which are categorized as non-switchers. The highly-cited EF taxonomy introduced by Miyake et al. (2000) provided evidence that individual differences in updating, inhibition, and shifting are separable but interrelated EF processes in young adults (see also Friedman et al., 2008, for genetic evidence supporting this model). While a systematic review of the latent-variable EF literature showed that the three factors of updating, inhibition, and shifting was not universally obtained in all samples, there was substantial evidence for the Miyake/Friedman model in many studies that tested young adults (Karr et al., 2018). These three separate components of EF are directly related to the results of Section 4's simulation in that EF inhibition is related to proactive interference in the model, EF updating is related to changes in system confidence in the model, and EF shifting is related to system-switching itself in the model. We tested this novel model prediction by measuring EFs in a sample of young adults and then testing them in a trial-by-trial system-switching experiment.

5.1 Methods

5.1.1 Participants

Fifty-nine undergraduate students were recruited for this study and were compensated with partial course credit for their participation. Participants were young adults recruited from the introductory psychology subject pool of Purdue University. All procedures were approved by the Purdue University Institutional Review Board.

5.1.2 Design

Participants completed two separate experimental sessions for the categorization and EF measures. Session order was counterbalanced across participants. The experiment was predominantly a between-subjects design where group (switcher or non-switcher) was determined at the analysis stage based on performance in the categorization task.

5.1.3 Materials

5.1.3.1 Categorization Task

Circular sine-wave gratings of constant contrast and size, occupying ~ 5° of visual angle were presented to participants on a 21-inch monitor (1,920 × 1,080 resolution). The stimuli were defined by a point in 2D space where the dimensions were frequency and rotation angle. Frequency was indicative of bar width and was calculated in cycles per degree (cpd), while rotation angle was the angle of the counterclockwise rotation of the bars from the horizontal as calculated in radians. The stimuli were the same as those used in Hélie & Fansher (2018) (and shown in Figure 7).

Stimuli were generated into an arbitrary 200 × 100 coordinate system using the randomization technique of Ashby and Gott (1988) and were separated into four categories arbitrarily labelled with letters A-D (See Figure 7). Category A and B structures are II and were generated using bivariate normal distributions: $\mu A = (42, 80)$, $\sum A = (145\ 135; 135\ 145)$, $\mu B = (58; 64)$, $\Sigma B = \Sigma A$. Category C and D structures are RB and were generated using bivariate normal distributions: $\mu C = (138, 72)$, $\sum C = (10\ 0; 0\ 280)$, $\mu D = (162, 72)$, and $\Sigma D = \Sigma C$. The arbitrary 200×100 coordinate system was then re-scaled into frequency × orientation space using a non-linear transformation (Hélie, 2017). This yielded stimuli ranging in frequency from 0.29 to 8.6 cpd and from 34° to 95° in orientation (counterclockwise from horizontal).

The screen background color during the task indicated the possible category choices to participants: II stimuli (A or B) were presented on a green background and RB stimuli (C or D) were presented on a blue background. To perform well, participants would have to rely on a MF system when categorizing A/B stimuli and the MB system when categorizing C/D stimuli.

The session was divided into 7 blocks of 100 trials (700 trials total). For each trial a crosshair was presented for 1,500 ms with either a blue or green background (signaling a RB or II trial respectively). Adding preparation time has been shown to reduce the accuracy switch cost for participants who can switch between systems on a trial-by-trial basis (Hélie, 2017). After 1,500 ms the crosshair was replaced by a stimulus where the background color indicated possible response choices (green - A/B, blue - C/D). The stimulus disappeared from the screen after the participant made a response and auditory feedback was presented: a high pitch tone for a correct response, a buzz sound for an incorrect response, and a two-note sound for an incorrect key selection (see Figure 7B for an example trial).

Stimulus presentation, feedback, and response recording were displayed and acquired using Matlab. Participants gave responses on a standard keyboard: the ‘s’ key was used for category A, the ‘d’ key was used for category B, the ‘k’ key was used for category C, and the ‘l’ key was used for category D. Response keys A and B were covered with blank green stickers indicating their use for II trials and response keys C and D were covered with blank blue stickers indicating their use for RB trials (matching the background). The category labels (A–D) were displayed at the bottom of the screen below the stimulus mapping the response buttons on the keyboard. Participants responded to A/B stimuli with their middle and index fingers on the left hand and responded to C/D stimuli with their middle and index fingers on the right hand.

Prior work has found that switching the locations of response keys affects II categorization, but not RB categorization (Ashby et al., 2003). To test whether degree of interference interacts with ability to switch between categorization systems, during the last block of the experiment, the button labels were switched. The button or key associated with category A was now the button or key previously associated with category B and vice–versa. Likewise, the button or key associated with category C was now the button or key previously associated with category D and vice-versa. During this block the labels at the bottom of the computer screen were changed to match this alteration (so they now read B, A, D, C).

5.1.3.2 Executive Function Tasks

Below we list the tasks used to measure EF, based on the framework originally specified by Miyake et al. (2000).

5.1.3.2.1 Continuous counters (Morey & Cowan, 2004; Redick et al., 2016; Shipstead et al., 2012)

Participants were presented with a series of shape stimuli and had to keep a running count of the number of squares, circles, and triangles presented for each trial. Shapes were presented one at a time, and the ordering of the different types of shapes was random. At the end of each trial the participant had to report the number of presentations for each shape which varied from three to six presentations. Participants made responses with the number keypad. During each trial the shape type presented to participants was changed six to seven times and the number of shape presentations varied. Following the presentation of a 500 ms fixation cross, each shape was presented until the participant pressed the spacebar to continue. At the end of each trial, participants had as much time as needed to recall the number of triangles, squares, and circles presented in the trial. Participants were told to be as accurate as possible in their recollections and speed of response was not emphasized. Participants completed three practice trials followed by 15 test trials.

5.1.3.2.2 Antisaccade (Hallett, 1978; Kane, Bleckley, Conway, & Engle, 2001; Redick et al., 2016)

Participants were tasked with identifying a backward-masked B, P, or R that was briefly presented on the screen for each trial. For each trial a duration fixation screen consisting of a string of asterisks was presented for a variable period of time (200, 600, 1,000, 1,400, or 1,800 ms), followed by a flashing equal sign cue (oncreen 100 ms, offscreen 50 ms, onscreen 100 ms). Immediately after the cue, the backward-masked B, P, or R was presented for 100 ms. Participants were responsible for identifying the presented letter with a key press. The left, down, and right arrow keys on a standard keyboard were labelled with stickers marked as B, P, and R, respectively. They were asked to use their index, middle, and ring fingers of their right hand on the buttons labelled B, P, and R to make their responses. Accuracy was emphasized to participants and there were no specific instructions regarding speed of response.

The experiment started off with 18 response mapping trials where both the cue and letter were presented in the center of the screen. In the first half of these trials, the cue (=) was presented for 250 ms and in the second half the cue was presented for 100 ms. This was to initially get participants acclimated to task timing as this would be the cue duration during the real trials. They then completed 18 practice trials where the first 9 trials were prosaccade, in which the cue and letter appeared on the same side of the screen, and the second 9 trials were antisaccade where the cue and letter appeared on different sides of the screen. These trials are crucial for measuring inhibitory control as attention tends to be captured by the flashing cue on the opposite side of the screen, making it difficult to identify the briefly presented letter. Feedback was provided for all practice trials. Following the practice trials participants completed 36 test trials, all of which were antisaccade where the stimulus presentation for each trial was equally divided between left and right locations. No feedback was provided during these test trials.

5.1.3.2.3 Go/no-go (Robertson et al., 1997; Wiemers & Redick, 2019)

Participants completed a numerical version of the sustained-attention-to-response task (SART) as a measure of response inhibition. Participants were presented with a series of individual numbers ranging from 0-9 and were tasked with pressing the spacebar with their dominant hand as quickly as possible each time a number was presented (“go” trials); however, they were asked to withhold this response when the number presented was a “3” (“no-go” trials). Each number was shown for a maximum of 300 ms before a row of uppercase X’s was presented as a mask for 900 ms. Participants were able to press the spacebar anytime within 1200 ms. If the spacebar was pressed during the first 300 ms, the program would then show the 900 ms mask. Each number presentation is considered to be a trial. Participants were given 10 practice trials followed by 240 real “go” and 30 real “no-go” trials that were randomly intermixed. They were told to respond as quickly and accurately as possible.

5.1.3.2.4 Running span matrix (Redick, 2016; Redick, Wiemers, & Engle, 2020)

During each trial participants viewed a 4 × 4 grid and were instructed that they would have to recall, in order, the locations of the last *n* red squares that would appear on the grid. Each red square was presented for 300 ms (200 ms ISI), and at the end of the trial, participants viewed a blank 4 × 4 grid and had to click the locations of the last *n* red square presentations in order. Accuracy was emphasized for this task and no instructions were given regarding speed of response.

Participants first completed four practice trials where $n = 2$, followed by 12 real trials where $n = 4$ (where there were 2 trials each of a list length of 4, 5, 6, 7, 8 and 9).

5.1.3.2.5 Keeping track (Engle, Tuholski, Laughlin, & Conway, 1999; Redick et al., 2016; Yntema & Mueser, 1962)

Before viewing a list of words presented one at a time, participants were given two to six different categories (metals, animals, colors, distance, countries, or relatives). All categories were cued an equal number of times during the task. Participants had to remember the last item presented in the list that belonged to each category. Each list consisted of 16 words, with each word shown for 1,500 ms (250 ms ISI). After the last word was shown, participants used the mouse to select the most recently presented exemplar for each category out of 6 presented words. Participants were told to accurately recount the exemplars and there was no emphasis on speed of response. Participants first completed four practice trials, two trials with one-category lists and two trials with two-category lists. They then completed the experimental block with three trials each of two-, three-, four-, five-, and six- category lists randomly intermixed.

5.1.4 Procedure

Undergraduate students were recruited from the introductory psychology participant pool to take part in a multi-session study. In one, 1-hour session participants completed all EF measures, and in a separate 1-hour session participants completed the categorization task, with session order counterbalanced across participants. Participants had to complete both sessions within a week-long time period and were not allowed to complete both sessions on the same day.

5.1.4.1 Categorization Session

Participants were told that they would complete a categorization task and that they would need to learn the category membership of stimuli through trial-and-error learning. Participants were told to accurately categorize the stimuli, with no instruction regarding speed of response. They were shown an example stimulus and were told that the bars of the sine-wave grating would vary in width and orientation, and that their categorization judgements would be based on these features.

The procedure was identical to the 1–session preparation (1S/PREP) condition in Hélie (2017). The experiment lasted about 55 minutes and consisted of 700 trials, equally divided into 7 blocks. Participants were allowed to take short breaks between blocks. Block 1 consisted of RB-only categorization, Blocks 2-5 consisted of II-only categorization, Block 6 intermixed RB and II trials and required participants to switch between MF and MB systems on a trial-by-trial basis, and Block 7 was similar to Block 6 except these trials included the button–switch component described earlier. They were given longer to learn II categories as prior work has shown that II category structures are more difficult to acquire than RB (Hélie & Ashby, 2012).

Prior to completing Block 1, participants were told that for trials with a blue background (RB trials), bar width would determine membership, that stimuli would belong to category C or D, and that they would respond by selecting one of the two blue buttons on the keyboard. Following Block 1, they were told that for trials with a green background (II trials), bar width and orientation would determine category membership, that stimuli would belong to category A or B, and that they would respond by selecting one the two green buttons on the keyboard. Participants were informed about the button–switch component of Block 7 prior to completing that block. Due to the complexity of the task instructions, the experimenter stayed with the participants for the first few trials to ensure that they correctly understood the task.

5.1.4.2 EF Session

Participants completed all five EF measures during this session in the following order: continuous counters, go/no-go, running span, anti-saccade, and keeping track. The experimenter gave participants instructions before the start of each task and was present during the entire session so that they could initiate the experimental program for each task.

5.2 Results

Data were excluded from five participants for being under the age of 18 (*n* = 1), failing to attend both sessions (*n* = 3), or experimenter error (*n* = 1).

5.2.1 Categorization Task

A model-based (DBM) analysis identified participants who could or could not switch between MF and MB systems on a trial-by-trial basis (see Ashby & Crossley, 2010; Hélie, 2017; Hélie & Fansher, 2018). To make this classification, participant performance in the intermixed trials block (Block 6) was separated by II and RB trials and then DBMs were fit separately to these data (Ashby, 1992; Maddox & Ashby, 1993). Hélie et al. (2017) describe three classes of decision-bound models including guessing and rule-based models (both MB), as well as procedural-learning models (MF). The RB and II data were fit to these models and the best models were selected using the Bayes information criterion (Hélie, 2006). The optimal model for the RB data was rule-based (MB), while the optimal model for the II data was MF (see Figure 7). Participants whose data were best fit by the optimal models were labelled as “switchers”, as they demonstrated that they could effectively switch between systems. All other participants were labelled as “non-switchers”. In line with previous studies with an undergraduate sample (Hélie, 2017; Hélie & Fansher, 2018) who found that approximately 50% of students were switchers, 46.30% of participants (n = 25 out of 54) were labelled as switchers.

5.2.2 Executive Function Measures

All tests were run as independent samples *t*-tests comparing means between “switcher” and “non-switcher” groups.

5.2.2.1 Updating

Three tasks were used to measure updating ability. The primary measure of updating was accuracy in the Continuous Counters task (Redick et al., 2016), as participants had to continuously update their mental tally of the number of times each shape had appeared. Participants in the “switcher” group performed significantly better on this measure than the “non-switchers”. Levene’s test for equality of variances was significant (F = 14.29, p < .001), so performance was compared between groups without the assumption of an equality of variances (*MD* = .08, t(33.87) = -2.55, $CI_{95\%}$ = [-.15, -.02], p = .02).

The total number of correct items on the Keeping Track task was also considered a measure of updating performance as one must continuously update each category with the most recent exemplar as the list of words is presented. Accuracy was compared between “switchers” and “non-switchers”, and there was no significant difference (*MD* = -2.9, t(52) = -1.4, $CI_{95\%}$ = [-7.2, 1.3] , p = .17).

The total number of correct items on the Running Matrix Span task was also compared between “switchers” and “non-switchers” as a measure of updating performance, as one must continuously keep track of the locations where red squares have appeared in the grid. There was no significant difference between switchers and non-switchers ($MD = -3.54$, $t(52) = -1.71$, $CI_{95\%} = [-7.69, .60]$, $p = .10$).

Lastly, a composite updating score was created by *z*-scoring and averaging the three previous measures together. Levene’s test for equality of variances was significant ($F = 4.82$, $p = .03$), so performance was compared between groups without the assumption of equality of variances ($MD = .49$, $t(45.38) = -2.40$, $CI_{95\%} = [-.89, -.08]$, $p = .02$), with switchers having a significantly greater updating composite score than non-switchers.

5.2.2.2 Inhibition

Two tasks were used to measure inhibition. The antisaccade task is considered a measure of inhibition as one must ignore an irrelevant flashing distractor. Accuracy on the antisaccade test trials was compared between “switchers” and “non-switchers” and there was a significant effect of switch status on accuracy ($MD = .10$, $t(52) = -2.04$, $CI_{95\%} = [-.19, -.002]$, $p = .046$), with switchers showing greater accuracy.

Performance on the go/no-go task was also considered a measure of inhibitory control, as one must refrain from pressing the spacebar when presented with a specific stimulus. Accuracy on no-go trials was compared between groups and there were no significant differences ($MD = .03$, $t(52) = -.60$, $CI_{95\%} = [-.15, .08]$, $p = .55$).

To create a composite inhibition score, anti-saccade and go/no-go accuracy were z-scored and averaged. There was no effect of switch status on the composite measure of inhibition (*MD* = .35, *t*(52) = -1.64, $CI_{95\%}$ = [-.79, .08], *p* = .11).

5.2.2.3 Shifting

To assess shifting ability, RT switch cost on the Continuous Counters task was examined. RT switch cost was defined as the difference in RT when one views two of the same shapes sequentially as compared to viewing to different shapes sequentially (Unsworth & Engle, 2008). Whether or not one was a switcher did not significantly predict switch cost on the Continuous Counters task (*MD* = 87.08, *t*(52) = -1.73, $CI_{95\%}$ = [-187.96, 13.79], *p* = .09).

5.3 Summary and discussion

Figure 11 summarizes the results obtained with the composite scores. As can be seen, successful system-switching in the categorization task was related to updating ability, with better updating for participants who could switch on a trial-by-trial basis. However, switchers and non-switchers did not significantly differ in performance on inhibition and shifting composites. Hence, system-switching was related to a specific aspect of EF, namely updating. This result partially supports the model predictions from the previous sections, in that updating in system confidence based on performance was an important component of the models for system-switching. However, the model also predicted that inhibitory processes would be important in reducing switch cost and thus facilitating switching. The experiment found partial evidence supporting this prediction, with switchers performing better in the antisaccade task. However, the inhibition composite score did not support this prediction in a young adult sample. Note that the model predictions were generated using different age groups. It is possible that the variance in inhibitory process among young adults was not sufficient to predict system-switching. In addition, Friedman and Miyake (2004) showed that there are distinct and separable aspects of inhibition that might differentially relate to system-switching. This could explain the different results obtained in the antisaccade and go/no-go tasks. Future work should address this possibility.

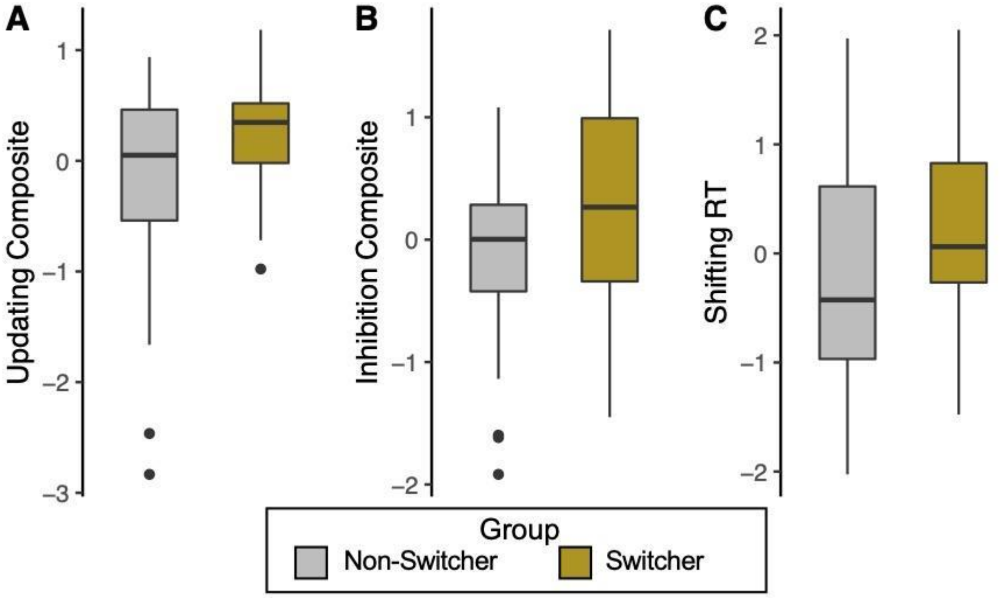

Figure 11. Performance on measures of executive function by switch group. Note that values on the y-axis represent *z*-scores, where a higher value indicates better functioning.

6 General Discussion

This article proposed a new computational model of how interactions between the prefrontal cortex and the striatum can be used to account for switching between MB and MF systems in category learning. The work began with the observation that many participants fail to switch away from a MB system to an optimal MF system when categorizing II stimuli (Ashby & Valentin, 2017), and results from human experiments were used to build a computational model that simulated a neurobiological circuit that facilitates learning system-switching in categorization tasks. The model was designed based on the hyperdirect pathway of the cortico-basal ganglia network. It incorporated Izhikevich's (2007) firing model for the neuronal cells in the brain areas involved, including the preSMA, STN, and PMd. Model-based and MF systems each generated their responses for every stimulus in every trial. In each trial, one response was selected as the output of the model. The proposed new model was focused on the selection process. The model was used to simulate two different types of system-switching: (1) self-initiated system-switching in an II categorization task published in Lim & Hélie (2019) (Section 3), and (2) trial-by-trial cue-based system switching of different age groups from data published in Hélie & Fansher (2018) (Section 4). The model was able to reproduce accuracy learning curves, predict the proportion of switchers for different age groups of participants, and predict the accuracy switch cost in trial-by-trial switching tasks.

The simulation results also suggested that system-switching ability may be related to individual differences in updating and inhibition (two executive functions). To test this hypothesis, Section 5 presented a new behavioral experiment that used a battery of EF benchmark tasks and the same participants were also put in a trial-by-trial system-switching task. The results showed that participants who were able to switch systems from trial-to-trial in the perceptual categorization task had a higher composite updating score, an important component of EF. The next subsections present a review of the most important features and accomplishments of the proposed new model.

6.1 Key Features

Unlike other models of category learning, the proposed new model focuses on the biological system-switching mechanism from MB to MF systems. In contrast, most of the available category learning models highlight the mechanism of response generation and selection. The emphasis on the neurobiological simulation enables a deeper understanding of how switching between two learning systems can be accomplished in the brain. In the model, system-switching is facilitated by the hyperdirect pathway in the basal ganglia. The brain areas involved are the preSMA, STN, and PMd. MB and MF systems are modeled as black boxes that output responses based on their respective accuracy probability in the current task. The responses from the two systems are generated independently. Critically, system-switching is depicted as the reduction of inhibition of the response of the MF system into PMd units. The STN acts as the gate for the MF system's response to activate the PMd units. If the activity of the MF system is lower than the inhibition from the STN, the MF system's response is prevented from activating the PMd units. However, if the activity of the MF system is higher than that of the STN, the response of MF system can activate the PMd units.

6.2 Model Predictions

The proposed model was able to show learning of system-switching through the reduction in STN's inhibition of the MF system's response into PMd units. System-switching was possible when the following criteria were met. First, MB-RL was not the optimal system to learn the task, e.g., when the MB system failed to provide accurate responses over time, the confidence in the MB system decreased with increasing inaccurate attempts at categorizing the stimulus. This was fed into the preSMA as feedback, which lowered the activation of the preSMA and reduced the

STN activity. With reduced activity, the MF system's response inhibition to the PMd units by the STN faded, allowing the response of the MF system to activate the PMd units. This increased the likelihood of selecting the response of the MF system as the overall response. This process showed system-switching when the MB system failed, and the MF system took over to respond. One important prediction of the proposed model is that it predicts a "hard" switch. Once the model has switched from the MB system to the MF system, it cannot switch back to MF. This is because confidence in the MF system can only increase, and the maximum confidence in the MF system is constrained to be higher than the maximum confidence in the MB system. The only case where the model can switch from MF back to MB is when the switch is prompted by a cue (as in Sections 4-5).

Second, with the success of categorizing the stimuli, after numerous trials, the MF system gained enough confidence whereby its activity exceeded the inhibition emitted by the STN. This allowed the MF system's response to be transmitted to the PMd units for action selection. This process may result in system-switching from MB to MF after extensive training, even if the MB strategy is optimal for the task. This is because the model predicts that system-switching should eventually happen regardless of the presence of perceptual cues even in the trial-by-trial switching tasks if the two criteria aforementioned were met. The ability to switch between systems was observed when parameters were adjusted to cater to low confidence in MB and high confidence in the MF system. This could provide a route towards the development of automaticity (Hélie et al., 2015).

Third, in addition to feedback-driven system confidence, the model also showed that individual differences in executive function could affect switching ability. We were able to fit the model to participants from different age groups in a category learning task that involved trial-by-trial switching and show how aging affects categorization system-switching. The model was able to reproduce the accuracy learning curve, switch cost, and proportion of switchers that were shown in the experimental results. The difference in the switching capabilities in young adults, older adults, and people with Parkinson's disease was simulated by adjusting the parameters that governed the learning rate of the MF system's confidence (as in previous simulations) but also the decay in proactive inhibition. We found that fewer participants in the older age groups (older adults and people with Parkinson's disease) had a high learning rate of the MF system's confidence, making system-switching difficult. It is unclear at this point where the MF system's confidence is located, but with their role in reward uncertainty and motivation, the ventral PFC and striatum are plausible loci (Hélie et al., 2017). In addition, more participants in the older age group suffered from proactive inhibition interference when tasks switched frequently. Proactive interference makes it difficult to switch when the tasks demand different responses to similar stimuli. Consistent with model results, previous work has shown that older adults (Hull et al., 2008) and people with Parkinson's disease (Dirnberger & Jahanshahi, 2013) generally have EF deficits. These deficits may be related to decreases in tonic dopamine levels (Hélie et al., 2012).

6.3 Extensions, Improvements, and Future Work

Once choice that needs to be made when designing any computational models is what processes should be directly modeled and what processed can be abstracted as black boxes. Should the visual system be modeled? Or should the model input be a feature-based representation? What about the motor output? In the proposed model, the decision systems were included as black boxes. This choice has some advantages. For example, the model is simpler and provides a more intuitive understanding of the switching process – which was the focus of the current work. It also makes the switching model more general. The decision systems could be replaced by one's favorite MF and MB models of category learning without changing the functioning of the switching model. However, this lack of detailed system modeling also came at a cost. The main one being that the possible interaction between the learning processes within each system and the switching mechanism is not accounted for. We now discuss consequences of this limitation in more details.

First, while the current model was able to match and predict system-switching through neurobiological circuits, it lacks the ability to simulate accurate response times in each trial. If the model could simulate response times, time-related switch costs could be simulated, which would add constraints to the model. From Hélie and Fansher (2018), switch cost was more apparent in response times as compared to just accuracy. Modeling the timing of each system (which are currently black boxes) and adding a motor component to the model could allow for this functionality. The result could provide a better reflection of the different switching capabilities of the different groups of participants.

Second, the black box systems generated output based on a single source of accuracy probability (one for each task and learning system). However, even in a single task, the accuracy probability should vary throughout the session. Initially, without grasping a rule, participants should select the category by guessing or by chance. Over time, more rules are generated by the MB system and each rule has its accuracy probability. Depending on the accuracy feedback of the learning system, its accuracy probability can be adjusted from guessing (i.e., 50% for a two-choice category task) to the maximum value. Future work should add this functionality.

Finally, the model can also be applied to non-human animal studies. Although some aspects of the model would have to be adjusted to rescale the cognitive limitations of non-human subjects, the hyperdirect pathway model can still be implemented to simulate the system-switching capabilities in other primates. This would allow for matching single-cell recordings in the affected brain areas of the animals and more directly testing biological assumptions by accounting for biological data.

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9 Appendix

The proposed model must meet the requirement of having computationally simple neurons that can generate firing patterns exhibited by actual biological neurons (Izhikevich, 2007). However, the intention of the model was not to quantitatively fit neural activation, but to instead seek for a qualitative agreement. The Izhikevich model proves to be computationally efficient in producing rich spiking and bursting dynamics, as exhibited by neurons when simulating multiple neurons in real-time, while maintaining a certain level of biological plausibility. Each neuron in the preSMA and PMd was simulated as follows:

$$100\dot{v} = 0.7(v+60)(v+40) - u + I + noise \tag{A1}$$

$$\dot{u} = -0.03[2(v+60)+u]$$

$$if\ v \geq 35, then\ \ v \leftarrow -50, u \leftarrow u + 100$$

where *v* is the membrane potential, *I* is the input, *u* is an abstract term that describes membrane recovery variable for Na+ and K+ ion channel gating, and *noise* follows a normal distribution of *N(*0,1*)*.

The STN cells were modeled using an adaptation of Izhikevich's firing model parametrized as follows (Michmizos & Nikita, 2011):

$$\dot{v} = 0.04v^2 + 5v + 145.5 - u + 1.3\ I_{STN} + noise \tag{A2}$$

$$\dot{u} = 0.02[0.2v - u]$$

$$if\ v \geq 25, then\ \ v \leftarrow -65, u \leftarrow u + 2$$

where, I_{STN} is input to STN cells. The parametrization of Eq. A2 was obtained by fitting the spike initiation dynamics of the STN cells.

Each unit of cells in the model represents the activities of a tightly interconnected cell group. For each trial, each neuron model was given a time frame of 2000 ms. The activity of preSMA and STN cells started at time = 0 ms, while with the burn-in period, the PMd units started receiving input at time = 500 ms. Figure 3 shows an example spike train for each modeled neuron.

Interneuron connections were simulated as synapses simplified by modeling the delays of spike propagation through the synaptic cleft. The simulation represented the gradual delivery of neurotransmitters from the presynaptic neuron to the postsynaptic neuron. A standard way of modeling the synapse is to use an α-function (Ashby & Hélie, 2011; Rall, 1967):

$$f(t_\alpha) = \frac{t_\alpha}{\lambda} exp^{(\frac{\lambda - t_\alpha}{\lambda})} \tag{A3}$$

where t_α is the time since the cell voltage reached v_{peak} and λ is a constant that determines the duration of signal propagation in the synapse. Greater λ values increase the delay in synaptic transmission. Every time the presynaptic neuron cell spikes, the α-function is delivered to the postsynaptic cell, with spiking time starting at $t = 0$. The α-function has a maximum value of 1.0 and it decays to .01 at $t = 7.64\lambda$ (Ashby & Hélie, 2011). If the propagation of neurotransmitters is still in process and a second spike is produced, a new α-function that corresponds to the second spike is added to the first α-function, giving an integrated α-activity. The latency in a typical synapse is generally less than 0.5 ms and this delay was approximated with $\lambda = 60$.

9.1 Model's Circuit

9.1.1 Response Generation in MB and MF systems

As can be seen in Figure 4, the MB system was connected to the PMd and the preSMA. The MB response was fed into PMd units as input (the blue line). The response was then checked for its accuracy, and feedback for both the MB and MF systems were given separately. The connection from the MB system to the preSMA (the orange line) served as the confidence for that system ($MB_{confidence}$), which was fed into the preSMA as input for activation. Greater $MB_{confidence}$ increased the activity in the preSMA. $MB_{confidence}$ was adjusted with feedback from responses through learning.

The response of the MF system, on the other hand, was directed only to the PMd. This connection was dependent on the inhibition of the STN and feedback from the response. The STN received its input from the preSMA, whose activity was increased by greater $MB_{confidence}$. Thus, greater $MB_{confidence}$ increased activity in the STN, preventing the response of the MF system from reaching the PMd units.

Since the proposed model focused on the mechanism that facilitates switching between the MB and MF systems, both the MB and MF systems were modeled as black boxes. It was hypothesized that MB responses would be preferred in the beginning with high confidence, which leads to the inhibition of MF responses and prevents its activation from reaching the PMd cells. As discussed earlier, different categorization tasks may require a different learning system to maximize accuracy. Rule-based tasks should follow MB responses, whereas II tasks should follow responses from the MF system. In II tasks, since responses from the MB system are considered suboptimal, early errors from the MB system decrease $MB_{confidence}$. This weakens the inhibition of the MF system, slowly allowing the MF response to reach the PMd units.

In a category learning task, participants are asked to categorize a perceptual stimulus. To simulate this situation, the model receives stimuli in the form of its desired categorization response.[3] In a two-choice categorization task, if the stimulus belongs to category 'A', then the desired categorization response for the stimulus is 'A'. The desired categorization response served as the input to the learning systems. Both MB and MF systems had preset accuracy probabilities (Acc_{MB}, Acc_{MF}), and generated responses based on the accuracy probability independently. For instance, if the probability of MB accuracy was 0.8, MB had an 80% chance of producing the desired categorization response. Else the response should be the incorrect category. The same process independently applied to the MF system. As a result, the response of each system was independent, and one system could be accurate while the other may not be.

The accuracy probability of each system is task dependent. For instance, the MB system has a higher chance of generating an accurate response in an RB task, as compared to its performance in an II task where the optimal solution requires relying on the MF system.

The proposed model was also able to simulate accuracy performance in category learning tasks that demanded changing of the responding system on a trial-by-trial basis. This was implemented in the model with perceptual cues. Perceptual cues give a contextual indication to the participant as to whether or not they are performing the same task. In the proposed model, there is proactive interference from the previous task when switching from one task to another. As a result,

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[3] As a reminder, the proposed model does not learn to categorize stimuli; it only learns to switch between categorization systems.

performance in the new task might dip in the first few trials after a switch. However, in a learned task, the accuracy should be able to recover to a certain extent depending on the persistence of the interference. Accuracy probability of a system, ACC_{MB} is given as follows:

$$ACC_{MB} = ACC_{MB_{Task}} - \left[R_{MB_{Task}}(1-D)^{N}\right] \tag{A4}$$

$$ACC_{MF} = ACC_{MF_{Task}} \tag{A5}$$

where, $ACC_{MB_{Task}}$ is the accuracy probability of the MB system in a given task, $R_{MB_{Task}}$ is the proactive interference affecting the accuracy probability of the MB system for the current task, D is an exponential decay rate, and N is the number of trials since the last task switch.

9.1.2 Model free system inhibition

The $MB_{confidence}$ indicated how confident the response from the MB system was, which affected the system switching process. $MB_{confidence}$ ranged from 0 to 1 and was initially set to 0.99 (in line with the bias observed in primates). As a result, the overall response followed the MB system at the beginning of the experiment, and this confidence could be adjusted based on trial-by-trial feedback.

With sufficient training, a participant may associate a RB task with an MB system response, and an II task with an MF system response. If a MB system response was 'preferred'[4] in a task, this part of the model increased the preSMA input to increase the inhibition of the MF system

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[4] We put 'prefer' in quote here because we are not assuming that subject have a conscious preference or make a volitional system switch. We take no position on whether participants can volitionally control system-switching.

response to the PMd cells. If a MF system response was ‘preferred’, the preSMA’s input was lowered to reduce the inhibition of the MF system response to the PMd cells.

The associations between task cues and systems are represented by A_{MB} and A_{MF}. These values were calculated as follows:

$$A_{MB} = S_{MB}[vc_{RB} + (1 - vc_{RB})R_S(1 - D)^N] \tag{A6}$$

$$A_{MF} = vc_{II} \times S_{MF} \tag{A7}$$

where, vc_{RB} and vc_{II} are the presence of perceptual cue for RB and II tasks (respectively), S_{MB} is the association of MB responding with a RB perceptual cue and S_{MF} is the association of MF responding with an II perceptual cue, R_S is working memory’s proactive interference decay effects on preSMA input, D is the exponential decay rate (same as in Eq. A4), and N is the number of trials since the last task switch.

In the proposed model, *vc* was represented in the form of a binary input; when the perceptual cue was present, *vc* = 1, whereas when the perceptual cue was absent, *vc* = 0. The presence of a perceptual cue for an II task (vc_{II} = 1) reduced the input to preSMA cells by a factor of S_{MF}, which in turn reduced activation of the STN, thus encouraging the use of the MF system as the overall choice response. On the other hand, the presence of a perceptual cue for an RB task (vc_{RB} = 1) increased the inhibition of STN with stronger input to the preSMA cells by a factor of S_{MB}. Note that even when vc_{RB} = 0, the interference of previously using an MB strategy may still linger with an exponential decay function even after the task was changed to an II task. Participants who failed to switch systems from task-to-task may have experienced a larger interference effect. These non-switchers might abandon an optimal responding system (e.g., MF responding in an II task) during the frequent task switching trials and stick to a suboptimal responding system (e.g., MB responding in an II task). Crossley et al. (2018) showed that in a task intermixed with RB and II trials, some participants abandon their MF strategies to use either guessing or an MB strategy in the II task, but optimal strategy use was unaffected in the case of the RB task in the intermixed trials task.

9.1.3 preSMA input and circuit connectivity

The STN exerted an inhibitory activity on the MF system output to prevent the MF system's response from reaching the PMd units. The activity of STN was dependent on the preSMA cells. The connection from preSMA to STN was excitatory. High $MB_{confidence}$ activated the preSMA, which led to the indirect inhibition of the MF system output. This resulted in the use of the MB response as the overall model response. I_{preSMA} fed into preSMA's Izhikevich firing model as input and activated the unit accordingly. The nonnegative input to preSMA cells was in the form of a square function that varied with the presence of perceptual cues and confidence of MB:

$$I_{preSMA} = 130 \times \left[A_{MB} - A_{MF} + MB_{confidence}\right]^{+} \tag{A8}$$

where, A_{MB} is the activation of the MB system with the presence of a cued RB task, and A_{MF} is the activation of the MF system with the presence of the cued II task (Eq. A6 and A7). $[a]^{+}$ is a function that returns a if a is positive and 0 otherwise.

9.1.4 STN input

The integrated α-activity from preSMA, α_{preSMA}, served as an input to the STN:

$$I_{STN} = \alpha_{preSMA} \quad \text{(A9)}$$

where the α- function is defined by Eq. A3.

9.1.5 PMd input and category selection

With greater activation of STN, when the accumulation of its integrated α-activity exceeded the activity of the MF system, the response of the MF system was inhibited. The equation that governs the inhibition of the response of the MF system was given by:

$$I_{PMd} = 70 \times \left\{ \left(\mathrm{MB}_{\mathrm{response}}\right) + \left[\left(MF_{response} \times MF_{confidence}\right) - (0.67\ \alpha_{STN})\right]^{+} \right\} - 20\ \alpha_{L} \quad \text{(A10)}$$

where, I_{PMd} is the input to PMd unit, $\mathrm{MB}_{\mathrm{response}}$ is the response of the MB system that feeds into the PMd unit, $MF_{response}$ is the response of the MF system that feeds into the PMd unit, $MF_{confidence}$ is the confidence of the MF system, and α_{STN} is the integrated α-activity of the STN (as calculated using Eq. A3). In addition to the input, each PMd unit received lateral inhibition from the other PMd units in the form of α_L.

Initially, when the value of $MB_{confidence}$ was high enough, the activity of the STN was high enough so that the value of its integrated α-activity was greater than the value of $MF_{response} \times MF_{confidence}$. The difference in the output from STN and the response of the MF system as shown in Eq. A10 was negative (which became 0 after applying the bifurcation function). Adding this term to the response of the MB system gave the input to the corresponding PMd unit. However, if the integrated α-activity of the STN was smaller than the value of $MF_{response} \times$

$MF_{confidence}(n)$, the difference was positive. Hence, the MF system's response was not inhibited, and the response from the MF system was added to the response of the MB system as the input into the PMd unit.

The PMd unit with the integrated α-activity that reached the decision threshold first was selected as the response of the overall system. If the α-activity of all units reached the threshold at the same time, the choice was random. If no units reached the threshold by the end of the trial, the unit with the highest activity was selected as the response of the overall system. This latter case was considered an informed guess when a forced choice was required.

9.2 Learning

MB- and MF-RL have been used to understand learning in biological systems in both cognitive and neural systems (Banino et al., 2018; Mattar & Daw, 2018). The Rescorla-Wagner (1972) model can be used to describe these types of learning. With a choice being made, the difference between the expected value of the chosen option, v_i, and the experienced outcome, r is computed. If the outcome exceeds expectations, the association strength of appropriate synapses is increased. If the outcome is worse than expected, the strength is reduced. The Rescorla-Wagner equation (Averbeck & Costa, 2017; Rescorla & Wagner, 1972) summarizes the process of value adjustment during learning for behavior in its simplest form, which is given by:

$$v_i(k+1) = v_i(k) + \gamma(r(k) - v_i(k)) \tag{A11}$$

where γ is the learning rate of the model that controls the size of each of the learning updates.

9.2.1 *Association of task cues and systems (learning system)*

Conditioned learning for each system to a cued task was modeled with the Rescorla-Wagner model as follows:

$$S(n+1) = S(n) + \left[vc(n) \times F_S(n) \times \gamma_S \times \left((S_{max}) - S(n)\right)\right] \qquad \text{(A12)}$$

where S is the association of a perceptual task cue to a learning system (S_{MB} for MB system and S_{MF} for MF system), γ_S is the learning rate for the Rescorla-Wagner model for the association, F_S is the accuracy feedback of the corresponding learning system when compared to the actual category of the stimulus, and S_{max} is the upper bound for S. In the presence of a perceptual cue, the corresponding S is learned with the accuracy feedback of a particular learning system (MB or MF). F_S took either the value of 0 or 1, with 0 representing mismatch of the learning system's response with the actual stimulus category and 1 as the accurate response of the learning system. When the particular learning system gave a correct response in the presence of a perceptual cue, the corresponding S increased with γ_S and the difference between S_{max} and the previous S value. As S approached its maximum value, the increment per trial decreased.

9.2.2 *Confidence in the MB system*

$MB_{confidence}$ was adjusted according to the success of the MB system response in each trial with Rescorla-Wagner learning:

$$MB_{confidence}(n+1) = MB_{confidence}(n) + \left[\gamma_{MB} \times \left(F_{MB}(n) - MB_{confidence}(n)\right)\right] \qquad \text{(A13)}$$

where, γ_{MB} is the learning rate for the Rescorla-Wagner model for the MB system confidence and F_{MB} is the accuracy feedback for the MB system. When the MB system gave a correct response, $MB_{confidence}$ increased with γ_{MB} and the difference between 1 and the previous $MB_{confidence}$. As $MB_{confidence}$ approached 1, the increment per trial decreased. When the MB system gave an incorrect response, $MB_{confidence}$ decreased with γ_{MB} and the difference between 0 and the previous $MB_{confidence}$. As $MB_{confidence}$ approached 0, the decrement per trial decreased.

9.2.3 Confidence in the MF system

The weight of the MF system's response varied with confidence in the MF system. Confidence was adjusted according to the response accuracy of the MF system, given by the Rescorla-Wagner learning model as follows:

$$\begin{aligned} MF_{confidence}(n+1) \\ &= MF_{confidence}(n) \\ &+ \left[K \times \gamma_{MF} \times \left(MF_{confidence_{max}} - MF_{confidence}(n)\right)\right] \end{aligned} \tag{A14}$$

and $K = \begin{cases} 0 & if\ respone\ of\ \ MF\ is\ incorrect\ or\ the\ system\ does\ not\ follow\ reponse\ from\ MF \\ 1 & if\ reponse\ of\ MF\ is\ correct\ and\ the\ system\ follows\ response\ from\ MF \end{cases}$

where, γ_{MF} is the learning rate of the Rescorla-Wagner model for $MF_{confidence}$. When the MF system gives a correct response, $MF_{confidence}$ increases with γ_{MF} and the difference between the maximum value of $MF_{confidence_{max}}$ $(MF_{confidence_{max}} > 1)$ and the previous $MF_{confidence}$. As $MF_{confidence}$ approaches $MF_{confidence_{max}}$, the increment per trial decreases.