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HEMISPHERIC SPECIALIZATION: EVOLUTION OR REVOLUTION

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Some twenty years ago, I addressed the Montreal Neurological Institute on the topic of temporal lobe function. My data were obtained from experiments performed with monkeys. Wilder Penfield was in the audience and opened the discussion with the question as to whether I believed that the difference between man and the nonhuman primates was quantitative or qualitative. My answer was that I believed the difference to be quantitative but of such an extent that qualitative changes emerged. I used the then new computer technology as an example. Vast increases in the capacity of the memory in central processors had changed computational power not only quantitatively but qualitatively. Penfield argued the case for a more fundamental distinction that distinguished man and we agreed to disagree.

My interest in the topic of this conference—hemispheric specialization—thus fits a larger set of issues, which in my Arthur Lecture to the Museum of Natural History I entitled, *What Makes Man Human?*[1] At stake are such theoretical stances as "evolution," "mind-brain dualism," "the origin of language" (the subject of a fascinating conference held in this Academy last year) as well as some very practical concerns as to the limits of applicability of animal research to our understanding of the human condition, the cure and prevention of disease, and the improvement of life on earth and in space.

How then are we to obtain substantive answers to the question posed by Penfield? I believe my reply of twenty years ago was correct in spirit if not accurate in expression. I did not then, nor would I today, hold that the only difference in brain structure and function between man and other animals is quantitative. Changes in organization, in chemical composition, in developmental sequence, and in time and duration of critical periods are only a few of the differences that might make the important distinction that we recognize as human.

But whether such differences constitute a revolution or evolution is an empirical not a theoretical issue. This was the point of my answer to Penfield and from the contents of the program of this conference I believe that my view is shared by our hosts. For, if and when we fill any knowledge gap in comparative biology with sufficient relevant data—and can, to some considerable extent, specify the mechanisms that lead from one data point to another—we arrive on the side of evolution, eschewing revolution or other form of discontinuity.

The task of this conference is therefore to chart the evidence for neural specialization, especially as it concerns lateralization of function, and to provide in each instance a possible or plausible mechanism that can stand the tests of scientific analysis. To the extent that we are successful, to that extent an evolutionary approach to the evidence is supported—despite the apparent revolutionary consequences that the evolutionary process has wrought.

THE NONHUMAN PRIMATE

In my own experience with monkeys the evidence for hemispheric specialization has until recently been sparse despite a rich yield in the localization of cerebral functions. An early study[2, 3] showed that handedness was about equally divided between left, right, and ambidexterity, and that unilateral resections of parietal cortex contralateral to the preferred hand would shift dominance to the other. After this initial investigation, the matter was dropped except for one experiment on the motor cortex where a similar result was obtained.[4] For the most part one-stage bilaterally symmetrical lesions were made that precluded an analysis of possible lateralization of function. The program of research has been successful in differentiating the functions of the frontal and limbic forebrain from those of the posteriolateral convexity and in delineating separate areas within the convexal "association" cortex that are specifically concerned with one or another sensory modality.[5]

A few years ago, however, James Dewson who had collaborated in defining the locus and extent of the cortical area involved in audition[6] became interested in the possibility that lateralization of function had evolved in the auditory mode early in phylogenetic history. He examined this possibility in a series of studies[7-9] and showed that left-sided resections of the superior temporal gyrus (the homologue of Wernicke's area in man) but not right-sided lesions would impair performance on a difficult auditory delayed match from sample task. Resections of primary auditory cortex had no such effect. Thus, a *primordium of lateralization of function in the modality that gives rise to verbal abilities in man is to be found in nonhuman primates.* A crucial data point had been inserted within a large gap in knowledge.

MECHANISM

The research mentioned earlier has provided important clues regarding the mechanism by which the modality specific "association" (or "intrinsic" as I prefer to call them) areas function. Much, though not all, of this evidence comes from experiments performed on the inferior temporal gyrus, which is associated with visual function.[2, 5, 10, 11] A multitude of studies has shown that radical disconnections of the input to this cortex from brain structures known to receive retinal connections—such as the geniculostriate system and the pulvinar nucleus of the thalamus—fail to have the devastating effect (often they have little or no effect at all) on visual discrimination performance that follows bilateral resections of the inferior temporal gyrus.[10, 12-15] By contrast, lesions of the output that leads to the basal ganglia of the forebrain from the inferotemporal cortex, as mapped electrophysiologically[16] and neuroanatomically,[17] have identical results to those obtained from the cortical resection.[14, 18]

The output from the superior temporal gyrus of monkey (the auditory intrinsic cortex) and its homologue the insulotemporal cortex of cat has also been studied extensively.[19] Here the pathways lead back to the auditory system rather directly and influence function at the collicular and olivocochlear levels.

The evidence, though far from complete as yet, thus indicates that this "association" or *"intrinsic" cortex, though sensory-mode specific, achieves its specificity through central "motor" control over input.* The central motor aspects of cerebral functions may therefore hold the key to understanding how and to what purpose hemispheric specialization has occurred.

Support for a "central motor" theory of the evolution of cerebral specialization derives from two series of studies on man. The first of these observations was made by Doreen Kimura[20] who noted that patients with aphasia are unable to transfer from one nonverbal motor pattern to another, a defect not observed in patients with lesions of the right hemisphere.

The second pertinent observation was made by Bela Kostik in Luria's laboratory. Kostik[21] was using speech shadowing in a dichotic listening task. He found that when simple passive recognition was substituted for active shadowing the usually obtained hemispheric differences disappeared. Only the active motor performance shows the specialization of function.

In summary, the evidence, though as yet sparse, suggests that *hemispheric specialization has come about by way of differentiation of the brain's motor mechanisms.* What then were the motor acts that over the course of evolutionary history, provided selection pressure to result in *Homo sapiens?*

HISTORY

Reynolds[22] has described a likely course of events that could have led to handedness in nonhuman primates. Arboreal existence made it mandatory to use the arms independently of one another—and sometimes even the fingers. The two hemispheres of the brain had therefore to work separately rather than in concert as they do in the control of swimming, walking, postural adjustment and the like. Another student and colleague then suggested that such independence of hemispheric control would prove detrimental to the operation of midline structures such as the tongue; and he then provided a simple demonstration that we are in fact mostly right-tongued as well as right-handed. (The demonstration consists of holding one side of the tongue between one's teeth and attempting to speak, then holding the other side, speaking and comparing the ease and intelligibility of the two expressions.) Finally, I added the speculation[23] that perhaps left hemispheric dominance results from a slight metabolic advantage that derives from the left-sided position of the heart. This speculation has since found anecdotal support from an observation that an unexpected number of cats have midline and right-sided hearts and from the report of our barber that hair almost invariably is thicker and grows more rapidly on the left than on the right; where the situation is reversed, the persons turn out to be left-handed. These observations may not be what we would agree to regard as evidence; still as leads for forming hypotheses and methods for testing them, why not take them as beginnings?

But such speculations do not account for the lateralization of function in the auditory mode discovered by Dewson. Here I suggest, the impetus is derived from the need to localize sound. Have you ever watched deer or dogs move their ears? Usually they move them in concert but occasionally, especially when sound localization is demanded, the ears will move separately much as one might move two antennae in order to locate a source of transmission. Now primates evolve into their arboreal existence where the reflection of sound from foliage makes this "antenna" method useless. Rather, sound becomes localized either by moving the entire head and in most instances the entire body, or through social structure where those closest to the sound source warn those more remote. In either case the sound localization mechanism, the motor mechanism that has become specialized as did that of the hand, now must come under the control of a single operator lest conflicting signals provoke chaos. As in the case of the tongue, hemispheric independence gives way to hemispheric dominance.

CONCLUSION

I have provided from my own area of expertise some new data points that begin to fill the knowledge gap that exists in our understanding of hemispheric function in the brains of nonhuman and human organisms. I have also speculated as to how we can connect these data points by plausible mechanisms and added some speculations on the evolutionary history of the development of cerebral specialization. Most of these speculations are at best hypotheses that can be used to guide further empirical search. Nonetheless, the data points and the hypotheses can provide the beginnings of an understanding in evolutionary terms of the great revolution that has "made man human."

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