Neurobiological Mechanisms of Cognitive Maintenance and Disengagement: Accounting for Dissociable Variance in Working Memory and Fluid Intelligence Task Performance

by

Ashley Nespodzany

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Graduate Supervisory Committee:

Mary Burleson, Chair
Nicholas Duran
Elias Robles-Sotelo

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ABSTRACT

Performance on working memory (WM) and fluid intelligence tasks (gF) is often highly correlated. However, recent research by Shipstead, Harrison, & Engle (2016) has suggested that dissociable cognitive processes underlie performance on WM and gF tasks, such that WM task performance is contingent upon maintenance of relevant information while gF task performance is contingent upon disengaging from irrelevant information so that updating can occur. The aim of the current study was to test the proposal that the dopamine gating system, a neurological mechanism underlying information encoding and updating, is a plausible mechanism underlying the abilities identified by Shipstead and colleagues that are separately unique to WM and gF. Sixty-three participants completed a task that measured ability to maintain and update information, and is neurologically known to reflect functionality of the dopamine gating system during updating performance. The results indicate that individual differences in updating performance are predicted by gF, but not by WM. This suggests that the ability to disengage from irrelevant information is facilitated by distinct processes in the dopamine gating system, and is a distinguishing component of gF.

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Working Memory

Working memory is the cognitive system that allows information to be continuously represented in conscious awareness, and it is considered an inherent component of human cognition. Working memory can be conceptualized as a system that holds relevant information online in the absence of stimuli so that information is still easily accessible. The purpose of maintaining representations in and accessible to awareness is to process and use that information to carry out goal-directed behavior. This system facilitates the execution of internal goal-directed behavior by regulating and biasing attention toward relevant internal and external information. A simple, real-world example of this faculty is listening to a friend state their phone number for you, and then you writing it down. The goal is to obtain the correct phone number from the friend, so while the friend is speaking each chunk of numbers (the stimuli) and usually in sets of 3-4 digits at a time, working memory encodes and maintains the sets of numbers as a mental representation (Cowan, 2001) so that the numbers can be accessed when you are ready to write them down (in absence of the stimuli).

Individual differences in working memory functioning are often psychometrically measured through measures of working memory capacity, as the system is believed to have limited storage and processing ability (Baddeley & Hitch, 1974). Researchers have therefore designed a variety of tasks that aim to measure how many units of information an individual can maintain in the contents of awareness, especially in the presence of distracting stimuli or tasks. For example, a traditional type of working memory task is span tasks, in which participants are presented with units of information that they have to recall immediately after the presentation of that information (Daneman & Carpenter, 1980; Turner & Engle, 1989). The amount of information that they can accurately recall would indicate that individual's working memory capacity, or the amount of information that could be successfully maintained in awareness.

These types of tasks can be made more complex, and ecologically valid, by including distracting processing tasks with the presentation of the to-be-remembered items (e.g., having participants solve a math problem while attempting to maintain a list of random letters). While some studies have purported to have discovered the storage limit of working memory, starting with Miller's "magic number seven plus or minus two" (Miller 1956), many factors influence just how much one can maintain in working memory, and there is still no clearly defined cut-off point. Nonetheless, there is a range of individual differences on these capacity measures, which has established them as useful tools for assessing individual working memory ability.

While working memory research was founded upon the idea that the working memory system had finite storage, it was also realized that the limitation of assessing capacity is that capacity is only one static part of the working memory process. Simple capacity measures are only useful in measuring the amount of information one is capable of maintaining in awareness. This is problematic because working memory is a system that requires multiple cognitive processes. These constituent processes are encoding, maintaining, and updating information, and they can be considered cyclical in nature (see Figure 1).

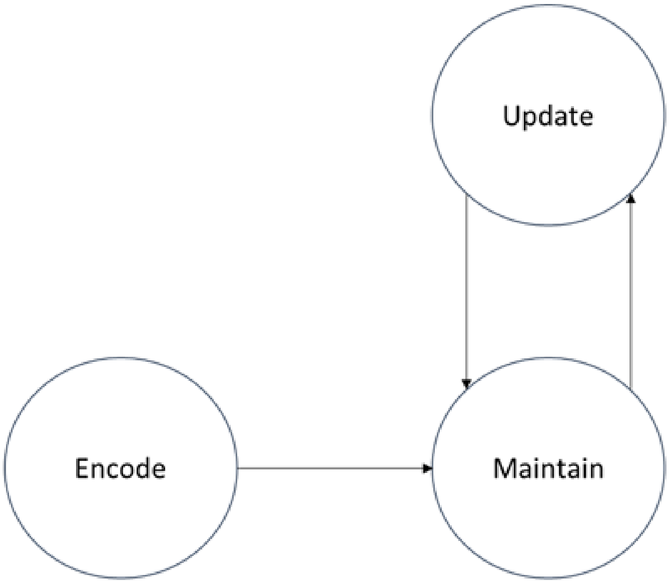

Figure 1. Cyclical processes of working memory. Information is encoded into the contents of working memory where it is then maintained. When information becomes outdated, new information is updated into the contents of working memory and then maintained.

First, information from the environment is encoded as a representation in awareness. Then, once a representation is made, it must be maintained so that the information is easily accessible (this would be the process measured by capacity tasks). Lastly, representations can become irrelevant or “old” when more relevant or new information is available/presented in the environment (Ecker, Lewandowsky, & Oberauer, 2010; Morris & Jones, 1990). When new or more relevant information is encoded as a representation in awareness, it essentially replaces the old information, and this process is called “updating.” This last step of updating is integrative of encoding because the act of updating is essentially the process of encoding new information, which is why these processes are somewhat cyclical. Individual differences in working memory can therefore also be psychometrically measured with tasks that gauge the effectiveness of updating; however, capacity measures are much more commonly used.

The working memory system is an essential component of learning, reasoning, problem solving, and other complex cognitive processes that are used in daily life, and render it “a crucial interface between perception, attention, memory, and action” (Baddeley, 1996, p. 13472). Individual differences in working memory capacity have therefore been linked to many facets of cognitive ability such as reading comprehension (for a meta-analysis see Daneman & Merikle, 1996), language acquisition (for a review see Baddeley, 2003), and general intelligence (for a meta-analysis see Oberauer, Schulze, Wilhelm, & Süß, 2005).

Fluid Intelligence

Amongst the many cognitive abilities that working memory has been correlated with, is fluid intelligence with which it shares between 50% (Kane, Hambrick, & Conway, 2005) and 80% (Oberauer et al., 2005) of their variance on task performance for most individuals. Fluid intelligence is characterized by the ability to solve novel-type problems that don’t require any preexisting knowledge or language (Cattell, 1963). Because fluid intelligence is a cognitive ability that is non-verbal and not contingent upon previously learned facts, tasks that measure it are also culturally fair measures of intelligence. Types of problems that measure fluid intelligence are dependent upon abilities to reason, use logic, and recognize patterns essential to establishing solutions (Carpenter, Just, & Shell, 1990).

A traditional task that measures an individual’s fluid intelligence is the Raven’s Progressive Matrices task (Raven, 1965). In this task, participants see a set of objects or shapes that follow a pattern. The last item in this set is missing, and it is the participant's job to select the item that will complete the set according to the pattern. This test measures the ability to reason, use logic, and recognize patterns because the participant is not informed what the pattern is; it is their job to first figure that out.

The theory of fluid intelligence as a construct was first proposed in the mid-nineteenth century (Cattell, 1963), however unlike the system of working memory, fluid intelligence has not been defined in terms of its constituent psychological processes. Namely, an issue with understanding the link between working memory and fluid intelligence is that fluid intelligence is not broken down into a model of separable cognitive processes. Fluid intelligence is considered to depend on the working memory system—essentially, fluid intelligence is believed to be facilitated by the cognitive processes involved in working memory.

Researchers have proposed that maintaining representations in awareness is critical to solving novel problems, by directing attention appropriately (Engle, 2002) and manipulating information relevant to the task at hand (Engle, Tuholski, Laughlin, and Conway, 1999). Colom and colleagues (2008) proposed that short-term storage capacity is what accounts for the largest amount of variance between working memory and intelligence tasks. Other research has suggested that mechanisms of interference control can account for common variance between fluid intelligence and working memory (Burgess, Gray, Conway, and Braver, 2011). Some theories do not clearly converge with each other, but regardless of perspective, all theories suggest that cognitive processes characteristic of the working memory system facilitate the execution of fluid intelligence tasks. Therefore, researchers believe the strong correlation between the two constructs is due to the working memory processes that are deployed during reasoning tasks.

The strong correlation between working memory and fluid intelligence has been further substantiated by the search for cognitive systems in the brain, and much of this research suggests that both working memory and fluid intelligence recruit common brain regions. Functional imaging, electroencephalographic experiments, and brain damage studies have related fluid intelligence task performance and working memory task performance to regions of the prefrontal cortex (Braver, Cohen, Nystrom, Jonides, Smith, & Noll, 1997; Burgess et al. 2011; Duncan, Burgess, & Emslie, 1995; Engle, Kane, & Tuholski, 1999; Gray, Chabris, & Braver, 2003; Prabhakaran, Smith, Desmond, Glover, & Gabrieli, 1997;). The dorsolateral prefrontal cortex (a sub-region of the prefrontal cortex) is especially crucial to performance of both task types (Colom et al., 2009; Kane & Engle, 2002). Volume of gray matter within this region has been linked to individual differences in cognitive measures as well.

Because cognitive and neurophysiological research has linked working memory and fluid intelligence together, these abilities are often researched as either emergent properties of one underlying cognitive-processing system (Engle, 2002) or under the assumption that the working memory system underlies and therefore causes the performance of fluid intelligence tasks (Oberauer, Süß, Wilhelm, & Sander, 2007). However, when examining each construct by definition and by psychometric methods, they seem to be measures of independent abilities; working memory is characterized by representing and accessing information in awareness while fluid intelligence is characterized by using reasoning in solving novel problems. Measures of working memory are designed to assess the ability to represent and maintain information relevant to task goals, while measures of fluid intelligence are designed to assess the ability to reach accurate solutions to novel problems.

Moreover, correlation does not imply causation, and therefore it is difficult to conclude that one of these abilities is the foundation for the other. Thus, both the construct definitions and psychometric measures of working memory and fluid intelligence provide little insight into why these separate ability measures share such a large portion of variance.

A study conducted by Shipstead, Harrison, and Engle (2016) investigated theoretical differences between the constructs of working memory and fluid intelligence by examining constituent mental processes involved in the performance of each task type. They concluded that separate cognitive mechanisms appear to underlie performance of working memory and fluid intelligence tasks. Specifically, they found that working memory measure scores are strongly related to acts of intentional maintenance, while fluid intelligence measure scores are related to the ability to disengage from outdated information (e.g., forgetting incorrect assumptions about the solution to a problem so as not to perseverate on an ineffective method).

Behavioral Predictions

With this finding, the shared variance in working memory capacity measures and fluid intelligence measures may be more related to mechanisms of specific cognitive processes, and not so much the entirety of the working memory system. When considering the constituent cognitive processes believed to give rise to working memory (i.e. encoding, maintaining, and updating), updating is a likely cognitive process that accounts for variance in performance of both fluid intelligence and working memory tasks. This is hypothesized because the process of updating relevant information into awareness first requires disengaging (i.e., the process identified by Shipstead et al. (2016) to be related to fluid intelligence performance) from old information to successfully update new and more relevant information into awareness. If this is the case, then working memory measures may be strong measures of one's ability to maintain relevant information, and fluid intelligence measures may actually be strong measures of one's ability to disengage from no longer relevant information so one may update newly relevant information (see Figure 2).

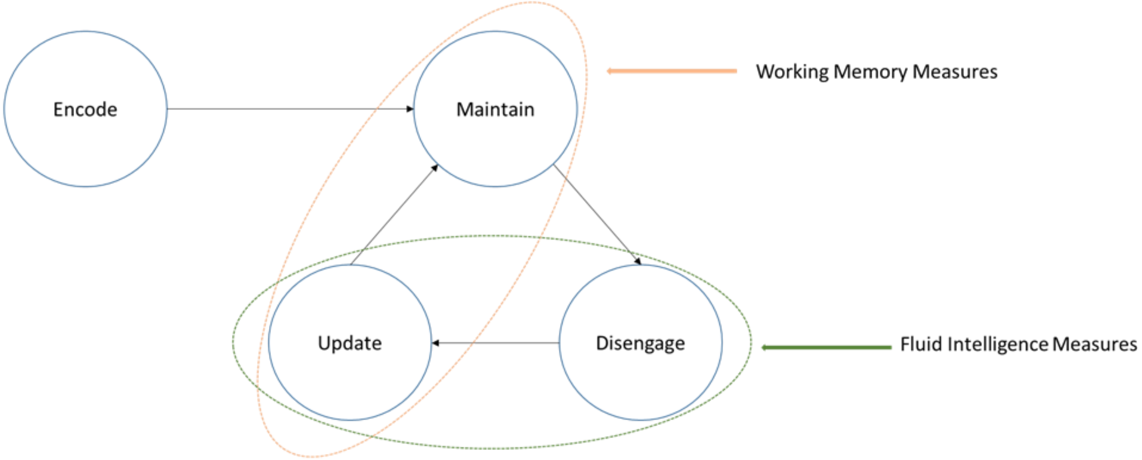

Figure 2. Incorporating the process of disengaging into working memory functioning. The process of disengaging precedes updating, as the previously maintained information must first be released from the working memory stores in order for new information to be represented without interference. Working memory tests likely tap into an individual's ability to maintain encoded and updated information, while fluid intelligence tasks likely tap into an individual's ability to disengage from outdated information so that updating can occur.

Hypothesis 1. The first aim of this study is to test the hypothesis that the cognitive process of working memory updating is uniquely related to fluid intelligence task performance and not working memory task performance. This would suggest, in concordance with Shipstead and colleagues' (2016) theory of maintenance and disengagement, that the ability to disengage from irrelevant information is an essential process in fluid intelligence task performance and a psychological process that likely accounts for the shared variance between fluid intelligence and working memory measures since both types of tasks often require disengaging/updating.

Identifying a Neurological System Consistent with Cognitive Research

As with behavioral research, cognitive neuroscience has traditionally sought to demarcate the components of working memory and fluid intelligence by searching for neural mechanisms that are common to both constructs. As previously mentioned, the frontal lobes have been identified as functional substrates correlated with performance of both working memory and fluid intelligence tasks (e.g., Burgess et al., 2011; Gray et al., 2003). However, in light of the recent work by Shipstead et al. (2016) that suggests that performance of working memory and fluid intelligence tasks are unequally reliant on independent cognitive processes, the reductionist approach of the neurocognitive paradigm should also begin to investigate the biological substrates and networks that are unique to working memory and unique to fluid intelligence. If distinct cognitive processes are facilitated by distinct neurobiological processes, then identifying the neural processes unique to each type of cognitive construct is important for understanding individual differences in cognitive ability.

A biologically plausible system that can account for each of the underlying components of both working memory and fluid intelligence while remaining consistent with the prefrontal cortex correlational research is Braver and Cohen's (2000) *dopamine gating system*. This system includes many brain regions consistent with imaging research that has related the psychological constructs of working memory and fluid intelligence to the prefrontal cortex, and the dopamine gating system includes neurological mechanisms associated with acts of both maintenance and disengagement.

Encoding and Maintaining. In the proposed dopamine gating system, the prefrontal cortex actively maintains representations through the excitation of local neuronal circuits that stabilize themselves with excitatory feedback, and inhibit activation of nearby circuits (Braver & Cohen 2000). The self-excitatory loop, is the circuit that, while active, maintains the information that has been encoded into it; it is the temporary store for working memory contents. Encoding is the initial activation of a self-excitatory loop in the prefrontal cortex. What initiates a loop in the prefrontal cortex is transient dopamine signaling, which is received by the prefrontal cortex from the ventral tegmental area, a dopamine-producing region of the midbrain.

This suggests an integral role for dopamine and the prefrontal cortex in cognitive processes attributable to encoding information temporarily in awareness. This neural system is responsible for the representation and stabilization of relevant information, and also responsible for the simultaneous inhibition of irrelevant information. Thus, the connectivity of the circuits projecting to and from the prefrontal cortex is also characteristic of the cognitive, top-down processing models of working memory and attention regulation. Essentially, the anatomy of this neurological system suggests that it underlies psychological processes that are involved in working memory, fluid intelligence, and attention control.

To elucidate how this system underlies the process of updating, dynamic dopamine firing from the ventral tegmental area signals the self-excitatory networks in the prefrontal cortex to either actively maintain information or to update new or more relevant information into the network. Thus, dopamine serves as a modulatory neurotransmitter for prefrontal circuits involved in information representation (O'Reilly, 2006) as well as the dynamic changing of such representations. Essentially, the dopaminergic input from the ventral tegmental area acts as a "gating mechanism" for the representational contents in the prefrontal cortex. Dopamine acts a signal for when working memory contents need to be updated; a signal that new and more relevant information is to be let in and maintained in the circuit (this can be considered as briefly opening the gate). This momentary signaling to open and close the gate not only allows the representation of updated information in the circuit, it simultaneously prevents irrelevant information from disrupting the currently activated network (the absence of transient dopamine signaling can be analogous to closing the gate, which keeps competing information out).

Investigators interested in the "when and what" to update into the prefrontal cortex have proposed two theories of how this system responds to stimuli and inputs. One is that the same dopamine system that modulates reward prediction error can train the gating mechanism to respond to inputs that will maximize reward—or in other words, the reward system trains the gating mechanism to update goals that will guide behavior toward reaching a reward (Braver & Cohen, 2000). A similar theory is that the basal ganglia enables the selection of the most relevant information by having a role in filtering out irrelevant information (McNab & Klingberg 2008). Functional MRI research conducted by D'Ardenne et al. (2012), has shown that simultaneous activation of the basal ganglia, substantia nigra (another dopamine producing cell body that projects to the basal ganglia), and ventral tegmental area occur during working memory tasks that require rapid updating of information.

The aforementioned fMRI research conducted by D'Ardenne et al. (2012) is particularly important in the present study. This research has shown that performance during an AX-Continuous Performance Task that requires updating of information is related to activation of the dorsolateral prefrontal cortex, ventral tegmental area, substantia nigra, and basal ganglia during the time-frame in which successful updating occurs. That is, correct behavioral responses to this updating task are contingent upon the cohesive operation of the dopamine gating system’s units. These findings not only connect the research on cognitive ability and the individual brain regions, they also suggest that cognitive updating is facilitated by appropriately timed dopaminergic signals to the prefrontal cortex within this circuit.

Cognitive Disengagement and the Dopamine Gating System

So far, this neural mechanism corroborates the theory that there are constituent, distinct processes involved in working memory, specifically: encoding, maintenance, and updating. While disengaging has been proposed in the cognitive model, it is novel to be considered a neural process within the dopamine gating system. However, if dopamine signals the prefrontal cortex to update, and updating is preceded by disengaging, then dopamine signals within this neural system are likely to also underlie the process of disengaging.

The following is to reiterate the mapping of the cognitive process model onto the processes facilitated by the dopamine gating system. *Encoding* of information is the step in the model where a dopamine signal from the ventral tegmental area to the prefrontal cortex briefly opens the gate for information to enter; the self-excitatory loop is essentially receiving the relevant information it needs to represent. The gate then rapidly closes—likely due to the absence of this dopamine signal from the ventral tegmental area to the prefrontal cortex—to lock in the representation and the neuronal self-excitation then maintains this representation. This is the process of *maintaining* information. When this representation is outdated or no longer relevant, the *updating* of working memory contents has to occur, which is facilitated by dopamine again being released from the ventral tegmental area to bind to dopaminergic receptors in the prefrontal cortex to start this process over with new information. As mentioned, it is this updating process that I propose is inclusive of the *disengaging* process.

While updating has traditionally been treated as a process that overrides old information with new, it is important to consider that new information likely cannot take the place of old information without first ridding working memory contents of the old information. If the contents of working memory were not cleared prior to adding information, new information would share attentional resources with old information. This phenomenon is known as cognitive interference. Again, because the system is confined by its storage capacity, interference must be minimized by removing the irrelevant information from awareness. With this in mind, it is likely that the dopamine signals that facilitate updating simultaneously facilitate the release of previously relevant information from the contents of memory. Essentially, the dopamine signaling that opens the gate to update new information is also releasing outdated information—which can also be conceptualized as the mechanism of disengaging. This process, as proposed by

Shipstead et al. (2016), is again an important process in performance of fluid intelligence type tasks.

Neurocognitive Predictions

Within the context of the dopamine gating system and within the context of the proposed separate abilities that underlie working memory and fluid intelligence, it is hypothesized that working memory tasks are likely tapping into the functionality of the self-excitatory circuits that maintain the most relevant information (acts of intentional maintenance), and fluid intelligence tasks are tapping into the functionality of the dopamine signaling that releases outdated information in these frontal circuits (disengaging and updating). If these hypotheses are correct, then the mental process of working memory updating is preceded by disengagement (an ability strongly related to fluid intelligence), and disengagement is neurologically facilitated by dopamine signals from the ventral tegmental area to the prefrontal cortex. In other words, updating is likely facilitated by the disengagement mechanism that is essential in performance of fluid intelligence tasks, and therefore updating ability is likely better related to fluid intelligence task performance than to general working memory task performance.

Hypothesis 2. The second aim of this study is to test the hypothesis that the dopamine gating system is likely the neurological system that facilitates cognitive processes that can account for shared and distinct variance in performance of working memory and fluid intelligence tasks. I believe that while the dopamine gating system underlies the execution of both types of tasks, the specific biological functions it carries out (maintaining and updating) can be separately related to the cognitive processes that are unique to each cognitive construct, e.g. fluid intelligence and working memory. It was predicted that eye-blink rate would be strongly related to fluid intelligence since it is assumed to be an index of dopamine induced disengagement. Because working memory performance should not be related to disengagement it was also hypothesized that working memory scores would not be related to spontaneous eye-blink rate. In summary, higher levels of dopamine (indexed by eye-blink rate) should correlate with higher scores on updating trials and higher scores on fluid intelligence tasks because dopamine induces cognitive disengagement within the dopamine gating system.

In the present study, a modified AX-Continuous Performance Task (see methods for a description) from D'Ardenne and colleagues' experiment was used to measure working memory updating and working memory maintenance. The AX-Continuous Performance Task was used because performance on this task reflects functionality of the dopamine gating system as demonstrated by D'Ardenne et al. (2012). Specifically, it is experimentally supported that updating performance during this task reflects the recruitment of the substantia nigra, basal ganglia, ventral tegmental, and dorsolateral prefrontal cortex, with the assumption that the correlated activation of both the dopamine producing cell bodies and dorsolateral prefrontal cortex is indicative of dopamine release to the prefrontal cortex (D'Ardenne et al., 2012).

Therefore, if fluid intelligence is uniquely related to updating performance on this task, then it can be inferred that the dopamine signaling characteristic of this system is also likely facilitating the process of cognitive disengagement in fluid intelligence task performance.

The role of the dopamine gating system and dopamine signaling in individual differences of fluid intelligence and working memory was tested by using spontaneous eye-blink rate as an indicator of dopaminergic activity in cognitive circuits. Primate studies involving destruction of dopaminergic cell bodies show that eye-blink rate is positively correlated with dopamine levels (Lawrence & Redmond, 1991). These studies are consistent with research in human subjects with dopamine related pathology such as Parkinson's disease and schizophrenia, as well as animal research on dopamine altering pharmacological treatments (Agostino, Bologna, Dinapoli, Gregori, Fabbrini, Accornero, & Berardelli, 2008; Kleven & Koek, 1996; Colzato, Wildenberg, & Hommel, 2008; Taylor, Elsworth, Lawrence, Sladek, Roth, & Redmond, 1999). Eye-blink rate has been implemented in cognitive research as an index of dopamine in striatal tissue of the basal ganglia. It is specifically associated with cognitive inhibition, switching, and termination of cognitive representations (Colzato, Wildenberg, Wouwe, Pannebakker, & Hommel, 2009; Chermahini & Hommel, 2010; Dreisbach et al. 2005; Irwin 2013).

Methods

Participants

Sixty-four undergraduates from Arizona State University's West Campus were recruited for the experiment. Participants' ages ranged from 18 to 35 years old with a mean age of 21.7 years. Fifty-two females and 12 males were recruited. All participants were students who were enrolled in psychology courses which required research participation for course credit.

Measures

AX-Continuous Performance Task (AX-CPT). Subjects completed an eight-minute AX-CPT modified from the task used by D'Ardenne et al. (2012). The AX-CPT is designed to measure updating accuracy and maintenance accuracy, and consists of these two discrete trial types that are also known to reflect dopamine signaling in the dopamine gating system.

The task presents letters on screen in a one-at-a-time sequence in the order of a cue letter then a probe letter. Cue letters (A or B) indicate a rule set for behavioral responses (pressing 1 or 2) when followed by probe letters (X or Y, see Figure 3). Consecutive trials either require an update of task rules (e.g., cue 'A' trial followed by a cue 'B' trial) or maintenance of the same task rules (e.g., cue 'A' trial followed by another cue 'A' trial). Therefore, updating trials are trials where cues differed consecutively, and maintenance trials are trials where cues did not differ consecutively. The research conducted by D’Ardenne and colleagues demonstrated that the dopamine gating system shows correlated activation during trial types that require memory updating. It is therefore inferred that accurate performance of updating trials in this task reflects functionality of the dopamine gating system. All participants completed both updating trials and maintenance trials in the task, and update and maintenance conditions within the task were randomized.

Working memory measures. To gather individual working memory scores, a battery of working memory tasks were completed by all subjects.

Operation Span Task. The operation span task presents a series of letters in a one-at-a-time manner where after each single letter presentation the subject completes a simple arithmetic problem. After a series of letters and arithmetic problems, the subject must recall the individual letters in their correct serial position. This task requires subjects to maintain the list of letters (ranging in length from three to five letters) in working memory in the face of the arithmetic distractors (See Figure 4). The letter lists were in random order, and each list length was presented twice.

Symmetry Span Task. Subjects are presented with a four by four grid where a to-be-remembered spatial location within the grid is highlighted. Subjects then judge the spatial symmetry of a picture, which is followed by another presentation of a to-be-remembered spatial location, and so on. Like the operation span, after several alternations between the to-be-remembered information and a distracting task, subjects are to recall the highlighted spatial locations in the grids in the order that they were presented (see Figure 5).

Visual Arrays Task. Subjects are momentarily presented with an arrangement of colored squares. This arrangement then disappears and subjects are presented with a blank screen until the arrangement is again presented. In the second presentation of the arrangement, or target array, it is the subject's job to determine if a selected square has changed colors or not relative to the initial arrangement (see Figure 6). Subjects were presented with an array that consisted of either 4, 6, or 8 squares per trial, and a change from initial array to the second array occurred on 50% of all trials. Score for this task is calculated as $k = N*(\text{Hits} + \text{CR} – 1)$, where N is the number of squares or items presented in a trial, hits are correct identifications of change, and CR are correct rejections of change.

Fluid intelligence measures. To gather individual fluid intelligence scores, participants also completed a battery of fluid intelligence tasks.

Number Series. Subjects are presented with a string of numbers that follow a pattern or rule. Subjects must discern what this pattern or rule is and complete the series with what would be the next number in the sequence (see Figure 7). Score for this task was computed as the sum of correct responses on as many trials as the subject completed in five minutes.

Letter Sets. A series of five letter strings (four letters in each string) are presented. The subject must discern what pattern or commonality they share, and identify which one of the five letter strings does not belong because it does not follow the pattern or have a commonality with the other letter strings (see Figure 8). Score for this task was calculated as the sum of correct responses on as many trials as the subject completed in seven minutes.

Ravens Progressive Matrices. The Ravens Progressive Matrices task is a non-verbal pattern recognition task where subjects are presented with a series of shapes that follow a pattern (in a 3 by 3 matrix). However, the last shape in the pattern is missing. Subjects are instructed to select the shape or object that completes the series in concordance with the pattern that the previous shapes and objects follow (see Figure 9). In order to select the correct shape or object, the test-taker must identify what the existing pattern in each trial is. Score for this task was computed by summing the amount of correct solutions a subject completed in 10 minutes.

Spontaneous Eye-Blink Rate. Participants had their spontaneous eye-blink rate measured with EyeLink 1000 eye tracking equipment. Participants were instructed to focus their gaze at a fixation cross presented in the center of a screen for 60 seconds. They were informed that this portion of the experiment was to further calibrate the EyeLink 1000.

Results

Hypothesis 1

A single score was made for each individual's working memory and fluid intelligence performance by creating z-score composites for each battery type. Updating scores from the AX-CPT were calculated as the sum of all correct responses on updating trials, and maintenance scores from the AX-CPT were calculated as the sum of all correct responses on maintenance trials.

Four cognitive task values were missing from the data set. These values were likely missing due to researcher error and not for systematic reasons, and the missing data values totaled less than 1% of the dataset. Therefore, the EM imputation in EQS was used to estimate these missing values. This method was selected over deletion due to the relatively small sample size.

To test the hypothesis that working memory would be related to maintenance accuracy and fluid intelligence would be related to updating, the relationships amongst all variables (working memory, fluid intelligence, maintenance, and updating) were first examined with bi-variate correlations (see Table 1). Consistent with the hypothesis, working memory was significantly related to maintenance trial accuracy, r (62) = .24, $p = .05$, while fluid intelligence scores were not, r (62) = .10, $p = .43$. Both working memory and fluid intelligence scores were significantly related to updating trial accuracy, r (62) = .39, $p = .002$, r (62) = .36, $p = .004$. As expected, working memory and fluid intelligence scores were significantly related r (62) = .62, $p < .001$, and performance on maintenance and updating trials from the AX-CPT were highly correlated, r (62) = .76, $p < .001$.

Table 1

Correlation Matrix for Cognitive Constructs and AX-CPT Trial Types

Measure	1	2	3	4
1. Working Memory	__	.60*	.24*	.39*
2. Fluid Intelligence		__	.10	.36*
3. Maintenance			__	.76**
4. Update				__

**p < .001, *p < .05

To test the unique predictive relationships between the cognitive constructs and updating ability, a three step hierarchical regression was conducted with maintenance accuracy, working memory score, and fluid intelligence as the predictor variables and updating accuracy as the dependent variable. Because maintenance trials and updating trials were highly correlated, the unique variance of updating predicted by each cognitive construct was tested with a hierarchical regression controlling for maintenance trial accuracy. It is asserted that maintenance trial accuracy should be controlled for because performance of updating trials are also encompassing of maintenance processes (i.e., the correct rule sets still must be maintained in awareness in order to accurately respond to updating trials), and this is likely why they are also so highly correlated. Thus, maintenance trial accuracy was entered at step 1 of the model as a control variable, working memory score was entered at step 2 of the model, and fluid intelligence score was entered at step 3 of the model (see Table 2).

Table 2

Hierarchical Regression for Working Memory and Fluid Intelligence Predicting Updating Accuracy

Step	Predictor	B	SE B	β	R^2	ΔR^2
1	Maintenance	.89**	.09	.78	.60**	
2	Maintenance	.84**	.09	.72	.64**	.04*
	Working Memory	.05*	.02	.21		
3	Maintenance	.85**	.09	.74	.68**	.04*
	Working Memory	.01	.02	.06		
	Fluid Intelligence	.07*	.03	.25		

**p < .001. *p < .05.

As expected, maintenance accuracy accounted for a significant amount of variance in updating accuracy, *F* (1, 62) = 93.44, *p* < .001. At step two of the model, working memory score accounted for an additional 4.2% of variance in updating accuracy and this R^2 change was significant, *F* (2, 61) = 7.14, *p* = .01. At step 3 of the model, fluid intelligence score accounted for additional 4% of variance in updating accuracy and this R^2 change was significant, *F* (3, 60) = 7.53, *p* = .008. When fluid intelligence score was included in the model at step 3, working memory score became a non-significant predictor of updating accuracy, and between the two cognitive constructs, fluid intelligence score was the only significant predictor of updating accuracy.

Hypothesis 2

To test the hypothesis that performance on fluid intelligence tasks and updating trials were related to individual differences in spontaneous eye-blink rate, a bivariate correlation was run with these variables. Working memory and maintenance trials were included to test the hypothesis that there would not be any correlation between processes involving maintenance and spontaneous eye-blink rate.

Counter to what was hypothesized, there were no significant relationships between spontaneous eye-blink rate and measures of cognitive ability.

Discussion

Cognitive Implications

Consistent with the hypothesis, fluid intelligence performance was the strongest predictor of ability to accurately update information. Essentially, in the AX-CPT task, individuals who performed well on fluid intelligence tasks were accurate on updating trials because they were able to successfully disengage from the outdated rule set used in the previous trial. That is, individuals who perform well on fluid intelligence tasks—or those who are adept at reasoning—are able to disengage from incorrect information so that the correct information can be updated into the contents of awareness. This suggests that fluid intelligence accounts for variance in cognitive processing that is contingent upon successful disengagement from outdated information. Moreover, it indicates that disengaging is an important process that precedes updating.

The present study supported that updating in isolation is uniquely predicted by fluid intelligence performance, which provides evidence that the cognitive process of updating is crucial in performing fluid intelligence tasks. However, this is not to say that updating is a process limited to fluid intelligence performance, it is also necessary in performance of certain working memory tasks. Virtually, working memory tasks that are more complex than simple span tasks also require updating, especially when switching between processing tasks or transitioning from previous trials to new ones. Within this framework, it seems plausible that updating can account for common variance between working memory task performance and fluid intelligence task performance.

Updating has been related to fluid intelligence task performance in previous studies. First, an experiment by Friedman and colleagues (2006) showed that updating is an executive function that is related to measures of general intelligence. This is similar to a study conducted by Chen and Li (2007) which showed that updating mediates the relationship between age differences and fluid intelligence. In summary, both experiments supported that updating is a critical psychological component of reasoning and intellectual ability. However, these experiments did not test the relationship of updating to measures of working memory, nor did they attempt to parse out unique variance in working memory and fluid intelligence related to updating (due to the researchers' attribution that the updating process is an executive function facilitated by the working memory system). Therefore, what is uniquely contributed by the present study is evidence for dissociable processes involved in working memory task performance and fluid intelligence task performance. Namely, that working memory task performance is highly dependent upon maintaining representations, and fluid intelligence task performance is highly dependent upon disengaging and updating.

The unique relationship between fluid intelligence and updating found in this study therefore suggests that updating is not a process limited to the working memory system, and in turn is counter evidence to the theory that the working memory system is causal to fluid intelligence. The more plausible model is that both fluid intelligence and working memory rely on related cognitive processes such as maintenance, disengaging, and updating.

The relationship between fluid intelligence and updating found in the current study also suggests that tasks that utilize measures of updating as an indicator of working memory function may be measuring psychological processes more important to performance of fluid intelligence tasks—or reasoning ability. Again, this is not to say that working memory tasks do not require the process of disengaging or updating, but more so that successful fluid intelligence task performance is much more dependent on disengaging and updating than working memory tasks are.

In effect, the current results also pose revolutionary implications for how the working memory system can be conceptualized. Traditionally, it is considered to be a mechanism that is responsible only for holding information online—or maintaining information that will facilitate the execution of goals. While this theory of maintenance was somewhat reified in the current study by supporting that the psychological process of maintenance is uniquely related to working memory task performance, it is important to note that updating—which encompasses disengaging—was strongly related to both working memory *and* fluid intelligence task performance.

This finding points to the notion that the working memory system may carry out functions that are more complex than simply maintaining information. This implies that the current working memory capacity tests that are gauging one’s ability to maintain information are not actually measuring working memory as a system. In other words, if traditional working memory tasks are designed to capture the amount of information that one can maintain, but the working memory system is more than just a cognitive storage unit, then traditional working memory tasks are not highly accurate measures of working memory function. In essence, simple span tasks—or tasks that are designed only to measure how many units of information one can maintain—aren't equipped to inform us about the working memory system; these tasks are only measuring how much the system can store in a static moment. Therefore, interpretation of scores on working memory capacity tests should be done with caution if one desires to use these tools to make inferences about the overall working memory system itself.

In short, the current findings suggest that both working memory and fluid intelligence are cognitive abilities that are facilitated by multiple, constituent cognitive processes, and both cognitive abilities require maintenance, disengagement, and updating. However, the degree to which each cognitive process is a critical component of working memory and fluid intelligence differs between the two constructs.

Working memory is *most* reliant on the process of maintaining information, and this is due to the necessity of directing attention to what is most relevant in carrying out a goal. Updating also facilitates performance of working memory tasks because relevant information and goals may change, and therefore new information must be stored in awareness. Disengaging is important to prevent interference between old and new information, however, simple working memory tasks aren't designed to measure how effective one is at disengaging, and therefore disengaging is least critical in performance of working memory tasks.

Fluid intelligence is *most* reliant on the process of disengaging from irrelevant information, and this is due to the necessity of forgetting incorrect assumptions or approaches to problems so that novel solutions can be generated. Updating is also an important process in facilitating performance fluid intelligence tasks because it is intermediate of disengaging from incorrect information and generating the correct information. Maintenance, or maintaining task goals and relevant information, is necessary for fluid intelligence, however this process is not as critical as disengaging or updating. Essentially, maintaining information may lead to perseveration on an incorrect assumption, and without being able to disengage from that outdated assumption, the generation of the correct answer may not be reached.

Simply put, working memory and fluid intelligence differentially rely on the same cognitive processes. Working memory relies on these processes in the rank order of maintenance, updating, then disengaging. Fluid intelligence relies on these processes in a converse order such that disengaging, updating, and lastly maintenance are critical processes in facilitating fluid intelligence performance.

Neurocognitive Implications

The relationships between spontaneous eye-blink rate and updating or fluid intelligence scores were not significant in providing biological evidence for the role of the dopamine gating system in cognitive tasks requiring disengagement. First, this relationship may not have surfaced because spontaneous eye-blink rate has been used as an index of striatal dopamine levels in previous research, and therefore may not serve as a generalizable index of dopamine in cell bodies of the substantia nigra or ventral tegmental area (the dopamine structures themselves). It is also plausible that changes in spontaneous eye-blink rate are not sensitive to nuanced differences in dopamine during cognitive task performance. While previous research has substantiated the relationship between eye-blink rate and dopamine availability, this research has been conducted with populations with disease and brain damage, yet the present study used a healthy population. It is also important to note that eye-blink rate was not measured during task performance in the present study, therefore measures of spontaneous eye-blink rate during the absence of cognitive tasks (as in the present study) may not relate to cognitive task performance like eye-blink measures during cognitive task performance.

While the current study was unable to provide evidence that there is a relationship between physiological indicators of dopamine availability and cognitive processes, the behavioral results of the AX-CPT still suggest that the dopamine gating system may underlie the process of disengaging. If performance on updating trials was related to activation of the dopamine gating system in an imaging study, then it can be inferred that performance of the same task used in the scanner is indicative of the recruitment of the dopamine gating system outside the scanner. Therefore, because performance of this task's updating trials was uniquely predicted by fluid intelligence scores in my experiment, there is indirect evidence for the relationship between the performance of the dopamine gating system and individual differences in fluid intelligence. However, without direct measures of neurological activity or neuroimaging evidence, no explicit conclusions can be made, but further investigation of this relationship should be conducted.

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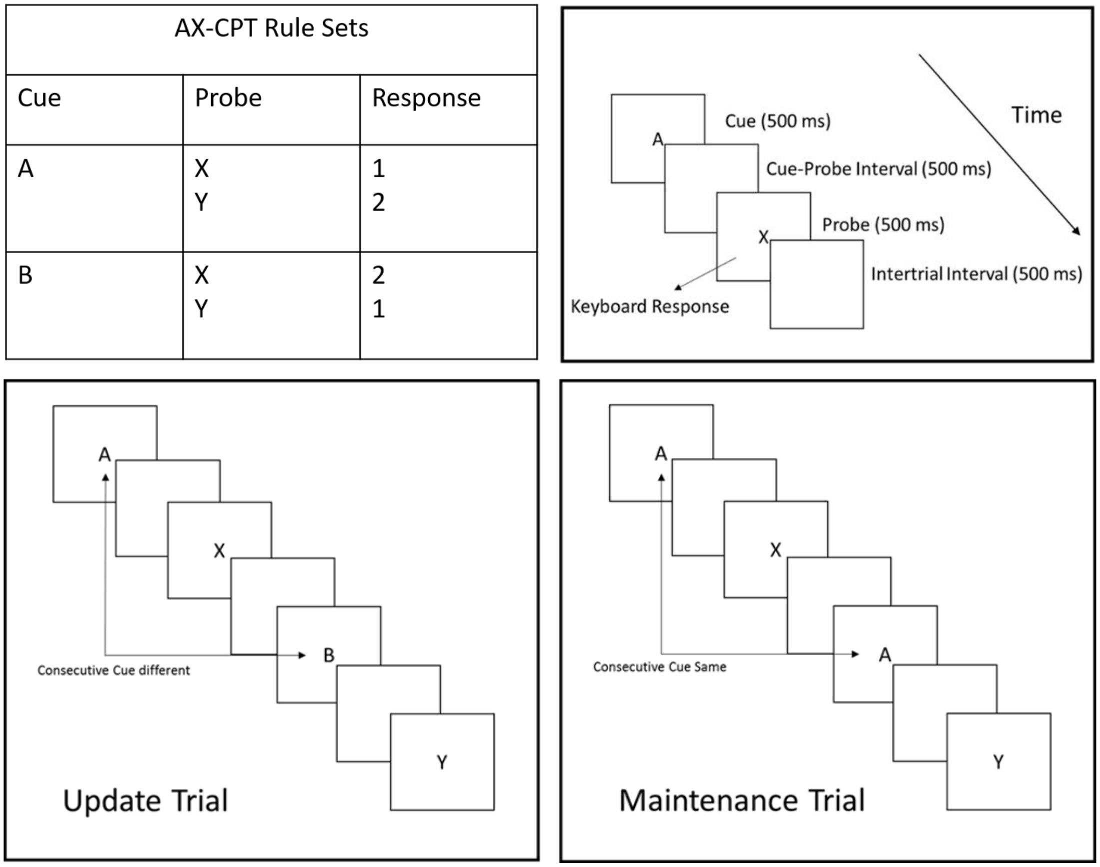
APPENDIX A

WORKING MEMORY TASKS



AX-CPT Rule Sets		
Cue	Probe	Response
A	X Y	1 2
B	X Y	2 1

Figure 3. AX-Continuous Performance Task. Subjects are given two rule sets to follow for responding to cue and probe pairs. Rules for responding to probes are opposite between “A” cues and “B” cues. Updating trials were where consecutive cue letters differed, whereas maintenance trials were where consecutive cues were the same.

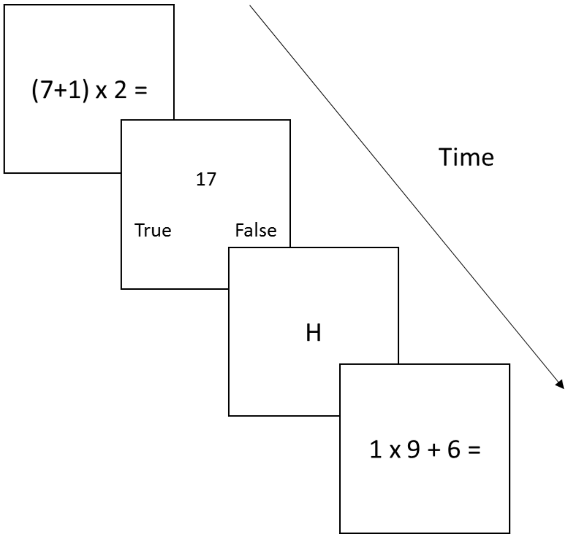


Figure 4. Operation Span Task. Subjects are instructed to remember a series of letters in the order they are presented in while solving math equations. Subjects then recall the letters in their serial position.

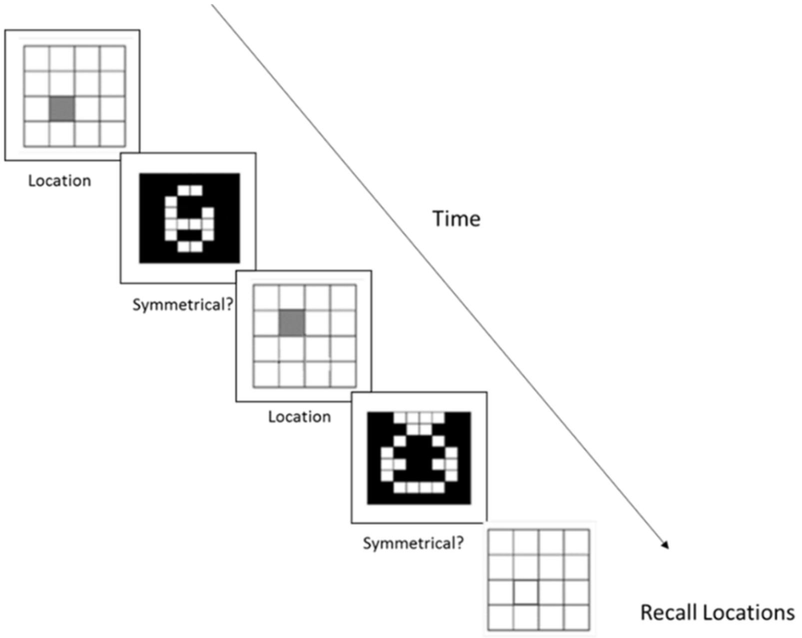


Figure 5. Symmetry Span Task. Subjects alternate between viewing a highlighted grid square in a matrix and judging the symmetry of a picture. Subjects are to recall the spatial locations of the grid squares in the order they were presented.

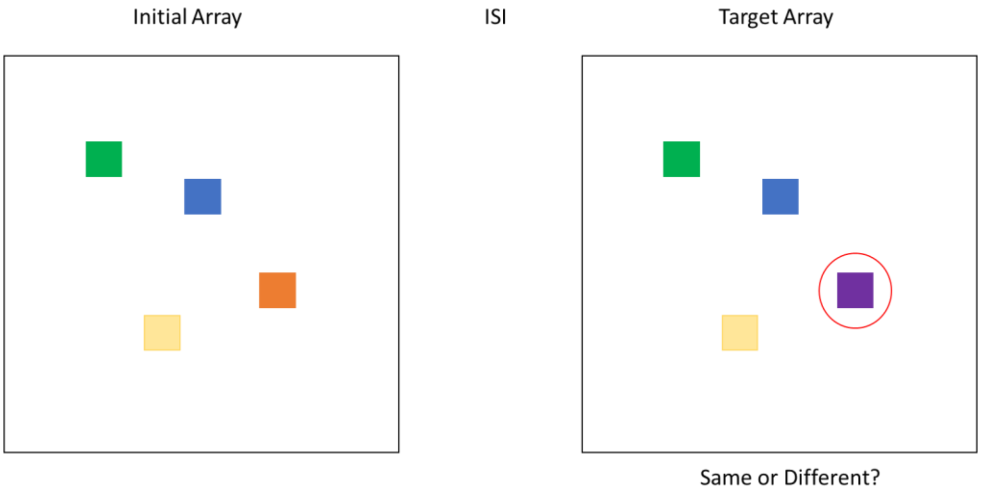


Figure 6. Visual Arrays Task. Subjects are presented with an initial array of colored squares for 500 ms. After the inter-stimulus interval, a target array is presented and subjects must determine if the selected square is the same or different from the initial array.

APPENDIX B

FLUID INTELLIGENCE TASKS

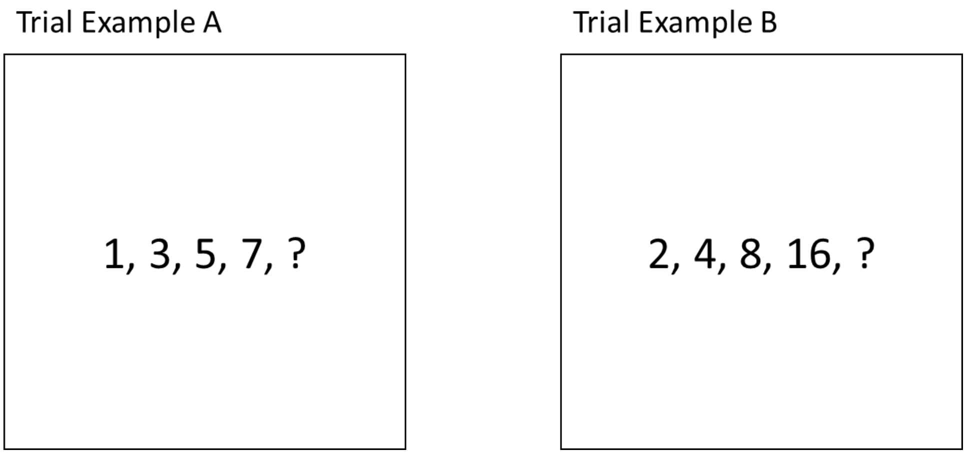


Figure 7. Number Series. Subjects are presented with a series of numbers that follows a pattern or rule. Subjects must discern this pattern or rule in order to complete the series.

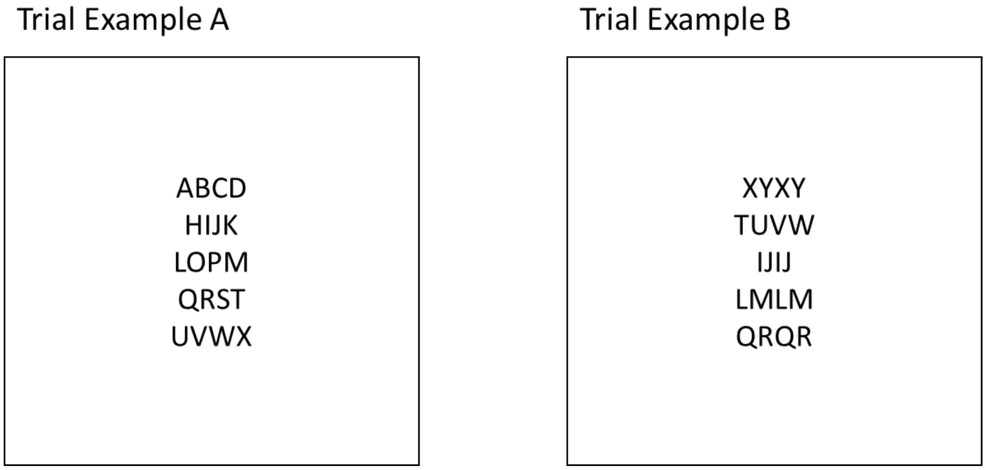


Figure 8. Letter Sets. Subjects view five letter strings where four follow a pattern or rule set and one does not. Subjects must decipher the pattern for each trial in order to select which letter string does not belong.

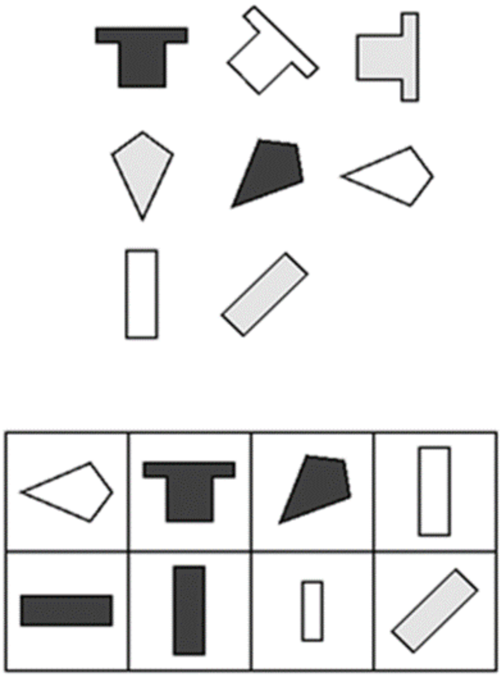


Figure 9. Adapted Ravens Progressive Matrices. Subjects are presented with a three by three matrix of objects that follow a pattern. Subjects must discern what this pattern in order to correctly select the object that completes the series.