What Have We Learned About Learning? Reflections from Developmental Psychology and Cognitive Neuroscience

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Learning is thought to be something at which human beings excel. They learn many things over the course of time from infancy to adulthood, such as how to communicate with others using language, how to manipulate objects, and how to solve problems effectively. But what is the science behind learning? How do people's brains change as they learn, and does this have anything to do with the strategies they use to learn? In this essay, we briefly outline the changes in how researchers approach the issue of learning across development, with a focus

INTRODUCTION

Human knowledge ranges from the marvelous to the mundane; a mind that can unravel the mysteries of particle physics can also understand how to make a cup of tea. And yet we are born without knowing how to do either of these; we learn such knowledge and skills through our experience with the world. Throughout childhood we encounter and acquire language, learn how to manipulate objects, and represent complex events from our environment. These are far from simple tasks. Yet infants achieve this kind of learning with relative ease. Societal interest in enhancing early learning has increased considerably in recent years, as evidenced by the remarkable popularity of infant learning products such as "Baby Einstein" and "Baby Bright." Alison Gopnik, a professor of psychology at Berkeley, suggests that this early capacity for learning may be what has provided human beings with an evolutionary advantage over other species (Gopnik, 2010). Here, we consider how learning may progress across the lifespan, extending from infancy and childhood into the adult years. We explore differences in accounts of learning across development while also highlighting similarities, such as the need for active engagement during learning. Accounts of the neural underpinnings of learning, through plasticity and dopaminergic learning models, are outlined briefly. These findings point toward the complexity of human learning as a multifaceted phenomenon extending across the lifespan.

DIFFERENCES IN LEARNING AND NEURAL PROCESSING ACROSS DEVELOPMENT

In the scientific world, neurological evidence is thought to exist for differences in learning between children and adults. Damage to the brain in adulthood, affecting the language networks, typically results in aphasia—an impairment of the ability to use language. However, the severity is markedly less if the injury occurs before or immediately after birth (Lennenberg, 1967; Bates, 1999). The outcomes of left-hemisphere injury are less debilitating in children on language learning, and discuss how current neuroscientific research complements what is known behaviorally about learning. We illustrate how various developmental and neural processing inputs interact with prior experience to facilitate learning. Further, the contributions of active learning over the lifespan, and the roles of novelty and motivation in enhancing learning, are considered. Approaching learning as a complex, multifaceted process will help researchers move toward more-integrated behavioral and neurobiological models of learning.

with perinatal focal lesions than when such injuries occur in adults, suggesting that at some point between birth and adulthood the way we learn language changes. Converging evidence suggesting a difference between adult and child language-learners is derived from behavioral studies. These suggest that it becomes harder over time to learn a foreign language (Johnson & Newport, 1989). However, there is considerable debate about how long this time frame is (Flege, Munro, & MacKay, 1995; Flege, Yeni-Komshian, & Liu, 1999; Zevin, 2012), and how individual differences may contribute to this difficulty. In addition, there are disputes about what aspects of language (syntax, pronunciation, vocabulary), are harder to learn after this time frame. For instance, categorizing speech sounds in a second language is more difficult in adulthood than it is earlier in development (Kuhl, 2004; Werker & Tees, 2005; Zevin, 2012). Little is known about where the boundaries of a "sensitive period" for learning language lie and how this period might relate to neural changes over development.

Can a consideration of these neural changes over development then serve to explain changes in learning, and perhaps this sensitive period? Many studies have shown that there are structural and functional neural changes over childhood and adolescence (Giedd et al., 1999; Lu et al., 2007; Sowell et al., 2004; Shaw et al., 2008), including changes in cortical thickness and white-matter volume, as well as structural and functional connectivity. These changes can be a result of age; for instance, cortical thickness changes as a result of age (Shaw et al., 2008), but can also relate to expertise and learning. Cortical thickness in the inferior frontal gyrus is related to grammatical proficiency (Nuñez et al., 2011) and phonological proficiency (Lu et al., 2007). Experience with a second language, as indexed by age of acquisition, can modulate the degree of structural neural reorganization. The earlier a second language is learned, the higher is the gray-matter density (i.e., the relative concentration of cell bodies, dendrites, axons, and glia in cortical volumes)

in the left inferior parietal region (Mechelli et al., 2004). But even in monolinguals, proportional changes in the graymatter density in the posterior supramarginal gyri bilaterally can be correlated with number of words learned (Lee et al., 2007). These findings demonstrate how neural changes can be bidirectional, with changes occurring in neural structure via learning and not simply as a result of maturational processes.

Neurobiologists today accept the idea of pluripotentiality-the capability of the cortex to take on a wide array of representations. In childhood, there may be early competition among neural areas for control over various behavioral tasks; regions that process tasks efficiently will win (Elman et al., 1996; Siegel, Donner, & Engel, 2012). Systematic functional neural changes might occur with expertise relating to a skill or an over-rehearsed task, resulting in either an increase or a decrease of neural activity within regions or changes in the network of regions involved in a task. Brown and collaborators (2005) demonstrate developmental changes in cerebral functional organization, from the ages of 7 to 32, for the relatively simple task of word generation. For this task, more cortical areas were recruited at younger ages, with greater involvement of prefrontal regions earlier in life. The process may thus be one of interactive specialization: neural processing in childhood may be diffuse in several regions across both hemispheres, and may become increasingly task-specialized and restricted to more-specific networks as expertise builds (Durston et al., 2006; Karmiloff-Smith, 2010). There is also event-related potential evidence supporting this theory: comprehension of single words in infancy (13-17 months) is processed in a more distributed, bilateral manner (Mills, Coffy-Corina, & Neville, 1997), becoming increasingly left-lateralized at 20 months of age. This may serve to explain the difference in the severity of language impairment mentioned earlier, as networks become more focal and specialized in adulthood. In old age, some evidence points to a converse reorganization of language processing (Federmeier, Kutas, & Schul, 2010), perhaps due to cortical atrophy (Tyler et al., 2010).

Further results from the Brown et al. (2005) study also indicate regions where children showed less activation than adults did, such as the lateral and medial frontal cortex and the left parietal cortex, suggesting that these regions were integrated into task-related networks over childhood. This suggests the importance of understanding neural changes, as these are regions typically associated with prolonged developmental courses, coming "online" during adolescence. The role and function of these regions are being explored, and they seem to relate to executive functioning, notably inhibition, attention, and self-knowledge. These neural differences were all observed for the same simple task, even when controlling for performance differences on the task. It therefore seems likely that young children use different neural resources than young adults do while performing the same task, even when their overt behavioral performance is identical. Thus, the neurological picture appears much more complex than that suggested by a "sensitive period," and it seems evident that understanding changes in neural activation will play a large role in illustrating the complex interplay between brain and behavior.

ACTIVE LEARNING STRATEGIES—FROM INFANCY TO ADULTHOOD

Characterizing the behavioral side of the learning process, developmental psychologists have conducted research revealing that babies are sophisticated learners and demonstrating their active role in the learning process. A simple example is the case of producing words; learning labelto-object mappings amid baby paraphernalia and a large number of toys is a challenge. Words are typically produced by many people whose voices vary considerably, and not always in isolation. As an example of the complexity this label-to-object mapping entails, the word "dog" can occur in multiple contexts: when looking at a pet, at a picture book, or in an animated cartoon, and also in reference to many breeds of dogs. It can also occur within nonliteral phrases such as "it's a dog-eat-dog world." To explain how children may learn words and grammar in this "busy world," many developmental psychologists have favored the idea of innate specification of function, perhaps shaped by evolution (Spelke & Kinzler, 2007). This includes the notion that we have special, inbuilt modules and neural mechanisms to help us parse language. The opposite notion is that of a tabula rasa, or blank slate, where the child is taught only through interaction with the environment. As we know from the neurological studies presented above, neither of these explanations is completely correct. However, most current approaches to understanding learning incorporate elements of both these approaches, and the argument may really lie in the relative role the environment plays. One such approach suggests that learning, whether in the visual, perceptual, motor, or language domain, can arise from identifying regularities in the environment around us, without any explicit instruction or even intention to learn (Perruchet & Pacton, 2006). For example, in English, within the phrase "sit down," the combination of the sounds within "sit" or within "down" is more frequent and acceptable than the combination of sounds between the two words-in this case, "tdo." Understanding how likely it is for sounds to be put together within a language may help us learn where word boundaries lie. As the reader may have realized when listening to a foreign language, these are quite difficult to parse in continuous speech. However, we know that adults are able to learn this kind of information within an hour of listening to a new language (Saffran, Aslin, & Newport, 1996), even if the language is stripped of all other cues such as intonation and meaning.

In the past few decades, researchers have made progress by leaps and bounds in our knowledge about what infants can comprehend. Primary evidence has come from studies that work on the principle of novelty-preference: infants look longer at occurrences that are novel. So if they have learned about an occurrence, they should look less at that occurrence, and more at an interesting novel phenomenon. (For a full review of this methodology, and some new directions, see Aslin, 2007.) Many such studies have shown that even 8-month-olds are able to segment continuous speech-to learn word boundaries, based on the statistical information within the speech stream-with less than two minutes of exposure and no explicit training (Saffran et al., 1996). There is evidence to suggest that infants as young as 2 months can learn regularities over complex visual patterns (Kirkham, Slemmer, & Johnson, 2002). This serves to illustrate that learning mechanisms can be powerful, implicit, and used to understand the world around us from a very young age. Extending the role of these learning mechanisms further, sound sequences that are highly probable within a language are more likely to be accepted as labels for words (Graf-Estes, Evans, Alibali, & Saffran, 2007). This strain of research demonstrates that babies are likely not passive listeners who simply learn the words parents teach them, but that they actively track the information available to them, and can use and generalize this information in other contexts.

Experience differs across children, so they may have different ways of learning the same information. For instance, early in development, monolingual children use a wordlearning constraint, the mutual exclusivity constraint (Markman & Wachtel, 1988). This constraint stipulates that an object cannot have more than one name; hence if the child already knows the word "car," he or she will not think that a new word refers to cars. At an early stage of word learning, before children start to learn synonyms, this is likely to be an effective strategy to learn label-toobject mapping. However, recent research (Houston-Price, Caloghiris, & Raviglione, 2010) suggests that bilingual children do not exhibit this phenomenon, as even early on, their experience tells them that two different labels can be used for a single object.

Infants also learn a lot about their environment by their interaction with it, and certain environmental experiences may change the learning of other related skills. This is not a consequence of simple growth, or maturation. The environmental demands infants are exposed to allow them to use the set of cognitive capacities they possess to change their cognitive ability, sometimes even across different cognitive domains. For instance, infants who were unable to grasp objects were given experience with Velcro sticky mittens. This enabled them prematurely to grab objects by simply swiping at them. When tested later, they showed increased visuo-motor coordination, and more mature grasping, than infants who were not given this unusual early Velcro experience (Needham, Barrett, & Peterman, 2002; Barrett & Needham, 2008). This suggests that even very young children use their prior sensory and motor experiences and expectations, when engaging with their environment, to a greater extent than previously believed, and that early experiences may have cascading consequences through development.

This kind of active experience may even be *crucial* for learning in childhood. For example, when children learn

from traditional interpersonal interaction with caregivers (as opposed to learning from television programs and educational videos), they are able to learn more (Kuhl, Tsao, & Liu, 2003). Further, they fail to generalize learning from one situation to the next when learning from recorded materials (Christakis et al., 2009). Successful screen learning may require a more dynamic interaction of the infant with the task at hand—for instance, new gaze-contingent training paradigms, which involve the stimulus changing based on where and how long an infant looks, do demonstrate improvements in cognitive control and sustained attention (Dekker, Smith, Mital, & Karmiloff-Smith, in preparation; Wass, Porayska-Pomsta, & Johnson, 2011).

Active engagement with the environment is equally important for adults in facilitating learning. The role of learning within adulthood has emerged as a growing area of enquiry, with particular emphasis on active engagement as a critical learning mechanism. James and collaborators (2002) examined visual learning in adults using a 3D object-rotation paradigm presented within a virtual reality environment. When participants actively manipulated the orientation of an object (relative to passive viewing) during familiarization, their results indicated enhanced response accuracies and decreased reaction times in testing. This result accords with other studies of active versus passive adult learning within spatial environments (Péruch, Vercher, & Gauthier, 1995). Active and passive learning may differ with respect to the relative contributions of visual and proprioceptive feedback, attention, decision-making, and cognitive manipulation (Chrastil & Warren, 2012). The mechanisms facilitating adult visuospatial learning involve an active, volitional process called "spontaneous revisitation," entailing the active rescanning of items immediately after they have been viewed (Voss et al., 2011). This process may selectively enhance learning via recognition memory and spatial memory for object positioning. Active engagement with view manipulation has been shown to engage neural circuitry encompassing the left hippocampus, left medial prefrontal cortex, and right cerebellum (Voss et al., 2011). However, depending on the modality of sensory input, there may be multiple, integrated neural pathways by which learning occurs. Learning mechanisms may allow for integration of these inputs into higher-level, task-focused schema (Iran-Nejad, 1990).

The interactive nature of learning has been exemplified by experimental paradigms entailing both active and passive processing of stimuli. Wade and Holt (2005) devised a novel "space invaders" computer game task, where visually presented aliens preceded a complex sound waveform. The adult participants were not instructed to engage actively with or learn these sounds. However, discrimination of sound categories was beneficial to in-game performance. The authors found that postgame discrimination accuracy for complex sounds was positively correlated with in-game performance. Furthermore, conditions where sounds showed a reliable pattern produced better overall performance than conditions where sounds were presented randomly. A subsequent fMRI investigation using the same paradigm revealed a significant correlation between changes in activation in speech-selective areas (left superior temporal sulcus) and behavioral accuracy in discriminating the passively encountered complex sounds (Leech, Holt, Devlin, & Dick, 2009). These findings suggest that for paradigms entailing some form of active engagement, learning may occur even when stimuli are encountered in an incidental fashion. Further, such learning might recruit neural regions specialized toward other cognitive or perceptual abilities, highlighting the potential for adaptation of cortical areas following active learning.

NEURAL UNDERPINNINGS OF LEARNING

Central to the learning mechanisms described above is the role of neural plasticity in allowing for experience to shape brain structure at both regional and circuitwide levels. A key scientific development in recent years has been the recognition of plasticity as a mechanism extending across the human life span. Developmental studies have reported increased myelination within subcortical whitematter tracts, including the left arcuate fasciculus and posterior corpus callosum, during childhood and adolescence. By contrast, grey-matter densities fluctuate during development, peaking in frontal and parietal regions at 10 to 12 years, before decreasing steadily into early adulthood (see Paus, 2005). Lövdén, Bäckman, Lindenberger, Schaefer, & Schmiedek (2010) argue that plastic changes in adult brain structure rely on a mismatch between the available functional capacity of brain networks and the cognitive demands placed upon those networks. Thus, a mismatch occurring within a network's range of potential performance may serve to spur neural plasticity, and hence facilitate learning (Lövdén et al., 2010).

Such mechanisms of plasticity can be considered from the perspective of second-language acquisition. The relative difficulty for adult learners in achieving nativelike proficiency in domains such as phonology is well documented (Birdsong, 2009; Ellis & Sagarra, 2011). Nevertheless, Birdsong (2009) highlights that adult second-language learners may display high proficiency within certain domains of language learning (e.g., syntax), compared to others (e.g., pronunciation; see also Flege et al., 1995). Lövdén and collaborators (2010) suggest that such disparities in language proficiency may reflect differences between the relative functional capacities of adult language networks and the functional pressures placed upon those networks. Thus, learning various facets of a second language (e.g., syntax versus pronunciation) may be driven by the existing capacity of a language network with respect to these facets, and the external, environmental pressures driving the network to master the facet most critical to the new language, in order to allow one to communicate effectively.

Neuronal plasticity may thus arise from differences in the capacities of networks to adapt to processing demands. The demands on functional neural networks will differ depending on the stage of learning. For example, recruitment of different neural circuits may occur at different stages of motor learning, and also at different times across development. Diamond (2000) notes that neocerebellar circuits are recruited most heavily during the early stages of motor learning, when task novelty is greatest. However, such neocerebellar circuits rarely achieve full development before early puberty, suggesting that their functional capacity in motor learning will differ both across development and across stages of learning (Diamond, 2000). The extent to which functional adaptation occurs within motor networks may also depend upon task demands. Reaching with a single hand when a force is applied to that hand produces a subsequent change in initial movement of the opposite hand; this pattern is not observed when a force is applied to one hand while reaching with both hands (Diedrichsen, 2007). This suggests that functional motor adaptation varies depending on the requirements of the task (i.e., functional pressure), and is based on the ability of the network to adapt following motor feedback, extending its functional capacity (Diedrichsen, 2007).

NOVELTY, MOTIVATION, AND LEARNING

The preceding accounts of adult language and motor learning highlight that mechanisms underlying plasticity and learning display a complex interaction with the functional capacity of neural networks. However, in considering why learning occurs, it is also important to recognize the relationship between learning and motivation. Researchers have long acknowledged the role of reward as a motivator of learning, acting to reinforce and increase the reselection of behaviors, based on coding of salient stimuli or events by the neurotransmitter dopamine (Dayan & Daw, 2008). However, recent neuroscientific investigations have questioned the role of reward, suggesting that rapidly occurring dopamine signals may facilitate learning depending on their occurrence with unexpected sensory events (Redgrave & Gurney, 2006). The novelty of events or stimuli may thus serve as a significant component accounting for motivation of behavior and learning (Bunzeck, Doeller, Dolan, & Duzel, 2012). Increased fMRI activation in the dopaminergic midbrain (substantia nigra/ventral tegmental area) in anticipation of novelty has been argued to display effects similar to the representation of reward cues, and may interact with activity in the hippocampal regions via dopaminergic input (Wittmann, Daw, Seymour, & Dolan, 2008). This loop of dopaminergic and hippocampal structures may form a motivational network with the medial prefrontal cortex, which can mediate representation of both novelty and reward. Such a system may further serve to motivate novelty-seeking, exploratory behaviors (Bunzeck et al., 2012). Thus, novelty may be a key factor underlying the motivation to learn, spurring pursuit of further novel stimuli or learning environments.

CONCLUSION

We have highlighted key changes in structural and functional neural organization over development, and have illustrated why brain-behavior links are likely to be bidirectional. We then have specifically addressed why learning in infancy may involve active, experience-driven strategies, to ground our understanding of learning in a context-dependent manner. Our goal is to incorporate what we know about active learning in adulthood, and the neural changes that may be associated with this form of learning. The specific examples highlighted in this paper illustrate the complexity and dynamism of the human learning process. Inputs into learning can be influenced by the developmental processing occurring at the time of learning, prior expertise, and learning biases, as well as engagement with the activity in question, novelty, and motivation in general. Learning a given skill can therefore involve differential processing and demands, based on interactions among the factors outlined above. Therefore we have emphasized that, from a cognitive and developmental standpoint, our understanding of learning will be limited until we can ground it in a multifaceted framework, explaining the interplay of brain-behavior relationships along with the role of active participation in dynamic environments.

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The authors have completed and submitted the ICMJE Form for Disclosure of Potential Conflicts of Interest. No conflicts were noted.

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