in Encyclopedia of Neuroscience Vol. I
George Adelman (Ed)
Birkhäuser: Boston

Corpus Callosum

Michael S. Gazzaniga

A major objective of neurobiology is to understand the development, distribution, and functional capacity of neural structures. A major objective of cognitive neuroscience is to understand the roles various brain structures play in producing cognition. These two interests converge on a single neural system, the corpus callosum. The corpus callosum is the largest neural tract in the mammalian brain, and serves to unite the separate neural activities of the two brain hemispheres. Insight into the functioning of this neural structure, a structure that is known to transmit information pertaining to the production of conscious unity, assists in the understanding of how neural systems produce the sensation of conscious awareness.

Interest in the callosum grew with the discovery that midline surgical section of the structure in the cat prevented the interhemisphere transfer of learning and memory. In the monkey, sectioning the smaller anterior commissure along with the corpus callosum was necessary to abolish interhemisphere transfer. With this surgery, visual discriminations trained to one half-brain, such as learning the difference between a "+" and a "0" for a food reward, were not known to the other half-brain. Normal animals, not surprisingly, showed complete transfer with the commissure intact.

In the 1960s, midline section of a human corpus callosum and anterior commissure was done. Behavioral testing revealed that, as in the monkey, there seemed to be little or no interhemisphere transfer. More recently, it has been determined that sectioning only the callosum prevents interbrain interactions just as in the cat. Mental activities carried out by the right half-brain go on outside the realm of awareness of the left half-brain and vice versa. It appears as if separating the two half-brains produces two separate conscious systems.

Neurobiological analysis of the callosum has revealed important characteristics of the system that give rise to clues to larger issues in cortical organization. First, it has been suggested that during development a glial sling forms across the midline, and through this tissue the callosal fibers cross over from one hemisphere to the other. Supporting this view is the fact that in the small percentage of animals born without the callosum, the glial sling does not appear. Such cases of agenesis usually give rise to grossly pathologic brains. Whether this sling hypothesis is true remains to be proved. Nonetheless, at a functional level patients with callosal agenesis appear to be able to cross-integrate the kinds of perceptual and cognitive information that callosum-sectioned patients cannot. This suggests that with early insult other commissures can take on the normal function of the callosum by keeping each hemisphere aware of the activities of the other.

Second, it has been clearly determined that during development there is an exuberance of callosal fiber growth into cortical regions. As development proceeds, the number of fibers innervating any one region decreases. Fibers originate in all layers of cortex except layer I. Their terminal fields are organized in columns oriented radially to the cortical surface. It has also been shown that a small percentage of the callosal neurons send out an axon to the ipsilateral hemisphere. The factors that determine these fine patterns as well as the number of callosal fibers innervating any given cortical zone remain unspecified.

Third, the callosum is organized topographically such that the more posterior regions interconnect visual and parietal areas of cortex; and more anterior regions, frontal and prefrontal cortex. This specificity is sufficient to cause selective breakdowns in interhemispheric transfer when only part of the callosum is sectioned. Thus, section of the posterior quarter of the callosum breaks down visual transfer between the two half-brains. The same humans, however, might well transfer tactile information. Conversely, a section that spares the splenium or posterior region, but disconnects more anterior regions in the posterior half may break down tactile information but not visual information. This kind of modality-specific action is not discernible with anterior lesions of the callosum. The functional significance of anterior regions remains poorly understood with one well-documented exception.

Case J.W. underwent staged callosal surgery in a medical effort to control his epilepsy. The posterior half of the callosum was sectioned first, and ten weeks later the remaining anterior half was cut. This made possible the neuropsychological analysis of his transfer capabilities through the anterior callosum, since the posterior callosum was severed. To understand J.W.'s special results it is important to realize that he possesses language in the right hemisphere as well as in the left. This is a rare phenomenon, but allows for some interesting tests.

In the first interoperative session, J.W. was not able to name visual stimuli presented in the left visual field, which projects to the right half-brain. The right brain, being mute, could not express its visual experience, and the posterior callosal section prevented the information from being communicated to the left, speech-competent hemisphere. Beginning in the second testing session, J.W., using a special strategy, started to name stimuli flashed to the left visual field. With further testing it became clear that it was not information concerning the actual visual stimulus that was being transferred through the remaining callosal fibers, but a semantic code. When the remaining callosum was sectioned, J.W. lost this ability to cross-integrate. However, in patients without right hemisphere language, such tests are not possible, leaving unspecified the type of information transferred in the majority of cases. Nonetheless, the anterior region appears to contribute high-order information, and in J.W. the information was semantically based.

Fourth, the final distribution field of callosal fibers varies both inter- and intraspecies. The intraspecies findings suggest that each animal has what might be called a cortical fingerprint. Such findings, which provide good evidence that the basic cortical anatomy of each individual is different, suggest a possible physical basis for variations seen in personality, memory capacity, and overall intelligence.

Finally, the anatomical finding that most callosal fibers arise in association cortex offers a possible explanation for its functional role in the production of conscious experience. In every cortical sensory region studied to date, and in every species, the primary sensory cortical areas send out only a few callosal fibers. Area 17 of the cat and monkey, for example, contributes but a few fibers. Areas 18 and 19, however, contribute richly to the callosal system. The same picture emerges from the somatosensory system where the primary hand area sends out few fibers but where somatosensory association cortex sends out massive projections to the opposite hemisphere. This suggests that the callosum is specialized for the management of encoded information of an associative or abstract nature, as opposed to being merely a simple sensory channel sending over a duplicate of the sensory information initially projected to a half-brain.

The callosum will continue to command attention from both neurobiologists and cognitive neuroscientists for many years. Discrete sectioning of no other brain structure produces such a distinct dissociation of function. Understanding the micro-anatomy of this structure should greatly expand the understanding of brain and behavior.

See also Brain Asymmetry, Animal; Brain Asymmetry, Functional Aspects; Cerebral Cortex; Mind, Neurobiology of

Further reading

Gazzaniga MS, LeDoux JE (1978): *The Integrated Mind.* New York: Plenum Press

Pandya DN, Karol EA, Heilbronn D (1971): The topographical distribution of interhemispheric projections in the corpus callosum of the rhesus monkey. *Brain Res* 32:31–43

Schwartz ML, Goldman-Rakic PS (1982): Single cortical neurones have axon collaterals to ipsilateral and contralateral cortex in fetal and adult primates. *Nature* 299:154–155

Sidtis JJ, Volpe BT, Holtzman JD, Wilson DH, Gazzaniga MS (1981): Cognitive interaction after staged callosal section: Evidence for transfer of semantic activation. *Science* 212:344–346

Sperry RW (1961): Cerebral organization and behavior. *Science* 133:1744

Van Essen DC, Newsome WT, Bixby JL (1982): The pattern of interhemispheric connections and its relationships to extrastriate visual areas in the macaque monkey. *J Neurosci* 2:265–283

Cortical Motor Columns

Hiroshi Asanuma

Within the motor area of the cerebral cortex, there are small volumes of tissue which, when electrically stimulated, produce contraction of individual muscles. These volumes extend perpendicularly from the surface to the depth of the cortex in a columnar shape and are called cortical motor columns or cortical efferent zones. The diameter of these columns is about 1 mm in cross section and the threshold current for producing contraction of the target muscle increases rapidly at the edges of the columns. Column edges overlap each other to form an overlapping mozaic. These cortical motor columns or efferent zones exist in the motor area of primates and carnivores and probably in rodents.

The motor area of the cerebral cortex is defined, physiologically, by low threshold electrical currents for eliciting contraction of limb and trunk muscles. Anatomically, this area contains almost no granular cell layer (layer IV) and is characterized by the presence of giant pyramidal cells (Betz cells) in layer V. Therefore, this area is often called gigantopyramidalis and its architectonic limits are easily determined. The pyramidal cells in layer V send fibers directly to motor nuclei of the cranial nerves and to the spinal cord. In primates, some of these fibers synapse directly on motor neurons in the ventral horn. These fibers constitute a major portion of the pyramidal tract, although some of the pyramidal tract fibers (40%) originate in the sensory cortex. The motor effects from the motor cortex are primarily transferred through the pyramidal tract because the section of the pyramidal tract substantially increases the threshold for the motor effect.

The mode of activation of the muscles from the motor cortex has been a controversial issue since the discovery of the motor cortex by Gustav Fritsch and Eduard Hitzig in 1870. At around the same time, Hughlings Jackson, based on his clinical observations, favored the idea of a widespread overlapping of the representations of muscle groups within the motor cortex. He concluded that the motor cortex "thinks" in terms of movements, not muscles. This view was supported by Sherrington and his collaborators. They stimulated the surface of the motor cortex of various primates including gorilla and orangutan and found that it was very difficult to produce contractions of a single muscle. On the other hand, Chang and co-workers were able to produce contraction of individual muscles, although only occasionally, by stimulating the surface of the monkey motor cortex. They concluded that there are foci for contraction of individual muscles and that these foci do not overlap. Thus, the results concerning the mode of motor representation were controversial until recently.

Around 1960, a new technique called "closed chamber method" was introduced for the study of the central nervous system. With this technique, it was possible to insert a microelectrode into the brain of awake animals without damaging the tissue to record activities of individual neurons in the depth of the cortex. This technique was first applied to the somatic sensory cortex and then to the visual cortex. In both cortices, it was found that neurons with similar properties were grouped together along the direction of radial fibers in the gray matter. These are called "cortical sensory columns" and are thought to constitute the basic modules of cortical function. Shortly after these discoveries, the same technique was applied to the motor cortex to stimulate a small volume in the gray matter, a technique called intracortical microstimulation (ICMS). With this technique, it was easy to produce contraction of a single muscle, and the threshold current for eliciting the contraction was less than 1/100th of the current necessary for producing contraction of muscles from the surface of the cortex. Hence, the accuracy of measuring the motor representation was increased substantially. It was found that the low threshold points for producing contraction of a given muscle were located in a small area within the depth of the motor cortex and the area extended along the direction of radial fibers constituting a columnar shape. These small areas were originally called cortical efferent zones to distinguish them from the cortical sensory columns, but were later called cortical motor columns.

Following the discovery of cortical motor columns, various studies were carried out to further characterize the organization of the projection from the small area of the motor cortex to the spinal cord. It turned out that each pyramidal tract neuron