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Article abstract—The concept of association cortex emerged from the tradition of an associationist view of human mentation and a localizationist view of cortical organization. Efforts to understand the function of association cortex proceeded under the influence of these philosophic foundations. An alternative to the associationist interpretation is that these parts of cerebral cortex are utilized by different functional systems at different times. This notion is compatible with the distributed systems theory of cortical function and has implications for the neurologist's approach to lesions of cerebral neocortex.

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The legacy of association cortex

Charles J. Duffy

The term "association cortex" refers to those parts of cerebral neocortex not recognized as being specifically motor or sensory in function. Uncertainty about the function of these parts of the brain is reflected in the hesitancy with which the term association cortex is used. Often it is followed by a disclaimer that the name is an inadequate descriptor of the function of these cortical areas. What then is the origin of this term and why does it persist?

The origin of this term is embedded in the history of associationism and cerebral localizationism. Associationism is the doctrine that views mentation as the product of the combination and interaction of mental events. Cerebral localizationism attributes specific functions to specific parts of cerebral neocortex. In the late 19th century, associationism and cerebral localizationism were united, generating theories of the neural basis of cognition. These theories continue to influence the design and interpretation of experiments on association cortex, impeding alternative interpretations.

The rise of associationism. Although seriously ill, John Locke, a retired physician, produced the fourth edition of *An Essay Concerning Human Understanding* in 1700.¹ In a new chapter, "Of the Association of Ideas," he stated the associationist view of mentation²: "Ideas that in themselves are not all of kin, come to be so united in some men's minds, that it is very hard to separate them. . . . This strong combination of ideas, not allied by nature, the mind makes in itself either voluntarily or by chance, . . ."³ This work greatly influenced David Hume who, at the age of 27, furthered the associationist doctrine in his *Treatise of Human Nature* (1738).⁴ Hume proposed that associations are made according to three relationships between ideas: causality, proximity, and similarity. He was the first to provide a psychological

explanation for associations, stimulating the search for a mechanism of association.^{5,6}

Hartley⁷ carried the search for a mechanism of associations into the realm of neurology. As a physician, he was aware of the theory of nervous system functioning advanced by Newton and incorporated this theory into his associationist philosophy. Hartley recognized the importance of this relationship to neurology and philosophy, "[Because] sensations are conveyed to the Mind by the Efficiency of corporeal causes upon the medullary substance, as is acknowledged by all physiologists and physicians, it seems to me, that the powers of generating ideas and raising them by association, must also arise from corporeal causes. . . ."⁷

Associationism gained momentum in the late 19th century, while scientific neurology began to flourish in Europe. Herbert Spencer, associationist philosopher and evolutionary theorist, extended associationism further into the growing discipline of empirically based neurology. For Spencer, the association of ideas was the formation of relations between feelings, "the discharges through fibres that connect nerve-vesicles are the objective correlatives of what we know subjectively as relations between feelings. . . so here we conclude that the association of each relation with its exact counterparts in past experience, answers to the reexcitation of the same connecting fibre or fibres."⁸

A somewhat different avenue was pursued by Alexander Bain in *Mental and Moral Sciences* (1868).¹⁰ He followed Hume's lead in recognizing a group of fundamental relationships between ideas that promote associations, and he related these to the phrenologist's notions of localized functions.⁹ Spencer's emphasis on connecting fibers and Bain's emphasis on cortical locations presaged a contro-

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versy regarding the mechanism of associations.

The rise of localizationism. Franz Joseph Gall¹¹ is usually remembered in connection with phrenology. However, he was also a respected physician and an accomplished neuroanatomist.¹¹ Gall introduced an empirical approach to the localization of cerebral functions and stated "that the different regions of the brain are devoted to different classes of functions."¹² His main antagonist was Pierre Flourens, then secretary of the French Academy of Sciences. Flourens introduced the experimental method into the debate by studying the effects of brain lesions in birds. He concluded that: "A point excited in the nervous system excites all others. . . . The nervous system, therefore forms one unitary system."¹³

The controversy about phrenology forced Gall to leave Vienna. When he arrived in Paris, he met widespread opposition from all levels of the scientific hierarchy.⁹ After Gall's death in 1828, J.B. Bouillard championed the concept of localized cerebral functions. Bouillard's contentious manner alienated his colleagues, but his unrelenting support for localizationism kept the issue alive through the early 19th century.¹⁴ Paul Broca's¹⁵ study of the relations between cortical lesions and aphasia firmly resurrected cerebral localizationism. His conclusions gained support from many workers, notably Dax, Jackson, and Wernicke.

Fritsch and Hitzig¹⁶ stimulated the brains of living animals, confirming the localizationist doctrine with evidence that motor and sensory regions were separate. They saw their findings as confirming Gall's views and contradicting those of Flourens. Their work established the concept of cortical localization as it is currently accepted.

The uniting of associationism and localizationism. John Hughlings Jackson provided strong support for cerebral localization.¹⁷ His theory of the organization of the brain integrated the evolutionary associationism of Spencer with modern neurologic thought. Jackson shared Spencer's hesitancy about strict cortical localization, "[I]t is to be understood that the unit of constitution of the whole nervous system is sensori-motor, and also that the so-called motor provinces, of the middle and highest levels at least, are supposed to be only *chiefly motor* and their sensory provinces only *chiefly sensory*."¹⁸ Jackson introduced the associationist doctrine as the fourth factor in nervous system evolution, the factor of increasing cooperation or "greater association" between nervous centers. He proposed that this trend is manifest by an increasing number of interconnecting pathways for the formation of associations.

Ferrier¹⁹ confirmed the results of Fritsch and Hitzig and supported the suggestion that corticocortical fibers play a role in the formation of associations. He was more of a localizationist than was Jackson, but in a chapter on "The Hemispheres Considered Psychologically," he revealed that he shared

Jackson's associationist views. Ferrier stated that specific motor and sensory areas are richly interconnected by "associating fibers" that facilitate interactions between them.¹⁹

In the United States, William James²⁰ similarly integrated the localizationist and associationist doctrines. Regarding cerebral localizationism, he wrote, "We thus see that the postulate of Meynert and Jackson. . . is on the whole most satisfactorily corroborated by subsequent objective research. The highest centers do probably contain nothing but arrangements for representing impressions and movements, and other arrangements for coupling the activity of these arrangements together."²⁰ In contrast to Jackson and Ferrier, James seemed to follow Bain in attributing the formation of associations to an area in cortex, not to cortical connecting fibers. James' associationist views were clearly expressed: "In the last chapter we already invoked association to account for the effects of use in improving discrimination. In later chapters we shall see abundant proof of the immense part which it plays in other processes, and shall then readily admit that few principles of analysis, in any science, have proved more fertile than this one."²⁰

It would be misleading to leave the impression that as the 19th century came to a close, associationism and localizationism had been harmoniously united into a theory of the cortical mechanisms of mentation. In fact, the cerebral localizationist movement contained within it significant disharmony. Neurologists argued how strictly to apply this doctrine. Were there truly pure motor and sensory areas in cortex or was all cortex sensorimotor?²¹ How strictly were sensory modalities parcellated in cortex? Ferrier¹⁹ had demonstrated separate visual and somatosensory areas, but Luciani²² had demonstrated areas of sensory overlap.

Around the turn of the century, Flechsig²³ suggested an alternative way of integrating associationism and localizationism. He proposed that specific parts of the brain are devoted to the formation of associations between motor and sensory centers and that these "regions have a different structure and are in connection with sensory pathways only by association systems. . . . I have called them association centers and deduction of this notion has led, as is well known, to the most vivid discussions."²³ This proposal was to have a profound impact on subsequent considerations of these matters.

The modern concept of association cortex. Bianchi presented the results of years of experimental work on association cortex in *The Mechanism of the Brain and the Function of the Frontal Lobes* (1922).²⁴ He claimed priority for the concept of association cortex, although he recognized that Flechsig was pursuing the same line. Based on differences in the number of corticocortical fibers, Bianchi suggested the existence of a hierarchy of association cortices. While specifying that the highest cortical

functions are located in the frontal lobes, he maintained that the central mechanism of those functions is association. "From all the foregoing, it seems clear that the whole mental edifice rests upon the law of association."²⁴

Bianchi's experiments and conclusions were criticized by Karl Lashley: "These experiments which he (Bianchi, 1922) reports seem to me far from conclusive. . . there are no controls to show that lesions of equal extent in other parts of the cortex are not attended by an equal deterioration."²⁵ Lashley made selective lesions of cerebral cortex in rats and tested their subsequent behavior. He concluded that no higher cortical function is uniquely dependent on the integrity of a particular cortical area, a concept that he called cortical equipotentiality. "The contribution of the different parts of a specialized area or of the whole cortex, in the case of non-localized functions is qualitatively the same."²⁵

In an effort to resolve this conflict, Jacobsen (1936)²⁶ specifically tested for unique higher functions in frontal cortex. He made discrete frontal lesions in rats and examined their performance in a battery of refined behavioral tasks. Jacobsen suggested that both Bianchi and Lashley were partly correct. He supported Bianchi's assertion that the frontal lobes are central to higher cortical functions. However, he also supported Lashley's assertion that intelligence, language, and logic are not localized functions. Jacobsen reconciled these views by proposing that the functions localized to frontal cortex are the neural mechanisms that contribute to higher mental processes.

This view was accepted in the new edition of Fulton's *Physiology of the Nervous System* (1943).²⁷ The magnitude of the change in attitude is seen in Chow and Hutt (1953)²⁸: "The question whether the term 'association cortex' is both structurally and functionally a meaningful entity awaits further clarification. . . on the one hand, no unique function can be assigned to the association area. On the other hand, there are separate foci within this area that are maximally concerned with a specific function tested. . . ." The associationist doctrine survived these changes but the mechanism of association had again been delocalized. There had been a return to the pre-Flechsig notion that associative functions are primarily the product of activity in corticocortical association fibers.

This trend was furthered by Geschwind's influential work *Disconnexion Syndrome in Animals and Man* (1964).²⁹ He related cortical pathway tracing experiments to studies of cortical pathology, concluding that higher functions rely on corticocortical and corticolimbic fibers. "I have attempted to show that many disturbances of the higher functions of the nervous system, such as the aphasias, apraxias and agnosias may be most fruitfully studied as disturbances produced by anatomical disconnexion of primary receptive and motor areas from one another."²⁹

This concept was supported by studies of cognitive functions after hemispheric disconnection by commissurotomy.³⁰

The notion that higher cortical functions rely on corticocortical connectivity was integrated into a general theory of cortical organization by Mountcastle (1978).³¹ He proposed that corticocortical connections form a network, allowing interactions between distant cortical modules and producing a group of distributed systems in cerebral cortex. Many of the differences between this theory and that espoused by Ferrier are related to the explosive enrichment of knowledge about the modularity and connectivity of cerebral cortex. For our purposes, a particular element is indispensable. With the cortical column as the fundamental module of cortical functioning and the extensive intracortical connectivity demonstrated throughout cerebral cortex, the number of possible combinations of processing units reaches astronomical proportions. "It is obvious that the total number of distributed systems within the brain is much larger than had once been thought, and perhaps by several orders of magnitude. . . . Distributed systems are thus composed of large numbers of modular elements linked together in echeloned parallel and serial arrangements."³¹

Current notions of cortical functioning have harmonized the associationist and localizationist doctrines. It has become clear that to unify these ideas it is unnecessary to follow Flechsig in hypothesizing the existence of association areas in cortex. In fact, the theory of distributed systems suggests that cerebral cortex has no need of special centers for association.

The auxiliary cortex hypothesis. Flechsig's suggestion of the existence of association areas was an associationist interpretation of Luciani's report of cortical areas of multisensory overlap. However, an alternative interpretation is justified—that cortical areas of multisensory overlap are shared by the resident modalities over time. These areas may be partially or wholly used by one modality at one time and by another modality at another time. The final section of this paper is devoted to the presentation of a line of evidence that supports this notion, the auxiliary cortex hypothesis. The evidence is assembled from three disciplines: the electrophysiology of multisensory neurons in association cortex, the neurophysiology of nonmodality specific human responses, and the cognitive psychology of modality-shared components of higher mental processes.

In the early 1950s, pial surface recordings demonstrated that auditory, somatic, and vestibular sensory pathways influence neural activity in overlapping areas of cat association cortex.^{32,33} It seemed unlikely that these responses were relayed from other cortical areas or nonsensory ascending systems, because they persisted after extensive cortical or reticular formation lesions.^{34,35} Quantitative analysis of evoked potentials demonstrated decremental

interactions between modalities, setting the stage for an associationist interpretation of the findings.^{6,37} These decremental interactions were confirmed and localized to four areas in cat cortex.^{38,39}

It seemed that association cortex was a unique entity allowing multisensory interactions. It was not known whether the multisensory responses were from tightly packed, sensory-specific neurons or a population of truly multisensory neurons. Extracellular single neuron analysis and intracellular recordings indicated that each modality evoked a different profile of postsynaptic potentials in multisensory neurons, suggesting that they are influenced by sensory-specific afferents.^{40,41} Subsequent work concentrated on complex interactions between and within neurons in these areas.^{42,43}

Studies of human association cortex have concentrated on time-locked, modality-varying aspects of scalp-recorded neural activity. A late, positive component of sensory evoked potentials, peaking about 300 milliseconds after auditory or visual stimulation⁴⁴ has been attributed to activity in association cortex.⁴⁵ Early work demonstrated that P_{300} is neither modality-specific nor directly related to the subject's level of arousal, but is dependent on the subject's expectations about the stimulus.⁴⁴ Subsequently, investigators viewed P_{300} as a measure of stimulus unpredictability or uncertainty resolution by sensory input.⁴⁶⁻⁴⁸ However, there is also a major effect of stimulus relevance to the ongoing task.⁴⁹ These findings were reconciled by the discovery that distinct psychologic events evoke varieties of the P_{300} wave. Courchesne et al⁵⁰ discriminated a frontal P_{300} related to the unpredictability of the stimulus and a parietal P_{300} related to the relevance of the stimulus. It seems that some cognitive analysis is a prerequisite for P_{300} ,⁵¹ and task difficulty influences it quantitatively.⁵² The P_{300} wave is now viewed as a product of nonmodality specific activity in association cortex,⁴⁵ related to attentional mechanisms,⁵³ and involved in the further processing of sensory information.⁵⁴

Early studies in cognitive psychology suggested that attention acts as a filter, protecting information analysis systems from input overload.⁵⁵ The observation that some nonattended inputs were perceived led to a model which incorporated parallel, as well as serial, mechanisms for perceptual selectivity. These theories required that several partially processed inputs must compete for further processing.⁵⁵ By involving a subject in two simultaneous tasks, one might monitor the allocation of information processing capacity. Treisman and Davies⁵⁶ used auditory and visual, linguistic and nonlinguistic stimuli to differentiate between interference based on modality and interference based on the nature of the stimulus. They found that modality-specific systems operated in parallel at an early stage of processing, while at later, more centrally located stages, modality non-specific systems serially process information of a

similar nature. This view was supported by experiments on the effects of interference between manual and verbal tasks.⁵⁷ Dual-task interference depends on both the extent to which the tasks require the same subsystems and the difficulty of the tasks.⁵⁸ There seem to be "psychological pathways" for processing information.⁵⁹ These pathways function in parallel, each performing some further analysis on a specific type of information, regardless of the modality of origin.

Taken together, studies in animal and human neurophysiology and human cognitive psychology are consistent with the notion that association cortices function as higher processing subsystems shared by modalities over time. The auxiliary cortex hypothesis does not deny the significance of multisensory interactions in these areas. Indeed, if an area of cortex is shared by several sensory systems, it might also be shared by nonsensory systems. These nonsensory systems are intrinsic to a shared region and are dependent on multisensory input. It is tempting to speculate that auxiliary cortex sharing created the potential for the interactions that support nonsensory association systems.

Several implications of the auxiliary cortex hypothesis must be considered in a wider perspective. Since antiquity, physicians have understood biology by drawing analogies to the machines of their era.⁶⁰ The analogy between auxiliary cortex and a time-shared computer is useful, if applied with restraint. Computer time-sharing allows several users to have intermittent access to the processor so that the processor is always in use and the efficiency of the system is optimized. Eighteen percent⁶¹ of human total body oxygen consumption is attributable to the brain; optimizing cortical efficiency might have enormous impact on energy requirements. Extending the analogy, the focusing of processing capacity on one of several available inputs can be viewed as temporarily enabling the connection between that input and an advanced processing capacity. The controller does not turn systems on and off. Rather, it regulates access to continually functioning systems. This view is consistent with optimization of efficiency and distinct mechanisms for controlling the level and focusing of cortical activity.

In computer time-sharing, many users have access lines to the computer's processor. This does not imply the existence of a hierarchy between the users and the computer; the information processing capacity of the system depends equally on both. Similarly, the convergence of corticocortical fibers⁶² does not necessarily imply hierarchic organization in cerebral cortex. Corticocortical convergence allows auxiliary areas to interact with the other components of the processing systems with which they are powerfully, though transiently, linked.

Conclusion. Corticocortical convergence led Bianchi to conclude that specific parts of neocortex

are the site of higher mental processes. This notion is closely related to Flechsig's associationist interpretation of Luciani's description of sensory overlap in cerebral cortex. Flechsig's hypothesis was consistent with contemporary ideas about cerebral cortex and mental processes, ideas that were well established in the natural philosophy of his era. The auxiliary cortex hypothesis is an alternative to the associationist interpretation. These hypotheses are to be considered complementary, not mutually exclusive. Such a view is compatible with the distributed systems theory of cortical organization. It is an essential element of the distributed systems theory that "even a single module may be a member of several (though not many) distributed systems."³¹

These matters have important implications for clinical neurology. Lesions in association cortex result in impaired sensation, attention, and other higher functions. No fundamental deficit has been found to unify symptoms conceptually.^{63,64} These syndromes may best be viewed as manifestations of the variety of cortical distributed systems that are partially dependent on these areas. The neurologist's effort to identify a single common denominator in cortical symptomology may be frustrated if conducted in the context of a traditional, localizationist view of cortical organization.

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