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Mechanisms of automaticity and anticipatory control in fluid intelligence

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ABSTRACT

The constructs of fluid (Gf) and crystallized (Gc) intelligence represent an early attempt to describe the mechanisms of problem solving in the vertebrate brain. Modern neuroscience demonstrates that problem solving involves interplay between the mechanisms of automaticity and anticipatory control, enabling nature's elegant solution to the challenges animals face in their environment. Studies of neural functioning are making clear the primary role of cortical-subcortical interactions in the manifestation of intelligent behavior in humans and other vertebrates. A tridimensional model of intelligent problem solving is explored, wherein the basal ganglia system (BGS) and cerebrocerebellar system (CCS) interact within large scale brain networks. The BGS and CCS work together to enable automaticity to occur. The BGS enables the organism to learn what to do through a powerful instrumental learning system. The BGS also regulates when behavior is released through an inhibitory system which is incredibly sensitive to context. The CCS enables the organism to learn how to perform adaptive behaviors. Internal cerebellar models enable gradual improvements in the quality of behavioral output. The BGS and CCS interact within large scale brain networks, including the dorsal attention network (DAN), ventral attention network (VAN), default mode network (DMN) and frontoparietal network (FPN). The interactions of these systems enable vertebrate organisms to develop a vast array of complex adaptive behaviors. The benefits and importance of developing clinical tests to measure the integrity of these systems is considered.

KEYWORDS

Automaticity; basal ganglia; cerebellum; fluid intelligence; large scale brain networks

The breakdown of Spearman's G into the broad constructs of fluid (Gf) and crystallized (Gc) intelligence represented an early attempt to describe the mechanisms of problem-solving in the human brain (Cattell, 1963). Since that time, modern discoveries have revolutionized our understanding of brain functioning (Cromwell & Panksepp, 2011). These discoveries demonstrate problem solving is based on mechanisms of anticipation, the prediction of the future impact of action on the environment (Pezzulo & Cisek, 2016). The traditional model within neuropsychology equates brain functioning with computer processing. Within that information processing model, input is processed leading to output. Applied to the brain, neural sensory signals are processed by "cognitive" structures which send neural action signals to motor structures (Miller, 1956). According to the information processing model, information is processed in sequence: first, we perceive, then we think, and finally we act.

Cattell anticipated the difficulty with sequential processing (e.g., Perceive-Think-Act), as reflected in his statements describing intellectual ability as an interplay between problem solving and stored experience, emphasizing the transitional flow of learning between fluid and crystallized intelligence. This emphasis is clear

in his statement, "This year's crystallized ability level is last year's fluid ability level" (Cattell, 1987, p. 189). He describes a temporal aspect to learning, such that "fluid" adaptation to novel situations becomes "crystallized" over time, allowing the organism to store that newfound knowledge for future use. Cattell's description of intelligent behavior as an interplay between Gf and Gc foreshadows current neuroscientific understanding of anticipatory control networks and automaticity.

Modern methods allow us to understand these mechanisms of adaptive behavior. Anticipatory control and automaticity provide the means for vertebrate organisms to flexibly respond to an environment that is both predictable and ambiguous, aptly described by Kim Sterelny (2003) as "translucent." The vertebrate brain evolved to allow the organism to shift between (a) exploitation of predictable environmental features through automaticity; and (b) slow, careful problem solving when faced with unpredictable and ambiguous stimuli (D'Ambrosio, Wenzel, Schwartzkroin, McKhann, & Janigro, 1998). When faced with familiar and expected cues, the vertebrate organism responds with implicit, automatic behaviors, allowing the organism to exploit these predictable environmental features (Griffiths, Morris, & Balleine, 2014). Conversely, when

faced with novelty and ambiguity, mechanisms of deliberate conscious control enable goal-directed problem solving, usually involving access to a library of stored knowledge (Goldberg, Podell, & Lovell, 1994).

Applying the constructs of anticipatory control and automaticity, the manuscript extends and modernizes Cattell's ideas regarding the interplay between fluid and crystallized intelligence. The parallel interactions of the basal ganglia system (BGS) and the cerebrocerebellar system (CCS) within large scale brain networks enable both anticipatory control and automaticity. Optimal problem solving requires a set of available action sequences to move, act, and react; these action sequences are made available through automaticity, which requires error correction from the cerebellum and associative learning from the basal ganglia. A tripartite model describing these interactions is reviewed in the following section, first describing the basal ganglia system (BGS) and cerebrocerebellar system (CCS), and then describing the interactions of these systems within large scale brain networks.

Tripartite model of automaticity and anticipatory control

The hallmark of “intelligence” is the ability to respond efficiently to changes in the environment. This manuscript focuses on action control systems relevant to environmental adaptation, while acknowledging the important roles of other brain systems for intelligent behavior, as described in detail elsewhere (Baddeley, 2012; Colom, Karama, Jung, & Haier, 2010; Fuster & Bressler, 2012). Optimal adaptation requires an automatic system to exploit predictable features of the environment and a novelty-detection system organized along a hierarchy to adapt to novelty and ambivalence. These systems control action. The vertebrate brain accomplishes the goals of automaticity and action control with two learning systems, working in parallel. The BGS, through implicit instrumental learning, enables the organism to anticipate/predict the potential outcome of any behavior and, over time, to accurately identify rewarding and punishing features of the environment (Doll & Frank, 2009). The CCS functions by way of anticipatory control to predict sensorimotor outcomes, resulting in an ability to automate any behavior (Imamizu, 2010; Ito, 2005). Both systems encompass cortical and subcortical structures, providing the mechanisms for what Cattell described as fluid and crystallized intelligence (Cattell, 1963).

Consider all the different things learned through experience. Just about any behavior is incredibly hard to do at first. Gradually, with repeated practice, the

activity becomes easier and easier, until the task is forgotten completely and can just be accomplished. This goes for everything from taking first steps to performing calculus. At some point in learning, the fluid reasoning involved in effortful problem solving becomes completely implicit and happens automatically, without any effort. This occurs without conscious awareness. At the point of automation, a behavior becomes effortless, and we can even engage in other thought and action while performing the automated behavior. Consider driving down a long stretch of highway in very light traffic; you might listen to the radio or think about what you'll be doing when you arrive home, but the *automated* task (in this case, driving) occurs without you having to think much about it.

This automated system also features “emergency responding.” Consider a significant change in context in the aforementioned example. While driving, you suddenly notice a child running across the highway; your automation system enables you to slam on the brake while steering to avoid the child. These responses occur rapidly, without any conscious thought. How does this elegant adaptive behavior occur in the brain?

The BGS and CCS work in tandem to accomplish the precision, speed, practicality, and elegance of automatic behavior. Functionally independent, dedicated, reciprocal, looped connections between the cerebral cortex, the basal ganglia, and the cerebellum enable the brain to gradually improve performance through repetition and practice. Chunks of behavior become sequenced and errors are corrected, resulting in the release of behavior with the greatest chance/probability of reward. We consider these learning systems in greater detail, beginning with the BGS.

Basal ganglia system

Although different functional neuroanatomists characterize the BGS in different ways encompassing multiple areas of the cortex and the basal ganglia, Middleton (2003) presents a model which includes a set of four basal ganglia structures. These include (a) the striatum (caudate and putamen), forming the primary inputs structures of all incoming sensory information; (b) the globus pallidus; (c) the substantia nigra; and (d) the subthalamic nucleus. The globus pallidus is an intermediate structure which projects to different thalamic regions. The substantia nigra, a primary source of dopamine synthesis, is an output structure projecting to the thalamus and the superior colliculus, an important structure for the control of eye movement. The subthalamic nucleus is the “rapid responder” of this system,

inhibiting behavior much more rapidly than other inhibitory pathways in this system (Mink, 2003). Understanding the neuroanatomy of the BGS is of crucial importance to grasping its role in intelligent behavior. Because an in-depth review of this system is beyond the scope of this manuscript, the interested reader is directed to two excellent review sources (Hikosaka, Kim, Yasuda, & Yamamoto, 2014; Koziol & Budding, 2009).

The basal ganglia receive cortical input from all primary cortices, including extensive connections with all frontal regions and the parietal and temporal regions associated with the attention networks. The primary input mechanisms of the basal ganglia are the caudate and putamen. The body of the caudate receives neural signals from the inferior temporal cortices while the tail of the caudate receives parietal projections (Middleton & Strick, 2000; Seger, 2009). The ratio of these connections are as high as 10,000 cortical inputs to a single spiny cell neuron (Houk, 2005), making the basal ganglia extremely sensitive to changes in environmental context (Seger, 2008).

Multiple potential actions are available at any one time and the basal ganglia release particular behavior based on anticipated outcome. Both anticipation of reward and avoidance of negative outcome influence this action control. Compelling literature indicates the mesolimbic dopamine system includes both tonic levels of dopamine release and phasic release representing learning opportunities (Walton, Gan, & Phillips, 2011). Phasic dopamine firing rates increase when unexpected rewards are encountered. Conversely, phasic dopamine firing rates dip below tonic levels when anticipated rewards do not occur, resulting in an unpleasant loss of dopamine resulting in avoidance of the punishment inducing behavior in the future (Montague, Dayan, & Sejnowski, 1996; Schultz, Dayan, & Montague, 1997). In this way, the BGS enables the organism to select actions having high potential for rewarding outcome and to avoid actions associated with negative (nonrewarding) outcomes (Nakanishi, Hikida, & Yawata, 2014).

Reward probabilities are anticipated through the formation of associations between perception and action, a process that occurs beneath the level of conscious awareness (Thach, 2014). As the vertebrate organism moves through the world, the BGS learns the reward value of various outcomes. This process occurs by way of the association between rewarding outcomes and specific perception-action linkages, which are strengthened within sensorimotor cortex (Dolan & Dayan, 2013). These perception-action linkages enable the prefrontal cortex to identify potential solutions to

novel or ambiguous situations by making use of previously successful behavior (Haber, 2011; Koziol, 2014; Paul & Ashby, 2013).

Automatic behavior is released by the BGS without the need for conscious cognitive control, because this prediction based system learns through repetition that particular actions are highly predictive of specific, anticipated outcomes. When you press the gas pedal, there is a strong expectation the car is going to start moving. When driving up to a red traffic light, the foot automatically goes to the brake pedal. Upon entering a dark room, you reach for the light switch. In each of these examples, experience forms powerful perception-action linkages, such that stimulus cues (darkness, a red traffic light) elicit specific actions which occur without conscious thought. If the expected outcome does *not* occur, phasic dopamine levels drop below tonic levels, resulting in rapid identification of significant contextual change (e.g., “The electricity must be out. The brake isn’t working!”).

These cues for contextual change can be subtle to the point of being experienced as intuitions. Many have experienced an internal warning sign when leaving a store at night that *something isn’t right*, possibly resulting in asking for an escort to your vehicle. We often sense if a loved one is in distress or angry before we are told. Intuition has been traced to implicit learning mechanisms of the BGS (Frank, O’Reilly, & Curran, 2006; Wan et al., 2011).

Basal ganglia system and continuous learning

The BGS brings sets of action-perception linkages together, resulting in the formation of adaptive skills, a process that some researchers have termed “chunking” (Graybiel, 1998; Jin & Costa, 2015; Jin, Tecuapetla, & Costa, 2014). When chunked behavior is performed successfully, tonic dopamine release strengthens the perception-action linkage formed to produce the behavior. This linkage is further strengthened with each repetition. The sensory and motor cortices involved in the behavior link together, becoming a new functional unit, ready to be “called up” at a moment’s notice.

This process is critically important to cognitive development in childhood and adolescence. Throughout childhood, the BGS chunks various behaviors together, resulting in learning and automating thousands of procedures across the developmental spectrum (Njiokiktjien, 2010; Welsh, Pennington, & Groisser, 1991). Examples of chunking include walking (which integrates balancing, standing, sequential movement, etc.) and performing multiplication (which integrates automated concepts including number sequencing and

addition). Each new ability involves a combination of several previously learned, implicit skills, which are “chunked” together, lending truth to Cattell’s 1987 observation, “This year’s crystallized ability level is last year’s fluid ability level” (p. 189).

The ability to exploit the environment for optimal adaptation requires anticipatory control. This necessitates an exquisite sensitivity to context. The striatum receives thousands of cortical inputs to a single striatal output, enabling it to rapidly identify and respond to any changes in the environment. The striatum anticipates both *what* is rewarding in the organism’s environment and *where* the rewarding situation will be located in time and space. In this respect, the extensive striatal connections with parietal and temporal cortex allow the striatum to “direct” the attention within large scale brain networks. When anticipated outcomes do not occur, the striatum immediately responds to the change in context by attempting to form new associations that better predict optimal outcome. In this way, a powerful mechanism of associative learning occurs. Instrumental activities of various sorts get chunked together, resulting in new behaviors and skills. Applied to fluid intelligence, the striatum is the mechanism that *identifies the parameters of a problem or novel situation* (Koziol, 2014).

Cerebrocerebellar system and cerebellar control models

Fluid intelligence requires a mechanism for vertebrate organisms to learn and execute adaptive actions with speed and accuracy. The traditional information processing model of cognition, based as it is on direct sensorimotor feedback, is much too slow for responding in real time. Considerable time and precious energy are required to execute a new behavior, as we all can attest from recalling the learning of just about any complex behavior, from toothbrushing to highway driving (Saling & Phillips, 2007). The brain needs a way to function in “real time.” Speed in behavior is necessary and requires constant adjustment. Nature’s answer to this problem is the predictive control mechanisms of the CCS.

Cortical information, projected to the cerebellum, allows the cerebellum to generate a copy of the sensory-motor information which is maintained within the cortex, called an internal cerebellar control model. The cerebellum performs the same singular activity on the neural information it receives from the cortex, whether that information is sensory, motor, cognitive, or social in origin (Molinari et al., 2008). In fact, the activity learned when tasks are being performed are

interpreted as activity within the cerebellar control model (Koziol, Budding, et al., 2014).

Automatic behaviors are expressions of internal cerebellar control models, as described by Ito (2011, pp.184–185). Learning a complex motor action requires the premotor and primary motor cortices to perform a motor action. These initial steps of learning proceed slowly, because motor cortices must rely on external sensory feedback. With repetitions, the cerebellum is increasingly activated, forming its own motor schema, a “copy” of the complex motor action. This “copy” is an “internal model” which includes all the sensory and motor information necessary to perform the behavior. The cerebellum “corrects” the contents of its own internal model each time the action is executed. This results in an increasingly efficient representation of the behavior; this efficient behavior is projected back to the cortex, allowing the cortex to retain what the cerebellum learned (Doyon et al., 2002; Galea, Vazquez, Pasricha, de Xivry, & Celnik, 2011; Koziol, Budding, & Chidekel, 2010; Shadmehr, Smith, & Krakauer, 2010).

The cerebellar cortex becomes very active during initial learning trials; neural activity gradually shifts to the cerebellar dentate nucleus (Doyon et al., 2002). While this process continues, the parietal cortex is recruited, and acquires a “motor schema,” or its own model of the action the premotor cortex is in the process of executing with each trial (Ito, Heilman, & Rothi, 2003). As the cerebellum “learns” the most efficient representation of the task/behavior, activity shifts to the dentate, and then on to cortico-striatal networks; and finally this is stored in cortical regions; the cortex retains what the cerebellum learns (Celnik, 2015; Galea et al., 2011; Grimaldi et al., 2014). This is observed in the results of neuro-physiological and neuro-imaging tasks, which demonstrate decreased cerebellar activation as the learning phase has been accomplished (Galea et al., 2011). For an in-depth review of cerebellar control models, see Masao Ito’s (2012) superb text.

The cerebellum has an impressively extensive set of connections with most areas of the cerebral cortex, including the prefrontal, premotor, and motor cortices, as well as various areas of parietal and temporal cortex (Schmahmann & Pandya, 1997). These connections provide the cerebellum with access to a rich tapestry of cortical action controls, including cortical areas involved in perception, planning, and motor action. A looped neural architecture originating in the cerebral cortex carries neural signals to the cerebellum, which regulates the amplitude of the neural responses. This neural regulation results in adjustments to the quality of all forms of behavior, even including social cognition, as recently shown (Van Overwalle, Baetens,

Marien, & Vandekerckhove, 2014, 2015). Following this cerebellar regulation, neural signals are sent back to their area of cortex from which they originated. This looped architecture allows the cerebellum to adjust the *quality* of cortical signals to improve behavior. Adjustments to the rate, rhythm, and force of behavioral expression makes cortical actions smooth and effortless (Schmahmann & Sherman, 1997).

The cerebellum performs the same important action on all the information it receives. In this respect, it is a “one-stop shop,” regulating the amplification of cortical signals to correct errors, with cerebellar feedback resulting in the formation of new and higher quality representations in the cortex (Ito, 2005; Ramnani, 2006). Every repetition results in refinement, improvement, increased learning, and improved quality. The cerebellum is a quality control mechanism of the brain.

By means of revising neural signals received from the cortex, the cerebellum guides anticipation and corrects errors on a moment-by-moment basis. “Perfected” behaviors are then stored in the various areas of the cortex required to implement the behavior. Therefore, the internal model “knows” what the cortex wants to do, and it contains every element necessary to execute the intended behavior. Cerebellar control models allow vertebrate organisms to shift based on the context of the situation. Then, in future settings, when a new but similar situation is encountered, the cerebellum copies the “revised” cortical information and modifies its own previously established “model” (Galea et al., 2011). As a result, the cerebellum is able to adapt learned behavior across similar settings/situations; the automatic behavior is adjusted, but it never has to be re-learned again.

The internal model of the cerebellum is focused on *anticipatory* control; based upon its copy of cortical content, the cerebellum *predicts* behavioral, or sensory-motor outcomes. With repeated execution of the behavior, the cerebellum continually refines the behavior, so that the behavior becomes efficient, effortless, automatic – and *implicit* – outside of conscious guidance and control. Error corrections occur rapidly, with minimal reliance on incoming sensory data (Shadmehr et al., 2010).

The cerebellum’s primary role is to improve the quality of *movement* and this has been known for the past two decades (Glickstein & Yeo, 1990). Its role in voluntary motor control enables humans and other vertebrates to learn extremely complex voluntary motor behaviors. In addition, recent evidence demonstrates the cerebellum has the same role in the regulation of cognition, emotion, language, and social cognition (Koziol, Budding, et al., 2014; Marien & Manto, 2016;

Strick, Dum, & Fiez, 2009; Van Overwalle & Marien, 2016). The cerebellum’s role in neural regulation makes it a prime candidate for involvement in adaptive learning of procedures, including “thought procedures.”

The cerebellum “teaches” the cortex how to anticipate thought outcomes, teaching the prefrontal cortex how to think ahead, allowing for thinking in real-time (Ito, 2008). The most efficient thought sequence is stored in the relevant areas of the frontal cortex, just as the most efficient motor sequence is stored in sensorimotor cortices (Galea et al., 2011). Koziol (2014) provides a useful example of a cerebellar thought control model. Consider solving the following subtraction problem: 82–38. The cerebellum assists in the formation of a thought procedure for regrouping, borrowing and carrying of numbers required to solve the problem. Once the subtraction procedure is learned, automated, and stored, then each time a similar configuration is identified, the brain anticipates this subtraction procedure will solve the problem. The procedural sequence may need to be practiced many times before it becomes fully automated and stored in relevant areas of the cortex; once learned, like riding a bicycle, the thought procedure is not forgotten.

Fluid intelligence and large scale brain networks

Mesulam (1990) was an early proponent of large-scale brain networks as being composed of functionally segregated, interactive systems. Various technologies led to increased understanding of large scale brain networks (LSBN), with a result that theorists began proposing LSBN’s represented a contrasting paradigm with traditional localization theories of brain functioning (Menon, 2011). In 2011, Yeo and colleagues identified seven functional brain networks in 500 participants, and then replicated the network identifications with a separate group of 500 participants. These findings represent confirmation of theoretical work which occurred years before (Yeo et al., 2011). Several specific networks appear to be directly involved in mechanisms of automaticity and anticipatory control.

Corbett and colleagues (Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002) described evidence for two systems working together to modulate attention. The dorsal attention network (DAN) activates in response to expectations that objects will be in particular locations or will move in certain directions. This is something with which we are all familiar. Consider the seating expectations in any classroom; without requiring verbal agreement or “seat assignment,” students typically sit in the same location throughout

a series of class meetings. The DAN contributes to the anticipation other students will be in their expected seats.

Research demonstrates the DAN is involved in specification of the parameters for action in the environment (Corbetta et al., 2008), informing the organism how to do an activity (Barsalou, 2008). The brain structures of the DAN include the intraparietal sulcus and the frontal eye fields, which enables the matching of visual attention with spatial location (Arnott & Alain, 2011). The DAN controls spatial attention, including shifting of attention. In relating the DAN to factors of intelligence, it is involved on both fluid problem solving and crystallized knowledge. The DAN directs the parameters for action in both novel and routine settings. In novel settings, frontal systems direct behavior through reciprocal frontoparietal connections. In routine settings, the DAN functions implicitly, specifying parameters of action in fully automated behaviors (Cole et al., 2013; Jacob & Nieder, 2014; Koziol, Barker, Joyce, & Hrin, 2014b). The DAN is part of the cortical library of stored and completely automated procedures which we engage in every day. Therefore, regions of the DAN direct both explicit problem solving and implicit procedures.

The ventral attention network (VAN) denotes what traditional neuropsychology refers to as the “what” pathway, representing neural circuitry flowing from the occipital visual centers, through the temporoparietal junction, forward through the supramarginal gyrus, frontal operculum and the anterior insula (Kolb & Whishaw, 2009). The relevant regions of the temporal and parietal lobes contain extensive reciprocal loops through the striatum (Seger, 2009). Identification of “what” encompasses much more than simple object categorization. The VAN enables object *salience*, including what an object can be used for, how it can be used; in short the object’s importance or relevance to the organism (Menon, 2011). The extensive VAN projections to the striatum make it critical for implicit, instrumental learning. Most of what we do is based on instrumental learning, which operates beneath the level of conscious awareness (Doll & Frank, 2009; Koziol & Budding, 2009). The primary “linking together” of the dorsal and ventral processing streams occurs in the entorhinal cortex of the medial temporal lobe memory system (Squire & Zola-Morgan, 2015); however, that representation of the external world is based on reward likelihood (e.g., anticipation), rather than accurate replication of the external world (O’Reilly, Munakata, Frank, & Hazy, 2012).

The default mode network (DMN) represents brain functioning “at rest” when the organism is not engaged

in any sort of problem solving or behavior (Sandrone, 2012). In healthy brain functioning, the DMN operates inversely to action-control networks, such that the DMN decreases when goal-directed activity is required (Castellanos & Proal, 2012). Dysregulation of DMN activity is found in various psychiatric disorders, including Schizophrenia, Attention-Deficit/Hyperactivity Disorder, and depressive conditions (Menon, 2011; Weissman, Roberts, Visscher, & Woldorff, 2006). At rest, the DMN engages in both self-referential thought and thinking about the future (Kinsbourne & Jordan, 2009).

Cole et al. (2013) identified a crucial role for the frontoparietal network (FPN) as a primary area of organizational control. The FPN has functional connections with many and varied brain systems. By way of “flexible hubs,” the FPN was shown to recruit relevant connecting areas to respond adaptively to whatever task was at hand. Various tasks across multiple domains recruited specific “hubs.” Furthermore, changing activity patterns as shown on fMRI enabled identification of the task that was performed! The FPN was a primary area of shifting when task change occurred, which was more so than any other network. Evidence of connectivity pattern “re-use” was also found, meaning new or novel tasks recruited well-established automated connectivity patterns (Cole et al., 2013).

The FPN engages when the organism performs effortful cognitive tasks requiring rules and information to be kept in mind. Thus, it is the network most associated with working memory functions. The FPN activates with both the DMN and the dorsal and ventral attention networks, but does so preferentially, based on hemispheric lateralization. Within the left hemisphere, the FPN engages preferentially with the DMN, focused on the internal cognitive context. Behavior is driven by routine, automatic settings and whatever one is thinking about. Conversely, the right hemisphere FPN preferentially couples with the attention control networks (Wardak, Ramanoël, Guipponi, Boulinguez, & Ben Hamed, 2012), enabling adaptive problem solving in response to unfamiliar or unexpected change identified in the external environment.

Functioning of this centralized network hub is highly correlated with intelligence, although the relationship takes a while to “come online.” For example, resting state fMRI of children found positive spatial maps associated with the left FPN correlated with intelligence. In adolescents, positive spatial maps of the right FPN were also correlated with intelligence (Li & Tian, 2014). Thus, we begin to see how any discussion of fluid intelligence without incorporation of the interactive mechanisms of these various LSBN’s is inadequate. On the other hand,

future contributions to the literature that incorporate principles of LSBN's represent an exciting area of growth.

Developmental aspects of anticipatory action control

The vertebrate brain is geared toward anticipatory action control, a process that occurs through sensorimotor interaction with the environment (Pezzulo, 2011). As an organism moves through the environment, knowledge of the world is formed, a process beginning soon after birth. The DAN and VAN develop early and are integrated as functional units by nine months of age (Kaldy & Leslie, 2003).

Movement is crucial to the development of anticipatory action control. Primitive reflexes such as sucking and latching on lead very quickly to a neonate's anticipation of nurturance. When children are unable to move normally, later deficits in action control occur. A study illustrating this concept followed a group of extremely-low-birth-weight (ELBW) children without severe brain injury or cerebral palsy over ten years, beginning at age three months. A General-Movement-Assessment given to the ELBW children at three months of age *predicted* neurocognitive deficits and brain pathology years later (Grunewaldt et al., 2014).

Several important studies demonstrate sensorimotor deficits influence adaptive outcomes. For example, sucking ability predicts later neurodevelopmental outcome (Poore & Barlow, 2009). Children with Developmental Coordination Disorder perform significantly worse than normal peers on measures of processing speed and working memory (Sumner, Pratt, & Hill, 2016). Adolescents who survived tumor of the posterior fossa of the cerebellum show deficits in forward thinking, inhibition, and mental flexibility. Ataxia scores of those adolescents correlated significantly with deficits in forward thinking (Koustenis, Hernáiz Driever, de Sonnevill, & Rueckriegel, 2016).

Early cerebellar damage results in significant disruptions linked to neurodevelopmental disorders. In a recent paper, Catherine Stoodley (2015) reviewed structural and functional cerebellar differences in attention deficit-hyperactivity disorder, autism spectrum disorders, and developmental dyslexia, demonstrating different cerebellar sub regions are involved in each disorder. Other researchers are identifying the links between cerebellum and action control associated with LSBNs. For example, Buckner and colleagues (Wang, Buckner, & Liu, 2014) identified neural fiber projections associated with action control linking frontal and parietal cortices with the cerebellum. Reciprocal hubs

of interactivity are clearly identified between the FPN and the cerebellum. These findings identify the importance of cerebellar regions in neurodevelopment, including intelligence. Cerebellar integrity may drive overall brain development (Wang et al., 2014).

Neuropsychological assessment of automaticity and action control

Commercially available neuropsychological tests measuring the integrity of the basal ganglia and cerebro-cerebellar systems have yet to be developed, despite research demonstrating that testing of these systems is possible. For example, researchers have evaluated the integrity of the BGS reward pathways. Patients with schizophrenia were found to have deficits in the acquisition of reward contingencies on probabilistic Go–No Go learning tasks, likely related to a deficit in procedural learning (Waltz, Frank, Wiecki, & Gold, 2011). In testing their computational model of frontostriatal dopamine, Frank and colleagues found unmedicated ADHD patients had deficits in both positive (Go) and negative (No-Go) reinforcement learning. Psychostimulant medication alleviated the Go learning deficits but the No-Go deficits remained (Frank, Santamaria, O'Reilly, & Willcutt, 2007). Thus, research supporting the practical benefit of measuring implicit functioning exists. Deficits in the ability to predict reward have been found within other clinical populations, including Parkinson's disease (Frank, Seeberger, & O'reilly, 2004), obsessive-compulsive disorder (Kaufmann et al., 2013); autism (Larson, South, Krauskopf, Clawson, & Crowley, 2011); cocaine addiction (Morie, De Sanctis, Garavan, & Foxe, 2014); and cigarette smoking (Potts, Bloom, Evans, & Drobles, 2014). Nevertheless, the only measure of reward processing available for use with clinical populations is the Iowa Gambling Task (Bechara, Damasio, Tranel, & Damasio, 2005).

A second important aspect of test performance is speed of problem solving. Research demonstrates slower performance on traditional measures of processing speed is associated with *increased* brain activation. Sweet et al. (2005) found slower processing speed on the Wechsler Symbol Search task was associated with greater activity in the bilateral medial occipital, occipitoparietal, occipitotemporal, parietal, and dorsolateral prefrontal cortices. The finding is consistent with the idea that automaticity enables faster processing; less automaticity requires increased activation of cortex, resulting in slower speed (Saling & Phillips, 2007). Impairments in automaticity contribute to developmental delays. For example, injury to the cerebellum due to premature birth is associated with developmental

impairments in motor, cognition, and expressive language (Limperopoulos et al., 2014). Archibald and colleagues (Archibald et al., 2004) found a significant relationship between posterior fossa lesion volume in the cerebellum and memory scanning speed in multiple sclerosis patients. Given the cerebellum's role in error correction (Ito, 1993) and timing (D'Angelo et al., 2009), the CCS is likely to influence the rate at which automaticity is achieved.

Commercially available testing of the speed at which automaticity is achieved could aid clinicians in identifying implicit learning deficits contributing to abnormal neuropsychological test findings. Koziol (2014) has proposed the use of repeated trials of commercially available or public domain tests to measure automaticity. One example is the administration of the well-known Trail Making Test, Part B over five learning trials, with the primary outcome measures being reductions in speed and errors across trials (Koziol & Budding, 2009). This idea is an application of verbal word-list learning paradigms to an implicit learning task (Marien & Manto, 2016).

The development of commercially available tests measuring aspects of BGS and CCS represents an exciting opportunity for the field of neuropsychology to integrate neuroscience into clinical practice. Tests measuring "automaticity acquisition" could be linked with practical behavioral and neuropsychological outcomes. Likewise, comparison of the implicit learning abilities of normal-controls with various brain-injured populations would enable progress in the field of neuropsychology. In discussing the need for measures of implicit functioning, Strauss, Sherman, and Spreen (2006) concluded that "current theoretical knowledge is not well integrated in clinical assessment, and, as a consequence, important information regarding patient functioning is likely missed" (p. 679).

Summary

Cattell's early, intuitive description of the interactive flow between fluid and crystallized intelligence represents an attempt to describe the mechanisms of problem-solving in the brain (Cattell, 1963). Since that time, neuroscientific discoveries are demonstrating that optimal adaptation involves an interplay between stimulus based and higher order control (Podell, Lovell, & Goldberg, 2001). Adaptive mechanisms allow vertebrate organisms to routinize the unfamiliar, enabling any type of behavior, no matter how complex, to become automatic, beyond conscious awareness (Bargh, 2014). This manuscript characterizes intelligent behavior based on the parallel

abilities to (a) exploit predictable features of the known environment through automaticity and (b) solve problems encountered in an unknown or unpredictable environment (Griffiths et al., 2014; Koziol, Barker, Hrin, & Joyce, 2014).

A tripartite model described how the brain accomplishes intelligent problem solving. The basal ganglia system provides the mechanism to learn (a) what to do through an instrumental learning system built to strengthen the sensorimotor interactions associated with rewarding outcomes (Hikosaka et al., 2014) and (b) when to release behavior through a powerful inhibitory system (Redgrave, Prescott, & Gurney, 1999; Schroll, Vitay, & Hamker, 2012). The cerebrocerebellar system tells the organism how to do an activity. Internal models allow the cerebellum to modify cortical signals without requiring direct sensorimotor feedback (Ito, 2008), enabling the prediction of future sensorimotor outcomes. Furthermore, evidence demonstrates what the cerebellum does for the motor system, it also does for cognitive and motivational systems (Ito, 2008, 2011; Koziol, Budding, et al., 2014; Marien & Manto, 2016; Schmahmann, 2013). These concepts have found significant support in neurophysiological studies of animals and neuroimaging studies of humans (Brown, Zatorre, & Penhune, 2015; Doyon, Penhune, & Ungerleider, 2003; Penhune & Steele, 2012). The BGS and CCS interact with large scale brain networks to optimize behavior, with a significant change in subcortical-cortical interactions across the developmental spectrum (Menon, 2013). The dorsal and ventral attention networks interact with the default mode network to provide and gather information regarding how the organism's action in their environment will impact the organism in the future. This brain prediction relies highly on the organism's reading of the current context in which it finds itself. Brain networks are intimately entwined with a BGS providing information about salience and context (D'Ambrosio et al., 1998) and with a CCS which sends control signals providing information instructing the sensory and motor systems how to respond to reach identified goals *in the future* (Ito, 2008).

Incorporation of the mechanisms of automaticity and anticipatory control into theories of fluid intelligence represents an exciting opportunity for neuropsychology. Many researchers are describing the role of cortical-subcortical loops in action selection (Caligiore, Pezzulo, Miall, & Baldassarre, 2013; Doya, 2000; Houk et al., 2007; Koziol, Barker, Joyce, & Hrin, 2014a). Theorists are also applying LSBN functioning to the understanding of intelligent behaviors (Jung & Haier, 2007; Vakhtin, Ryman, Flores, & Jung, 2014). Both the BGS

and CCS influence motor, cognitive, and motivational functions (Mars, 2011; Middleton & Strick, 1994). Despite multiple learning systems being well established in neuroscientific literature (Ashby & Crossley, 2012; Squire & Dede, 2015), few tests measuring implicit learning or the efficiency of automaticity acquisition are available to the practicing neuropsychologist.

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