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Learning through the ages: How the brain adapts to the social world across development

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ABSTRACT

In a number of ways development can be understood as a specialized form of learning. As new neuronal circuits are maturing they are molded by environmental experiences much in the way that experience molds synaptic strength in traditional learning models. Furthermore, many of the same mechanisms that underlie synaptic changes in learning also mediate changes that occur across development. This is true at both the molecular level in remodeling of dendritic spines and at the systems level via emotional amplification of associations. A key difference between the two however is that while learning can occur within virtually any circuit at any time, developmental plasticity is much more restrictive in both domain and time window. In this manuscript I review some of the mechanisms associated with developmental neuroplasticity and then provide specific examples from the development of social cognition.

1. Introduction

The maturation of the nervous system is extremely protracted relative to other physiological systems. Earliest stages of brain development begin soon after conception and, in most species, regulated changes in growth and refinement of brain circuits continue into early adulthood (Stiles, 2008). In humans this process begins about two weeks after conception, and is not complete until well into the third decade of life (Gogtay et al., 2004; Huttenlocher, 1979; Petanjek et al., 2011; Sowell et al., 2003). In this paper, I will argue that an important aspect of this prolonged maturation process is to incorporate neuroplasticity and adaptation into the framework of brain development. I will compare some of the mechanisms that are shared between brain maturation and learning, and will elaborate on some of the specialized features of learning that occurs in immature brain circuits; a concept I am referring to as *developmental learning*. I will then briefly provide some concrete examples of developmental learning principles from the domain of social development, in which the prolonged process of maturation is particularly apparent in both brain and behavioral responses.

By developmental learning I am referring to the *active guidance and modulation of regulated growth by experience*. Developmental learning differs from traditional learning in that it can only occur when new synapses and circuits are undergoing growth and maturation. Although developmental learning often employs the same mechanisms as traditional learning, developmental learning refers to learning which is directly moderated by the maturation process. Learning which impacts circuits that are more (or less) receptive to modification as a function of developmental state is developmental learning. In many ways developmental learning reflects the concept of sensitive or critical periods in development (Hensch & Fagiolini, 2005; Knudsen, 2004; Lewis & Maurer, 2005). However, critical periods tend to be applied in a very restrictive manner to

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specific early life experiences. My conception of developmental learning is a more expansive application of sensitive period concept. Developmental learning applies whenever regulated changes in brain circuits occur in development. By this definition developmental learning can occur well beyond early life and can extend even into what is traditionally considered early adulthood (Gogtay et al., 2004; Petanjek et al., 2011). It should be noted that this paper is aimed at integrating developmental findings from a variety of disciplines (including both animal and human based studies) to generate theoretical concepts of neural maturation. I have tried to indicate clearly which models I am referring to in the text but in order to focus on general principles, they have not been segregated.

2. Developmental learning as an intermediate form of adaptation

A primary function of the nervous system is to optimally match behavioral and physiological systems with the environment in which the individual is embedded. Adaptations can occur via genetic modifications across generations, or via changes brought about by learning within the individual. I will argue that, developmental learning, as a specialized form of traditional learning, is a third category of adaptation that, in terms of stability, flexibility, and cost, lies in between these two other forms of adaptation.

Some environmental features are relatively stable, like gravity and climate. However, there are also many aspects of the environment that change dramatically across generations, seasons, or days. Examples of fluctuating environmental features include sources of food, potential predators, and social structure. Adaptations brought about by intergenerational shifts in the genome provide optimal fit between the organism and the more constant features of the environment. However, such shifts do not provide adequate flexibility for more rapidly changing features like food sources or social structure. If a primary source of food disappears within a generation, for example, inherited tendencies to seek out that food-source would lead to starvation. On the other hand, traditional learning provides a much more flexible and rapid means for the organism to adapt to the environment, because adaptations are individually customized and tailored to specific circumstances. There are, however, costs associated with learning. Frequent, dramatic changes to the wiring of the nervous system can be energetically expensive and sluggish. In addition, using a trial and error based strategy can be deadly if the wrong food source is chosen or social affiliations are directed at the wrong individual.

In developmental learning, emerging brain circuits are highly susceptible to environmental experiences during their formation, but are much more stable thereafter. This generates a specified period of time when environmental context can mold adaptations but it does so within certain parameters. In the classic example of the critical period for visual system development, for example, visual circuits are refined by experience rather than being created de novo. In addition, the refinements are restricted to a particular period of time in development which restricts the cost and effort dedicated to specific structural development. As such, developmental learning is an intermediate form of adaptation – in terms of flexibility, stability, and cost.

There are several important differences between traditional and developmental learning, even though the mechanisms of circuit change are similar. First, developmental learning is more rapid but also more labile than traditional learning. The ultimate outcome of developmental learning occurs on a much slower time scale. Secondly, developmental learning occurs within relatively narrow constraints, because the overall architecture is determined in the genome and experience can only make relatively minor changes to its implementation. Finally, developmental learning proceeds along pre-determined timelines and sequences, as the maturation of the brain unfolds over time. Developmental learning tends to be less flexible than traditional learning because it is more sequential and hierarchical (eg. you must walk before you run). On the other hand, because developmental learning depends on actively maturing brain circuits, it is also more robust and resistant to extinction than traditional learning. To use the classical example of visual system development as an example again, once ocular dominance columns are established they are generally very resistant to change.

3. Mechanistic similarities between developmental plasticity and learning

For many years brain development was thought to be orthogonal to environmental experience (Meaney, 2010). However, it is now widely recognized that maturation of brain circuits cannot be dissociated from adaptations to the local environment, and indeed brain development can only be understood in the context of an interaction between nature and nurture (Meaney, 2010). From this perspective, environmental influences are a constant factor on brain maturation throughout brain development, and brain development should be construed as a form of learning. Indeed, from a mechanistic standpoint many of the same factors that govern change at the synaptic and circuit levels involve establishing and stabilizing contacts between cells. Cellular research on models of learning and development indicate similar mechanisms are employed in both circumstances. In addition, the recent surge of interest in epigenetic modulation of genetic expression has indicated another area in which common mechanisms seem to be employed in learning and maturation related processes. In this section I will review several models that reveal common mechanisms for brain change in development and learning.

Long-term potentiation, or LTP, is a model of activity-dependent synaptic plasticity that has served as a model of learning for many years. LTP critically depends on the synaptic contacts between cells mediated by small dendritic protrusions called spines (Kasai, Fukuda, Watanabe, Hayashi-Takagi, & Noguchi, 2010). Across the lifespan, spines, and synapses more generally, ebb and flow, thereby generating intermittent contact between cells (Caroni, Donato, & Muller, 2012). When co-activity between cells occurs, transient spines strengthen and stabilize, and new more lasting neural associations are created.