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Revisiting Kaas and colleagues: The homunculus: The discovery of multiple representations within the "primary" somatosensory cortex

Leah Krubitzer and Mary Baldwin

There are a few truly momentous occasions in life and most do not occur through any machinations on the part of the individual who enjoys such occasions. Rather, they are happenstance and simply require one to be in the right place at the right time. Such was my experience (Leah Krubitzer) in the 1980s when I found myself lucky enough to be a graduate student in the laboratory of Jon Kaas. A serendipitous twist is to find myself writing this chapter with Mary Baldwin, a fellow student who succeeded me in Jon's laboratory some 20 years later, and today finds herself in the right place at the right time to recount with me this important discovery of our mentor. I began work in Jon's laboratory in 1983, on the heels of his discovery that the sensory neocortex of primates is more complexly organized than previously believed. In the 1970s, the Kaas laboratory utilized multiunit electrophysiological recording techniques in novel ways in visual and somatosensory cortex in non-human primates.

Together with John Allman, Kaas demonstrated that the visual cortex was composed of multiple, topographically organized subdivisions that extended beyond the borders of the traditionally defined primary (V1) and secondary (V2) visual areas (Allman and Kaas, 1971 (MT), 1974 (MTc), 1975 (DM), 1976 (M)). A few years later, in the study that is the highlight of this chapter, Jon discovered that what was once considered a single cortical area, the primary somatosensory area (SI), was actually composed of at least three separate cortical fields with distinct functions (Kaas et al., 1979). This was much more than a point scored by the splitters over the lumpers in their pursuit of defining a functional map of the primate brain. Below we argue that this seminal paper was revolutionary because it demonstrated the power of surveying a large expanse of cortex and the importance of directly relating structure to function, and provided a new perspective on the complexity and number of sensory maps in the primate neocortex.

But before we can address how the field has advanced from this work, it is important to appreciate where we were before these discoveries were made, how these discoveries changed our theoretical framework, and how the use of particular techniques to uncover aspects of cortical organization revolutionized the field.

BEFORE 1979: A BRIEF HISTORY OF CORTICAL CARTOGRAPHY

Appreciating the impact of Jon Kaas's contribution requires that we step back about a century or so. In the late 1800s and early 1900s there were a number of prominent anatomists detailing the cytoarchitecture and myeloarchitecture of the human neocortex, such as Constantin von Economo, Percival Bailey and Gerhardt von Bonin, Oskar and Cécile Vogt, Korbinian Brodmann, Alfred Walter Campbell, and Grafton Elliot-Smith (for reviews see Nieuwenhuya, 2013; Nieuwenhuya et al., 2015; Triarhou, 2007a, b; Kaya et al., 2016). Using Nissl and myelin stains, and in one case unstained, wet tissue and the naked eye (Elliot-Smith, 1907), these scientists pioneered the idea that the neocortex in humans is not a homogeneous structure, but is composed of multiple subdivisions with distinct laminar thicknesses, cell densities, staining and myelination (see Figure 4.1). If the currency of neuroanatomy is others' adoption of one's nomenclature, Brodmann may be the most renowned because his illustrations of the subdivisions of the human neocortex are still found in most textbooks. In fact, Brodmann proposed that these divisions were separate "organs" of the brain that had distinct functions (Brodmann, 1909, cited in Garey, 1994).
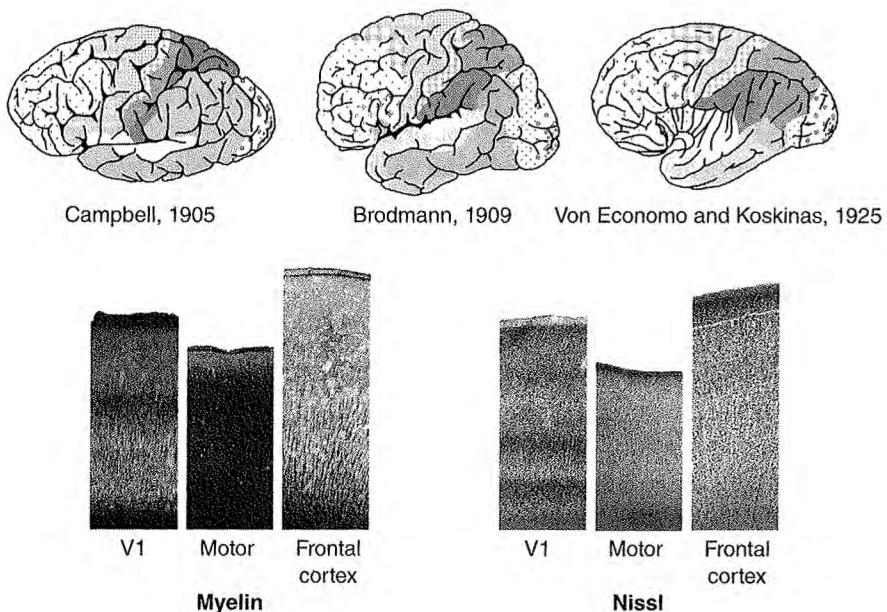

| Campbell, 1905 | Brodmann, 1909 | Von Economo and Koskinas, 1925 |

V1   Motor   Frontal   V1   Motor   Frontal
                 cortex   cortex

Myelin   **Nissl**

Figure 4.1 Architectonic maps of the neocortex proposed by early anatomists (top row). These maps were constructed by examining sections stained for Nissl substance or myelin (bottom row). Multiple cortical fields were identified in anterior parietal (plaids), posterior parietal (dark gray), occipital (dots), and frontal (crosses). Although the divisions of different anatomists varied, they all agreed that cortex was not homogeneous. Close examination of Nissl and myelin stains reveals clear laminar differences in V1, motor, and frontal cortex.

Despite his work on the human brain, what we consider to be Brodmann's most important contribution to the field goes largely unappreciated: his extensive comparative analysis. He cut and processed tissue from multiple species, including hedgehogs, ground squirrels, rabbits, flying foxes, kinkajous (South American carnivores), lemurs, marmosets, guenons, and humans, and generated a numerical naming system for different cytoarchitectonic fields, some of which were similar across species. Much of his terminology is still commonly used today, including areas 17 and 18 of the occipital lobe, areas 3, 1, and 2 of the parietal lobe, and area 4 of the frontal lobe.

While he and others inferred that these architectonically distinct areas of the neocortex corresponded to functional subdivisions, it was not until the middle of the twentieth century that physiologists such as Clinton Woolsey, Philip Bard, Richard Lende and Wilder Penfield demonstrated that the parietal cortex contained distinct representations of the body surface. These individuals used surface evoked potential techniques to examine where in the neocortex inputs from different portions of the body were represented. Their functional subdivisions roughly corresponded to previously defined architectonic subdivisions by Brodmann and others, although they did not directly relate their functional data to histologically processed tissue. Specifically, a single representation of the contralateral body was found in non-human and human primates in the anterior parietal cortex (see Figure 4.2), a region that roughly corresponded to areas 3, 1 and 2 of Brodmann. This functional field was termed the "primary somatosensory cortex" and abbreviated to SI. Today, arabic numerals have replaced roman numerals in this abbreviation, which is now commonly written as S1. These maps of the body were complete and topographically organized, such that adjacent portions of the skin were represented in adjacent portions of the neocortex. It was during this time that the term "homunculus" became popularized. While Penfield enjoyed much of the notoriety for his studies of the human parietal cortex, it was Clinton Woolsey and colleagues who demonstrated the ubiquity of SI in numerous species including humans.

Lateral to SI, a second representation of the body observed in humans and other mammals was called SII (now commonly referred to as S2) (see Figure 4.2). It should be noted here that during this time the primary auditory area (A1) and the primary visual area (V1) had also been defined in a variety of mammals, roughly corresponding to architectonic divisions of the neocortex (Brodmann's areas 41 and 17 respectively). However, it was not common during this era for physiologists to cut and process the brains from which they recorded. Therefore, a direct relationship between function and structure was rarely well established.

There were several extremely important (and sometimes counterproductive) theoretical concepts that emerged from this era of scientific discovery that still persist today. The first is that when two fields of a given sensory modality were described in evoked potential mapping studies, these were regrettably termed "primary and secondary sensory fields". This, of course, reinforces current theories on hierarchical processing networks in the neocortex, which imply that fields such as the primary somatosensory, auditory and visual areas have ascendency
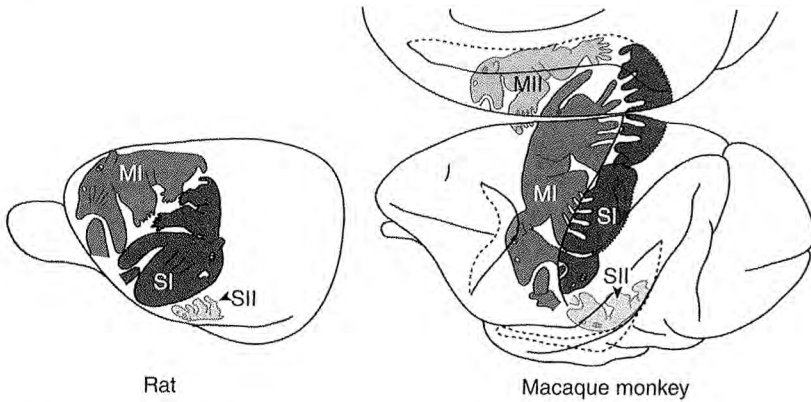
Rat   Macaque monkey

Figure 4.2 Maps of the somatosensory cortex and motor cortex generated from evoked potential studies in anesthetized rats and macaque monkeys. The first (SI) and second (SII) somatosensory areas are depicted as homunculi, or a miniature of the body (normally referring to humans). These maps were originally generated by Clinton Woolsey (see Harlow and Woolsey, 1958).

over secondary areas such as S2 and V2. In addition, this terminology impacted our ideas of cortical field evolution in mammals, perpetuating the idea that primary areas are older, secondary areas are more recently evolved, and other areas (such as V3 and V4) have evolved subsequently and in order. Interestingly, at the time of discovery Woolsey appreciated that the terminology was problematic and stated that these areas were named simply in order of discovery and not ascendancy.

The second theoretical concept that emerged from this era, thanks to the extraordinary comparative studies of Brodmann and later Woolsey, is that mammals share common features of neocortical organization, such as the presence of common anatomical and functional brain areas including S1, S2, V1, V2, and so on. This realization that there were common brain features across species had, and still has, extremely important implications for theories of cortical evolution, and provides a basic framework for assigning homology and understanding the possible cortical organizational scheme that was present in our earliest mammalian ancestors. Of course, since the time of Brodmann's and Woolsey's studies, additional methods have been used to establish the homology of different cortical fields in mammals, but these early works provided the first firm foothold in the field of comparative neuroscience.

The third important consequence of these early comparative studies has been the promotion of the term "association" cortex. In these preparations one or two maps of the sensory epithelium were described. In mammals with small brains, such as rats, the first and second sensory areas (e.g. S1, S2, V1, V2) assumed most

of the cortical sheet. In species with larger brains, such as macaque monkeys, these fields were separated by a relatively large expanse of cortex where responses to tactile, auditory or visual stimuli could not be evoked in the anesthetized preparations used to study non-human mammals. This unresponsive cortex consisted of a much larger percentage of the cortical sheet in monkeys and apes than in small-brained mammals, and included the region of cortex between S1/S2 and V2, now known as the posterior parietal cortex. Because stimulation failed to evoke a response, these physiologists assumed this region corresponded to the "association cortex" identified by anatomists at the beginning of the century (e.g. Campbell, 1905; Fleshig, 1905). The association cortex was proposed to be a region where sensory inputs were combined and translated, and perhaps where consciousness was seated (Zeki, 1993). Over time the notion of the posterior parietal cortex (PPC) as the association cortex gradually gave way to an appreciation that the PPC contains a large, complex network of cortical fields, many of which process sensory inputs.

It would be remiss if we did not briefly mention the important contributions by Vernon Mountcastle and his colleagues in the 1950s and '60s. Probably the most significant was his work on the awake behaving monkey, where he directly related neural activity to some aspect of behavior. Discoveries that neurons respond to specific sensory modalities, that particular features of a stimulus such as orientation and direction are coded by specific neurons, and that receptive fields of neurons have a complex organization such as center-surround were also made during this time (see Mountcastle, 1995a, 1995b). Subsequently, he described the cortical column and promoted the notion of a "basic uniformity" of the neocortex at the level of the microcircuit. However, that is a separate story for another day.

1979: THE GAME-CHANGING DISCOVERY OF MULTIPLE REPRESENTATIONS IN THE "PRIMARY" SENSORY CORTEX OF PRIMATES

We have outlined not only the scientific discoveries that occurred before the 1979 Kaas paper but also the theoretical framework prevalent at this time, so that the reader can appreciate why the 1979 study by Kaas, Nelson, Sur, Lin, and Merzenich was so important. Utilizing extracellular electrophysiological recording techniques in a number of New and Old World monkeys under anesthesia, Kaas and colleagues recorded from hundreds of sites within the parietal cortex in each animal while stimulating different body parts. Unlike single-unit studies in which only a few sites within a given monkey cortex are surveyed and stimuli are controlled, in these studies the body was stimulated by handheld probes (a technique termed "hand mapping") lightly tapping or brushing the skin surface for cutaneous stimulation. Deep receptors were stimulated by manipulation of joints or probing muscles. Because neural responses to these manually applied stimuli can be

ascertained very rapidly, it is possible to record from hundreds of sites across centimeters of the neocortex. Kaas and his colleagues directly related hundreds of recording sites to cytoarchitectonic boundaries (like those first demonstrated by Brodmann and his contemporaries) to generate functional maps of cortex with architectonic borders.

By sampling so many locations, these studies demonstrated there were multiple representations of the body surface in the parietal cortex rather than only one, each of which was co-extensive with an architectonically distinct field (see Figure 4.3). They found a very detailed and complete representation of the cutaneous body surface in area 3b in which neurons had relatively small receptive fields. Furthermore, a complete mirror reversal representation of the body surface was observed in area 1, and an additional representation of the deep receptors of the muscles and joints was found in area 2. Although they did not characterize a body map in area 3a, they proposed that a separate representation existed there as well, and a complete map of the body in area 3a has been subsequently described in a variety of mammals (see Figure 4.3C; also see Krubitzer et al., 2004, for a review). Thus, rather than a single map or homunculus of the body that spanned four cytoarchitectonic fields (see Figure 4.3A), Kaas and colleagues discovered two topographically organized representations corresponding to areas 3b and 1, and one roughly topographic representation of deep receptors that co-registered with area 2 (see Figure 4.3B).

This discovery that the anterior parietal cortex was much more complexly organized than was previously believed was the game changer, because for the first time fundamental questions could be asked about the hierarchy of information processing, about homology across species, and about the evolutionary genesis of cortical field formation (i.e. how new cortical fields were added). For example, how can we determine which areas emerged early in mammalian evolution and which areas evolved more recently if more than a single sensory area is present in some mammals versus others, as is the case for the classical macaque monkey SI (now known to contain areas 3a, 3b/S1, 1 and 2) versus rodent SI? Further, of those more recently emerging areas, which ones are or are not shared across extant species, and which areas are specializations to a particular clade, or even species? Finally, as new areas emerge in the course of evolution, to what degree is their contribution to the network dependent on the processing that occurs in already-existing areas? It seems highly unlikely that fields are added into a network in a strictly sequential or hierarchical fashion (despite the unfortunate nomenclature of V1, V2, V3, V4, etc.), but instead emerge between existing areas within the network.

In addition to changing the theoretical framework of how we think about the organization and function of the somatosensory cortex, this study was an important demonstration of a methodological approach that complemented other techniques. For example, Kaas underscored the importance of combining different techniques to subdivide the neocortex accurately. Unlike most previous studies, he directly related his electrophysiological recording data with his
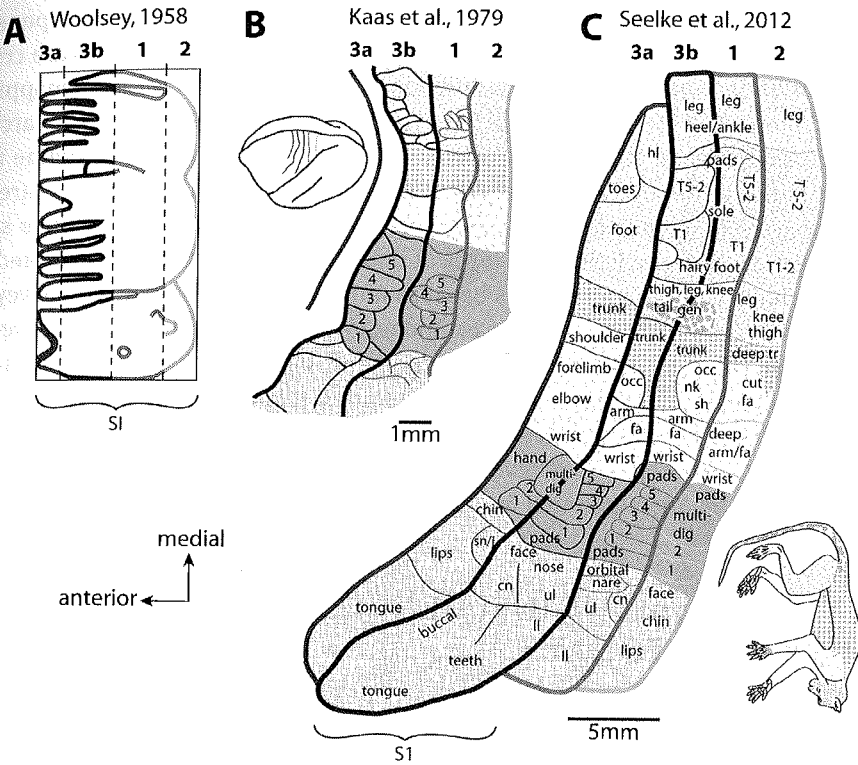
Figure 4.3 Changing concepts of the organization of somatosensory cortex over time. Early evoked potential maps of Woolsey (A) suggest that a single representation of the body was co-extensive with four cytoarchitectonic fields (3a, 3b, 1, and 2). The 1979 study by Kaas and colleagues discovered that cytoarchitectonic areas 3b and 1 each contained a separate and complete representation of the body (B). Subsequent studies summarized by Seelke et al. (2012) demonstrate that detailed maps of the body exist in each of the four cytoarchitectonic fields, at least in macaque monkeys (C).

cytoarchitectonic data. In subsequent papers and reviews he argued convincingly that the best way to subdivide the neocortex was to use multiple criteria, including an examination of the connection patterns of a presumptive cortical field (Kaas, 1982). In addition, the use of multiunit electrophysiological recording techniques made surveying a huge swath of cortex possible, and allowed one to pose questions about the overall cortical organization. While a number of important discoveries in parietal and posterior parietal cortex in the same era were made using single-unit electrophysiological techniques (see Mountcastle 1995a, b, for a review), the types of results yielded by the two techniques were synergistic rather than mutually exclusive. Studies of single neurons in awake animals are limited in terms of the amount of cortex that can be surveyed, but they allow one to determine the response properties of neurons in much greater detail and with

more precision. Moreover, it is extremely valuable to study neural responses while an animal is conscious and even behaving. While both techniques are critical to our understanding of cortical function, the extracellular multiunit mapping method pioneered by Kaas and colleagues, especially when combined with architectonic analysis and studies of connections, allowed investigators to define the overall organization of the cortical sheet including the number of cortical areas, the topographic organization of individual cortical fields, and the relative size and location of cortical fields. This type of information could not be elucidated in awake behaving single unit studies because not enough cortex could be surveyed in a single animal. This is still the case today. While the multiunit mapping techniques that were used to uncover the mysteries of the mammalian brain have showed staying power over a number of decades, it is perhaps unfortunate that with the advent of powerful new techniques to probe cortical networks we tend to throw out techniques that revolutionized the field and still remain the best method to probe organizational features of the neocortex.

BEYOND 1979: THE INFLUENCE OF THIS STUDY TODAY

The fundamental issue that was resolved in the 1979 publication was that there are three or four distinct maps of the body surface in primates that correspond to three or four cytoarchitectonically defined areas, only one of which is homologous to S1 (area 3b) as defined in non-primate mammals. Unfortunately, many scientists who work on the anterior parietal cortex in cats and monkeys still refer to these multiple architectonic fields as S1, a bone of contention that Kaas himself appreciated and vocalized in a compelling review entitled "What, if anything, is S1?" (Kaas, 1983). This is more than a semantic issue. The inappropriate use of the term S1 promotes a misunderstanding of both cortical circuitry and homology.

In a number of ways the seminal paper by Kaas and colleagues (1979) has laid the foundations for much of what we know about cortical organization and function today. First, this study re-emphasized that there is often a good correspondence between structure and function. That is, the Kaas multiunit mapping studies demonstrate that the multiple anatomically identified cortical areas in the anterior parietal cortex correspond with topographically organized somatosensory cortical fields. Further, multiple somatosensory fields not only exist in primates but are also found in squirrels, rats, flying foxes, tree shrews, and a variety of other species (see Figure 4.4).

Second, the 1979 study was pivotal in the discovery of cortical plasticity. In a series of studies published in subsequent years by Jon Kaas and Mike Merzenich, using the same multiunit extracellular techniques as those used in the 1979 study, they demonstrated that there were large alterations in cortical maps in S1 (3b) in adults that emerged as a consequence of alterations in the periphery, such as a
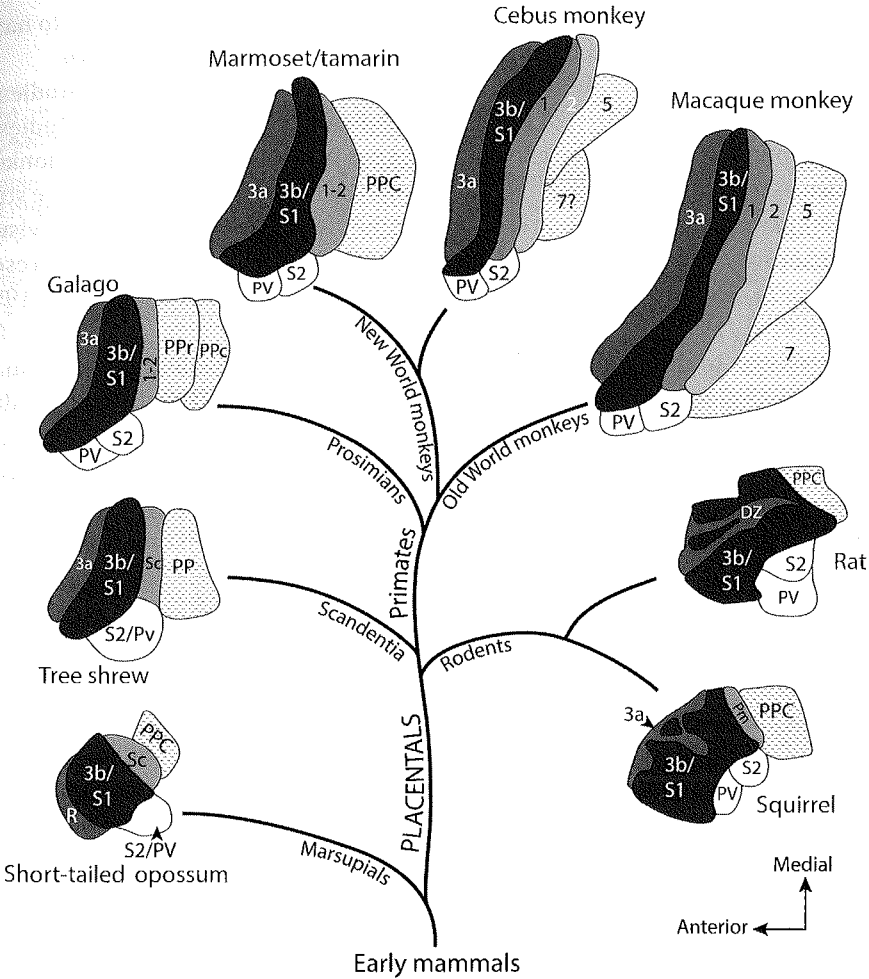
Figure 4.4 A cladogram showing the phylogenetic relationship of different species of mammals and the organization of their parietal cortex. Modern comparative analysis utilizes multiple techniques (e.g. electrophysiological and architectonic) to subdivide the neocortex. This figure demonstrates that all species examined have a primary somatosensory area (S1) and a second sensory area (S2). Recent studies demonstrate that a field rostral to S1 (termed area 3a or R) has been identified across groups as well as a posterior parietal cortex. However, the posterior parietal cortex is greatly expanded in primates. To date only primates have four separate anterior parietal fields (3a, 3b, 1 and 2), only one of which (area 3b) should be considered as S1.

nerve section or a loss of digits and limbs due to injury (Merzenich et al., 1983). This led us to re-examine the idea of strict critical periods during development. It also led to an explosion of experiments in both labs and spawned a new generation of investigators who studied adult plasticity, including Gregg Recanzone,

Hubert Dinse, Tim Pons, Jim Jenkins, Randy Nudo and Preston Garraghty, to name but a few, all of whom used techniques pioneered by Kaas and Merzenich.

Additionally, the 1979 study was the basis for non-invasive imaging studies in humans. The first generation of functional magnetic resonance imaging studies in humans sought to validate the existence of areas previously described in monkeys in which extracellular multiunit techniques were used to define a field. These studies in humans confirmed the presence of multiple representations in the visual, somatosensory and auditory cortex, including the presence of separate representations in 3a, 3b, 1 and 2 (Binder et al., 1994; Sereno et al., 1995; Lin et al., 1996; Disbrow et al., 1999).

Subsequent to the publication of the 1979 study, investigators began to more thoroughly explore the posterior parietal cortex to see whether distinct subdivisions were present, like the multiple areas described in the anterior parietal cortex. Most of the studies in PPC are executed in awake animals since neurons here do not respond well in anesthetized preparations. While it is beyond the scope of this chapter to consider all of the single-unit studies on the posterior parietal cortex, it is clear that these types of studies in monkeys, and non-invasive imaging studies in humans, demonstrate that this region of the neocortex is composed of multiple cortical fields that have both sensory and motor functions (particularly regarding the hands and eyes). Specifically, in primates the anterior portion of the posterior parietal cortex in the intraparietal sulcus and on the inferior parietal lobule (including areas 5, 7a and 7b of Brodmann and PF and PG of von Economo) is dominated by areas involved in intentional reaching and grasping, preshaping the hand to match a visual target, and matching grasp postures to shape and behavioral context. These regions are also involved in monitoring tactile and proprioceptive information from anterior parietal fields to code reach and grasp kinematics. Finally, these regions are involved in higher-order functions such as parsing self motion from object motion, generating an internal representation of the self, and possibly coding the intention of others (Snyder et al., 1997; Fogassi et al., 2005; Bisley and Goldberg, 2010).

What is probably the most important concept to have emerged in recent years is that the parietal cortex, including both the anterior and posterior parietal cortex, is actually involved in motor control, and not strictly in sensory processing (Gharbawie et al., 2011a, 2011b; Stepniewska et al., 2014). Further, we now know that neurons in somatosensory areas in the parietal cortex and lateral sulcus are modulated by attention, and even by stimulation from other modalities such as vision (Haggard et al., 2007; Burton et al., 2008). Thus, function is distributed across cortical networks that are made up of individual nodes or cortical fields, rather than being strictly localized to a particular cortical field. This means processing is not strictly hierarchical, that there is not a one-to-one correspondence between cortical field and function, and that differential activation of nodes within a network can generate a variety of complex behaviors. It is our hope that the next generation of scientists will seek to understand how characteristics such as perception, intention and consciousness emerge from such networks and the multiple cortical fields that compose them.

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