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"The Organization of Sonatosensory Callosal Projections: A New Interpretation"

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THE ORGANIZATION OF SOMATOSENSORY CALLOSAL PROJECTIONS

A New Interpretation

Herbert P. Killackey

INTRODUCTION

Our understanding of the function of the corpus callosum at the psychobiological level has increased enormously over the past 30 years. The now classic study of Myers and Sperry (1953) demonstrated the role of the corpus callosum in the interhemispheric transfer of information. This finding was extended to a much more general and exciting level with the demonstration of a breakdown in the interhemispheric transfer of information related not only to the sensory and motor spheres, but also to more global cognitive functions in man (Gazzaniga *et al.*, 1962, 1965, 1967; Gazzaniga, 1970). However, our understanding of the corpus callosum at the neurophysiological and neuroanatomical levels has not kept pace with these exciting developments. In this chapter I focus on the callosal projections of the somatosensory system of rodents and primates, emphasizing research in which I have been involved. I will attempt to provide a somewhat novel interpretation of the anatomical organization of the corpus callosum based on this research, but I will begin by presenting what I consider to be the consensual view of the relationship between the corpus callosum connections and the somatosensory cortex.

It is now generally recognized that different regions of the somatosensory cortex vary considerably in the density of the commissural projections that they send and receive. For example, in the opossum (Ebner, 1967), cat (Ebner and Myers, 1965; Jones and Powell, 1968), raccoon (Ebner and Myers, 1965), monkey (Jones and Powell, 1969; Karol and Pandya, 1971), rat (Wise and

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Jones, 1976; Akers and Killackey, 1978), mouse (Yorke and Caviness, 197 and squirrel (Gould and Kaas, 1981) zones of the somatosensory cortex sociated with distal limb regions as well as other regions are almost free commissural input, while in other regions, such as the trunk representatic there are dense interconnections. It is important to note that this conclusi was largely reached by comparison of anatomical data with previously pu lished maps of the primary somatosensory cortex determined by evoked tentials, such as those of Woolsey (1958), and conclusions are dependent both the detail of the published maps and the accuracy with which the a tomical data can be related to these maps. With respect to the primate, most often referenced maps were the summary maps published by Wool (1958). Thus, comparisons were made with summaries of the physiologi data rather than directly between anatomical and physiological data. Furth the physiological data themselves, while the most accurate at the time, based on surface evoked potential recordings, where the source of the tential is located at a cortical depth (approximately 1 mm) that is roughly h the width of the surface map. This results in relatively large receptive fie whose centers are difficult to locate accurately, and introduces a degree uncertainty into the data from which the summaries were prepared.

Two different interpretations have been put forth to account for differential distribution of callosal projections and their relationship to figurine map of the primary somatosensory cortex. The first view was tl the separate maps of the contralateral body surface in each hemisphere connected along the representations of the dorsal midline of the body throu the corpus callosum so as to form a continuous or joined representation the entire body surface. This view was first developed by Ebner and My (1962, 1965) and was a logical extension of their findings in the visual syst that the representations of the two visual hemifields are strongly interc nected along the representations of the vertical meridian at the border of first and second visual areas. Given this evidence, it was reasonable to g eralize to the principle that discontinuities in the representations of sens surfaces that result from representation in separate hemispheres are join by midline callosal connections. An alternate but not mutually exclusive pothesis sought to explain the lack of callosal projections in portions of matosensory cortex in terms of an exclusivity of projection systems. It w suggested that regions of sensory cortex that specialize in processing sens information and receive dense, specific thalamic projections are relatively of callosal projections. From this interpretation it would be expected areas of sensory cortex associated with highly developed peripheral recep organs would receive sparse commissural projections. While this interpr tion is consistent with the anatomical evidence, it raises a most intrigu question. If the distal forelimbs are not connected across the corpus callos how does information transfer across the midline occur for tactile discri nations learned with the forelimbs, and why is such transfer lost follow sections of the corpus callosum (Myers and Henson, 1960)? This funct could be attributed to the second somatosensory area, but its organization hardly seems precise enough to account for the complexity of the information transferred. I suggest an alternate hypothesis of the organization of the somatosensory callosal projections, which can account for the above observations and interprets callosal connections in terms of specialized cortical areas and the processing sequence of somatosensory information.

CALLOSAL PROJECTIONS IN THE RODENT

As mentioned above, a major limitation in our current understanding of the organization of somatosensory callosal projections has been the relatively indirect way in which anatomical and physiological data have been compared. This problem can be easily overcome in the rat. In this species there are readily identifiable cytoarchitectonic features of the somatosensory cortex with which both physiological and anatomical data can be compared (Welker and Woolsey, 1974). In the rat, primary somatosensory cortex is characterized by a particularly dense fourth layer of granule cells, which in certain regions (the posteromedial barrel subfield, PMBSF, which contains the vibrissae representation) can be related to the body surface on a one-to-one basis on anatomical grounds alone. Furthermore, the entire distribution of the layer IV granule cells can be related to the somatotopic map of the body surface (Welker, 1976). By comparing the distribution of thalamic or callosal projections to the somatosensory cortex with intrinsic cytoarchitectonic features of this cortex, one can more closely relate patterns of projections with somatotopic mapping data than was previously possible. We and others have previously done this in the rat and have found that the thalamic input from the ventrobasal complex is largely coextensive with the granular cortex and its coextensive body surface map or "ratunculus." This provides a relatively objective anatomical criterion for defining primary somatosensory cortex. The callosal projections, on the other hand, largely arise from and terminate in areas of cortex that surround and interdigitate the primary somatosensory cortex, although there is a less dense but appreciable callosal projection to the PMBSF (Olavarra *et al.*, 1984). This is illustrated in Fig. 1. This cortical region giving rise to callosal projections is characterized by a poorly differentiated layer IV, which contains few granule cells. We have referred to it as "agranular" or perhaps more appropriately as "dysgranular" (Akers and Killackey, 1978; Killackey, 1983). Physiological studies in the rat have found this region to be much less responsive to stimulation of the body surface than the primary somatosensory cortex (Welker, 1976; Simons, 1978). In this dysgranular cortical area pyramidal cell bodies that give rise to callosal axons are arranged in vertical arrays located chiefly in layers III and Va, with fewer neurons in layers Vc, upper Va, and layer II, and with still fewer callosal projection neurons in the other layers (Wise and Jones, 1978; Ivy and Killackey, 1981). The terminations of the callosal projections have a similar vertical and laminar distribution. The evidence suggests that callosal projections are largely homotopic, that is, they arise from and terminate in the same cortical areas and laminae. The ipsilateral granular or primary somatosensory cortex provides a second major input to the "dysgranular" cortical area (Akers and Killackey, 1978). Thus, this cortex receives tactile information from the entire body surface. Finally, in addition to projecting across the corpus callosum, this cortical region projects rostrally to the motor cortex and may consequently be regarded as the final processor of somatosensory information. Somatic callosal projections in another rodent species seem to be organized in a similar fashion. In this instance, the pattern of callosal terminations as determined by anterograde degeneration techniques was compared directly with the physiologically determined map of the body surface in the same animal (Gould and Kaas, 1981). These authors report that in the squirrel, like the rat, the cytoarchitectonically distinct "unresponsive zones" in the somatosensory cortex are the major site of callosal terminations. To summarize, there is strong evidence in two rodent species that major concentrations of callosal projections in the somatosensory cortex lie outside of what can be defined as the primary somatosensory cortex in the classical sense. I would hypothesize that it is this cortical area that plays a major role in the transfer and integration of tactile information across the midline.

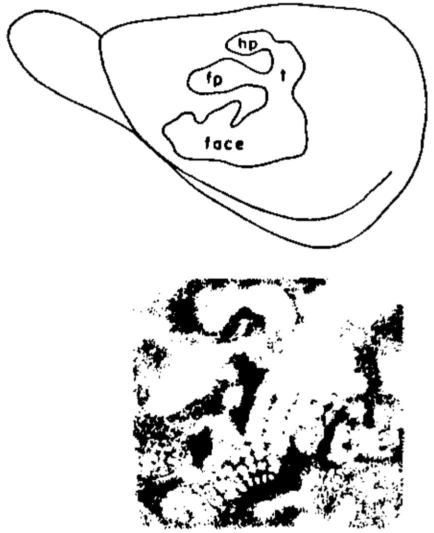

FIGURE 1. The distribution of callosal projections in the rat somatosensory cortex. From Olavarria *et al.* (1984).

CALLOSAL PROJECTIONS IN PRIMATES

The relatively indirect way in which patterns of callosal projections have been compared with body surface maps in primates alone provides a basis for reassessing these relationships. However, the considerable evidence resulting from recent detailed mapping studies, which indicate that what has previously been considered to be the primate somatosensory cortex consists not of one but of several maps of the body surface, provides an even more compelling reason to reassess the relationship between callosal projections and somatic maps in the primate somatosensory cortex (Paul *et al.*, 1972; Merzenich *et al.*, 1978; Kaas *et al.*, 1979). Traditionally, the primary somatosensory cortex has been defined as a single somatotopic map coextensive with four striplike cytoarchitectonic fields (areas 3A, 3B, 1 and 2). However, recent evidence suggests that there are two separate and complete representations of the body surface receptors in areas 3B and 1, a representation of muscle receptors in area 3A, and a representation of deep and cutaneous receptors in area 2. Recently, I, along with several collaborators in the laboratory of Dr. Jon Kaas, have directly related physiological maps to patterns of somatic callosal projections in both owl monkeys and rhesus monkeys (Cusick *et al.*, 1982; Gould *et al.*, 1982; Killackey *et al.*, 1983). We made multiple injections of both anterograde and retrograde tracers into one hemisphere and then extensively mapped the body surface representation in the other hemisphere of the same animal. To further facilitate a comparison of callosal projections and body surface maps, we prepared several hemispheres by a flat mounting procedure, which allows direct and extensive comparisons of callosal projections and physiologically defined areas to be made in single sections.

We found that in both species there were major differences in the densities of callosal projections in the different cytoarchitectonic fields of the postcentral gyrus (Fig. 2). In general, there was a gradient of callosal connections such that they were most dense in area 2, less dense in area 1, and least dense in area 3B. Further, within a given cytoarchitectonic zone there were regional differences in the density of projections. Callosal connections were least dense in the representation of the hand and foot and denser in the regions representing the limbs, trunk, and much of the head. These regional differences were more pronounced in the rhesus monkey than in the owl monkey. However, it should be emphasized that no part of the body representation is truly devoid of callosal connections, although area 3B in the rhesus monkey approaches this condition. On the other hand, there are relatively dense concentrations of callosal projections throughout all parts of the body representation in area 2, particularly in the owl monkey. Thus, it should be pointed out that previous conclusions that distal limb representations are devoid of callosal projections at best applies to area 3B of the rhesus monkey and fails to recognize important differences across species and other cytoarchitectonic fields (areas 1 and 2) that also contain maps of the body surface. Along the same lines, it should also be pointed out that previous studies that emphasized "midline" callosal projections were, in fact, basing this conclusion on the observation that callosal connections in area 2 are denser than in area 1 or area 3B. This increased density of callosal connections is related to the map of the entire body surface and not just the midline. This evidence does not support

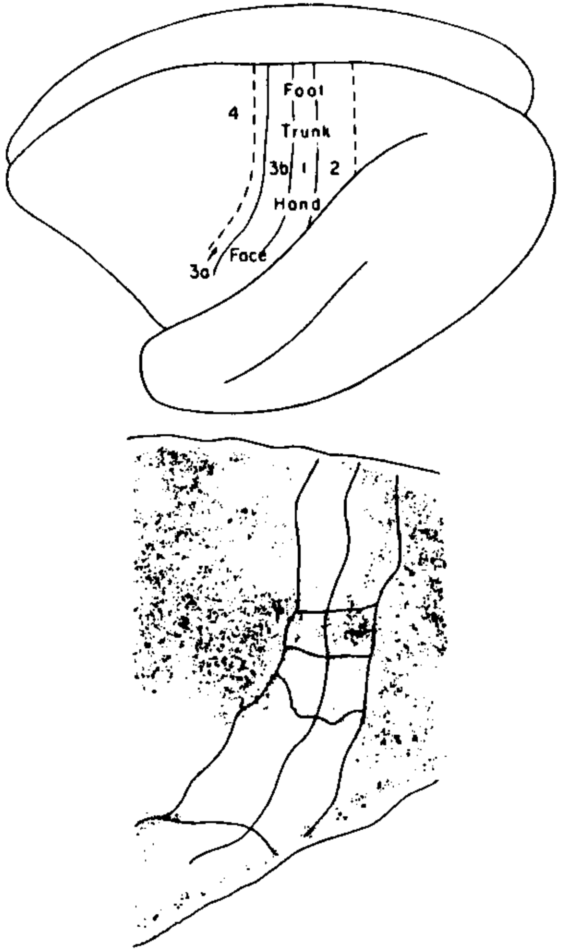

FIGURE 2. The distribution of callosal projections in the owl monkey somatosensory cortex. From Killackey *et al.* (1983).

evious contentions of a particular relation between callosal projections and
e midline representation. Indeed, it is now recognized that callosal projec-
ns are also more widespread in extrastriate visual areas and include more
an the visual midline (Newsome and Allman, 1980; Van Essen *et al.*, 1982).

We also found evidence that callosal projections in the primate somato-
nsory cortex are not as highly homotypic as they appear to be in the rodent.
st, our results suggest that the distribution of callosal terminals is more
stricted than the cells that give rise to callosal axons. Second, we found that
ere are laminar differences between the sites where callosal projection neu-
n cell bodies are located and where they terminate. In some cortical areas
B and 1) the distribution of anterograde label largely overlaps that of the
trogradely labeled neurons in the superficial layers. On the other hand, in
rtions of area 2 and in other parts of the posterior parietal cortex there
e extremely dense callosal terminations in layer IV, which is devoid of
llosal projection neurons. This finding is particularly interesting because
er IV is usually closely associated with thalamic input, but in area 2 regions
alamic input is concentrated in the lower part of layer III (Jones and Burton,
76). These findings may be interpreted as evidence for specializations in
e anatomical organization of callosal projections in the primate that are not
esent in the rodent.

Overall, there are similarities in the patterns of callosal projections in the
imate and rodent that deserve emphasis. In both, a portion of somatosen-
ry cortex (SI in rodent and 3B in primate) is characterized by a dense
alamic input and a stellate cell-rich fourth layer in which callosal projections
e relatively sparse. In both, another portion of the somatosensory cortex
ceives major input from this first region (the unresponsive zone of rodents
d area 2 of primates) and in turn is densely interconnected with the opposite
misphere and ipsilateral motor cortex (Akers and Killackey, 1978; Jones *et*
, 1978). The process of callosal transfer of information seems to take place
specialized cortical areas beyond the cortical areas in which sensory infor-
ation is initially processed. In this view, the cortical processing of somato-
nsory information is a sequential process involving several distinct areas
th unique connectional patterns. In primates this process is further com-
icated both by the multiplicity of representations of the sensory surface and
fferences in areal and laminar patterns of callosal connectivity. A careful
alysis of these complexities may provide insights into the evolution and
nction of the primate brain.

EVELOPMENT OF CALLOSAL PROJECTIONS

The development of callosal projections has been most extensively studied
rodents. The developmental process can be conveniently subdivided into
o phases. In the first phase, which is largely a prenatal event, the corpus
llosum is formed. The second phase takes place postnatally and during its
urse the pattern of callosal projections is established.

The formation of the corpus callosum is preceded by the formation of

an early glial bridge or "sling" (Silver *et al.*, 1982). The first callosal axons grow across the midline on the surface of the glial "sling" to the opposite hemisphere. The sling is formed by a population of glial cells that migrates medially from the ependymal zones of each hemisphere and fuses at the midline on embryonic day 15 in the mouse. Two days later (embryonic day 17) the first callosal axons can be seen to have reached the midline traveling along the surface of the glial substrate. During the next several days there is a massive migration of axons across the midline, which continues into the early postnatal period, during which time the glial sling disappears. The same authors have also demonstrated that the corpus callosum does not form in a strain of mice in which the glial sling is absent or in normal mice in which the glial sling has been severed in the embryo soon after its formation. In rats the corpus callosum can be developmentally altered after the formation of the glial sling (Jensen and Altman, 1982). Irradiation on embryonic days 17–21 results in a progressively less severe reduction in the size of the corpus callosum as measured in the adult. The corpus callosum is lacking in some animals irradiated on embryonic day 17 and slightly reduced in size in animals irradiated on day 21 (Jensen and Altman, 1982). This effect is probably largely due to an elimination of the cells that project callosally, as there is a correlated reduction in the size of the supragranular layers. Curiously, there seems to be no concomitant reduction in the infragranular layers, which also make a major contribution to the corpus callosum in rodents. By the time of birth many callosal fibers have reached the opposite hemisphere. However, they do not immediately invade the opposite cortex. They appear to wait several days in the white matter before invading the cortex (Wise and Jones, 1976). This "waiting period" signals the end of the first period of callosal development.

During the second period the pattern of callosal projection neurons undergoes a series of ontogenetic changes before achieving their adult pattern of distribution at roughly the end of the second postnatal week (Fig. 3). The callosal axons grow into the maturing cortex during the first postnatal week (Wise and Jones, 1976; Killackey and Akers, 1979). Their ingrowth roughly matches the maturational state of their target cortex, in that the lateral to medial gradient of cortical development is matched by a similar gradient in callosal fiber invasion of the cortex. In general, laterally directed fibers reach their target roughly 24 hr before more medially directed ones (Killackey and Akers, 1979). We have also found that the callosal axons invade the cortex in a relatively specific fashion. We detected patterns of advancing anterograde label in only those cortical regions of the young rat that were destined to be callosally connected in the adult. Consequently, we concluded that the establishment of the pattern of afferent callosal projections is specific developmentally as well as in the adult state. This initial specificity of afferent callosal projections is in marked contrast with the initial distribution pattern of the neurons that project across the corpus callosum (Ivy *et al.*, 1979; Ivy and Killackey, 1981). From postnatal day 0 to day 4, callosal projection neurons

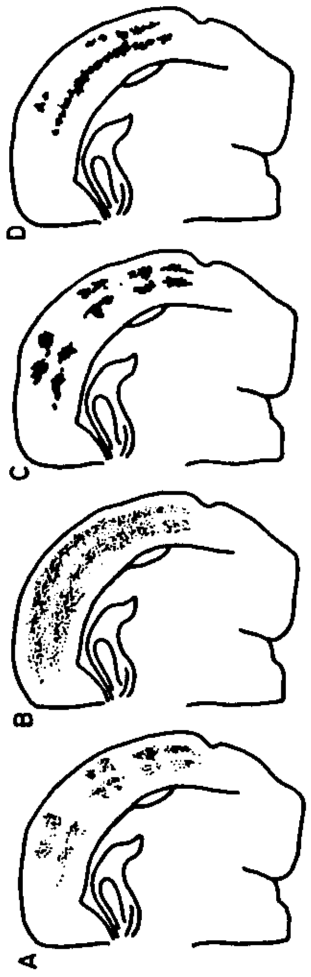

FIGURE 3. (A) The discrete distribution of callosal projection neurons in the somatosensory cortex of the adult rat. (B) The continuous distribution of callosal projection neurons in the somatosensory cortex of the neonatal rat. (C) Results of double-label experiment demonstrating that callosal "drop out" neurons do not die. The dye fast blue was injected at birth and nuclear yellow at 3 weeks of age (both injections were made contralaterally). Stippling indicates the distribution of surviving fast blue-labeled cells, and dots indicate cells that were labeled via the corpus callosum at 3 weeks of age. (D) Results of double-labeling experiment demonstrating that many neurons that initially project across the corpus callosum maintain a projection to motor cortex. The dye fast blue was injected contralaterally at birth and nuclear yellow was injected into the ipsilateral motor cortex at 3 weeks. Stippling indicates the distribution of surviving fast blue-labeled cells, and dots indicate the distribution of cells labeled with both nuclear yellow and fast blue. From Ivy and Killackey (1982).

are distributed in two continuous bands, which extend throughout the cortical subplate. During the next several days there is a progressive labeling from inward out of cells in the cortical plate. During this period gaps in the continuous pattern of labeled cells first appear. By postnatal day 8 the adult pattern of callosal projection neurons is well on the way to being established, but an appreciable winnowing in the distribution of callosal projection neurons continues until postnatal day 15. Thus, the initial pattern of callosal projection neurons differs considerably from both the adult pattern and the initial distribution of callosal afferents. Similar distributional changes in callosal projection neurons during the course of ontogeny have been reported in the visual system of rodents (Rhoades and Dellacroce, 1980) as well as in the somatosensory and visual systems of the cat (Innocenti *et al.*, 1977; Innocenti and Caminiti, 1980). In addition, we have found evidence that several other populations of cortical projection neurons undergo similar ontogenetic changes in their distribution (Ivy and Killackey, 1980; Bates and Killackey, 1980).

The question of what happens to neurons that project transcallosally in the neonate but not the adult has been addressed in several recent studies (Innocenti, 1981; O'Leary *et al.*, 1981; Ivy and Killackey, 1982). All of these studies utilized the fluorescent marker fast blue, which has the property of remaining in cells for several weeks, enabling it to function as a neuronal "fate marker." This label was coupled with a second dye (nuclear yellow) to enable the labeling of projection patterns at a second time. All of the studies determined that the inital callosal projection neurons located in callosal-free regions of the adult do not die. We extended this result by determining that initially at least some callosal projection neurons also project ipsilaterally to the motor cortex. In the adult the projection to the motor cortex is maintained and the neurons lose the contralateral process, or at least the ability to transport label from the opposite hemisphere. The mechanisms underlying the changes in the distribution of callosal projection neurons are unclear. Various mechanisms, including actual elimination of an axonal process or perhaps a change in transport capabilities due to the formation of a sparse terminal arbor, may be involved. Another important question is: What factors guide the adult distribution of callosal projection neurons? It appears as if some factor associated with either the dense thalamic input or the granule cells of layer IV of the primary somatosensory cortex prevents callosal axons from penetrating the cortical plate in this region, consequently preventing the establishment of synaptic relations. Interestingly, the normal areal pattern of callosal connections is established in the cortex of the reeler mouse in spite of the severely disturbed pattern of cortical lamination (Ivy *et al.*, 1982).

In summary, the evidence suggests that the development of the somatosensory callosal projection system differs somewhat from that of the primary somatosensory system. First, the development of the callosal system seems to follow that of the thalamocortical system. Second, the callosal system undergoes distributional changes patterned by the preformed thalamocortical system. In general, the development of the primary somatosensory system can characterized as "hard-wired" and more closely attuned to the periphery omparison to the callosal system. Perhaps the advantage of an initial "soft ing" of callosal circuitry is that it allows the benefits of early experience to in sculpting a cortical network that is better adapted to the animal's internal external environments. The development of callosal projection systems been most extensively studied in the relatively simply organized rodent. emains a major challenge to study and understand the development of osal projections in the more complex primate brain, in which the basic ern of callosal connections has been complexly embellished.

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