



# The neuroscience of active learning and direct instruction

Janet M. Dubinsky<sup>\*,1</sup>, Arif A. Hamid

Department of Neuroscience, University of Minnesota, Minneapolis, MN, USA

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## ABSTRACT

Throughout the educational system, students experiencing active learning pedagogy perform better and fail less than those taught through direct instruction. Can this be ascribed to differences in learning from a neuroscientific perspective? This review examines mechanistic, neuroscientific evidence that might explain differences in cognitive engagement contributing to learning outcomes between these instructional approaches. In classrooms, direct instruction comprehensively describes academic content, while active learning provides structured opportunities for learners to explore, apply, and manipulate content. Synaptic plasticity and its modulation by arousal or novelty are central to all learning and both approaches. As a form of social learning, direct instruction relies upon working memory. The reinforcement learning circuit, associated agency, curiosity, and peer-to-peer social interactions combine to enhance motivation, improve retention, and build higher-order-thinking skills in active learning environments. When working memory becomes overwhelmed, additionally engaging the reinforcement learning circuit improves retention, providing an explanation for the benefits of active learning. This analysis provides a mechanistic examination of how emerging neuroscience principles might inform pedagogical choices at all educational levels.

## 1. Introduction

Neuroscience exploration of both associative and reinforcement learning (RL) in experimental animals and humans has deepened our understanding of learning and memory from a mechanistic, biological point of view. However, extending these mechanistic ideas to the real-world application of human education in formal schooling is limited. Education suffers from the tension between the goal of transferring content information to students versus the goal to train them to become skilled independent creators, critical thinkers and users of knowledge. These goals are exemplified and embodied in two distinct pedagogical approaches, direct instruction (DI) vs active learning (AL, see [Box 1](#) for definitions and elaboration). DI focuses upon transferring content knowledge (e.g. lecturing) and providing directions for accomplishing academic tasks. AL emphasizes the engagement of students in the process of manipulating new knowledge.

The critical contrast between AL and DI pedagogical approaches is whether the student is an *active* agent during class. In DI, the instructor actively delivers course content and students passively receive the material. In contrast, AL pedagogies require the student to actively manipulate and explore the disciplinary space ([Box 1](#)). In DI, students

only become truly active agents when *and if* they study by purposefully recalling or manipulating the material, usually outside of class, and/or rephrase and summarize during note-taking ([Abel and Roediger, 2018](#); [Karpicke et al., 2009](#)). Educational psychologists have documented behavioral practices that improve student learning, including retrieval practice, spacing and interleaving of content during studying ([Agarwal and Roediger, 2018](#)). These practices require students to initiate or engage in specific studying practices, self-testing or otherwise evaluative functions. An instructor who organizes in-class activities for students provides practice, models effective studying behaviors and promotes learning. All of these recommendations involve students actively remembering, practicing, making decisions, solving problems, and evaluating progress. Thus, one practical mechanism to achieve student agency (exerting effort and making choices) is to have both active classroom learning and active out-of-class studying ([Hood Cattaneo, 2017](#); [Lombardi et al., 2021](#); [Sinha and Kapur, 2021](#); [Smith and Baik, 2021](#)). Additionally, AL pedagogies include group work that engages social interactions among students, further motivating learning.

In meta-analyses at the university level, AL pedagogies produce better student outcomes as measured by improved performance on summative tests, lower failure rates, and more equitable outcomes

\* Correspondence to: Department of Neuroscience, University of Minnesota, 6-145 Jackson Hall, 321 Church St SE, Minneapolis, MN 55455, USA.

E-mail address: [Dubin001@umn.edu](mailto:Dubin001@umn.edu) (J.M. Dubinsky).

<sup>1</sup> ORCID ID: 0000-0001-9520-3780

(Deslauriers et al., 2019; Freeman et al., 2014; Haak et al., 2011; Theobald et al., 2020). Since students learn in both situations, can neuroscience provide mechanisms to support the greater learning gains seen in AL? Suggestive evidence comes from the finding that an undergraduate-level understanding of synaptic plasticity resonates with K-12 educators, as it provides a foundational explanation for how the classroom behaviors they orchestrate translate into the content and skill mastery desired for students (Dubinsky et al., 2019, 2013). Indeed, after learning neuroscience, teachers use synaptic plasticity, among other neuroscience ideas, to justify their choices of AL pedagogies (Dubinsky et al., 2019; Friedman et al., 2019; Schwartz et al., 2019; Tan and Amiel, 2019). Here, we explore how contemporary neuroscience explains the advantages and benefits of active, student-centered pedagogies compared to teacher-centered information transfer, while examining the neural mechanisms for both.

A key gap in understanding educational methodology is why learning is enhanced when student agency-centered pedagogies are employed. Does AL promote more synaptic plasticity in relevant brain areas than DI? Do brain reward and motivation circuits differentially regulate learning in active vs passive environments? What neurobiological components bolster learning when student agency and social interactions are engaged? This paper examines how the brain mechanisms underlying plasticity, agentic decision-making, error evaluation, and social interactions augment networks for learning. We suggest that these neural mechanisms form the basis for why AL can be more efficacious than DI. In making these arguments, we interpret and apply insights from contemporary literature in systems and cognitive neuroscience to learning in formal educational settings.

Our general hypothesis is inspired by prior studies across multiple

disciplines. We posit that AL promotes a more robust synaptic plasticity in students' brains as they actively engage with task learning objectives. The agentic, social, and motivational components of AL synergistically amplify signals in the reward circuit to make the experience and course content more valuable, meaningful, and memorable (Daniel and Pollmann, 2014; Miendlarzewska et al., 2016). On exposure to new content, students do not know which information will be useful for the future (e.g. exams), blurring the relative value of new content. Students face the challenge of sorting course information, predicting what information will be useful to retain vs. what will not. Such sorting entails manipulating the information, projecting and iteratively practicing how to apply it to problems or anticipated exam questions. When studying, students must direct their own learning towards gaps in judgment or understanding (Markant et al., 2016). In making these content-related decisions, learners implicitly ascribe value to learning objects or 'cognitive skills' as they build mental models of the disciplinary world. Rather than hope students do this on their own, AL provides opportunities for *all* students to explore the content space in a guided yet challenging way, taking advantage of social interactions. Finally, during assessments, students apply the learned world models and further evaluate the correctness of externally or internally generated possible answers using the inference machinery trained during classroom practice and study. Thus, from a neuroscientific perspective, AL classroom behaviors parallel those studied in experiments on decision making and cognitive processing, making those neuroscience findings relevant to classroom learning.

### Box 1

#### Active Learning vs Direct Instruction.

Direct instruction (DI) represents traditional pedagogy based upon transmission or transfer theory or the banking model. DI is often called teacher-centered, or sage-on-the-stage (Goswami, 2019). Active learning (AL) refers to pedagogies based upon constructivism and is variously called student-centered, cooperative, collaborative, project-based, flipped, or participatory (Goswami, 2019; Hood Cattaneo, 2017; Lombardi et al., 2021). In this paper, we contrast these approaches as if they were polar opposites. In reality, these form a continuum, with combinations and gradations of distinction among pedagogies. Instructors at all educational levels are capable of adapting these general categories of pedagogies to the developmental level of their students.

DI focuses upon traditional information transfer pedagogies like lecturing. The instructor organizes and delivers content that students listen to, annotate, hopefully internalize and then recognize appropriately or manipulate on a high-stakes exam. The roles here are clear: teachers deliver knowledge and students absorb it. The immediate value of acquiring the day's knowledge portion may be low compared to the distal goal of finishing the course in good standing. All internalization and mastery occur when students study the material outside of class, at best doing problem sets, without any instructor guidance. Most frequently, students reread notes only in preparation for the exam (Karpicke et al., 2009). Students schedule their own studying and maintain their own motivation. Student agency for their learning depends upon how motivated they are to utilize optimal study techniques and metacognitive evaluation on their own. Motivation to learn is left up to each student and their long-term achievement goals.

AL structures learning experiences where students have to encounter and manipulate the material. Pre-class preparation can require written summaries, quizzes, assigned problem sets, readings, or viewing videos or pre-recorded lectures. In-class time encompasses discussing or applying the content to real world problems, solving problems, going over quiz answers, designing projects, etc. Such activities engage students in recalling, manipulating the information, evaluating their own level of mastery (metacognition) and teaching each other. Requiring end of class summaries focuses everyone on the important ideas. Assessments are often interleaved into the daily activities as performance pieces, providing both students and instructors with formative feedback prior to, or in place of, summative assessments. In AL, students initially struggle with content, statistically exploring the disciplinary content, then practice and refine those ideas through in-class participation where they receive feedback for metacognitive evaluation of their own understanding. The salience and value of daily challenges, group work, and the sense of a class community working towards a goal maintain motivation, making it harder for less motivated students to become neglectful. For AL, student agency is built into every daily preparative and class activity. The instructor designs the course structure and guides activities to promote student mastery of the desired knowledge and skills through practice, application and correcting one's own mistakes. Course structure requires student effort, forcing them to engage in daily practice enroute to mastery (Lombardi et al., 2021).

Both DI and AL may be appropriate at different times within the same classroom (Lombardi et al., 2021; Yannier et al., 2021). Learning takes place in all circumstances, but to a higher level and more equitably during AL (Deslauriers et al., 2019; Freeman et al., 2014; Haak et al., 2011; Theobald et al., 2020). Notably, the educational gap in STEM learning between majority and underrepresented populations can be reduced using AL pedagogies (Haak et al., 2011). As with any human endeavor, the quality of instruction may vary with both pedagogies, as performance in some AL classrooms does not surpass DI (Klahr and Nigam, 2004; White et al., 2014).

## 1.1. Overview

In explaining the neuroscience mechanisms supporting both AL and DI, we review neuroscientific concepts related to learning and memory from across a broad range of experimental levels; from the cellular and synaptic level, to the anatomically connected circuit level, to the functional connectivity derived from fMRI at the network level. Reviewed mechanisms include i) synaptic plasticity and its modulation by dopamine, ii) the multiple roles of dopamine in the reinforcement learning circuit for decision making (also called the reward circuit), and iii) large scale brain networks supporting learning, error processing, and memory. The reviewed neuroscience evidence draws mostly from experiments on humans, but is supplemented with animal experiments when additional detail is needed.

There are strong parallels between academic instruction and laboratory-based associative and reinforcement learning experiments studying naturalistic foraging behaviors in model organisms. Specifically, classroom learning leverages brain mechanisms for exploring intellectual domains that perform operations on world-model representations. Thus, learning a concept, how to apply it, and how long to remember it are analogous to learning to navigate and make survival decisions in an ecological environment (Johnson et al., 2012; Metcalfe and Jacobs, 2010). For example, the rodent and human hippocampus can map physical space for navigation but also uses the same relational representation to organize, explore, manipulate, and plan through abstract knowledge spaces (Knudsen and Wallis, 2021; Theves et al., 2019). Moreover, in the reward learning domain, motivational principles for allocating and sustaining physical effort to pursue rewards (Salamone and Correa, 2012) are identical to those that regulate the cognitive effort required to search internal memory, deliberate, and simulate potential solutions (Vaidya and Badre, 2022; Westbrook et al., 2021).

The central focus is that neuroscience mechanisms are able to explain how learning and memory occur in situations created by different pedagogical practices. We first describe neuroscientific mechanisms that are largely synaptic and cellular in nature for a group of pedagogies that are common to both AL and DI; spacing, novelty and prior knowledge. Second, the mechanisms supporting AL are covered in detail as they involve multiple roles for dopamine (DA) and the RL circuit. This section considers the RL circuit's role in intrinsic motivation, agency, error evaluation, curiosity, and social interactions. Third, neuroscience mechanisms for DI are discussed regarding following instructions, the social nature of knowledge transfer, and working memory (WM). Prior to concluding, the last section addresses intersecting issues; the value of effort, interactions between WM and RL processes, the emergence of generalization, and the impacts of AL on individuals and groups. The neuroscience literature regarding attention and metacognition, topics highly relevant to education, has not yet, in our opinion, converged on clear mechanisms and refer the reader to relevant reviews (Cortese, 2022; Fleur et al., 2021; Lindsay, 2020).

To maintain the emphasis on behaviors relevant for human education, the text is organized by pedagogical categories. In each section, we present the educational practices first, followed by applicable neuroscience mechanisms. Educational examples draw primarily upon the university level with K-12 examples provided sparingly. This is appropriate since subjects in the majority of neuroscience experiments still draw from young adult populations. We recognize, but do not address, the rich literature on child development. The underlying neural mechanisms of learning and memory are not expected to be completely different in children; rather children's capacities may be limited by structural and network maturation which itself may be experience-dependent (Donato et al., 2021; Goswami, 2020).

## 2. Neuroscience mechanisms of spacing, novelty and prior knowledge

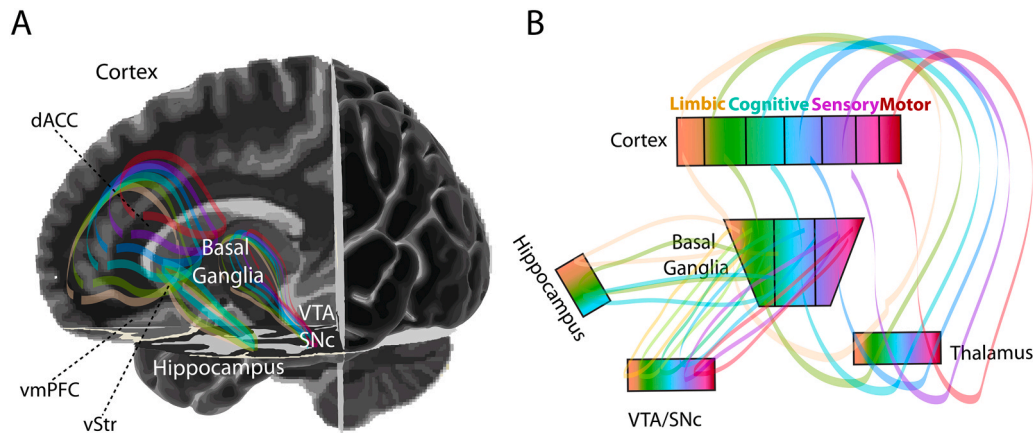
### 2.1. Plasticity

Three educational practices common to all good pedagogy - spacing, novelty and prior knowledge - can be explained by synaptic plasticity. Educational psychologists advocate for using spaced learning and retrieval practices as pedagogical strategies that improve student performance (Agarwal and Roediger, 2018). While both strategies are based on synaptic plasticity, retrieval practice additionally involves agency and will be discussed in Section 3.6. Moreover, investigation into the modulation of synaptic plasticity suggests that novelty and arousal can contribute to didactic learning. The associative property of plasticity (Barriónuevo and Brown, 1983; Nicoll et al., 1988), its modulation by novelty and arousal (Lisman and Grace, 2005; McGaugh, 2015), and the overlapping encoding of temporally associated novel and old memories (Chowdhury et al., 2022; Redondo and Morris, 2011; Sehgal et al., 2018) can explain why educators should always establish students' prior knowledge before introducing new material and why making sense of a topic requires multiple passes through the material.

Synaptic plasticity constitutes the central mechanism for learning and memory in all nervous systems (Kandel et al., 2016; Schaefer et al., 2017). The central function of plasticity is to strengthen or weaken the cellular connectivity between communicating cells. Plasticity can arise from cellular and intracellular changes involving biochemical, structural, and genetic mechanisms for learning on multiple time scales. Synaptic strengthening occurs both at the time of encoding and upon reactivation during memory recall (termed reconsolidation or reorganization), serving as the general mechanism for learning and remembering across timescales (Kandel et al., 2016; Moscovitch and Gilboa, 2022; Schaefer et al., 2017).

DA modulates synapses and circuits through a diversity of mechanisms at multiple levels. DA regulates synaptic activity through intracellular signaling pathways, modulation of neurotransmitter release and postsynaptic receptor function, perturbation of membrane potential and excitability, and interaction with other neurotransmitter systems (Tritsch and Sabatini, 2012). DA neurons from different midbrain nuclei project to widespread targets - sometimes more than one as axons can send collaterals to distinct brain areas (Björklund and Dunnett, 2007; Haber and Knutson, 2010; Tritsch and Sabatini, 2012). In parallel pathways from cortex through striatum, DA produces opposing excitatory and inhibitory signals to alter transmission of synapses, resulting in permitting or restricting the flow of information back to cortex via the thalamus (Cox and Witten, 2019; Shen et al., 2008; Surmeier et al., 2007). Thus, the Go/No Go nature of these DA control circuit-level signals act to gate information flowing through orthogonal cortico-basal ganglia-thalamic loop circuits that traverse the striatum (Badre, 2020; Haber and Knutson, 2010) (Fig. 1). Beyond these well-worked out mechanisms, we focus upon the information that DA modulation of cortical, striatal and hippocampal synapses provides for circuit and network calculations regarding cognitive behaviors (Berke, 2018; Cools, 2019; Cox and Witten, 2019).

While most mechanistic evidence that synaptic plasticity supports learning and memory comes from animal studies, investigations in humans confirm this relationship (Mansvelder et al., 2019; Spriggs et al., 2019). Plasticity can be directly measured as LTP and LTD in clinically resected human brain tissues (Beck et al., 2000; Chen et al., 1996; Mansvelder et al., 2019) and as transcranial magnetic stimulation invoked changes in motor-evoked potentials (Stefan et al., 2000). In recordings from clinically implanted depth electrodes in the human medial temporal lobe, single-unit neuronal firing responds to paired novel pictures or to anticipate the picture sequences being learned, demonstrating plasticity and the ability to predict future events (Ison et al., 2015; Reddy et al., 2015). In humans, cortical volume and connectivity changes have been observed after sensory, motor and cognitive



**Fig. 1.** Schematic of reciprocally interacting cortico-basal ganglia-thalamic pathways and their relationship to the RL circuit. Illustration of regional brain circuit interactions (A) and expanded overview diagram with regional connectivity (B) between cortico-basal ganglia-thalamic pathways and the reinforcement learning circuit. Cortical regions project in a topographic manner to the underlying basal ganglia input region, the striatum. Basal ganglia outputs to thalamic areas that subsequently project back to cortex complete the long-loop cortico-basal ganglia-thalamic pathways (Alexander and Crutcher, 1990). Topographically, more medial regions represent limbic or emotional processing; intermediate regions represent cognitive functioning; and more lateral regions are concerned with sensory-motor functions. This topographical arrangement is preserved in reciprocal dopaminergic connections between VTA/SNc and the striatum. The striatum to VTA/SNc connections also project to laterally adjacent regions (from medial to lateral) providing for spiraling feed forward integration of control signaling across the striatum and the associated functional long-loop pathways. The vmPFC and dACC are specific cortical regions contributing to limbic and cognitive valuation and monitoring functions in the RL circuit. Finally, hippocampal projections reciprocally innervate the limbic ventral striatum providing a pathway for control of encoding and remembering of emotional and value signals (Haber and Knutson, 2010). Additional connections between hippocampus and cortex are not shown. For a full description of anatomical connections in the RL circuit, see (Haber and Knutson, 2010). Abbreviations: dACC, dorsal anterior cingulate cortex; vmPFC, ventromedial prefrontal cortex; VTA/SNc, ventral tegmental area/substantia nigra pars compacta; vStr, ventral striatum. Image in A from the Allen Human Atlas - Brain Explorer.

learning (Draganski et al., 2006; Taubert et al., 2010; Wenger et al., 2021), consistent with synaptic proliferation seen in animal models of learning (Schmidt et al., 2021). These changes shape network activity across multiple, distributed cortical and subcortical brain regions (Bassett and Gazzaniga, 2011; Bassett and Sporns, 2017). As in vivo mechanistic studies in human learning expand, the evidence connecting synaptic plasticity to the networks generating cognitive learning will solidify further (Mansvelder et al., 2019; Rutishauser, 2019; Szegedi et al., 2016). For a synopsis of the neural circuitry contributing to the higher-order cognitive processes involved in learning and memory, see Box 2.

## 2.2. Encoding and spacing

Studying information multiple times over varying time scales, known as spacing, produces deeper learning than studying in a single cramming session before a test (Gerbier and Toppino, 2015; Wimmer et al., 2018). In humans, spaced learning exceeds massed learning for recall of vocabulary, content, skills, generalization ability, and reward values (Cepeda et al., 2006; Smolen et al., 2016; Wimmer et al., 2018). Spaced training results in greater retention of associated reward values for learned images in the ventromedial prefrontal cortex and hippocampus (Vaidya and Badre, 2020; Wimmer et al., 2018). Studies on massed learning indicate that performance is proportional to and may be limited by WM capacity, the short term capacity to retain information needed for immediate thoughts or action (Wimmer et al., 2018).

Experimentally, the better recall and error tolerance of spaced learning has been investigated at cellular and systems levels and recreated in models of neural networks. In brain slice preparations, maximal hippocampal LTP and associated structural changes are readily induced by stimulations that mimic natural hippocampal complex spikes, spaced 60 min apart, which appears to allow maximal integration of intracellular second messenger cascades that support plasticity (Diamond et al., 1988; Smolen et al., 2016). Moreover, memory reorganization during sleep improves learning spaced over days (Klinzing et al., 2019). Simulation of learning in neural networks attributes this difference to the nature of network connectivity as synapses become strengthened

(McClelland et al., 1995). When faced with how to store new information that crosses categorical boundaries of learned associations, networks that initially encoded information in a massed manner were subject to rapid failure. In contrast, networks that encoded initial information more broadly from spaced or interleaved encounters could incorporate the ambiguous novel information more rapidly and make fewer misclassification errors. In other words, interleaving provided the CNS network model for this information with the flexibility to identify, acknowledge, and incorporate exceptions to rules (McClelland et al., 1995). This network model correctly identified and emphasized the importance of the hippocampus as an intermediate stage of cortical information processing (McClelland et al., 1995). Therefore, the mechanistic explanation neuroscience provides for spacing indicates active pedagogies place students in situations where spacing and interleaving are inherently part of repeatedly addressing content during multiple applications. In contrast, lecturers must consciously plan to incorporate spacing into their content delivery.

## 2.3. Novelty and arousal enhance plasticity

For students, much of academic content is novel, even if the experience of attending class and listening is not. Emotional arousal, whether from social interactions, laughter, fear, or boredom, occurs in school settings and is most often disassociated from the academic content. After a psychology lecture, viewing an emotionally engaging video, unrelated to lecture content, resulted in better performance on the final exam for questions pertaining only to that lecture (Nielson and Arentsen, 2012). The demonstration that this type of arousal can alter academic outcomes suggests regular lectures could include arousing content to engage such mechanisms.

Arousal and novelty act at the cellular level via several mechanisms involving the neuromodulators norepinephrine and dopamine to alter synaptic plasticity and associated memory formation (Dudai, 2012; LaLumiere et al., 2017; Lisman et al., 2011; Lisman and Grace, 2005; McGaugh, 2015; Redondo and Morris, 2011). Human dopamine neurons respond to a novel image and when synchronized with cortical theta activity, predict memory formation (Kamiński et al., 2018). In arousal,



**Box 2****Synopsis of the Neural Substrates of Human Learning and Memory.**

The hippocampus rapidly encodes specific memories while the cortex slowly integrates these to extract generalizations across multiple episodes based upon task demands. In this arrangement, the hippocampus binds together memories based upon spatial, temporal, and abstract characteristics and acts as an index to their cortical representations, as they contribute to future planning (O'Reilly et al., 2014; O'Reilly and Rudy, 2001). Replay and reactivation of hippocampal signals immediately, over time and during sleep contribute to coordination of encoding, reorganization, and recall across downstream cortical networks (O'Reilly et al., 2014; Swanson et al., 2020). Over time, memory traces reorganize, representing a dynamic interplay between hippocampal and cortical representations that integrate new experiences into existing cortical networks. This has been called memory systems reorganization (replacing the older term systems consolidation, (Gilboa and Moscovitch, 2021; Moscovitch and Gilboa, 2022)).

Only a limited number of ideas can be cognitively manipulated at once, termed working memory (WM) (Cowan, 2010). WM involves rapid representations in multiple parts of cortex. The hippocampus contributes to WM if the WM task is long enough (>12 s) to require indexing of retrieval of recent medial temporal lobe memory for inclusion in the current WM task (Cabeza et al., 2002; Oztekin et al., 2009). WM contributes to setting the expectations for the reinforcement learning (RL) circuit. The WM and RL systems interact reciprocally such that low WM loads favor rapid encoding, without a RL contribution, whereas high WM loads engage the RL circuit to sort through relative values in a slower process that favors longer term retention (Collins and Frank, 2018).

Within the RL circuit (also called the reward circuit), DA provides signals for which memories, events or items are important or valuable enough to retrieve or use (Pennartz et al., 2011). Value calculations based upon prediction errors (PEs) computed in the striatum act to gate which ideas or rules held in working memory (WM) prevail in controlling subsequent decisions and actions (Collins and Frank, 2018; O'Reilly and Frank, 2006). Striatal dopaminergic inputs represent differences between expectations and experience (PEs), acting as learning signals to update expectations and gate which policies control subsequent actions or encoding (Schultz, 2016)(Box 4). Generalized subjective value calculations during deliberation and outcome delivery are made in two overlapping networks at the core of the RL circuit in humans (Bartra et al., 2013; Suzuki et al., 2012). The anterior insula, dorsomedial prefrontal cortex and more dorsal and caudal striatum produce a U-shaped response representing arousal or salience. During decision making, the anterior ventral striatum and ventromedial prefrontal cortex calculate a linear, valence-sensitive response representing overall subjective value that can be dynamically scaled relative to context. At outcomes, the posterior cingulate and anterior insula also signal subjective value (Bartra et al., 2013; Tobler et al., 2005). This holds for both physical and cognitive efforts (Bartra et al., 2013; Westbrook et al., 2019).

The RL circuit functions to control information flow through intersecting circuits (Badre, 2020). Dopaminergic signaling in the basal ganglia gates traffic through long-loop cortico-striatal-thalamic circuits that intersect and spiral through it in distinct anatomical subregions (Fig. 1). Circuits intersecting the human anterior caudate (dorsomedial striatum in rodents) are associated with cognitive functions, the posterior putamen (dorsolateral striatum in rodents) are associated with sensorimotor functions, and ventral striatum (ventral striatum/nucleus accumbens, in mammals) are associated with value, effort or goal-driven RL-related behaviors (Balleine, 2019; Suzuki et al., 2021). The hippocampus and ventromedial prefrontal cortex are part of the medial loops intersecting the ventral striatum, consistent with their role in RL (Haber and Knutson, 2010; Pennartz et al., 2011; Shohamy and Adcock, 2010). The medial to lateral spiraling nature of information through these loops suggests that signals move from value calculations to cognitive assessment prior to motor execution (Pennartz et al., 2011). This explains why i) RL is hippocampal dependent while procedural motor learning is hippocampal independent and ii) initial, slow, effortful motor learning and habit execution are respectively gated through the striatum from more anterior to posterior in humans or dorsomedial to dorsolateral in rats (Balleine et al., 2015; Pennartz et al., 2011).

While memories are broadly encoded throughout cortex, different regions appear to contribute more to specific domain general behaviors. MTL supports recognition memory, or familiarity while recall depends upon the hippocampus (Yonelinas, 2002). Bidirectional connections between the hippocampal area/medial temporal lobe and ventromedial prefrontal cortex provide a route for the ventromedial prefrontal cortex to contextually control encoding and retrieval (Preston and Eichenbaum, 2013). The presence or absence of modulatory cholinergic signals shifts the temporal dynamics of theta oscillations to bias hippocampus and medial prefrontal cortex towards memory encoding or retrieval, respectively (Gedankien et al., 2023; Haam and Yakel, 2017; Hasselmo et al., 1996; Kukulja et al., 2009). Generally, more anterior cortical structures set intentions whose associated actions are directed by more posterior portions of prefrontal cortex through spiraling cortical-striatal pathways with more caudal than rostral projecting connections (Badre and D'Esposito, 2009; Haber and Knutson, 2010). The dorsolateral prefrontal cortex processes incoming information and generalizes relationships, extracting rules and building conceptual understanding of a context while the ventrolateral prefrontal cortex maintains goals, policies or rules in communication with the hippocampus (Blumenfeld and Ranganath, 2007; Dehaene et al., 1998; Miller and Cohen, 2001).

norepinephrine, in conjunction with glucocorticoids, changes the level of activity in basal lateral amygdala neurons, increasing activity in widespread areas supporting multiple memory systems (McGaugh, 2015; Schwabe et al., 2022). Dopamine (DA) neurons also respond to novelty (Bunzeck and Düzel, 2006; Schott et al., 2004; Schultz et al., 1997), and modulates synaptic plasticity in the striatum, cortex and hippocampus to regulate reward learning, cognitive function, and memory storage (Duszkiewicz et al., 2019; Lisman and Grace, 2005; Puig et al., 2014; Shen et al., 2008; Shohamy and Adcock, 2010).

Two dopaminergic mechanisms contribute to novelty-enhanced encoding. First, DA activation contributes to hippocampal memory both within minutes and also after a 12-hour delay following the initial experience (Hansen and Manahan-Vaughan, 2014; Rossato et al., 2009). In mice, locus coeruleus neurons projecting to the hippocampus release

DA and norepinephrine during the encoding of novel events, enhancing learning within minutes (Duszkiewicz et al., 2019; Kempadoo et al., 2016; Takeuchi et al., 2016; Wagatsuma et al., 2018). These locus coeruleus-derived DA signals may be the novelty detectors that trigger the ensuing hippocampal interactions with other dopaminergic mesolimbic structures (Hansen and Manahan-Vaughan, 2014). Second, dopaminergic signaling can enhance hippocampal activation memory through synaptic tagging and capture. This process is hypothesized to spread proteins associated with strong LTP formation to adjacent synapses activated by weaker encoding and strengthen their long-term memory (Dunsmoor et al., 2022; Frey and Morris, 1997; Redondo and Morris, 2011). To be influenced by synaptic tagging, weakly encoded events must occur within specific time windows, roughly 0.5–3 hr before or after the more memorable event (Ballarini et al., 2009; Frey

and Morris, 1998; Redondo and Morris, 2011). The ability of DA to modulate synapses at distal and prior time points becomes important later in this discussion when considering how an outcome signal can retrogradely influence the strength of synapses that were active during the initial planning and execution of the actions leading to that outcome (see Section 3.3).

Behavioral tagging extends the idea of synaptic tagging to posit that novel experiences may enhance the learning of cognitive tasks (Dunsmoor et al., 2022), as suggested in these examples. Elementary student story or picture recall was enhanced when paired with a novel music or science lesson a few hours earlier (Ballarini et al., 2013). High school students' long-term retention of a copied graphic was greater when preceded by a novel change-blindness or sex education lesson (Ramirez Butavand et al., 2020). Beyond timing concerns, the relatedness of the novel and target experiences and students' prior knowledge may impact memory-making (Dunsmoor et al., 2022; Quent and Henson, 2022).

Given the broad temporal window for strengthening of weakly encoded memories by a stronger novel experience (Dunsmoor et al., 2022), replay mechanisms and other aspects of memory reorganization (e.g. sleep) may also be contributing to these memory enhancements (see Box 2). Novelty and arousal are alerting, but do not necessarily reward one's actions, as the latter engages other mechanisms discussed below (Section 3). While arousal, emotions, and novelty can't be easily distinguished in these educational experiments, the evolving mechanistic neuroscience understanding of these phenomena supports the utilization of engaging teaching practices to bolster learning and memory. Whether new lecture content, but not format, is sufficient to activate such mechanisms remains unknown. Considering the temporally contiguous nature of lessons throughout a school day, spacing breaks or varied activities between lessons could possibly promote the potentially beneficial effects of novel experiences on academic learning (Kelley and Watson, 2013; Menon and Levitin, 2005). This also raises questions about whether adding humor to lectures (demonstrated to activate reward centers (Bekinschtein et al., 2011; Neely et al., 2012)) could raise arousal neuromodulators sufficiently to enhance retention (Li et al., 2020; Mobbs et al., 2003; Zauli et al., 2022).

## 2.4. Prior knowledge

Prior knowledge provides an existing structure for integrating new information into one's understanding of a subject (Shing and Brod, 2016). Having an existing schema or mental model of an academic subject facilitates the encoding of further information into that schema, sometimes after only a single exposure, and potentiates its subsequent recognition (Shing and Brod, 2016; Tse et al., 2007; van Kesteren et al., 2014). Across multiple behavioral paradigms, retrieving, activating and addressing prior knowledge facilitates learning and memory (Brod et al., 2013; Council, 2000).

At a cellular level, linking of new and old information implies integration or similarities among synaptic connections (Brunec et al., 2020). Overlapping populations of neurons encoding temporally close experiences permit the linked recall of one memory by the other. Mechanistically, increases in intrinsic excitability modulated by DA, CREB activation, and/or synaptic tagging support memory linking (Sehgal et al., 2018). In rat hippocampus, DA induces place cell reorganization and links sets of synapses representing old and new spatial memories, promoting overlap and stability without altering memory formation (Chowdhury et al., 2022; Gonzalez et al., 2021). Analogously, a DA novelty signal depotentiates mouse ventral hippocampus to medial prefrontal cortex synapses in preparation for new synapse formation associated with learning of the novel information (Park et al., 2021). The associative nature of LTP and the reactivation of plasticity during recall also underpins the benefits of connecting new information to old memories (Council, 2000; Wang and Morris, 2010). In humans, the influence of these DA signals may extend beyond the hippocampus to memory encoding in the entire medial temporal lobe (Eckart and

Bunzeck, 2013).

Functional connections among cortical regions also support a role for prior knowledge in learning and memory. University neuroscience and education students learned more new facts about their respective fields, but not about the opposite field, when presented with sentences containing both old and new information than when presented with sentences containing only new information (van Kesteren et al., 2014). Activity in the medial prefrontal cortex, but not the medial temporal lobe, was correlated with successful encoding of the associated new information and predicted subsequent year academic achievements (van Kesteren et al., 2014). Different hippocampal subregions may be responsible for retrieving linked new and prior knowledge (Guo et al., 2023). In subjects with prior knowledge of a narrative, cortical event-related activation patterns emerge in anticipation of the upcoming story events (Baldassano et al., 2017).

These experiments demonstrate DA-modulated plasticity incorporates new knowledge into existing schemas, justifying educators' need to connect new information to prior knowledge. We use old memories to make predictions regarding future behaviors and states of the world. Activating prior knowledge not only provides opportunities for encoding via overlapping sets of synapses, it also enables students to make predictions regarding how the new content may impact the old. Together, synaptic plasticity and its modulation with time and exposure to DA constitute a cellular level basis for all forms of learning and memory.

## 3. Neuroscience mechanisms of active learning

By positioning students to make choices in discussions, problem solving, or other class activities, AL gives them agency and engages the RL system as we argue here. When exerting agency, an actor must evaluate action outcomes to determine if goals are met and iteratively change behaviors to reach goals. This process describes RL, supported operationally in the brain by the RL system (Sutton and Barto, 2018). DA signaling, underpinned by DA modulation of synaptic plasticity, remains at the heart of the RL system contributing value calculations to discriminate salient information or events (Bartra et al., 2013; Scimeca and Badre, 2012). Whether or how much the RL system becomes activated in a DI situation where a learner passively receives information without the opportunity to apply it towards a goal remains undetermined.

Given the breadth of modulatory DA synaptic mechanisms, multiple temporal, anatomical, and contextual roles of DA in cognitive processing are to be expected. DA signals differ within the RL circuitry temporally based upon the progression of the behaviors themselves. DA signals anticipation, cost of effort (Box 3), reward prediction errors (PEs, Box 4), and agency at times roughly, but not exactly, corresponding to cue, intervals anticipating or during actions, outcome or reward receipt, and evaluation, respectively (Hamid, 2021). Each of these contributes distinct information to the overall value calculations in the RL circuit. Midbrain DA cell spiking updates expectations useful for future decisions, whereas fluctuating DA levels in striatum regulate the current motivation to pursue an ongoing goal (Berke, 2018; Hamid et al., 2016). During progress to the goal, ramping DA levels proportional to the anticipated future reward, are used to discount time or effort costs required to attain the goal (Hamid et al., 2016). This motivational signal invigorates ongoing behaviors, while the outcome-associated, ventral tegmental DA spiking conveys a reward PE that acts as feedback to invested effort, time, plan, and action (Berke, 2018; Hamid, 2021; Mohebi et al., 2019). Moreover, the overall success rate of the animals' policies are encoded by tonic dopamine levels that are observed to correlate to reward rate and modify behaviors over longer times scales (Hamid et al., 2016). A recently observed wave like DA rhythm following reward acts to reinforce synapses that created the current state (Hamid, 2021; Hamid et al., 2021). This latter mechanism is hypothesized to contribute to the behavioral, circuit, and network level results

**Box 3****The Value of Effort.**

Scholastic learning requires effort in both AL and DI environments. The physical or cognitive effort required to accomplish a task can act as an energy barrier to beginning the task, reducing motivational engagement (Inzlicht et al., 2018). Under these high effort conditions, learning may be perceived as aversive because it requires students to leave their comfort zones and exert energy to explore new concepts (Finelli et al., 2018; Nguyen et al., 2017; Owens et al., 2020). Cognitive effort associated with a high WM load can produce anxiety (Moneta et al., 2007) or be aversive as evidenced by some people's choice of thermal pain in place of completing a large N-back task (Vogel et al., 2020). Similarly, students identify multiple costs associated with 'doing school': costs of effort for the assigned tasks, costs associated with conflicting responsibilities, costs of lost alternative opportunities, and emotional costs (Flake et al., 2015). Most students respond positively to AL, citing their agency. Student resistance to AL can be dispelled by instructor explanations justifying AL strategies (Finelli et al., 2018; Nguyen et al., 2017; Owens et al., 2020). Despite these costs, effort also can be rewarding as effort increases personal investment and overall value calculated retrospectively, concurrently, and prospectively (Inzlicht et al., 2018). Therefore, success is sweeter the more effort one exerts and contributes to future willingness to work hard, especially in an academic setting. Effortful success builds a love of learning, a universal goal of schooling (Anderman, 2021; Ontario. Royal Commission on Learning et al., 1995).

The value of work required to offset effort costs to complete a task is calculated by the mesolimbic DA signals in the ventral striatum (Gan et al., 2010; Hamid et al., 2016; Salamone and Correa, 2012). Effort calculations reflect the amount of work expended and must be weighed against expected rewards (Inzlicht et al., 2018; Salamone and Correa, 2012). In non-human primates, firing rates of mesolimbic DA neurons' PE signals are enhanced following costly actions leading to faster stimulus-reward learning (Tanaka et al., 2019). PEs included the cost of effort as well as the value of the juice reward, indicating that the RL circuit integrates both costs and benefits (Tanaka et al., 2019). In humans, DA appears to bias choices towards the benefits as opposed to the costs of cognitive effort or timing depending upon the task, the striatal subregion activated, and an individual's genetically-determined regional dopaminergic synthesis capacity (Cools, 2019; Westbrook et al., 2021). More difficult tasks, with more associations to be remembered or more difficult multiplications to perform, produce greater ventral striatal responses suggesting that greater applied cognitive effort generates greater reward signals and may represent intrinsic motivation (Dobryakova et al., 2017; Hernandez Lallement et al., 2014). Thus, RL circuit value calculations scale with the cost of effort, are biased by eventual benefits, and include the values of the learning goal and agency. Giving students the agency to control their own learning permits them to make decisions about expending cognitive effort, triggering additional activity in the RL circuit.

demonstrating that agency boosts declarative learning, described next.

### 3.1. Learning is enhanced by agency

AL requires students to exert agency; hence the term 'student-centered learning' (Lombardi et al., 2021; Smith and Baik, 2021). Exerting agency requires some level of intentionality and commits one to a course of action (Bandura, 1997). Volitional production of goal-directed actions also augments learning (Katzman and Hartley, 2020). Thus, a concrete advantage of AL over DI is the volitional, agentic exploration of the content space in classroom settings. Developmentally, learning via self-generated actions facilitates learning eye-hand coordination, depth perception, spatial cognition, sound recognition, and learning to write (James, 2017). Agency also enhances cognition and reasoning abilities. Preschool children exerting agency have expanded capabilities to develop communication, planning and problem solving skills (Adair, 2014). Similarly, both children and adults exhibit stronger memories for outcomes resulting from their own actions when compared to actions outside of their control (Katzman and Hartley, 2020), suggesting that agency can modify the influence of rewards on strength of memory encoding and recall (Rotem-Turchinski et al., 2019; Ruggeri et al., 2019; Voss et al., 2011). Moreover, from a behavioral flexibility standpoint, remembering the consequences of one's actions is adaptive for planning future behaviors and assigning appropriate credit to executed actions. Because humans and animals exhibit strong preference for the opportunity to freely choose among options (Leotti and Delgado, 2014, 2011), mechanistic insights into agency-related enhancements of content memory during AL may leverage specialized brain circuits for reward and motivation. Given the centrality of motivational and reward learning processes to educational contexts, we provide a brief summary of brain circuits for RL, and how their interactions may contribute to the benefits of AL. For more explanation of PEs, see Box 4.

### 3.2. RL circuit activation during intrinsically motivated and self-directed learning

Canonically, agency has been recognized as an intrinsic reward (Bandura, 1997; Deci and Ryan, 1985). The neural correlates of exerting agency involve brain reinforcement learning pathways (or the *RL circuit*) that imbue environmental stimuli or outcomes with subjective reward values. Thus, the RL circuit uses the estimated values of current and future states to guide actions exploring or exploiting the environment. Feedback from outcomes or rewards reinforces, both positively or negatively, subsequent value calculations and actions to prioritize or increase the saliency of instrumental actions or internal curiosity that guide exploratory behaviors (Bartra et al., 2013). RL circuit calculations have been considered as a common currency for multiple dimensions of value, including the value of information itself and whether or not the information has instrumental applications (Bartra et al., 2013; Bromberg-Martin and Hikosaka, 2011; Marvin and Shohamy, 2016). Exerting agency produces a signal that adds to these value calculations (Hamid, 2021; Hamid et al., 2021).

Intrinsic rewards activate the RL circuit and subsequent learning as exemplified in the following example. To assess how the RL circuit is involved in intrinsically motivated learning, new word learning was examined in the context of two sentences where the implied word meaning was either congruent or contradictory. Without any extrinsic rewards, brain areas associated with the ventral striatum, substantia nigra/ventral tegmental area and the hippocampus were activated during successful understanding of correct meaning during second sentence presentation, indicating that DA signaling was involved in this intrinsically motivated learning process (Ripollés et al., 2018, 2016, 2014). Moreover, the degree of functional connectivity between these regions at encoding was proportional to the success of recall a day later (Ripollés et al., 2016).

Evidence also suggests that intrinsic motivation may increase sensitivity to feedback and improve memory. Specifically, increasing intrinsic motivation, by having subjects explain how important the task is midway through learning a long set of word pairs, increased

**Box 4****Prediction Errors as Learning Signals for Cognitive Learning.**

At a mechanistic level, DA signals the difference between expected and attained rewards, called prediction errors (PEs), providing feedback that can be used as a teaching signal in RL (Schultz, 2016; Schultz et al., 1997). PEs are calculated in the RL circuit for determining utility, subjective value, and saliency, all necessary for making decisions and evaluating feedback. PE signals are associated with classical conditioning (O'Doherty et al., 2003), instrumental learning (Pessiglione et al., 2006; Zaghoul et al., 2009), declarative memory formation (Ergo et al., 2020), information seeking (Bromberg-Martin and Monosov, 2020), and cognitive control (Chatham et al., 2014). In humans, PEs associated with evaluative and learning behaviors, can be extracted from PET (Thut et al., 1997), event-related BOLD signals (O'Doherty et al., 2003), EEG signatures during declarative learning (Ergo et al., 2020), and extracellular single substantia nigra neuron recordings during DBS implantation (Zaghoul et al., 2009). BOLD signals corresponding to PEs associated with reward-based learning across multiple categories of experiences appear centered on the ventral striatum or its inputs (Bartra et al., 2013; Daniel and Pollmann, 2014; Schultz, 2016). In these various pathways, PEs provide learning signals to guide circuit behaviors towards goals.

Dopaminergic PEs identified with learning in cortico-basal ganglia motor circuits have been proposed to apply to cognitive behaviors trained in education, as these long-loop feedback pathways also include frontal and parietal cortices and the dorsomedial striatum which serve cognitive functions (Berke, 2018; Johnson et al., 2012; Metcalfe and Jacobs, 2010; Westbrook et al., 2021)(Fig. 1). Within the cortical-basal ganglia-thalamic loops, dopaminergic striatal signals regulate motivation, higher cognitive goals, selection of more or less practiced motor or habitual behaviors, and the learning that occurs as actions approach goals (Westbrook et al., 2021). Humans value the opportunity to be able to make a choice, as represented by anticipatory neural signals in the bilateral ventral striatum even if the anticipated outcome is a monetary loss (Leotti and Delgado, 2014, 2011). The dorsolateral and central striatum code the value of the ability to choose, while the central striatum also codes the value of individual items (Fujiwara et al., 2013). The fact that agency signals are observed in the same striatal structures that calculate value suggests that agency itself has value (Balleine et al., 2021; Hamid et al., 2021) both for motor and cognitive behaviors.

During memory retrieval and gating of WM, PEs generated in the RL circuit, and ventral striatum in particular, assess the value of the knowledge needed to meet a goal (Bartra et al., 2013; Scimeca and Badre, 2012). At encoding, reward anticipation, novelty and positive, but not negative, emotional valence further enhance ventral striatal activity and long-term memory formation (Adcock et al., 2006; Wittmann et al., 2008b, 2008a, 2007, 2005). The PEs in the ventral striatum scale *adaptively* to reward variability or WM load. Lower variability or WM load leads to faster learning while greater variability or load is associated with slower learning, higher error related negativity signals in the EEG (see Section 3.4) and improved immediate retention (Collins et al., 2017; Collins and Frank, 2018; Diederer et al., 2016; Diederer and Schultz, 2015; Rac-Lubashevsky et al., 2023).

PEs are recruited by both primary and secondary extrinsic rewards (e.g. sex, food, money), depending upon the context (Bartra et al., 2013). Moreover, intrinsic or self-generated rewards such as musical pleasure or high-value information similarly activate the RL circuit (Blain and Sharot, 2021; Bromberg-Martin and Hikosaka, 2011; Mas-Herrero et al., 2021). In a trivia learning task, both external and internal rewards activated the RL circuit but at different times; the ventral striatum was active when the question was posed for external rewards or when the answer was given for internal rewards (Duan et al., 2020). In a combined reinforcement learning task, intrinsic rewards activated the ventromedial prefrontal cortex more than extrinsic rewards (Chew et al., 2021). These studies indicate that timing or contextual scaling of activity as well as the extent of overlap in the participating regions may contribute to the intrinsic/extrinsic motivation distinction but support the general role of the RL circuit in calculating the value of information (Mas-Herrero et al., 2021).

recognition (DePasque and Tricomi, 2015). Reward processing regions were activated more by positive than negative feedback after the conversation. These motivational interviews increased the sensitivity to the feedback, ameliorated the natural decline in attention and motivation, and increased activity in the parahippocampal gyrus, leading to improved memory (DePasque and Tricomi, 2015). Moreover, the intrinsic rewards associated with exerting agency contribute to increased self-efficacy, a known factor that influences learning outcomes (Blain and Sharot, 2021). Nonetheless, it remains to be determined if neural signatures of increased intrinsic rewards in one learning context persist to strengthen future intrinsic motivation, as desired in an academic context.

Tasks which provide subjects with the agency to choose during learning also engage the hippocampus in conjunction with the RL circuit (Murty et al., 2015; Ripollés et al., 2016; Voss et al., 2011). When subjects chose to uncover a hidden symbol-object pair to study, they learned the pairings better than when instructed to uncover a specific pair (Murty et al., 2015). Concurrent fMRI demonstrated activation of the orbital frontal cortex and ventral tegmental area, regions involved in valuation, plus an association between striatal activation during the choice cue and hippocampal activation during encoding. The extent of this coupling was proportional to memory strength. Thus without explicitly offering a reward, the exertion of agency engages reward circuitry and enhances declarative learning (Murty et al., 2015). A similar paradigm for learning objects and their positions on a grid probed subject's agency by permitting uncovering single objects in a

self-directed sequence vs in a directed, yoked sequence (Brandstatt and Voss, 2014; Voss et al., 2011). Actively controlling the sequence of grid openings to study the contents produced fewer positional errors and better object recognition than passively moving through the grid. fMRI of normal subjects revealed greater hippocampal activity during active exploration while individuals with hippocampal damage did not benefit from the active viewing condition (Voss et al., 2011), indicating a critical interaction of RL and hippocampal circuits during agency. Simply choosing to view or continue to view visual stimuli enhanced their memory a day or a week later (Rotem-Turchinski et al., 2019; Yebra et al., 2019).

The agency-induced memory enhancement may also be influenced by the utility or value of the available choices. In games where the relative values of agentic control to choose and the values of the choices were individually varied, the ventromedial prefrontal cortex computed the value of agency (Wang and Delgado, 2019). In behavioral experiments with subjects from 8 to 25, agency increased memory for objects that were associated with the ability to make the choice especially when the agency had high value (Katzman and Hartley, 2020). Thus, the RL circuit combines agency in making a choice, a key component of AL pedagogies, with the intrinsic value of the learning object to impact learning and memory.

### 3.3. Dopamine agency signals

A recent analysis of agency-linked DA signals across the rodent



striatum indicate spatiotemporally multiplexed decision-signals that manifest as wave-like patterns (Hamid et al., 2021). Carefully timed, DA waves traveling on the medio-lateral axis signal the animal's agency to run at self-determined speeds towards distant rewards. When the rodent did not have to run to receive rewards, the waves traveled from lateral to medial (Hamid et al., 2021). Because the striatum can be anatomically subdivided into smaller regions by virtue of differential cortical connectivity (Aoki et al., 2019; Hintiryan et al., 2016; Hunnicutt et al., 2016; Matamalas et al., 2020), the sweep of the DA waves provides a means to integrate actions across various cortical-basal ganglia loops. In this view, the waves serve as credit assignment signals to adjacent striatal subregions to strengthen synapses associated with producing the desired outcome (Hamid et al., 2021). The mechanisms for influencing the strength of previously active synapses are related to those discussed above, including synaptic tagging. DA waves may also serve to deliver value signals to related circuits or may provide for multilevel cognitive control (Hamid, 2021).

This positive modulation of learning by DA waves forms the basis for a hypothesis explaining the increased effectiveness of epistemic learning in situations involving student agency. If present in humans, such spatiotemporal DA waves could similarly provide a specific agency signal that dynamically regulates planning, monitoring and executing flexible cognitive operations in service of academic content learning. Moreover, the acute or chronic disruption of these spatiotemporal DA waves has been hypothesized to underlie moments of behavioral disengagement, attentional drifts, and uncertainty about behavioral control (Vinogradov et al., 2022). While the exact circuit and behavioral mechanisms that orchestrate the spatiotemporal coordination of DA release are under intense investigation, these empirical findings and their theoretical interpretations may provide additional support for how agency enhances learning. This hypothesis will drive future research.

### 3.4. Active learning involves recognizing and correcting one's own errors

Educators have long recognized the importance of learning from errors (Metcalfe, 2017; Ohlsson, 1996; Wong and Lim, 2019). Arguments favoring error-less teaching methods are falling into disfavor as evidence accumulates that learning from errors produces longer term retention and transferability (Clark and Bjork, 2014; Kapur, 2008; Wong and Lim, 2019; Zhang and Fiorella, 2023a, 2023b). Initially struggling with difficult or ill-structured problems produces immediate failures ('desirable difficulties', 'productive failures'), but when followed by practice on well-structured problems, errors improve performance on measures of near and far transfer (Clark and Bjork, 2014; Kapur, 2008). This practice has been termed 'problem solving prior to instruction' where students review and discuss the difficulties encountered. Teachers leverage such reflections to provide subsequent instruction. Reversing the order, instruction followed by problem solving, results in lower performance (Loibl et al., 2017; Sinha and Kapur, 2021). In all versions of these error-focused pedagogies, learners exert agency when struggling initially in an unfamiliar content space, when generating ideas to solve the problem, when reflecting upon their performance to correct errors, and when iterating this process.

Intentionally generating incorrect statements and subsequently correcting those ideas produces better immediate recall and far transfer effects than the errorless processes of simply reading the material, generating correct statements with synonymous meanings, or correcting peers' errors (Metcalfe, 2017; Wong, 2023; Wong and Lim, 2022). Generating false statements produces more repetitive interactions with the material (e.g. recognize correct concept and its limits, generate error, fix error) than simply studying (i.e. recognize correct concept), generating synonyms (recognize correct concept, generate synonym), or simply correcting others (recognize correct concept and its limits, fix error) (Wong, 2023; Wong and Lim, 2022). Thus, generating content relevant ideas forces students to explore the content's limits, evaluate veracity, and reflect; all cognitively agentic acts. While fMRI correlates

of this behavioral paradigm have not yet been explored, the combined extra agency, retrieval and value judgements for generating and correcting errors would be predicted to engage the RL circuit.

Learning from errors is central to the Montessori method, which develops independent student mastery of motor skills and intellectual concepts through exploration of limited object sets. Students play, correct errors, repeat, and practice until they feel the reward of accomplishing the task (Montessori, 1912). Comparing students from Montessori and environmentally matched traditional schools, the Montessori students were more likely to self-correct (Denervaud et al., 2020a, 2020b). When distinguishing correct from incorrect math problems in the fMRI scanner, functional connectivity was greater between the anterior cingulate and the orbital frontal cortex following incorrect trials for Montessori students relative to traditional students. By contrast on incorrect trials, traditional students had stronger coupling of the medial frontal cortex and the hippocampus relative to Montessori students. This suggests that Montessori students may be more attuned to error monitoring while traditional students may rely more upon memory for recalling correct answers. Together, these experiments support the idea that self-directed, agentic learning influences error recognition, performance monitoring, and goal-adaptive behaviors during academic content learning (Denervaud et al., 2020a).

How do behavioral errors in classroom learning relate to neural PEs considered to be learning signals? In an experiment more closely aligned with academic learning, human subjects were scanned when receiving feedback on answers to a history test, representing semantic knowledge acquired a day earlier from reading an assigned passage. Activity in the ventral striatum, dorsolateral prefrontal cortex and parietal cortex correlated with the PEs and predicted subsequent memory performance a week later, confirming the importance of recognizing errors during practice (Pine et al., 2018). PEs and the associated response monitoring circuitry of the dorsal anterior cingulate contribute to evoked error-related negativity in EEG that arrives ~90 ms after inaccurate choices in RL tasks (Cockburn and Frank, 2011; Debener et al., 2005; Frank et al., 2005; Holroyd and Coles, 2002). Characteristics of the error-related negativity match those expected of a PE in a RL model and predict learning from the errors being signaled (Frank et al., 2005; Fusco et al., 2022; Holroyd and Coles, 2002; Philiastides et al., 2010). Moreover, intracranial and scalp recorded error-related negativities correlate with firing of single neurons in human dorsal anterior cingulate in response to recognized errors. This activity predicts post-error slowing of subsequent behavioral responses, consistent with the role of the anterior cingulate in error monitoring (Debener et al., 2005; Fu et al., 2019). Although error-related negativities do not rise to consciousness, error-related positivities (~300 ms following the error) do. These error-related positivities appear to indicate the awareness of having committed the error and predict subsequent post-error slowing in the next trial (Kirschner et al., 2021; Murphy et al., 2012; Nieuwenhuis et al., 2001) (but see (Debener et al., 2005)). Learning from getting things wrong increases both error-related negativities and error-related positivities compared to learning from getting things right (Frank et al., 2007). Thus, ventral striatal PEs do not themselves trigger conscious error awareness. However, the larger conflict monitoring RL circuit combines with top down cortical inputs to produce error awareness and post-error slowing providing a neural mechanism for conscious identifications of errors and the potential to learn from them (Cockburn and Frank, 2011). From the larger perspective of developing cognitive networks, making mistakes is critical for learning the higher-order statistical properties of academic content and their relationships within the disciplinary space (Lynn and Bassett, 2020).

### 3.5. Retrieval practice for learning

Making and correcting one's own errors, i.e. acting agentially, improves performance, consistent with retrieval practice as a productive strategy for learning (Montessori, 1912). When learning paired

associations, repeated recall under testing conditions is superior to simply viewing the pairings during repeated studying (Karpicke and Roediger, 2008) or even to manipulating the material when constructing a concept map (Karpicke and Blunt, 2011). Actively retrieving the content, out loud or to oneself, appears to improve retention on a delayed test more than simply viewing the content or monitoring the process of doing the retrieving (Abel and Roediger, 2018). Engaging in retrieval practice with feedback also serves to increase learner motivation to continue to investigate the topic at hand (Abel and Bäuml, 2020). Critically, learners exert agency during retrieval. Learners search their own memories to retrieve a target object and internally evaluate whether the found object or idea is correct, i.e. meets expectations. This agentic, repeated practice would be expected to engage the RL circuit and hippocampal associated processes of reorganization and replay.

Several fMRI studies highlight contributions of hippocampal memory functions and regions associated with reward processing to the success of retrieval practice, also called the testing effect. Activity in ventral striatum or putamen figured prominently during the studying and testing phases of word-pair learning for self-testing compared to restudying (Marin-Garcia et al., 2021; van den Broek et al., 2013; Wing et al., 2013). During the practice phase, self-testing, compared to restudy, engaged the lateral temporal cortex, medial prefrontal cortex and anterior hippocampus for successfully remembered pairs. Regions functionally coactivated with the hippocampus that predicted final learning one day later included the posterior cingulate, ventromedial and ventrolateral prefrontal cortex (Wing et al., 2013). New learning after an error was correlated with activity in the posterior inferior parietal lobule, an area associated with recognition memory, suggesting that retrieval practice works because this activity serves to refresh the associations being encoded during subsequent practice (Nelson et al., 2013). In line with its role in recognition memory, the inferior parietal lobule cumulatively calculates and compares the relative expected value of information regarding choices in the current context (Louie et al., 2011). Thus, detection of RL circuit contributions to the testing effect suggests active recall or self-testing, in addition to increasing plasticity, increases motivation, effort and/or agency signals while bolstering associations for learning and memory.

### 3.6. Curiosity, information, and the intrinsic rewards of knowledge acquisition

Active learning encourages and enhances student curiosity. Curiosity has been characterized as exerting agency while seeking information to enhance learning and memory (Kidd and Hayden, 2015). Curiosity represents the intrinsic motivation to autonomously decide to become familiar with an unknown object, environment or intellectual space (Harlow, 1953; Tolman, 1926). Among college students, intrinsic motivation from learning content in order to teach it to others produced greater conceptual learning than simply learning content for the extrinsic motivation of doing well on a high-stakes test (Benware and Deci, 1984). When learning foreign language vocabulary words, long term memory was better when participants were self-motivated than when they received monetary rewards (Kuhbander et al., 2016). AL increases university students' intrinsic motivation, measured psychometrically and as demonstrated in an increased focus on learning biochemistry content rather than getting good grades (Cicuto and Torres, 2016). Asking students to make predictions regarding hierarchical relationships across a series of geography questions generates curiosity and improves immediate retention (Brod et al., 2018). In all of these instances, rewards gleaned from satisfying intellectual curiosity enhance conceptual learning.

Comparisons across multiple primate and human experiments on curiosity indicate that elements of both reward and memory-associated circuits are involved (Cervera et al., 2020; Kidd and Hayden, 2015). In non-human primates, circuits for seeking, integrating and appraising information involve striatum, anterior cingulate, the lateral habenula

and other frontal and parietal areas (Bromberg-Martin et al., 2022; Bromberg-Martin and Monosov, 2020; Cervera et al., 2020; Jezzini et al., 2021; White et al., 2019). In humans, activity in the substantia nigra/ventral tegmental area, their afferents, ventral striatum, hippocampus, and their interconnections increased in proportion to the degree of curiosity, willingness to pay, and subsequent recall of content and incidental information present during trivia learning (Gruber et al., 2014; Kang et al., 2009). Reward signals between the substantia nigra/ventral tegmental area and hippocampus are also present during rest post-learning, contributing to reorganization (Gruber et al., 2016). When choosing to see information predictive of task or gambling outcomes, the subjective value of information is encoded in the ventral striatum with variable contributions from ventromedial and orbitofrontal prefrontal cortex and medial frontal gyrus (Charpentier et al., 2018; Kobayashi and Hsu, 2019). In addition to RL circuit activation, intrinsic motivation may engage more elaborate cortical processing beyond that associated with external rewards, as learning trivia to satisfy curiosity, but not for financial gain, engaged the frontoparietal network (Duan et al., 2020). Accordingly, agentic, intrinsic motivation engages learning through activation of both reward and cortical association pathways.

In academic environments, inherent motivation to engage in information search may be very low when the subject matter appears overwhelming, unknowable, not applicable or already known (Gottlieb and Oudeyer, 2018). Schools at all levels are designed to short-circuit this arduous search task by providing a *guided* path through the acquisition of skills and background knowledge. The inherent tension that develops is the trade-off between providing every bit of background knowledge through DI versus providing an iterative combination of some content and appropriate AL challenges for learners to explore within the given context. In the latter situation, the partial introduction raises questions, providing greater (but not overwhelming) uncertainty and associated curiosity among learners (Gottlieb and Oudeyer, 2018).

### 3.7. Social interactions activate the RL circuit

From an educational perspective, group social interactions, as part of AL, motivate and engage reluctant learners, eliciting agency broadly among students. Learning socially in groups increases student accuracy and confidence, generates valuable information about the academic context, and produces intrinsic motivation (Tullis and Goldstone, 2020; Vélez and Gweon, 2021). Discussing low stakes quiz answers with peers in dyads helped students correct errors by practicing recall, forcing verbalization and hence crystallization of reasoning, stimulating metacognition to recognize errors, and creating new knowledge (Tullis and Goldstone, 2020). Even in a genetics "lecture" class, small group discussions constructing answers to clicker questions engendered greater individual conceptual understanding that benefited initially naïve students and were not attributable to social conformity (Smith et al., 2009).

From a neuroscience perspective, people learn socially from advice, instruction and observing others (Clark and Dumas, 2015). Learning by observing how others respond can increase the observers' successes (Daniel and Pollmann, 2014). Brain mechanisms contributing to the benefits of social learning include the RL circuit. The central ideas emerging from a thorough synthesis of the social basis of learning and neural networks processing social interactions are i) social interactions promote subsequent learning through stimulation of the RL circuit and ii) social interactions involve individuals' agency, as part of the intrinsic drive to be socially engaged (Clark and Dumas, 2015). The social aspects of learning in groups creates additional motivational, salience and contextual neural signals to reinforce encoding and recall (Redcay and Schilbach, 2019). Cooperation is inherently rewarding as evidenced by activation of reward structures during mutual cooperation in prisoner's dilemma and trust games (King-Casas et al., 2005; Rilling et al., 2004). Information exchange among students in groups represents similar mutual cooperation. When learning in groups, activity in ventral

striatum and ventromedial prefrontal cortex may signal conformity with the majority suggesting that value calculations contribute to social learning or reciprocally, social interactions contribute value to making decisions about what is important to learn (Olsson et al., 2020; Redcay and Schilbach, 2019). Learning from viewing others' choices contributes to expected value calculations, producing a social PE in the left putamen, and increasing confidence in choices (Zhang and Gläscher, 2020). These socially generated value signals resemble and combine with signals related to self-choice during decision making (Ruff and Fehr, 2014; Zhang and Gläscher, 2020). The striatum computes social PEs for pro-social behaviors, judging other people with respect to oneself, learning about others or from others vicariously, choosing to follow normative social values, and assigning credit for agency (Báez-Mendoza and Schultz, 2013; Ruff and Fehr, 2014). Social learning also draws upon metacognitive processes that can augment learning about one's progress regarding specific content (Heyes, 2016; Olsson et al., 2020). Overall, learning in a social context further activates the RL circuit and adds value to the content to be learned.

Even the simplest form of social interactions - eye contact - enhances learning. Perceiving that a social partner's gaze and attention are cooperatively aligned with one's own, indicative of a social interaction, activates the ventral striatum and mesolimbic dopaminergic system (Pfeiffer et al., 2014). Jointly gazing with another person towards a common object activates the ventral striatum and ventromedial prefrontal cortex among other brain regions (Schilbach et al., 2010). The ventral striatum was uniquely activated when the subject exerted agency to initiate the joint gaze with the experimenter. Less activation occurred with a video of the experimenter or a computer as a companion (Redcay and Schilbach, 2019; Schilbach et al., 2010). This joint attention promotes memory (Kopp and Lindenberger, 2011; Schneider and Pea, 2017).

These findings indicate that even nonverbal social interactions are inherently rewarding and promote learning. Moreover, these learning enhancements of social interactions range from eye contact and communication to feedback on how to interact socially and how to adjust to novel ideas and situations (Clark and Dumas, 2015). The benefits of group work in AL classes derive from activating the RL circuit and are absent in a conventional lecture class.

#### 4. Neuroscience mechanisms of direct instruction

Lectures directly and efficiently depict information about the disciplinary world, eliminating the need for trial-and-error exploration of an entire body of knowledge (French and Kennedy, 2017). Informative lectures provide disciplinary insights, arguments, and context. These lectures can engage, enlighten, explain, and entertain while building attentional and note-taking skills. However, lectures can also overload attentional systems or become boring (French and Kennedy, 2017). Adults rate teacher quality lower if teachers fail to communicate the full range of useful knowledge (Bass et al., 2015). University physics students felt they learned more in DI than AL classes, despite empirical demonstration that they learn more with AL, reflecting the cultural expectation that knowledge transfer is more valuable than application (Deslauriers et al., 2019). Even preschoolers infer adults' intention to teach and assume that the content demonstrated includes all possibilities, a process that decreases subsequent exploration and self-discovery of additional, undemonstrated toy properties (Bonawitz et al., 2011). Thus, the expectations that formal education efficiently provides knowledge rather than the opportunity to explore knowledge spaces may be set early in the educational trajectory.

##### 4.1. Following instructions

One easy form of information transfer adaptable to experimental tasks is instruction delivery. Teachers provide both content knowledge and directions. Understanding instructions can be viewed as

constructing a mental model. With increasingly longer instructions, performance drops, with the latest additional rule having the least impact on behavior (Dumontheil et al., 2011). By analogy, a lecture describing disciplinary rules may lose impact the longer it proceeds; however, information devaluation has not been examined experimentally. The more comprehensive the instructions, the more model-based the human performance (Feher da Silva and Hare, 2020). Explicit instruction in the changing probabilities encountered in two step experimental tasks increased the number of subjects exerting control using model-based rather than model-free approaches. This suggests that when given knowledge of contextual probabilities, subjects formed a mental model of the task faster than when acquired through trial and error (Castro-Rodriguez et al., 2022). This supports the position that students need instruction and should not have to learn every disciplinary idea through trial and error.

Information transfer would be expected to activate different cortical networks than AL. During instruction delivery, retrieval and implementation, widespread cortical activation occurs, indicative of a transient global reorientation to the presentation of the new rule(s) (Hampshire et al., 2019; Kang et al., 2022). Frontoparietal network activation builds tonically as rules are added and subsides sequentially with time and along the rostral to caudal axis as short-term rule following becomes routine (Dumontheil et al., 2011; Hampshire et al., 2019, 2016). In a stimulus-response WM task, frontoparietal network coding of procedural information predicts instruction implementation, with the parietal cortex encoding both instructions and procedures, and the frontal cortex only encoding procedures (González-García et al., 2021). Rapid procedural rule following, where rules change on each trial, involves lateral prefrontal cortex, an area associated with cognitive flexibility during novel task execution (Cole et al., 2016, 2013). Procedural instructions occur in both DI and AL classrooms and would be expected to activate comparable cortical networks. Learning instructions, analogous to rules governing a disciplinary space, transiently appears to preferentially activate the frontoparietal and related networks (Cole et al., 2016, 2013; Hampshire et al., 2016). Verification that these same networks are engaged during lectures is warranted.

##### 4.2. Direct instruction as social learning

DI is a social interaction in the classroom and might be expected to activate the RL circuit. However, this only happens under limited circumstances. Following instructions can itself be rewarding, especially if that instruction was delivered by a human, eliciting conformity to a socially acceptable norm, as in a classroom (Biele et al., 2011). When teachers provide correct answers, this may positively or negatively reinforce students' own answers and self-evaluation. However, providing correct answers also qualifies as information transfer, especially if students did not work the problems themselves. After following advice, increased activity in the left caudate and septum may signal increased trust in the advice through downstream oxytocin release (Biele et al., 2011). Consequently, following instructions may be rewarding and bias the evaluation of effort towards favoring instructions, even when they are incorrect and PEs are negative (Doll et al., 2011, 2009). In these cases, maintained compliance with incorrect instructions results in a bias. Striatal value calculations become distorted to confirm this instruction (confirmation bias) and reject the calculated error from contradictory evidence (Doll et al., 2011, 2009). Moreover, false instructions appear to override experiential learning among adults (Decker et al., 2015), suggesting that DI may result in false beliefs.

DI may also diminish activity in the RL circuit that regulates flexible behavioral engagement. Dorsolateral prefrontal cortex representation of the instructed task was associated with the suppression of activity in ventromedial prefrontal cortex, ventral striatum and parahippocampal gyrus, suggesting acquired knowledge of the task removed the need to recall and evaluate outcomes via RL (Atlas et al., 2016; Koban et al., 2017; Li et al., 2011). Thus, the striatum only contributes to



frontoparietal network behavior *at initial instruction onset* where it may be involved in gating cortical activity or selecting rules (Hampshire et al., 2019, 2016; Koban et al., 2017). This observation supports the flexible motivation hypothesis that states ventral striatum and DA are required for flexible behavioral engagement but not cued performance in rodents (Nicola, 2010). Indeed in humans, instruction greatly diminishes PEs and BOLD activity in the ventral striatum, ventromedial prefrontal cortex and the hippocampus for reward-based associative tasks, suggesting that subjects do not exert as much effort or agency when following advice (Biele et al., 2011; Li et al., 2011). Instead of valuing the content and one's agency in learning it, during DI, the ventromedial prefrontal cortex, ventral striatum, and RL circuit become responsible for evaluating how well experiences match the instructed state (Koban et al., 2017).

#### 4.3. Working memory during direct instruction

During lectures, students listen to instructor explanations, possibly view slides or whiteboards, and take notes as they hopefully construct a mental model of the disciplinary content space. All of these activities require WM. Working memory limits cognitive load capacity, subsequently constraining retention during lectures (Jordan et al., 2020). When engaged in greater cognitive effort, i.e. greater WM load, reaction times of responses to interrupting probes increase, permitting relative comparisons between cognitive loads during different tasks (Piolat et al., 2005). Writing requires more cognitive resources than either reading or listening (Tindle and Longstaff, 2015). Note-taking during lecture, while slightly less demanding than composing original text, is comparable to the effort expended by an expert planning a chess move and more demanding, because of time pressures, than note-taking while reading (Piolat et al., 2005). Auditory and visual information can also compete for learners' attention. Overloaded lecture slides can suppress encoding and retention of lecture information only presented orally (Wecker, 2012). Thus, during a lecture, students' efforts are highly dependent on WM capacity (Piolat et al., 2005). Cycles of student inattention are regularly observed, even during short lecture segments of 9–12 min, and can begin within 30 sec of lecture onset, as assessed when chemistry students self-report lapses by tapping a clicker (Bunce et al., 2010). Interspersing student-centered pedagogies such as clicker or test questions into lectures decreases mind-wandering in their aftermath and increases performance on subsequent content tests (Bunce et al., 2010; Szpunar et al., 2013).

A full explanation for how information in WM becomes either long term memory or forgotten remains elusive. Proposed neural mechanisms for WM range from reverberation within local cortical synaptic connections to large scale network interactions (Braun et al., 2015; Miller et al., 2018). Insights into the mechanisms of memory formation when learning from natural sequences of events may eventually provide a model for learning from sequenced ideas in lectures. Experimentally, memories associated with event boundaries have been explored using movies, audio files, and written naturalistic narratives (Ben-Yakov and Henson, 2018; Davis and Campbell, 2023; Michelmann et al., 2021). Event boundaries discerned from abrupt changes in neural activity (EEG, electrocorticogram) or BOLD signals agree with human segmentation of these natural storylines (Baldassano et al., 2017; Michelmann et al., 2021; Silva et al., 2019). During listening to a narrative, cortical representations of information appear as temporal or meaningful chunks that may later be encoded into memory by the hippocampus at the end of an event. These chunks can be nested producing a hierarchy of temporally resolved events (Baldassano et al., 2017). When initially listening to stories, information flows from cortex to hippocampus at natural boundaries between events within the story. When listening a second time, information flow is reversed at a peak in hippocampal activity, predictive of a memory being recalled (Michelmann et al., 2021). At event boundaries, the hippocampus retrieves past events and integrates immediate and distal past events into sequences associated

with coherent narratives (Cohn-Sheehy et al., 2021). Functional communication between the hippocampus and subnetworks or regions associated with the default mode network are also increased at event offsets (Barnett et al., 2024). The amount of boundary-associated hippocampal pattern reinstatement predicts accuracy in natural recall of story elements, both immediate and delayed by 2 days (Barnett et al., 2024; Cohn-Sheehy et al., 2021). From a neural processing perspective, an event boundary indicates the current mental state has ended and the mental model requires updating (Bruneć et al., 2018) but the cellular mechanisms for event boundary transitions remain unknown. Moreover, large reward PEs can act as event boundaries in serial task paradigms (Rouhani et al., 2020), but whether PEs related to predicted state transitions are related to learning event boundaries remains unexplored (Hamid et al., 2021).

This event-boundary information exchange from cortex to hippocampus has been proposed to contribute to one time learning via information transfer (Michelmann et al., 2021), an ideal, putative mechanism for learning from DI. From an educational point of view, several questions are raised. Is nonfictional content delivered in lectures parsed and remembered according to similar event boundary functional communication? What constitutes an event boundary in a lecture, especially when prior knowledge is low? How does the emotional quality of events influence the strength of the hippocampal-cortical communication at offset boundaries? While didactic content often unfolds as a sequenced story about objects in the subject domain (e.g. the cyclic movement of neurotransmitter during synaptic transmission), it remains to be determined if such hippocampal reinstatement occurs for abstract objects. Most importantly, how does this event-based segmentation of memorable semantic content interact with the value calculations within the RL circuit? A deep mechanistic understanding of such interactions will inform choices regarding the optimal mixture of AL and DI pedagogies.

### 5. Intersections

#### 5.1. Interactions between working memory and reinforcement learning

DI relies upon WM, which is limited (Cowan, 2010; D'Esposito and Postle, 2015). AL engages students in experiences that reduce the statistical uncertainty regarding how the disciplinary world behaves. In learning course material, students use WM to keep topic content and goals in mind while using the RL system to explore options, solve challenges, and reduce personal uncertainty by gaining confidence in appropriate interpretations.

Mechanistically, WM and RL cooperate with WM setting the expectations to be evaluated by the RL circuit (Collins and Frank, 2018). Both BOLD- and EEG-derived measurements of WM and RL were tracked during experiments in which subjects learned through trial and error sets of action associations for varying numbers of symbols. The two systems cooperated dynamically from stimulus presentation to feedback. When the number of stimulus associations was low and easy to learn rapidly, WM measurements predominated. As the number of associations increased, learning slowed and the RL measurements dominated with the feedback expectations set by WM (Collins et al., 2017; Collins and Frank, 2018). This powerful interaction between learning mechanisms needs to be verified for longer term retention times.

During lectures, students' WM system is primarily engaged, limiting the cognitive power applied to understanding and internalizing the current content. As the instructor sets the pace of information delivery, learners' WM is taxed as they struggle to keep up with unfolding ideas and take notes. While the high WM load should increase concurrent RL PE signals (Collins et al., 2017; Collins and Frank, 2018), students have no time to reflect, connect content or question, processes that would engage their RL circuits. They retain more when they summarize rather than type verbatim during note taking (Feng et al., 2019; Horbury and Edmonds, 2021). Interleaving AL exercises with content delivery would



be expected to engage students' RL system, helping to sort through the applicable possibilities kept in mind through WM.

## 5.2. Generalizing and higher order thinking

Educators strive to develop students' higher order thinking or the capacity to use basic knowledge to generalize, apply, analyze, synthesize, infer, and evaluate information (Bloom, 1956). While Bloom's taxonomy has been revised multiple times, the idea that analysis and knowledge utilization are built upon retrieval and comprehension retains elements of its hierarchical heuristic (Anderson and Krathwohl, 2001; Marzano and Kendall, 2007). The additional practice afforded by AL approaches increases students' ability to perform at the higher levels of Bloom's Taxonomy. For example, in reforming an undergraduate neurophysiology course, introduction of clicker questions, more homework, group work, and feedback sessions improved student performance on course exams while simultaneously increasing the Bloom's levels of thinking skills on test questions (Casagrand and Semsar, 2017).

From a neuroscience perspective, shared conceptual representation, schemas, or their neural representations, cognitive maps (Tolman, 1948), are critical for incorporating new ideas, formulating abstractions, and generalizing across contexts (Behrens et al., 2018; O'Keefe and Nadel, 1978; Redish, 1999; Shenav et al., 2017; Vaidya and Badre, 2022). Replay, repetition, and remapping contribute to the generalization process (Knudsen and Wallis, 2021; Liu et al., 2019). The hippocampus maps the details of the current task structure while the PFC extracts task commonalities across multiple encounters leading to generalization (Mansouri et al., 2020). Ensembles of neurons within primate dorsolateral prefrontal cortex, anterior cingulate, and hippocampus code for the generalization of context, stimulus, and value variables as decisions are being made, reducing the dimensionality of the possible decision space (Baraduc et al., 2019; Bernardi et al., 2020; Knudsen and Wallis, 2021). When contexts shift, inference occurs utilizing the information within these ensembles to generalize, promoting more rapid learning (Bernardi et al., 2020; Park et al., 2020). In human hippocampus and entorhinal cortex, activation patterns resemble abstract grids, signal contextual relationships, and integrate and map temporal, spatial, categorical and contextual dimensions (Brunec et al., 2020; Constantinescu et al., 2011; Theves et al., 2019). Ventromedial prefrontal cortex value calculations distinguish among common elements (Cortese et al., 2021). In RL tasks, the entorhinal cortex, medial prefrontal cortex, and frontoparietal networks generalize responses from similar contexts, but not from widely differing task structures (Baram et al., 2021; Vaidya et al., 2021). Thus, broad network activity appears to create the mental flexibility for making inferences across generalized experiences and their associated cognitive maps (Park et al., 2020; Vaidya and Badre, 2022). Whether such generalization can occur in the absence of agency or the RL circuit, i.e. just by observing yoked progress through experimental tasks, remains to be tested.

When modeled mathematically, artificial neural networks must be trained repeatedly, slowly, and simultaneously on two separate but related tasks to mimic the ability to generalize and rapidly adapt when confronted with a novel situation (Botvinick et al., 2019; Wang et al., 2018). Additionally, mathematically nested RL algorithms create a progression of flexible behavioral changes encompassing initial trial and error, inference regarding missing information, generation of subjective preferences through comparisons, and finally generalization for novel contexts (Eckstein and Collins, 2020). The hierarchical stages emerging from this model are reminiscent of Blooms' taxonomy. Thus in experiments and models, the ability to generalize arises slowly out of prior exploration of multiple examples. In human education, such exploration requires repeated AL opportunities.

Together these experiments demonstrate how synaptic plasticity and its modulation by dopamine underpin cognitive as well as motor learning. Both neuronal and circuit mechanisms contribute to more robust memories and understanding when learning episodes are spaced.

The varying time scales of dopaminergic arousal or novelty signals that enhance plasticity boost learning of attended, incidental or temporally aligned events. The associative property of synaptic plasticity plus the overlap of encoding among neuronal populations contribute to the enhanced encoding when prior knowledge is linked to current topics. Synaptic plasticity builds circuits for intellectual actions that over multiple encounters of similar examples in different contexts leads to deeper understanding and generalization. All of these neural mechanisms may contribute to the success of active, engaging classroom strategies.

## 5.3. Active learning benefits individuals and reduces achievement gaps

The benefits of AL over DI that inspired this analysis have mostly been demonstrated at the aggregate course level (Freeman et al., 2014; Haak et al., 2011; Sinha and Kapur, 2021; Theobald et al., 2020). The significant performance differences on exams are not huge, on the order of 10–15%, testifying that students learn in both AL and DI situations (Deslauriers et al., 2019). These meta-analyses and the studies within them are drawn from cross-sectional comparisons of different student populations experiencing learning in different environments. An initial explanation for this difference might be that it is harder for students to be left out in an AL classroom. This appears to be the case for non-traditional students in science classes. Synaptic strengthening through practice and circuit mechanisms may also contribute to the benefits of AL. Evidence for both explanations follows.

AL science courses ameliorate minority student underperformance. In a multiple year, cross-sectional study, performance among students qualifying for an educational opportunity program improved almost 3 times more than other students when the introductory biology course transitioned from lecture to a highly structured AL format (Haak et al., 2011). In a meta-analysis of AL in collegiate STEM courses, the achievement gap for minority groups decreased by about a quarter of a standard deviation on final exam scores with half as many failures (Theobald et al., 2020). More AL experiences correlated with a narrower gap. These results are consistent with greater student participation, more opportunities for individual practice, and more scaffolding in AL classes. Thus, AL improves outcomes for all students and reduces the achievement gap for those with less privileged or practiced academic backgrounds (Theobald et al., 2020).

AL pedagogies also improve learning for individual students as demonstrated in two experiments. Using a cross-over experimental design and two comparable topics in undergraduate physics classes, students performed better on topic exams in AL classrooms than in fluent lectures but felt they learned more in the latter (Deslauriers et al., 2019). Data here were presented in aggregate form, so actual changes in individual student achievement could not be discerned. In a second, more complex experiment, instructor-student pairs respectively taught and learned different introductory psychology concepts through either explaining content directly or using a scaffolded, question and answer Socratic approach, in sequential blocks (Pan et al., 2020). Additionally, instructors and students wore functional near-infrared spectroscopy headsets over frontal and temporal portions of the scalp to monitor interpersonal brain synchrony. On an immediate post-test, knowledge gains were higher for the scaffolded compared to the didactic content, with a majority of individuals showing greater retention from the Socratic approach. Interbrain synchrony was higher in frontal cortices during scaffolded compared to didactic instruction. The degree of synchrony correlated with learning outcomes. Thus the active, Socratic questioning pedagogy produced a stronger instructor-student relationship as well as more robust learning, validating the benefits of active learning for individual students (Pan et al., 2020).

## 6. Conclusion

No experiment in this review decodes human declarative content

acquisition in real time in a classroom setting with sufficient detail to reveal exact cellular or system level mechanisms of optimal learning and memory. However, parallel studies in animals and humans that are challenged to learn the statistical properties of experimental tasks do yield insights into the brain processes supporting learning. Mechanistically, plasticity, agency, and social interactions engage the RL circuit, hippocampus, and associated cortical networks to support and augment learning and memory. Behaviorally, mastery and generalization arise from multiple encounters with the disciplinary material, where learners have opportunities to manipulate content. Neurally, this entails encoding the content in overlapping sets of synapses (plasticity) that gain value as the learners predict how to apply the content in explaining relationships or solving problems, exert agency, evaluate success, and iterate the process (RL circuit). Social interactions among students or between instructors and students further recruit the RL circuit.

This review associates these mechanisms of learning and memory with the opposing pedagogical approaches of DI and AL. Here, DI refers to instructor-supplied knowledge transfer. AL encompasses opportunities for students to manipulate and apply content individually or through social interactions. Thus, the greater student learning associated with AL over DI pedagogies (Deslauriers et al., 2019; Freeman et al., 2014; Haak et al., 2011; Theobald et al., 2020) may be attributable to the greater neural ‘value’ ascribed to information gained through one’s own effort, evaluation, or social interactions compared to information obtained from lectures. DI, at least for directions, appears to preferentially activate frontal-parietal structures and to rely upon WM (Dumontheil et al., 2011; González-García et al., 2021; Hampshire et al., 2016; Vaidya and Badre, 2022). WM, while rapid and sufficient for manipulating or encoding a low cognitive load, is insufficient for juggling a larger load which requires evaluating and comparing new information with old, a slower encoding process (Collins et al., 2017). DI provides an environment where uncertainty is low. Instructors paint a definitive picture of the disciplinary world intended to support rapid learning. When uncertainty is low, so is episodic memory, attention and cognition (Monosov, 2020; Rouhani et al., 2018). In comparison, when uncertainty is high, episodic memory, attention and cognition are high as active exploration is required to resolve the uncertainty (Collins and Frank, 2018; Diederer et al., 2016; Monosov, 2020; Rouhani et al., 2018). Learning rates might be slower, but retention is higher (Collins and Frank, 2018; Rouhani et al., 2018). This is the contribution of AL. AL provides an environment where uncertainty is relatively high and students have agency to resolve it. AL provides learners with challenges that create RL experiences, engage the value-generating RL circuit and as the RL process is iterated, provide the repetitions needed for both synaptic plasticity and generalization.

Content-wise, the goal of the educational system should be for students to form mental models of the disciplinary space, complete with relationships and associations for applying content to real world problems. A content focused approach to learning supports DI pedagogies. However, the learner will not acquire the cognitive evaluation, decision making or application skills without practice. AL pedagogies provide such practice and develop motivation. The RL circuit-hippocampal interactions during AL provide evaluative signals that raise the relevance of the associated materials and applications to ensure retention. Motivation for learning derives from curiosity, a drive to perform a task oneself, social engagement, and social approbation. All of these intrinsic motivators engage the RL circuit. Extrinsic motivators such as points, grades or competitions also engage the RL circuit but the occasions for learning from graded iterations may be limited by the frequency of these events. Intrinsically, exerting agency to discuss, solve problems or answer questions within the disciplinary space, making and correcting mistakes, and evaluating one’s progress generate anticipatory and feedback signals in the RL circuit. In applying content, students engage in multiple passes through the material, developing connections within cortical networks and extracting structural commonalities that lead to generalization and higher order thinking.

Classrooms should provide students with optimal learning opportunities. The neuroscience explanations reviewed here support learning both from DI and AL pedagogical strategies. Optimally, a calculated balance between DI and AL is needed for learning disciplinary content and its appropriate application. By itself, lecturing inadequately prepares learners to remember and apply content. Similarly, AL without contextual explanations can leave students floundering. Classroom material and student interactions with that material should evoke curiosity and evolve such that each repetition adds or reinforces content and builds a more complex understanding. By utilizing AL pedagogies, instructors provide opportunities for practice and application in the classroom, engaging deeper learning mechanisms and modeling behaviors for independent student studying. Critically, summarizing concepts, a form of DI, after each AL lesson brings everyone together with a common understanding. Instructors must help students recognize their own mistakes are not failures but opportunities to use errors as ‘learning signals’ to improve performance (Denervaud et al., 2020a). Emphasis should not be placed upon ‘getting all answers correctly’, but rather on flexibly providing students with opportunities to correct their own errors and maximize improvement (Metcalfe, 2017). As recently as 2018, 75% of university STEM class time was DI and only 18% of observed classes met criteria for being ‘student-centered’ (Stains et al., 2018). Shifting these proportions will improve student outcomes. At the university level, faculty, especially neuroscientists, should understand how the evolving neuroscience of learning and memory can be applied to guide their teaching strategies.

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## Declaration of Generative AI and AI-assisted technologies in the writing process

All text in this paper was written by the human authors. No generative AI or AI-assisted technologies have been used.

## Declaration of Competing Interest

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