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Plasticity in Sensory Systems

Jennifer K. E. Steeves and Laurence R. Harris

Over the past ten or so years, brain plasticity has become an extremely hot scientific trend and a huge commercial enterprise. From the parent who wants to give his or her newborn an enriched environment to promote superior brain growth to the aging adult who wants to stave off Alzheimer's disease, exercising, enriching, and training the brain has become a multimillion-dollar industry. Hundreds of brain promotion companies have sprouted up, such as The Baby Einstein Company, LLC, and hundreds of new books are published each year on brain enrichment. "Brain health," "brain training," and "brain fitness" are terms that are bandied about in the advertising world, suggestive of the possibility of improving and prolonging intellectual health. However, this "brain improvement" commercialism, although occasionally overstated, is not without some foundation in hard science: the discovery of brain plasticity.

The roots of the concept of "brain plasticity" can be traced to William James's seminal work, *The Principles of Psychology* (1890), in which he clearly understood that behavior, habits, or instincts are governed by certain physiological limitations. He states, "Plasticity, . . . in the wide sense of the word, means the possession of a structure weak enough to yield to an influence, but strong enough not to yield all at once. . . . Organic matter, especially nervous tissue, seems endowed with a very extraordinary degree of plasticity of this sort; so that we may without hesitation lay down as our first proposition the following, that the phenomena of habit in living beings are due to the plasticity of the organic materials of which their bodies are composed" (p. 106). The notion of plasticity was, however, largely ignored until Donald Hebb (1949) revived it in his influential book, *The Organization of Behavior*. Hebb, describing how cells

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connect with one another, developing the "cell assembly theory": the notion of cell connectivity altered through experience. This important concept is best described by the following statement: "When an axon of cell A is near enough to excite cell B and repeatedly or persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells such that A's efficiency, as one of the cells firing B, is increased" (p. 62). This concept has become known as "Hebb's postulate" or "Hebb's rule." He also described the contrasting situation in which a lack of stimulation leads to a loss of connectivity between cells. These principles have come to be known by the lay phrase "Cells that fire together, wire together" and as the "use it or lose it" phenomenon. What Hebb described is the foundation of the principle of cellular learning, which is sometimes referred to as "Hebbian learning." Today we know more about some of these mechanisms at the chemical level in the synapse with the phenomenon known as "long-term potentiation" (LTP) (Cooke and Bliss, 2006).

Around the same time that Hebb was developing cell assembly theory, microelectrodes, which were invented by 1st Baron Adrian in 1928 (Adrian and Bronk, 1928), were being perfected and used, notably by Vernon Mountcastle, to clarify the organization of the cortex (e.g., Mountcastle, 1957). The earliest experimental studies of experience-dependent physiological coding were famously carried out by Hubel and Wiesel in the visual cortex of the cat in the late 1950s and early 1960s (e.g., Hubel and Wiesel, 1959, 1962). One of Hubel and Wiesel's many classic experiments in experience-dependent coding showed that the distribution of the influence of the left or right eye on cells in the visual cortex was drastically altered if vision through one eye was disrupted early in life. The proportion of cells driven by the deprived eye was, as one might expect, drastically reduced, but, unexpectedly, the number of cells influenced by the nondeprived eye was dramatically increased. This was the first direct observation of Hebb's postulate in action, demonstrating plasticity in a neural system (Hubel et al., 1977; Wiesel and Hubel, 1963, 1965a, 1965b). This work led to Hubel and Wiesel being awarded the 1981 Nobel Prize in Medicine and greatly influenced the direction of research in neurophysiology for decades.

Not only did Hubel and Wiesel's pioneering work demonstrate neural plasticity, but it also indicated that the timing of sensory deprivation played a key role in behavioral outcomes because only visual deprivation that occurred early in life seemed to have adverse effects on vision. This gave rise to the notion of critical or sensitive periods as specific developmental "moments of opportunity" during which the visual system could be modified in response to visual input. Originally it was believed that critical periods were fixed temporal windows during which each particular aspect of visual behavior developed and its corresponding wiring was laid down. After that time period, the theory went, neural systems became

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fixed and could not be modified; that is, the window was closed forever from that moment forward (Fox, 1992; Hubel and Wiesel, 1970). Many researchers have since elaborated the effects of early visual deprivation on visual coding, and it has become clear that there are multiple critical periods, each specific to a different aspect of visual function. Similar principles emerged in other sensory systems, including hearing (Nakahara et al., 2004; Popescu and Polley, 2010) and touch (Richardson and Wuillemin, 1981). Clinicians have used the concept of critical periods to justify early intervention in an attempt to correct childhood sensory disorders of hearing or vision. Many socialized health care systems now provide neonatal hearing tests and early childhood vision tests as part of standard clinical practice, rushing to detect sensory problems before the close of the relevant critical period to optimize the chance of successful intervention.

However, the notion that the adult brain is hard wired once the critical windows of postnatal development close has been challenged. Michael Merzenich's seminal work on somatosensory (Kaas et al., 1983; Merzenich et al., 1984) and motor (Nudo et al., 1996) cortex in the nonhuman primate demonstrated that the adult brain can remap itself in response to changes in sensorimotor input. His research showed that deafferentation of cells in somatosensory cortex following digit amputation led to recruitment of those deafferented cells by adjacent digits in a way directly comparable to the change in distribution of cell responses in the visual cortex after removal of their primary input, as demonstrated by Hubel and Wiesel. Importantly, these experiments demonstrated that cortical maps in somatosensory cortex could be changed not only during early development but also in the adult brain as a result of sensory or motor experience. This directly supports Hebb's postulate of forty or so years earlier, which did not impose any requirement that plasticity could only occur during certain developmental phases. Here was proof that remapping and reorganizing the brain were possible in the mature brain in response to experience. This revolutionary finding indicated that critical periods are not, in fact, critical and that the brain is not completely hard wired in adulthood. The implications of this observation are enormous. It not only gives clinical patients hope for recovery from brain disease or trauma, but it also gives the average person hope that his or her brain could also be honed with experience or practice to expand or improve its cortical processes and thereby support substantially improved, or even supernormal, abilities. In terms of clinically assisted recovery from disease and trauma, the huge expansion of physical and occupational therapy facilities seen in recent years is based on the new hopes arising from this knowledge of neural plasticity. In a general context, the demonstration of adult neural plasticity has given optimism for recovery from stroke trauma (Sterr and Conforto, 2012). Plasticity across sensory and motor systems now seems a natural adaptive compensatory mechanism for disease and trauma.

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It is a commonly held belief that individuals who have lost vision have enhancement in other sensory systems such as hearing and touch, and that individuals who have lost hearing have enhancement in vision. In fact, as reviewed in this book, neural plasticity across sensory modalities can be rigorously demonstrated and even manipulated to assist people with sensory problems. No amount of plasticity can restore sight to the blind, at least not with current camera and neurosurgery techniques; however, in the 1960s, Bach-y-Rita developed the first sensory substitution device (Bach-y-Rita et al., 1969) allowing information that is normally available only through the visual system to be provided to a person through another sense. Blind people may be particularly good candidates for sensory substitution because of existing neural plasticity that allows a remaining sensory system to take over unused visual cortex (Collignon et al., 2011), but plasticity is certainly not limited to compromised systems. Neural plasticity is a wonderful example of how a basic science observation, aimed at understanding how the brain works, can find highly significant application in the real world. Reestablishing neural substrates for sensory and motor function is the ultimate goal of neural rehabilitation in the future. This book explores the phenomenon of neural plasticity, particularly how it relates to vision and its loss, and how plasticity can be called into service to help restore function.

The book is divided into three sections comprising three different themes in the field of sensory plasticity. Section I examines visual and visuomotor plasticity. In this section, Chapter 2 (Op de Beeck) describes how parts of the brain change as a result of learning about the visual aspects of an object, whereas Chapter 3 (Salomonczyk, Cressman, and Henriques) expands this theme to include the more usual type of learning associated with visuomotor actions. Chapter 4 (Neichwiej-Szwedo, Goltz, and Wong) completes this section considering how visuomotor adaptation is affected in people with early visual deprivation resulting from amblyopia. Section II of the book considers examples of what might now be called "classical plasticity": changes that occur during the conventional developmental "critical periods" as a consequence of clinical cases of disrupted visual experience. Although Chapter 5 (Maurer and Lewis) examines visual plasticity and visual loss in the recovery from congenital cataract, the other chapters in this section contemplate cross-modal plasticity in which deprivation in one sense results in gains or adaptations in other sensory systems. The clinical cases of visual deprivation that are considered are the surgical removal of one eye early in life (Chapter 6, Kelly, Moro, and Steeves) and early blindness (Chapter 7, Collignon, Dormal, and Lepore, and Chapter 8, Rauschecker).

Section III of this book contends with the more controversial topic of adult plasticity and how it might best be exploited for rehabilitation. Chapter 9 (Hess and Thompson) reviews the topic of visual plasticity in both healthy and amblyopic adult brains. Chapter 10 (Barry) describes the author's personal experience

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of recovering depth perception from stereopsis as an adult after an intense program of vision training, and Chapter 11 (Gall and Sabel) discusses one type of visual rehabilitation therapy that manipulates cortical plasticity. The last chapter (Chapter 12, Maidenbaum and Amedi) reviews many rehabilitation techniques, including the effectiveness of sensory substitution for visual problems, and thus neatly rounds out the book by demonstrating the advantages and disadvantages, as well as the successes and failures, of harnessing cross-modal plasticity to achieve functional vision in visually challenged individuals.

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PART I

VISUAL AND VISUOMOTOR PLASTICITY

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2

The Distributed Nature of Visual Object Learning

Hans P. Op de Beeck

Introduction

We mostly take object vision for granted, simply because our brain makes it seem easy. As a consequence, most of what we learn about objects during both development and adulthood goes unnoticed. Once the input to the system is in order (so excluding retinal disorders), almost all people can recognize cars, Coca-Cola bottles, and Barbie dolls. We only get a glimpse of the complexity of the underlying processes when we go through the most challenging tasks that we are typically confronted with. For example, some people have below average skills in face recognition. In this respect, interindividual differences in the most challenging object recognition tasks, created either naturally or in the lab by manipulating experience, serve as a gold mine for trying to understand the brain's exceptional ability to recognize objects.

My favorite example of an idiosyncratic object recognition talent is Gudrun, my eight-year-old daughter. She has a favorite teddy bear, are affection that developed when she was only a few months old. When Gudrun was one year old, my wife and I bought a second identical bear (just in case the first one was lost). Obviously, she noticed the difference between the old bear (which she calls "pretty bear") and the new one. It was also easy for us parents to differentiate between the old worn bear and the new exemplar. However, over the years these differences became very minor, and now no one can reliably differentiate "pretty bear" from "new bear." When I ask Gudrun, she can point to a few small details that, if I pay careful attention and look closely, are indeed informative about the identity of the bears (Figure 2.1). However, Gudrun does not have to be so

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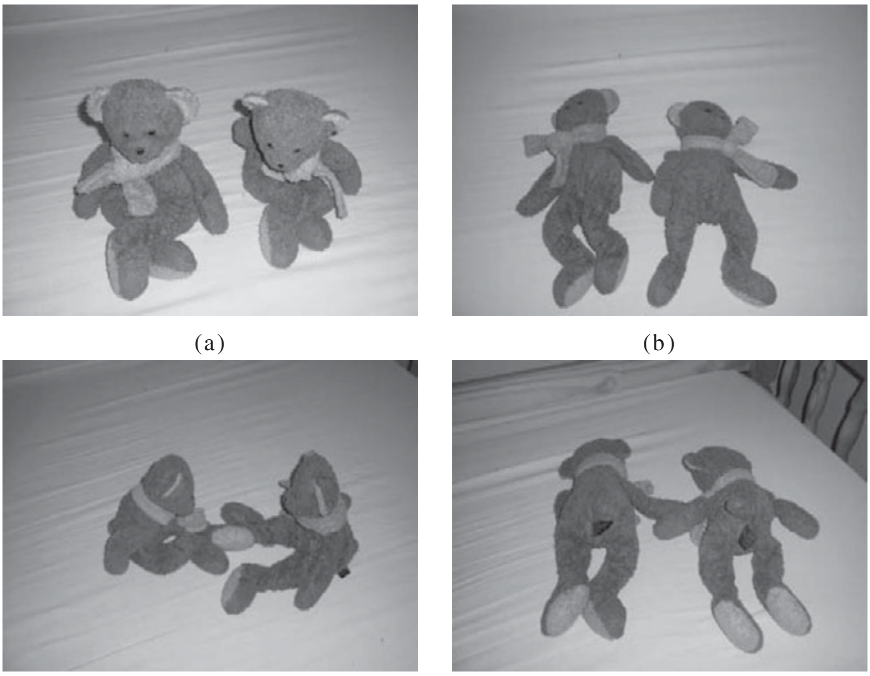

(a) (b) (c) (d)

Figure 2.1. Objects of expertise of a "pretty bear" expert. The use of multiple dimensions, including the darkness of the ears, the darkness and the length of the scarf, the expression of the face, and the thickness of the body allow for the discrimination of "pretty bear" (right, right, left, and right in panels (a)–(d), respectively) from its counterpart, "new bear."

attentive. She can enter her bedroom, spot the two bears at a distance of several meters and partially covered with other stuff (and, yes, there is always a lot of stuff in her room), and she knows immediately which bear is her favorite. She is a "pretty bear" expert.

There is no reason to assume that the brain, whether Gudrun's or anyone else's, would have been specifically designed to recognize teddy bears. In contrast to, for example, faces, teddy bears have no substantial evolutionary significance as far as we know. This chapter is mostly about this type of de novo expertise of which there are many examples. We have, among others, visual word form experts (readers), car experts, bird experts (ornithologists), radiologists, plane experts, fingerprint experts, Greeble experts, Ziggerin experts, martial rock experts, and Smoothie/Spikie/Cubie experts. In this chapter, I focus on the large body of work while trying to ascertain which brain mechanisms are involved when we learn about objects. As the reader will notice, this field has dealt with important controversies that shaped the field but that, in my opinion, can be left behind, given the current state of the art. The discussion of the studies is divided between

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