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Holism and Associationism in Neuropsychology: An Anatomical Synthesis

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INTRODUCTION

Neuropsychological theories make implicit assumptions about brain organization and the relationships between structure and function. These include assumptions about the movement and representation of information within brain structures and neural circuits and about the phylogenesis and development of these substrates. Unfortunately, our knowledge of human neuroanatomy remains incomplete and is particularly lacking in detailed information about the patterns of axonal connections—the basic circuits of the brain. As a result, the anatomical assumptions of neuropsychological theories are often represented by no more than diagrams of logical relationships between operationally defined functions, where the relationships are attributed to connections and the functions are assigned to areas.

The last decades have seen remarkable advances in experimental neuroanatomy using nonhuman species. Since the discovery of autoradiographic and peroxidase axonal tracer techniques in the 1970s, the development of information concerning the connective patterns of monkey, cat, and rat brains has proceeded at an explosive rate. It is probably not too ambitious to expect that the details of the connective anatomy for the brains of these model laboratory species will be thoroughly catalogued well before the turn of the next century. Although we still lack the means to directly analyze human brain circuitry at a comparable level of detail, the remarkable similarity in cellular and connective anatomy in mammalian brains makes it possible to apply many of these general findings to the problem of understanding human brain anatomy.

If the 19th century "diagram makers" were guilty of inventing, singling out, or oversimplifying neural connections to fit their psychological models of brain processes; neuropsychological theories at present are

guilty of ignoring the growing body of "diagrams" of empirically identified neural connections. Maps of the direct and indirect pathways through which information can be transmitted within the brain, and of the general patterns these pathways exhibit, can provide rigorous constraints within which to guide development of models of brain function. Perhaps for the first time in the study of the human brain it is possible to ask what sort of neuropsychological theories are suggested by the anatomy rather than the other way around.

Neuroanatomical evidence can provide us with a kind of information about mental processes not accessible through neuropsychological investigations alone. Ultimately the relationships between cognitive functions are a reflection of brain organization. But the human brain is not a computing device originally designed with the performance of these functions in mind. The neural architecture of the human brain was determined by the happenstance accumulation of successful evolutionary accidents over the hundreds of millions of years before the appearance of *Homo sapiens*. Consequently human neural systems carry within their architecture the imprint of past adaptations. Present functions that have inherited these systems are constrained by the logic of these past functions at least as much as by present demands. Even the neural logic of such a uniquely human activity as language is undoubtedly constrained by more ancient and unrelated neurological adaptations that have only recently become recruited to serve this new function (e.g., see Deacon, 1988). The evolutionary constraints within which human brain functions have had to develop are unlikely to be evident except through comparative neuroanatomical investigations.

In the discussion that follows I focus on two very general attributes of the connectional anatomy of cerebral cortical circuits: the reciprocity and the directionality of cortico-cortical connections. The existence of reciprocal connectivity for most cortical connections has been recognized for some time but has not been appreciated for its implications with respect to neuropsychological theories. The "directionality" of these connections is defined with respect to certain asymmetries in laminar organization. This systematic asymmetry of connections provides important clues for comparing directional or hierarchic patterns of cortical organization and may, therefore, help settle one of the oldest disputes in neuropsychology: that between ~~localizationist-connectionist-associationist~~ theories and anti-localizationist-microgenetic-holistic theories. These overly clumsy designations are meant to capture both the historical and theoretical sense of a long and changing debate between two major rival paradigms for modeling the organization of brain processes. The debate is of such general character that at times it has taken on an almost philosophical tone.

Nonetheless, the neurological implications of each of these alternative views are of more than historical interest. They have been translated into the paradigms of clinical practice and experimental design that have guided the treatment of neurological disorders and the investigation of neural processes.

TWO NEUROPSYCHOLOGIES: A BRIEF HISTORICAL REVIEW

Since the early part of the 19th century mainstream neurology and neuropsychology have embraced one of these general approaches at the expense of the other, and as is so often the case with major competing theoretical paradigms in science, the history of the field has seen a series of pendulum swings from associationism to holism, and from localizationism to antilocalizationism. Although the underlying ideas trace back to perennial philosophical debates over associationist theories of mind, the origins of these polar perspectives in neurology can be dated to the phrenological theories of Franz Josef Gall (1791; Gall & Spurzheim, 1810–1818) and the criticisms of this view by Pierre Flourens (1824–1894).

The associationist perspective begins from the underlying premise that each mental event and its corresponding underlying brain process can be analyzed into component mental events and neural processes. The idea that component processes are initially independent elements that may or may not enter into some higher-order process has further led to the view that different component processes may be carried out by different, relatively independent neural structures or circuits (localizationism). Higher-order functions are derived by linking together the functions of these separate structures and by collecting together the results of their activity in specialized centers whose specific functions are to integrate these diverse inputs. This analysis essentially models cognition as a sequential hierarchic process where the simplest component neural analyses must be completed before passing their results on to higher centers to be integrated into more complex analyses. Higher-order mental processes and lower-order processes are described by the same associational logic, but the content of the operations at each level differs. The resultant progression is from simple to complex, from simple component features to complex integrated wholes. The difference between the smallest sensory stimulus element and an abstract concept is treated as a difference in hierarchic complexity. Presumably, following the associationist logic, concepts can be analytically decomposed in a series of steps into relationships among minimal sensory elements. Correspondingly, brain processes in higher

centers are seen as operating on the results of the calculations in the next lower centers in the hierarchy while brain processes at the lowest most primary levels are seen as operating directly on sense data.

In contrast, the holistic (or anti-associationistic) perspective begins from the premise that mental processes are not decomposable into sub-processes that can exist independent of the whole cognition in which they are involved. Holistic theories argue that cognitive processes are not more complex relationships among simpler perceptual or motor processes, but that these fractional units are artificially abstracted glimpses of aspects of an indecomposable whole. Often this has led to the further argument that localized brain structures cannot be treated as though they have functional autonomy. Rather, mental activities are processes of the whole brain and the functions of the parts reflect their relative positions within the entire network. Many holistic theorists have argued that perceptions, intentions, memories and other mental events cannot be localized to specific structures (anti-localizationism). Consequently, the function of the whole should not be deducible from an analysis of the functions of the parts. Where associationism views cognitions as built up piecemeal from smaller more basic units collected from different areas of the brain, holism views cognitions as emerging whole and integrated from the outset, with different aspects of the whole developing in parallel in all regions of the brain. Thus, the holistic model is more akin to a parallel processing model of neural function in which all parts of the system are simultaneously at work on a different aspect of the same integrated process.

The difference between the two approaches is most evident in the interpretation of behavioral changes after focal brain damage. From an associationist-localizationist perspective the loss of brain tissue is expected to be correlated with either the loss of a specific function or the interruption of the interactions between intact **functions—disconnection**. From a holistic-antilocalizationist point of view the total amount of damaged tissue is more critical than its exact location. The greater the loss of brain tissue the more disturbed all cognitive functions become. Because each cognitive act is the product of a process encompassing the whole brain, the coherence of every motor act and every perceptual process is expected to be degraded by the damage.

Associationism and localizationism have had a long theoretical partnership in neuropsychology. Critiques of these theories tend to treat them as interdependent, and the acceptance of one has historically implied acceptance of the other. The same can be said for alternative theories. Anti-associationism and antilocalizationism arguments seem to reoccur and support each other in most holistic theories. However the debates over associationism and localizationism can in part be separated and individual theorists have supported one and not the other in some contexts.

The Development of ~~Localizationist-Connectionist~~ Theories

The modern form of the debate between localizationist and antilocalizationist theorists began to take shape at the end of the 19th century when Paul Broca (1861, 1863, 1865, 1866) demonstrated that localized damage to the left inferior frontal lobe of the brain caused loss of speech. This appeared to vindicate the discrete localization of function proposed by Gall a half century before. The next major step in this direction was taken by Carl Wernicke (1874), who identified a posterior temporal locus of damage in cases with the amnesic form of language disturbance. Wernicke's impact on neuropsychology was not so much determined by his discovery of another form of aphasia as by his synthesis of clinicoanatomical findings with a conception of the nervous system composed of functional centers linked together by connections that relayed information from one center to the next like a telegraph system.

Wernicke's theory, an important advance over the preceding localizationist ideas, grew directly out of the anatomical studies of Theodore Meynert (1866, 1867). Meynert had traced fibers from the auditory nuclei in the brain stem to ultimate termination sites within the superior temporal lobe and had also recognized that the sensory/motor division between postcentral and anterior cortical areas might thus comprise part of a sensory-motor reflex arc. Wernicke saw the implications of emphasizing connectional patterns within the brain for the analysis of brain damage. The result was a synthesis of ideas about the localization of functions with an anatomical interpretation for the means by which separated functions became associated: *connectionism*. His connectionistic interpretation of the aphasias set the stage for most subsequent associationist-localizationist theories. He distinguished motor (Broca's) aphasia from sensory (Wernicke's) aphasia in terms of damage to two corresponding functionally specialized centers. He reasoned that Broca's (motor) aphasia resulted from damage to the motor memory area for speech production and that his own cases of sensory aphasia resulted from damage to the auditory memory area for the sound structure of words (it was at the time still thought that the cortex was not directly involved in sensory reception and motor production, but only in higher level cognitive and mnemonic processes). But Wernicke went beyond this localized centers approach by also suggesting that disconnection of either language area from the "subcortical" centers involved in direct sensory or motor processing would produce distinguishably different sorts of impairments than the two forms of cortical aphasia (termed subcortical sensory or motor aphasia). He also reasoned that disconnection of cortical areas from one another should also produce unique deficits. Disconnecting the sensory from the motor language areas would effectively sever the speech "reflex arc" and should

produce repetition and speech production deficits, disconnecting visual areas and the temporal language area should produce reading deficits, and disconnecting the writing area in the frontal lobe from either the temporal or visual areas should result in writing or copying deficits. This approach provided a wealth of testable predictions, many of which were in some way vindicated by subsequent investigators (e.g., Lichtheim, **1885**; Liepmann, **1912, 1913**; Liepmann & Pappenheim, **1914**).

The clinico-anatomical evidence for connectionism was supplemented by new neuroanatomical discoveries. Fritsch and Hitzig (**1870**) had electrically stimulated the cerebral cortex of animals and demonstrated both localization of function and a direct role for cortex in the production of movement. This was a serious blow to the view that the cerebral cortex was involved only in "higher" cognitive functions, and not directly involved in simple sensory reception or movement, and strongly supported the idea that functions could be localized in cortex. The development of new histological staining methods for neurons and myelin also contributed to the influence of connectionism. A number of neuroanatomists, using different techniques, began to recognize that the cerebral cortex could be subdivided into distinct areas on the basis of cellular organization. Campbell (**1905**) and Brodmann (**1905; 1909**) produced maps of cortical areas based on cellular architecture and Flechsig (**1900; 1901**) and Vogt and Vogt (**1919**) produced corresponding maps based on myelin patterns. The Vogts additionally analyzed the correspondence between their myeloarchitectonic divisions and the electrical excitability of motor areas. These studies led many to hypothesize that the architectural parcellation of cortex corresponded in a one-to-one manner with functional localization.

Out of these studies a new synthesis of neuroanatomical and neuropsychological theories developed. According to the classic model put forward by Campbell in his **1905** monograph, there were three major tiers of neocortical areas within the cortical hierarchy for each sensory/motor modality: primary areas with direct peripheral connections, secondary "belt" areas that were adjacent to and connected with a particular primary area, and association areas that were connected with adjacent belt areas and with each other but had no direct peripheral connections.

In posterior cortical areas, according to this view, each of the highly specialized sensory areas was presumed to be a passive recipient area for registering sensory inputs. The adjacent belt area, which received its input from this receptive area, served a perceptual-psychic function. The "output" of the perceptual-psychic area was a completed perception. The association area for each modality received as its input the completed

perceptual information from the sensory-psychic area. Association areas were thought to be the center for storage of sensory memories, and by virtue of interconnections between different association areas, the substrate for sensory-motor integration and abstract conceptualization.

Motor areas appeared to be organized in a similar hierarchic triad, but with the direction of information flow reversed. Motor responses were assumed to be activated by particular stimulus associations relayed into the frontal lobes from posterior association areas. In prefrontal cortex these sensory associations are associated with motor associations and the intention to act is formulated. This behavioral plan is then relayed to the motor "belt" zone (premotor cortex) where the components of the movement are assembled together; then this region sends its output to primary motor cortex which executes the components of the movement.

These interpretations were further supported by ontogenetic and phylogenetic investigations of cortical parcellation. Flechsig (1901) demonstrated that during early childhood the primary sensory and motor areas reach adult levels of myelin development first among all cortical areas, the belt areas reach adult levels next, and the association areas reach adult levels last. In the prevailing recapitulationist atmosphere of the period, this progression was taken as strong evidence that "primary" areas served the most primitive and basic functions of the cortex—simple sensation and motor output—whereas association areas performed the most highly evolved and complex functions. Elliott-Smith (1910) further bolstered this interpretation by demonstrating that in phylogenetically "lower" brains (e.g., hedgehog) primary areas appeared to occupy most of the cortical surface, whereas in more "advanced" brains (e.g., primates and humans) most of the surface appeared to be occupied by association cortex. In recent research this phylogenetic hierarchy has been almost exactly reversed, with association areas considered to be most ancient and specialized primary sensory or motor areas most recent neocortical areas (Sanides, 1969; 1970). This finding has played an important role in the development of an alternative model (Brown, 1977); see the following discussion.

In sum, the connectionist model maintained its reflex arc pattern of organization through a three tiered cortical hierarchy, with information entering through primary sensory areas and exiting from primary motor cortex. Although the hierarchic schema has been elaborated and the distinctions between receptive and sensory-psychic functions has blurred, the broad outlines of this model can be found essentially intact in most modern texts on neurology or neuropsychology (e.g., Kolb & Whishaw, 1984; Mesulam, 1986).

The Development of Holistic Theories

Not long after Broca had presented his findings on the speech area this view was criticized in a discussion with the British neurologist John Hughlings Jackson (Luria, 1980). Although Jackson's prescient criticism (1869) was largely overshadowed by the success of the connectionist approach at the end of the 19th century, his theories and case studies would eventually play a central role in articulating an alternative (Jackson, 1932; 1958). His critiques were both antiassociationist and antilocalizationist. Although he was one of the early champions of localization of function in opposition to the tradition of Flourens, he nonetheless felt that the atomistic localizationism of Broca and Wernicke was equally in error. He particularly criticized the logic of identifying the symptoms that result from damage to a specific area of the brain with the function of that area. And he noted many cases where even total loss of a presumed functional center typically left some residual functionality. But more importantly, he criticized connectionism for its lack of attention to the "vertical" organization of mental functions.

According to Jackson, mental processes develop through a hierarchy of increasingly complex stages. Mental events develop through progressive levels of differentiation from "lower" spinal and brain stem structures, to simple sensory-motor systems, and finally to the "highest" cortical integration centers in a quasiphylogenetic hierarchy (Jackson, 1884). The earliest stages reflect primitive unarticulated mental content, the intermediate stages reflect superficial input-output relationships, and the highest stages represent the integrated development of conscious thought. Brain damage should alter the pattern of this developmental process, not just eliminate some specific functions. The loss of some function, a "negative sign," is then only part of the effect of the destruction of brain tissue. There should also be alteration of the products of cognition, "positive signs," that reflect the altered development of thoughts and intentions.

For example, with respect to aphasia, Jackson (1868, 1878) argued that the connectionist focus on the component parts of the speech act (e.g. sounds, words, movement of the vocal musculature) was limited to the merest surface aspects, the more easily localized input-output processes of speech. In contrast, he emphasized the dynamic and intentional aspects of language, the fact that speech is not just the stringing together of words, but rather an intentional act of conceptualizing and communicating a whole proposition. Jackson argued that the defining symptom of aphasia was not, strictly speaking, loss of language, but rather a disruption of the ability to propositionalize and comprehend propositional speech. He cited cases of paradoxical enhancement of emotional ejaculatory speech in many aphasic patients. This was, he presumed, an expression of the

release of intact "lower" centers also involved in speech after higher language processes were compromised. True aphasia in Jackson's sense was a disorder of a central symbolizing function, which could not be understood on the model of a sensory-motor reflex arc.

Jackson envisioned a parallel between the hierarchic stages of developing action and the anatomical hierarchy of motor control. Jackson's hierarchical conception of neural organization was in sharp contrast to the simple reflex model proposed by connectionists. Subsequently, however; connectionist models began to emphasize hierarchic organization, whereas holistic models downplayed it. For example, Sherrington (1906) later translated Jackson's hierarchic model into a theory of motor functions based on a hierarchy of reflex arcs upon reflex arcs (a view also expressed in Russian neurology at that time by Pavlov). For Sherrington, reflex reaction and feedback was seen as the basis for the organization of action at higher levels. Jackson had focused instead on reflexes as positive signs of lower systems released from their integration with higher systems. Sherrington's "reflexology" approach to the origins and regulation of movement retained the hierarchic structure of Jackson's conception of motor function but sacrificed its developmental features. In contrast, many later holists were to sacrifice the anatomical-hierarchic features of Jackson's model but retain its integrated developmental view.

A number of articulate critics of localizationist-connectionist theories began to gain a wide audience in the beginning of the 20th century. Experimental studies by Goltz from 1876 to 1884, and insightful critiques by Freud (1891), Marie (1906), Pick (1913, 1931), Head (1926), and others began to expose both the oversimplification of the clinico-anatomical associations and the tenuousness of some of the claims for precise localization of functions (although localizationist claims continued, e.g., Henschen, 1920-1922; Kleist, 1934). The most devastating anti-localizationist critique of the new connectionism came from the work of Karl Lashley (e.g., 1929, 1931b, 1933, 1946, 1951, 1952). Though not a neurologist, his impact on neuropsychology was enormous both as a critic of accepted ideas and as an innovative experimentalist who endeavored to devise ways of testing many prevailing assumptions. Included among his critiques of the associationist-connectionist models of brain function are four central claims: (a) that the architectonic divisions of the cortex do not correspond with either connectional or functional divisions; (b) that association connections within the cortex are not necessary for the development of learned associations between the modalities thereby connected; (c) that specific memories and learned associations are diffusely represented within the cerebral cortex as a whole; and (d) that motor functions could not be controlled by sensory feedback via reflex arcs but instead have to be

understood as unfolding from preset internally originating motor programs (Diamond, 1982).

Lashley's evidence came largely from maze-learning studies with rats. In the face of prevailing connectionist expectations his experiments demonstrated that extensive disruption of cortico-cortical connections (sensory-motor reflex arcs) did not eliminate previously learned sensory-motor associations nor destroy the ability to learn new associations. With respect to specificity of function, he found that the best predictor of functional deficit was the total size of the damaged cortical area rather than the specific location of the damage. Although, in hindsight, it might be argued that his choice of experimental animals and the non-specificity of his experimental paradigms may partially be responsible for the negative results, this research played an important role in pointing out the poverty of prevailing models of cortico-cortical association. Lashley's critique of cortical associationism was further underscored by the discovery that the so-called association areas of the cortex did not depend upon primary projection areas for all their input, as was assumed by the connectionist view, but also received extensive thalamic projections of their own (LeGros, Clark, & Northfield, 1939; Rose & Woolsey, 1949; Walker, 1938).

Henry Head (1926) and Kurt Goldstein (1926, 1927, 1948) best exemplify the subsequent translation of antilocalizationism and holism into the neuropsychology of the first half of this century. Although both recognized the localizability of brain damage in a wide range of syndromes they carefully distinguished between the effects of damage to peripheral input-output channels from the reorganizational effect that the same damage might have on central cognitive processes. For both, following Jackson, disruption of a central regulative feature of thought processes was always evident and proportional to the extent but not specific locale of damage. Head argued that this might be manifested as an impairment of intelligence, or, in aphasic cases, as a general disturbance of symbolic function. Goldstein termed this central reorganizing effect a disturbance or loss of "abstract attitude," characterized by a shift toward more "concrete" and stimulus-bound thought processes and behavior. He viewed this as a generalized disintegration of intellectual processes that always accompanied damage to the cerebral cortex (Goldstein, 1926, 1948).

By the early 1950s the influence of these holistic views began to fade with experimental demonstrations that many of the antilocalizationist anticonnectionist claims could not be supported to the extent suggested by Lashley's early rat experiments. Electrophysiological mapping of cortical areas demonstrated that multiple representations of topographic sensory and motor maps corresponded with architectonic boundaries (e.g., Rose & Woolsey, 1949). Cortical lesion experiments in animals (e.g., Lashley, 1948; Chow & Hutt, 1953; Harlow, 1953; Pribram, 1954, 1958) and focal brain damage cases in humans (e.g., Denny-Brown, 1951; Teuber, 1959;

Luria, 1980) accumulated as evidence that highly specific deficits could result from damage to distinct association areas, and disconnection experiments with animals (Myers & Sperry, 1953; Myers, 1955, 1956; Sperry, Stamm, & Miner, 1956; Sperry, 1958, 1961; Mishkin, 1979) and human commissurotomy patients (Bogen & Vogel, 1962; Gazzaniga, Bogen, & Sperry, 1962; Sperry, 1970; Sperry, Gazzaniga, & Bogen, 1969) demonstrated that long cortical connections did play important roles in the communication of information between cortical areas.

Although antilocalizationism has lost considerable ground since Lashley, the antiassociationism that was behind the holistic theories of Jackson, Goldstein, and others is not necessarily directly challenged by the demonstration of localized functional specialization nor by the importance of cortico-cortical association connections. The historical marriage of anti-associationism and antilocalizationism as a response to the connectionist doctrine was not intrinsic to either critique. One contemporary theory has incorporated both a role for functional specialization and a role for association connections and yet retains a holistic foundation. Jason Brown (1977, 1979) argued for a theory of brain function related to Jackson's (1884) model though Brown's theory incorporates considerably more information about functional localization and is influenced by a somewhat different theory of brain phylogeny (Sanides, 1969, 1970). Brown's theory incorporates the differential function of distinct cortical areas, correlated hierarchic differentiation of structure and function, and a major functional role for associational connections. Despite this rapprochement with localization, the theory is explicitly antiassociationist.

Brown, like Jackson, argued that developing perceptions and actions proceed through a hierarchy of stages that correspond to neural processes in a quasiphylogenetic hierarchy of brain structures. These cognitive events originate in primitive core brain structures then develop within limbic areas, then generalized cortex (association areas), then focal cortex (belt areas), and reach their culmination of development in specialized sensory and motor areas (note that Jackson's model places primary sensory-motor processes midway between "lower" and "higher" brain functions). The specific areas comprising each tier of cortex, from limbic to specialized areas, are assumed to be both structurally and functionally discrete (in contrast to Lashley's notion of mass action and equipotentiality). Brown used the term **microgenesis** to refer to this hierarchic unfolding of perception and action by direct analogy to developmental processes in embryology and evolution. Each momentary conscious event is the culmination of a microgenetic process extending through all levels of the central nervous system. Compared with **associationist-connectionist** models the direction of development is reversed, and primary sense data appear to play a terminal rather than initial role in the development of perceptions, thoughts, and actions.

Although association connections are important to Brown's theory, their functional role is quite different than for connectionist theories. In Brown's view the association connections that link adjacent cortical areas into a hierarchical series do not relay perceptions (or partially analyzed perceptions) from one area to the next. Rather, they provide areas at a subsequent level with information concerning the degree to which processing at the previous level is complete. Similarly, intermodal association connections are thought to coordinate the independent development of processes in different modalities rather than to carry sensory or motor information between them. This explanation of the function of cortical connections would not be incompatible either with the findings of Lashley or with disconnection experiments. In this way Brown retained the emphasis on global unity and parallelism of mental processes that has long characterized the holistic view without denying specific differentiation of local function.

Brown's interpretation of the effects of brain damage follows Jackson in its focus on the way that damage alters the developmental processes of thought. Because the function of each hierarchic level is, in a sense, complete in itself, damage to some structure midway in the hierarchy does not truncate the developmental process. The disruption of function in that structure, because it represents a level in a developmental process, will be manifested as a restructuring of performance in which the normally "buried" or "submerged" content of that level emerges into the foreground (Brown, 1977). The form that this takes has been variously described as "regression" (Brown, 1977), the expression of (pathological) content from a more "preliminary level" (Brown, 1979), "prematurely displayed" moments in a developmental "flow," desynchronization of processes at different levels, and retardation or slowing of a particular stage of a microgenetic process with respect to the others (Brown & Perecman, 1986). The pathological development of sensory processes may be expressed as sensory imagery, hallucination, or dreams (Brown, 1985b). The pathological development of action may be expressed as perseveration, disturbance of intention, or the inability to inhibit the insertion of irrelevant actions or emotional expressions within a behavioral sequence (Brown, 1985a).

ANATOMICAL IMPLICATIONS OF MICROGENETIC AND ASSOCIATIONIST MODELS

The importance of Brown's theory in the present context is that it makes explicit certain anatomical implications of a holistic perspective. By articulating a holistic developmental model of brain processes in anatomical

terms, it allows some interesting comparisons with the alternative associationist models. Both models correlate functional levels with distinct cortical levels. They differ with respect to the developmental sequence and temporal order *chat* hierarchical processes follow, and where (and how) these processes originate. This difference is most clearly evident in the explanation of perceptual processes.

Because associationist models consider sensory input as primary, the first stage of the perceptual hierarchy has its locus in "primary" sensory cortex. The basic building blocks of perception are extracted here from die incoming sense data as discrete disconnected bits of information. These primary sensory features are then conveyed by connections to secondary (belt) areas where they are combined into higher-order features, and finally through a series of such stages complex features are combined to form a complete sensory gestalt that is "recognized" in the highest level association areas (Hubel & Wiesel, 1962; 1965; Gross, Rocha-Miranda, & Bender, 1972). Figure 1.1 diagrams this hierarchic model with respect

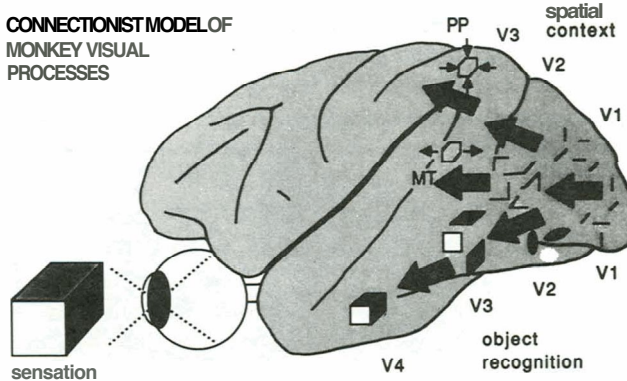


FIGURE 1.1. Diagram of the monkey brain showing a highly schematic summary of a current connectionist interpretation of visual processes (elaborated from Mishkin and Appenzeller, 1987). Sensory stimuli enter the eye and are relayed to the primary visual area (V1) via the lateral geniculate nucleus of the thalamus. In V1 neurons respond to simple oriented line elements and relay these features and color information to the first "belt area" (V2) where color and more complex properties of the perceptual object are analyzed, depicted by shaded areas and convex angle-edges. In the next tier (V3) these previous properties are further assembled into more complete features, depicted as colored sides. In the final step of the ventral process (V4) the final gestalt is assembled, "recognized" and remembered. In a parallel dorsal pathway attributes of spatial context (indicated by arrows and an outline of the object) are analyzed in the posterior parietal area (PP). Association of V3 and V4 processes with information from adjacent Limbic areas (L--hidden on the medial surface of the cortex) supplies affective associations to the perception.

to visual perception. Via connections between association areas and limbic areas these perceptions are also imbued with emotional significance and thereby capable of being paired with reward systems essential for learning and the consolidation of memories (Geschwind, 1965; Mishkin, 1979).

This is a sequential, or serial processing model, in which one stage depends on the completion of a previous stage for its raw materials. It can be compared to the operation of an assembly line, in which a small number of components are assembled into a subassembly at one stage in the sequence, and then **this** subassembly is passed on to a subsequent stage where it will become one of the basic components of a larger more complex subassembly. Only at the last stages does the product actually begin to take shape and become a recognizable whole.

In contrast, the **microgenetic** model of perception proceeds in exactly the reverse order (Brown, 1985b; see Fig. 1.2). A perception begins as an undifferentiated mental image, confounded with the body image and the state of affect, which is not at this stage differentiated from the self as an external object. According to Brown (1977), **this** earliest stage is realized within midbrain and limbic areas. The next stage in the differ-

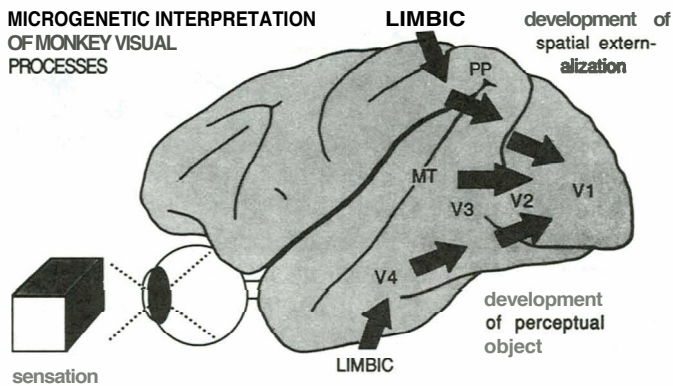


FIGURE 1.2 Diagram of the monkey brain showing a **schematized** model of a microgenetic interpretation of visual processes. Abbreviations are the same as in **figure 1.1**. Note the reversal of direction with respect to the connectionist model. The development of a **perceptual** object or image **begins** in **limbic** structures, and **through** a series of stages, each successive level of **cortex** from V4 and PP to V1 contributes to the differentiation of this **perceptual** object. The **arrows** do not indicate the movement of **perceptual** content from one level to the next **only** the progressive direction of activation and development. To parallel the current evidence for independent analysis of spatial, movement and object-oriented features I have depicted dorsal and **ventral** visual processes as separate **microgenetic** pathways.

entiation of the perceptual object takes place in temporo-parietal association areas where it develops into a preperceptual image differentiated in spatiotemporal modality and externalized from the body image but as yet without explicit form. Finally, in focal and specialized sensory cortex the image becomes differentiated in its precise detail as an external physical object. Some aspect of perception and recognition occurs at all levels, but as the process develops into its final differentiated form, the lower-level processes recede into the unconscious. Only disruptions of the process cause these earlier moments in the development of perceptions to emerge. Two examples of such truncated processes are suggested: mental imagery, in which the final levels of the process are not constrained by an actual external object, and hallucination, where earlier stages of image development may intrude into consciousness as though they were completed perceptual objects (Brown, 1983 & 1985b). Cases of blindsight or deep dyslexia are also demonstrations of emergence of these early phases of perception.

Although the associationist model might be compared to an assembly-line process, the microgenetic view is best compared to the process of sculpting. What begins as a relatively formless mass at an early stage is progressively carved first by broad strokes into the crude shape of the model and then by more delicate and precise strokes as progressively more refined levels of detail become revealed. Only at the last stages do we come to recognize the specific expression of the object. Associationist models of cognition begin with the fine details, whereas the microgenetic model ends with them.

However, with respect to motor processes the distinction between the two theories is not so clear. In Sherrington's (1906) classic reflex theory of motor behavior and the views of subsequent behaviorist theorists, motor behavior could be understood as comprised of sequences of individual reflex movements compounded together into more complex movement patterns in the course of learning. Here again, in assembly line fashion, the process begins from the smallest units of behavior (sensory-motor reflexes) and hierarchically builds more complex wholes (see Fig. 1.3). Complex skilled behaviors were presumed to be built up and organized via multiple levels of sensory feedback triggering multileveled motor outputs.

This view was seriously challenged by Lashley's seminal paper on the problem of serial order in behavior (Lashley, 1951, but see also Lashley, 1931a) demonstrating that the unfolding of a complex skilled movement is too well integrated and happens too quickly for feedback to control the parts independently. Contemporary connectionist theories incorporate some degree of central preprogramming of motor acts into their models of motor function, although it is still a source of debate whether sensory

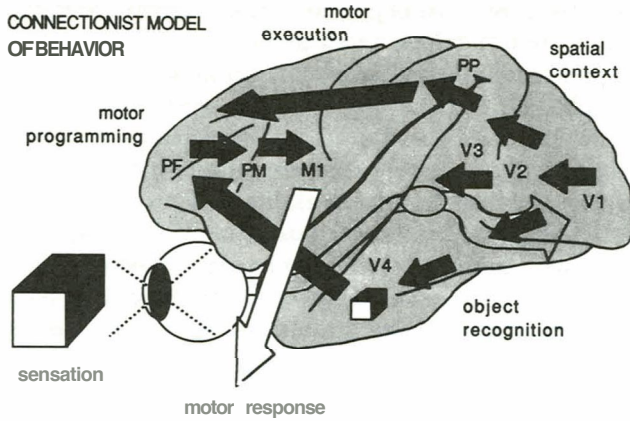


FIGURE 1.3. Diagram of the monkey brain showing a schematized model of a connectionist interpretation of sensory-motor relations in the production of action. Abbreviations for visual areas are the same as for figure 1.1. Notice the continuity of the "forward" progression of the developing action from sensory association areas (V4, IP and PP) to prefrontal association cortex (PF) then to premotor cortex (PM) and finally to primary motor cortex (M1). This requires that the information progresses from specialized to association areas posteriorly and then from association areas to specialized motor cortex anteriorly.

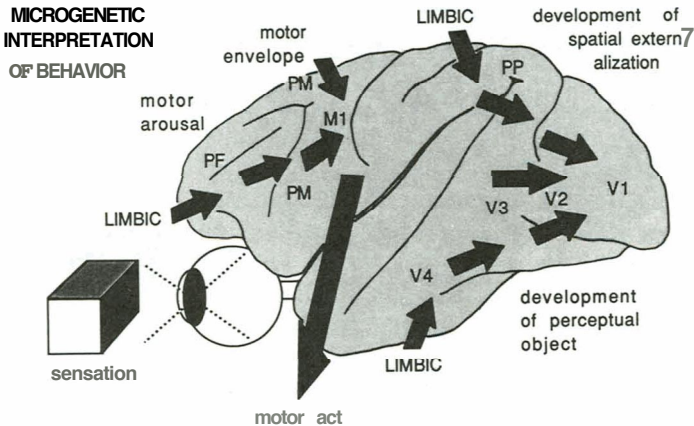


FIGURE 1.4. Diagram of a monkey brain showing a schematized interpretation of the microgenetic view of the development of actions. Abbreviations are the same as for figure 1.3. Notice that both anterior and posterior systems develop in parallel from limbic origins with endstages in primary areas (M1 and V1). Long association connections have been depicted as bidirectional and are not presumed to be directly involved in the development of either the perceptual or motor act except insofar as they coordinate the parallel unfolding of these processes in the production of action.

information acts as a direct stimulus for initiating these programs or simply provides information to them after they have been more centrally initiated (Berman, 1982). In either case connectionist models presume that the long association fibers linking posterior to anterior association areas carry this sensory information forward into the motor system where it is necessary to activate motor activities. For example, the explanation for the role of inferior parietal damage in the production of apraxic disorders has often been described as disconnection between parietal and frontal areas (e.g., Geschwind, 1965). The connectionist hierarchy for the initiation of an action follows a multisynaptic pathway that originates in the lowest level of the sensory hierarchy, projects by stages to sensory association cortex, projects from sensory association cortex to polymodal prefrontal areas, projects from prefrontal areas to premotor cortex, which finally projects to the primary motor area, the lowest level and final common output pathway for behavior (Jones & Powell, 1970).

The microgenetic theory also views primary motor cortex as the final stage in motor processes (Fig. 1.4). However, due to its focus on a central origin for action it differs with regard to the role of sensory information and the sort of information that passes from one level to the next in this hierarchy. As in the development of a perception, this hierarchy begins from activation within the core midbrain followed by activation of anterior limbic cortex, then prefrontal cortex, then premotor cortex, and finally agranular motor cortex. The earliest stage involves the development of an integrated sensory-motor arousal in which the developing sensory object-to-be and action-to-be are not distinguished. This is followed by the differentiation of a "motor envelope" within mesial and prefrontal cortical areas that incorporates all of the constituents of the to-be-realized action and its object into an undifferentiated unity. Subsequent premotor and motor cortex processes comprise the final levels of this differentiation in which discrete motor elements begin to gain independence and serial order emerges.

Although sensory information is seen to play a role in the microgenesis of action it does not play an initiatory role as it does in many associationist theories. A complementary sensory image of the developing motor action develops simultaneously within each sensory modality and the long association connections are assumed to play a predominantly coordinating role synchronizing these parallel processes. Brown (1987) does not, however, replace the sensory activation model with a central role for volitional activation. The sense of volition develops with the unfolding action and is not a separate agency or stimulus for action. He argued that "the phase of initiation actually precedes that of awareness and the feeling of agency."

CONNECTIONAL ANATOMY AND THE HIERARCHICAL ORGANIZATION OF NEOCORTEX

The Classical Hierarchy

The development of the first axon degeneration tracing techniques in the 1940s marks the beginning of the modern field of comparative neuroanatomy. With such techniques it at last became possible to examine the patterns of long connections in the brain. By the beginning of the 1970s considerable evidence from these techniques pointed to the existence of major cortico-cortical connections that correspond to the predictions of the connectionist models of the cortical hierarchy. Jones and Powell (1970), in a classic paper on cortico-cortical connections in the monkey brain, demonstrated that axonal connections linked adjacent areas within a modality exactly as would be necessary for information to pass from primary sensory areas to secondary sensory areas, and from there to tertiary association areas. They also showed that the posterior association areas have long projections that terminate in the prefrontal cortex and that the prefrontal cortex projects onto the premotor area, which finally projects to primary motor cortex.

Newly developed electrophysiological techniques of the 1960s allowing single cell recording further supported this hierarchic model. For example, Hubel and Wiesel (1962) demonstrated that the primary visual area receives strictly retinotopic inputs and that many of its cells are fine tuned to respond to simple visual features. These include precisely oriented line elements in specific positions within the visual field. However; the precision of retinotopic representation decreases and the complexity of the features capable of driving cortical cells increases in extrastriate areas progressively distant from the occipital pole (Hubel & Wiesel, 1965). Most notably, in inferior temporal areas there is little evidence of retinotopy, cells have typically large visual receptive fields, and many cells appear to be preferentially driven by the presence of such specific and complex stimuli as hands and faces (Gross et al., 1972). Lesion experiments done with monkeys verified that removal of striate cortex results in cortical blindness, whereas removal of the inferotemporal visual areas disturbs visual learning processes but does not impair simple discrimination (Mishkin, 1966). Although, it has proven somewhat more difficult to characterize the functional hierarchies of non-visual modalities, distinctions between precise sensory or musculotopic maps in primary areas and more diffuse maps in association areas have been found in all other modalities, as has the more crucial role of association areas in the learning of complex discriminations (Mishkin, 1979; Pandya & Seltzer; 1982a).

Reciprocal Connections

The recent development of high-resolution tracing techniques (utilizing autoradiographic, peroxidase, and fluorescent tracers) has added yet more connectional information. Tigges, Spatz, & Tigges (1973) and Tigges, Tigges, & Perachio (1977) demonstrated the existence of reciprocal (not just unidirectional) projections between areas 17 and 18 in the squirrel monkey brain. They also noted that these reciprocal projections were asymmetric with respect to their laminar origin and termination patterns within each region. Parallel studies in parietal areas (Jones & Wise, 1977; Jones, Coulter, & Hendry, 1978) also demonstrated that connections between areas at different stages in the somatosensory hierarchy were reciprocal and exhibited distinct laminar patterns. Rockland and Pandya (1979), Tigges et al. (1981), and Maunsell and Van Essen (1983) subsequently analyzed connection data in the entire range of monkey visual areas and concluded that the connections of adjacent areas throughout the visual cortical hierarchy are generally reciprocated and exhibit the same systematic laminar pattern of terminations and origins as do areas 17 and 18. Connections originating in more caudal regions terminate most densely within middle cortical layers (iii-c-iv) in their rostral targets whereas caudally directed reciprocal projections terminate most densely in the most superficial and deep cortical layers (i and vi) while avoiding middle layers. Cells from which rostral directed projections originate are predominantly supragranular in origin (e.g. layer iii) while the reciprocal projections arise more numerous from cells in infragranular layers (e.g., layer v). This relationship is diagrammed in Fig. 1.5 (but see next section for terminology). In hierarchic terms, projections directed away from primary visual cortex, up the hierarchy, toward association areas all share one set of laminar characteristics while projections directed toward primary visual cortex, down the hierarchy, all share another.

These reciprocal projections also exhibit systematic differences in the tangential as well as radial aspect of their termination patterns (see Fig. 1.5). Projections from primary to secondary areas (and from secondary to tertiary, etc.) terminate in discrete columnar fields within the middle cortical layers. In contrast, the reciprocal projections terminate in a sheet-like pattern that extends across the territories of many columns in cortical layer i (and to a lesser extent in vi). As a result, in one direction the termination pattern is relatively discrete and focused, whereas in the other it is relatively diffuse.

Subsequent investigations of laminar patterns in nonvisual sensory modalities (Deacon, 1985, 1988; Friedman, 1983; Friedman, Jones, & Burton, 1980; Galaburda & Pandya, 1983; Jones, Coulter, & Hendry, 1978; Pandya & Seltzer, 1982b) and non-primate species (Bullier, Kennedy, & Salinger,

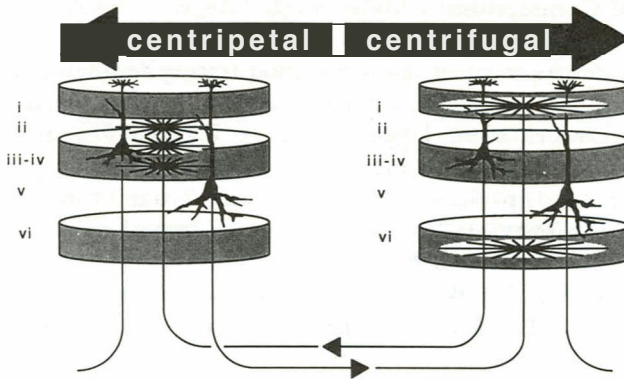


FIGURE 1.5. Simplified diagram of the **connectional and laminar relationships of intracortical reciprocal projections between adjacent cortical areas**. The roman numerals i-vi indicate cortical layers and the major termination layers are depicted as disks. Neurons projecting centrifugally are shown in gray, and neurons projecting centripetally are shown in black. Note that the centrifugal axons fan out in layers i and vi, whereas the centripetal axons terminate more focally in columns in middle layers *iii-iv*.

1984; and Sesma, Casagrande, & Kaas, 1984) have demonstrated this same basic correlation between laminar termination patterns and the direction of projections with respect to cortical hierarchies. This correlation has two significant implications for neuropsychological as well as neurophysiological models of cortical function. First, information is transmitted in both directions not just one; and second, there is a systematic difference in the termination patterns of projections directed either toward, or away from, primary sensory areas. This difference likely correlates with a difference in the kind of information transmitted in either direction.

An explanation of this relationship (for the visual system) that integrated it into the prevailing connectionist model of visual function was proposed by Maunsell and Van Essen (1983; Van Essen & Maunsell, 1983) although the idea **was** implicit in the terminology used by a number of papers (e.g., Tiggles et al., 1977). The basic idea was that projections from primary to secondary and from secondary to tertiary areas (and so on) relayed primary visual information up the visual hierarchy where at each stage it became progressively more complex, analogous to the way **geniculo-cortical** projections relayed visual information from the thalamus (where it is presumed only simple analysis is performed) to the striate cortex (where it is presumed that more complex analysis is performed). These ascending projections were termed forward projections (also *orthograde*), whereas the reciprocal projections were termed

feedback projections (also retrograde). Although there was no functional role specified for these feedback projections in connectionist theories, they were presumed to relay information about the progress of the higher-order analysis of a visual input back to its previous source. These were compared to reciprocating cortico-geniculate projections. Despite the terminological integration into the connectionist model, evidence directly pertaining to the function of either cortico-cortical or cortico-geniculate feedback projections is still lacking.

Centripetal/Centrifugal Organization and Laminar Patterns

To avoid any confusion that might arise when using terminology that distinguishes different anatomical relationships but also connotes different theoretical positions regarding function, let me introduce some descriptive terms that define the patterns and directions of projections solely on the basis of anatomical features. I suggest that we use the terms internal and external termination patterns to distinguish between projections that terminate predominantly in middle cortical layers (internal) and those that terminate predominantly in the most superficial and/or deep layers (external). A majority of both cortico-cortical and thalamo-cortical connections can be distinguished on the basis of these criteria. The remaining forms can be treated as mixed or intermediate.

To describe the direction of a projection within some cortico-cortical gradient let me also introduce two terms that indicate the quasi-hierarchic relationship between primary sensory and motor areas, their association areas, and limbic areas. I have chosen these terms in order to avoid higher/lower analogies, which confuse anatomical designations with a theoretical interpretation of priority of functions in these areas. I propose identifying the direction of a projection with respect to a dichotomy posed between centrally organized systems (e.g. limbic cortex) and systems that more precisely reflect peripheral sensory or motor constraints in their organization (e.g. primary sensory and motor areas). Connections that originate from cells in a more centrally organized structure and terminate in a more peripherally organized structure are termed *centrifugal* projections, while connections that originate from cells in a more peripherally organized structure and project to a more centrally organized structure are termed *centripetal* projections (see Fig. 1.6). Thus, projections from primary visual cortex (area 17) that terminate in belt cortex (area 18) are termed *centripetal* projections and the reciprocal projections from belt cortex to primary cortex are termed *centrifugal*. Because of the close correlation between direction and laminar pattern many ambiguous cases may be resolved when both laminar pattern and direction are considered together.

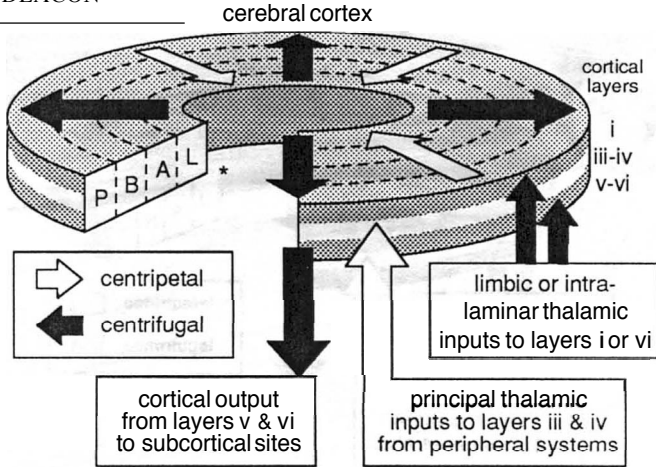


FIGURE 1.6. A highly schematized diagram showing the relationship between centripetal and centrifugal pathways of the cerebral cortex, including some subcomcal connections. Centrifugal projections are shown in black, and centripetal projections are shown in white. The letters P, B, A, and L refer to major tiers in the cortical hierarchy (P = peripherally specialized areas; B = belt areas; A = association areas; L = limbic areas). The cerebral cortex is depicted as a disk to emphasize the central-peripheral gradient of organization. Cortical inputs and outputs are also divided into centripetal (from peripheral to central) and centrifugal (from central to peripheral) projections. Centrifugal subcomcal outputs from layer v project to striatal, brain stem, and spinal targets, and those from layer vi project to thalamic targets. The thalamic afferents to the cortex are subdivided into centrifugal and centripetal projections on the basis of principle layers of termination (centripetal = middle layers, depicted as a white band; versus centrifugal = deep or superficial layer) and with respect to the origin of the thalamic information (peripheral sensory-motor sources; versus central limbic or midbrain sources). This suggests that the centrifugal/centripetal pattern of organization can be generalized beyond cortical circuits.

With these terms it becomes relatively easy to summarize the findings regarding the laminar organization of cortico-cortical projections within the visual, auditory, and somatic modalities. In each system it appears that centripetal projections exhibit the internal termination pattern while centrifugal projections exhibit the external termination pattern. The interpretation of the functional role ascribed to these types of projections by current connectionist theories can be stated as follows: Centripetal, internally terminating projections are characteristic of the "forward" progress of sensory analysis as sensory information passes from areas where simple reception and feature extraction take place to a terminal area where higher-order perceptual recognition takes place. Centrifugal, externally terminating projections on the other hand, are serving a "feedback" function, and do not convey primary information.

Sensory-Motor Association Connections

The long association connections that link posterior cortical areas with prefrontal and motor areas are also reciprocal (Deacon, 1985; Pandya & Yeterian, 1985). Like the reciprocal connections within sensory modalities these association connections are also asymmetric with respect to laminar termination patterns. Projections from posterior association areas that terminate within the prefrontal cortex exhibit a slightly modified internal pattern. They project most heavily upon middle layers in a clearly columnar pattern. Unlike most internal termination patterns in posterior areas some of the sensory-prefrontal projections have an additional dense termination in layer ii. The reciprocal frontal-sensory projections appear to terminate in a fairly typical external pattern with most dense terminations in deep and superficial layers, extending well beyond columnar dimensions in a sheetlike pattern (Deacon, 1985; in press).

Although prefrontal cortex is not in any obvious sense included in the same cortical hierarchy as are any of the posterior association areas, its laminar interrelationships with these areas suggest that we treat sensory projections to prefrontal cortex as centripetal and prefrontal projections to sensory areas as centrifugal connections. This distinction agrees with connectionist expectations about the forward flow of information from sensory to frontal areas. However, it may be at odds with Brown's view that long association connections serve a coordinating role with respect to the parallel elaboration of processes in sensory and frontal areas. Coordination between symmetric frontal and posterior hierarchies might rather have suggested symmetrical termination patterns.

Frontal Lobe Organization and the Failure of Forward/Feedback Theories

Both the forward/feedback terminology and the connectionist explanation of the role of reciprocal cortical connections run into difficulties when connections within the frontal lobes are considered. As in posterior cortical areas nearly all major frontal lobe projections are reciprocal and have distinct laminar organization. On the analogy with the projection patterns discerned in posterior systems we should be able to correlate the direction of forward information flow with internal termination patterns and the reciprocal feedback connections with external termination patterns. According to connectionist (as well as holist) theories of motor function, the forward flow of information is in the direction of motor outflow. In other words, projections from prefrontal, to premotor, to primary motor cortex (centrifugal projections) should exhibit internal termination patterns.

This expectation is the reverse of the association between direction and laminar patterning found in sensory areas because the direction of information flow is reversed in frontal areas.

Tracer studies in the frontal lobes do not support such a reversal of laminar patterning. The earliest reports of laminar findings that might have been interpreted as troublesome for this view come from the work of Kunzle (1978). In an analysis of somatic, premotor, and motor cortex interconnections he noted that premotor projections to the motor cortex exhibit a predominantly superficial termination pattern, whereas projections from motor cortex to premotor and somatic areas are columnar and focused on middle layers. More recently, preliminary reports of monkey studies by Deacon (1984, 1985, in press) with respect to arcuate and prefrontal connections, and by Primrose and Strick (1985) with respect to supplementary motor and premotor connections, indicate that this termination pattern is characteristic of the major types of frontal connections. In general, the association between centripetal projections and internal terminations and centrifugal projections and external terminations is the same in the frontal lobes as in posterior areas. Within the prefrontal cortex this relationship is more complex, with intermediate patterns of termination (Deacon, in press). It is also unclear which prefrontal to prefrontal projections (if any) are to be considered centrifugal and which centripetal.

How do forward/feedback interpretations fare with respect to these connectional findings? According to the connectionist interpretation, where internal patterns are associated with forward and external patterns are associated with feedback processes, there is some difficulty interpreting the frontal projection patterns. There are two possible connectionist interpretations: (a) The forward direction within the frontal lobes is from primary motor to premotor to prefrontal areas (analogous to treating the primary motor area as koniocortex) and the premotor area is merely supplying feedback to motor cortex; or (b) the different laminae within the frontal lobes have exactly reversed their functional roles in frontal as opposed to posterior areas so that external terminations correlate with the forward flow of information and internal terminations correlate with the feedback flow. Both of these interpretations are problematic.

With respect to the first interpretation, considerable neurophysiological and neurological evidence can be cited that contradicts it. For example, motor cortex damage invariably produces paralysis, especially of distal musculature, whereas damage to premotor or prefrontal areas more typically results in praxic disorders where movement capability is intact but organization or initiation of movement may be disturbed (Stuss & Benson, 1986; Wise, 1985). Studies with monkeys have shown that prefrontal, supplementary motor and premotor areas are most active preceding an action, during preparatory or choice phases, rather than synchronized with

the resultant movement (Gemba & Sasaki, 1984a, 1984b; Kurata & Tanji, 1986; Mauritz & Wise, 1986; Ono, Nishino, Fukuda, Sasaki, & Nishijo, 1984). The reverse appears to characterize motor cortex. This preparatory and initiatory role of supplementary motor and premotor areas cannot be described as feedback to the motor cortex, and even if we were to accept such an interpretation it still provides no account of a "forward" process from motor to premotor cortex.

The second interpretation is troubled by more basic considerations. If the forward/feedback interpretation of functional-connectional relationships does not hold for frontal lobe circuits, it must also put in doubt the corresponding functional interpretation of posterior cortical circuits. If we retain the forward/feedback interpretation for posterior cortical areas but not for frontal areas that exhibit the same connectional patterns we must be willing to give up an otherwise well-founded expectation that similar structure implies similar function within the nervous system. The widespread distribution and systematic nature of the correlation of centripetal pathways with internal layers and of centrifugal pathways with external layers strongly suggests that the same sorts of general neural calculations are being performed within these circuits throughout the cerebral cortex. Given the fact that posterior and frontal cortical circuits are organized in the same way, is there a single interpretation of this asymmetric cortical connectional pattern that applies to both sensory and motor processes?

In this regard the symmetry of Brown's microgenetic theory is much more promising (see Fig. 1.7). Both perceptual and motor functions are envisaged as unfolding in parallel along the same hierarchic trajectory, from central processes in primitive midbrain and limbic structures to highly differentiated processes in specialized sensory or motor areas of the cortex. In the anatomical terms introduced here these are centrifugal processes and immediately suggest that centrifugal pathways may be involved. In both perceptual and motor processes the microgenetic theory assumes that what passes from one level to the next in the cortical hierarchy is the product of processes affecting stimuli at that level, not (as might be suggested by associationist motor theories) some unfinished "content" produced at previous stages and passed on to the next stage to be further completed. When one stage of a sensory or motor act is differentiated it is complete *at that* level and although the subsequent levels of differentiation are constrained by this result they don't operate on the content of the previous stages. Motor and sensory processes are only distinguished by the end product of their development, otherwise the "act of perception" and a "motor act" are not differently organized.

In many ways the microgenetic theory treats all forms of mental process as motorlike. It emphasizes the similarity between the kinds of

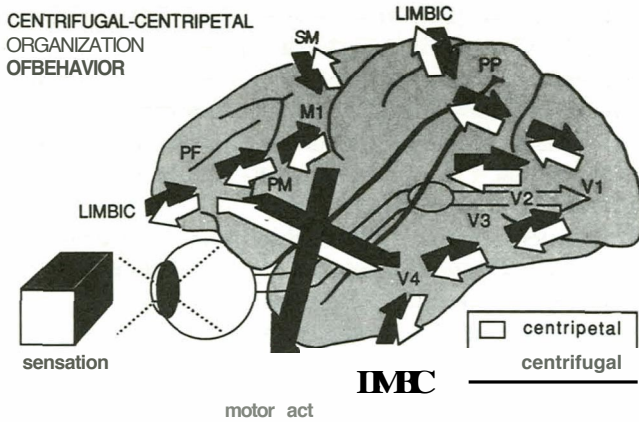


FIGURE 1.7. Diagram of the monkey brain showing a **schematized** model of the centrifugal and centripetal organization of sensory-motor processes. Abbreviations are the same as in figures 1.1-1.4. Centrifugal projection pathways are indicated by dark arrows and centripetal projection pathways are indicated by white arrows. Note the **symmetry** between posterior and anterior "hierarchies" and the **centrifugal/centripetal** relationship between **posterior** and frontal areas, indicated by the projection from **inferotemporal cortex** (V4) and parietal cortex (**IP** and **PP**) to **prefrontal cortex**.

mental "efforts" necessary to focus sensory attention, elaborate a mental image, recall a past conversation, mentally plan a **behavior** or control the execution of a difficult skilled behavior. And it seems to provide models for explaining a number of phenomena that are most difficult to explain in associationist terms. But **like** the alternative connectionist-associationist theories, microgenesis seems to systematically ignore at least half the cortico-cortical connections of the cerebral cortex (centripetal connections), and as a result provides insufficient explanations for a wide range of phenomena explained well by the connectionist alternative.

Despite his focus on centrifugal processes, Brown (1977) did in places describe a role for peripheral input at each level in the perceptual process. Brown's theory denies two assumptions of the associationist approach: (a) the idea that sense data are the content of perceptual experience and (b) the idea that information constituting one stage of the perceptual process is transmitted to the succeeding stages (in adjacent cortical areas) as a perception is analyzed or developed. Nonetheless, for his model to be complete and explicit it must still incorporate some account of the transmission of neural information from region to region and specify the form this information **takes**, if different than described by associationist theories. This must include the means by which information from the external objects of perception influences the developing mental image and some means for coordinating or synchronizing the activities of the

separate levels or stages of microgenetic processes. Both sorts of information must converge at every stage. With respect to the first requirement Brown (1977) said that "the perception-to-be, is shaped or determined by sensory information in the direction of the external object" and that there is a "reiteration of sensory control [at each stage to] maintain cognitive development in the direction of the object" (p. 95), although his theory is not explicit about the neural substrates through which this sensory information is conveyed to each area. With respect to the second requirement Brown (1979) referred to the role of association connections between cortical areas in terms of the coordination and synchronization of microgenetic processes in parallel cortical hierarchies. The implication is apparently that these intracortical connections play some sort of activational or inhibitory role with respect to their target areas but do not necessarily convey any perceptual or conceptual content from one area to another.

Although anti-associationist theories have historically been associated with holistic interpretations of neuroanatomical-neuropsychological relationships, Brown's approach demonstrates that the two aspects are separable, and that anti-associationism and holism may not be incompatible with regional specificity of function. The lack of explicit anatomical hypotheses regarding information transmission in microgenetic theory may not so much be a necessary feature as it is an attempt to focus attention away from associational relationships (between cortical areas) and focus instead on developmental relationships in cognition (within cortical areas and between cortical and subcortical systems).

THE ANATOMICAL BASIS FOR A SYNTHETIC VIEW

Two Halves Don't Necessarily Make a Whole

The systematic laminar termination patterns of cerebral cortical connections have provided reasons to doubt the consistency and completeness of either of these seemingly polar views of cognitive processes. Can these data also provide guidance for either bringing these two views into harmony with one another or alternatively replacing both with a more general synthesis that overcomes the major weaknesses of each?

In order to begin sorting out the relationship between the connective anatomy and these two neuropsychological paradigms one must first recognize that each view effectively ignores a particular half of the neural pathways linking cerebral cortical areas together. In sensory cortical areas the associationist models focus only on centripetally directed information processes while in prefrontal and motor areas they focus only on

centrifugally directed information processes. The microgenetic approach does not suffer from the same anterior–posterior inconsistency but nonetheless focuses exclusively on centrifugal information processes in all cortical areas. Can the two approaches be integrated such that each will explain distinctly different processes within each sensory modality?

Because neither view has a place for frontal centripetal processes, a combined theory would still be somewhat incomplete. However to a certain extent the complementarity of the two approaches does allow centrifugal and centripetal processes to be treated independently, at least with regard to sensory processes. For example, within sensory areas we can apply connectionist interpretations to centripetal processes and microgenetic interpretations to centrifugal processes. Beyond a mere juxtaposition of the two theories, this comparison suggests a number of structure–function relationships not implicit in either theory alone.

Centripetal projections terminate in precise cortical columns, interdigitated with columns receiving colossal terminations (callosal projections have a mixed termination pattern; e.g., see Goldman & Nauta, 1977). Consequently, they conserve the point-by-point, column-by-column *topography* of their area of origin and are well suited to convey complex spatially organized information from area to area. In contrast, centrifugal projections terminate in broad sheets that extend across the territories of many columns and probably do not conserve the topographic integrity of their place of origin. However, the more distributed termination pattern of a centrifugal projection system is likely capable of conveying the *temporal patterning* of the internally correlated neural activity of one area and conveying it in synchrony to a large sector of a recipient cortical area. In summary, there is a promising correspondence between the characteristics of centripetal pathways and the requirements of connectionist theory and between the characteristics of centrifugal pathways and the requirements of microgenetic theory. Centripetal pathways may preserve the topographic organization of peripherally originating information as it is conveyed from projection areas to association and limbic areas, whereas centrifugal pathways may preserve the temporal patterning and synchrony of distributed cortical activity as it is conveyed from limbic and association areas to specialized areas. In more general terms the centrifugal projections might be described as enhancing or inhibiting activity patterns that are intrinsic to the areas in which they terminate, whereas centripetal projections might be described as introducing extrinsic patterns of activity that selectively enhance or inhibit intrinsic tendencies.

With this dichotomy in mind a number of perceptual functions can be associated with each major pathway. For example, shifting and focusing sensory attention, the production of states of sensory anticipation and expectation, and the elicitation of sensory "imagery" or memories can be

associated with progression along the centrifugal pathway, whereas the extraction of perceptual detail and abstraction of higher-order pattern can be associated with a progression along the centripetal pathway. Disorders of perception can likewise be associated with disturbances preferentially affecting a particular pathway.

Syndromes that result from damage to peripherally specialized sensory cortical areas (e.g. cortical blindness) should significantly impair perceptual abilities but, according to this view, should not impair "mental imagery" in that modality to the same degree. However, the retained mental imagery should lack a certain level of differentiation and detail—a feature that would not be predicted from traditional connectionist approaches. Recognition of sensory objects in the disturbed modality should persist only insofar as peripheral input is independently supplied via alternative thalamocortical routes and should also be limited to global stimulus attributes (e.g. as in blindsight). More intriguing is the possibility that the reduction of centripetal information might release typical constraints on centrifugal processes and result in a transient enhancement of relatively unregulated mental imagery in the form of hallucinations.

Syndromes that result from damage to cortical areas more centrally located (e.g., posterior parietal, inferior temporal, and prefrontal cortex) should exhibit aspects of attentional and/or volitional disturbance with intact perceptual and motor functions. These disturbances indicate the effects of depriving primary and secondary areas of limbically originating centrifugal information. A typical visual system example is Balint's syndrome, (Balint, 1909; Benton, 1979) likely due to damage to posterior parietal areas, where there is a particular difficulty shifting attention and gaze to different aspects of the visual stimulus and difficulty interpreting complex spatial relationships. Conversely, inappropriate activation of centrifugal visual circuits, such as originating from limbic disorders such as schizophrenia or epilepsy, tend to produce hallucination (Brown, 1985b).

A number of optical illusions exemplify the interplay between these two systems insofar as these illusions are based upon cases where global gestalt information and attentional expectations interfere with the "literal" perception of the stimulus. Typical examples include gestalt inversions of figure/background or three dimensionality (e.g. the "Necker Cube"), inappropriate judgments of linearity or length because of the proximity of other elements that differentially direct visual attention, and dynamic optical illusions such as the apparent expansion or contraction of visual objects following a period of staring at a rotating spiral. In dynamic optical illusions we see that the entire perceptual experience can be distorted in a dramatic and systematic way by attentional adaptation. The duration (up to 10 seconds) and progressive decrementing of dynamic

optical illusions may provide some estimate of the temporal lability of centrifugal process effects.

The connectional symmetries between frontal and posterior cortical systems suggest that there may be similarities between the function of posterior centrifugal pathways and motor processes. One of the major biases that associationist theories have introduced is the assumption that sensory input and motor output are somehow opposite functions—that the brain's input and output systems are separated and linked by association areas and connections. The parallel organization of circuits in sensory and motor areas requires us to reevaluate this simple dichotomy between input and output areas.

Diamond (Diamond & Hall, 1969, Diamond, 1979, 1982) challenged this sensory-motor dichotomy on other grounds. The somatic sensory areas and motor areas of the monkey and human brain are organized so their most peripherally specialized areas (MI and SI) lie adjacent to each other forming parallel topographic body maps. Both areas contribute major projections to the pyramidal tracts, both can independently support motor functions (Sasaki & Gemba, 1982), and both receive subcortical afferents conveying somatosensory information (Jones, 1986). In a number of presumably primitive mammals (including opossum and hedgehog) there even appears extensive overlap in these areas (Diamond, 1979). For these (and other) reasons Diamond suggested that the somatosensory and motor areas be treated as a single somatic projection system.

These criticisms of the dichotomy between input and output areas of the cortex can be applied to all modalities. All cortical areas have subcortical outputs that arise from layers v and vi in sensory as well as motor cortex. These projections terminate in the thalamus, basal ganglia, and brainstem and spinal cord sites (see Fig. 1.6). The subcortical outputs from frontal and sensory areas have different output functions because they are differentiated by axon termination sites (Kuypers & Catsman-Berrepoets, 1984). For example, brainstem efferents from visual areas predominantly terminate in the superior colliculi, brainstem efferents from auditory areas predominantly terminate in the inferior colliculi, and the corresponding efferents from somatic and motor areas predominantly terminate within the spinal cord. In this sense the skeletal muscle projection cells are merely a special subclass of cortical efferent cells. As the skeletal muscle projections constitute the final common pathway of the frontal centrifugal projection system, so too, the brainstem projections of the sensory areas are the final common pathways of the posterior centrifugal projection systems.

In posterior systems the centrifugal pathways have been described as providing activational information from more centrally organized areas to more peripherally organized areas. The same logic can be applied to

frontal areas. Both theories describe the development of motor output in terms of a series of stages along the centrifugal pathway from limbic and prefrontal to premotor to motor cortex. The connectionist view suggests that motor programs are somehow resident in prefrontal and premotor areas and executed by the motor cortex. If this were the case we should expect that complex spatially organized information must be passed centrifugally. But the centrifugal pathways are not organized in a way that would suggest that they preserve spatial information. Like their posterior counterparts they exhibit broad termination patterns rather than discrete columns (Deacon, in prep.). Brown's view that subsequent motor levels receive only activational information from previous levels is more consistent with the relatively more diffuse organization of centrifugal pathways.

The activational role of the motor centrifugal pathways is clearly evident in the progression of disorders associated with damage to progressively more centrifugal areas. At the centripetal end, damage to anterior limbic areas results in various degrees of akinesia and suppression of spontaneous behavior (Damasio & Van Hoesen, 1983). Damage to the supplementary motor area also results in reduced spontaneous behavior, difficulty in the initiation of movements, and a loss of volitional control of movement (Stuss & Benson, 1986). The "alien hand sign" has been attributed to supplementary motor damage (Goldberg, 1985; Goldberg, Mayer, & Togliola, 1981). In this syndrome volitional control of the hand appears lost but movement ability remains. The hand often exhibits spontaneous motor patterns (e.g., grasping objects, spontaneously manipulating touched objects, such as unbuttoning a button; moving the arm and hand in the direction of tactile stimuli), and the patient may attribute this to an alien volition somehow resident in the hand itself. In a sense, it is a pathologic embodiment of the classic reflexology model of motor behavior. Damage to premotor areas is typically associated with limb-kinetic apraxia, some slight paralysis and the disorganization of complex skilled movements, though not with the same sense of a loss in volition that accompanies more central damage (Wise, 1985). Proximal musculature seems more affected in both supplementary motor and premotor damage and some degree of spasticity is also evident (Luria, 1980). Finally, damage to motor cortex is invariably associated with some degree of paralysis, particularly of distal musculature, but without signs of spasticity in spared movement abilities (Denny-Brown, 1951; Luria, 1980; Stuss & Benson, 1986). In summary, the centrifugal development proceeds from proximal to distal, whole behavior activation to individual movement execution, and from volitionally regulated to automatically released movement patterns. The role of prefrontal cortex in this hierarchy, via its additional centrifugal projections to supplementary motor and premotor

areas is more complex and will be addressed after a brief discussion of frontal centripetal pathways.

Drawing on the analogy of sensory centripetal pathways, we are now in a position to provide a more general interpretation of frontal centripetal processes. The centripetal projections within the frontal areas are organized so as to preserve topographic detail from area to area. As in posterior areas, they likely carry complex patterned information from more peripheral sources. Two major classes of peripheral inputs enter the motor cortex, those relayed from the cerebellum and those relayed from somatosensory sources. By analogy to posterior systems, this peripheral information is conveyed via centripetal pathways to premotor, supplementary motor, prefrontal and eventually limbic areas. In this sense, following Luria (1980), the frontal complex can be described as a "motor analyzer." Information from discrete musculotopic motor programs and somatic tactile input (e.g., kinesthetic sense) is "analyzed" by the centrifugally developing action as sensory information is analyzed by the developing attentional activation of posterior systems. The centrifugal projections likely provide information that plays a selectional role in motor behavior, differentiating and biasing intrinsic activity patterns initiated by more central processes of the prefrontal and limbic cortex.

Although skilled motor behavior is centrally organized and activated, its final expression is "filtered" and biased by peripheral sensory information. In addition, complex movement sequences require both sustained activation and millisecond-by-millisecond gating of successive motor cortex activation patterns. Sensory feedback is too slow to account for this sequencing (Lashley, 1951). However, centripetal motor projections also provide premotor and supplementary cortex with topographically precise information about the just previously-activated motor event (including automatic cerebellar programs). This information may play a crucial role in "gating" the successive steps in a rapidly unfolding movement sequence. This interpretation of a dynamic interplay between the two pathways is explored more fully in the final section.

A parallel explanation also applies to the role of posterior projections to frontal areas. These inputs also arrive via centripetal projections, and so might be assumed to contribute to the centripetally developing analysis in frontal areas rather than the centrifugally developing motor activation. This interpretation differs slightly from that provided by either theory. Traditional connectionism would attribute more of an activational role to these projections, although Brown argues that they serve only a coordinating role. Only postcentral and parietal cortex posterior-frontal projections terminate in motor cortex, premotor cortex (Jones, 1986) and supplementary motor cortex (Jurgens, 1984), whereas projections from all

modalities terminate in arcuate (Deacon, 1984) and prefrontal areas (Pandya & Yeterian, 1985) of monkeys. This multimodal aspect of the frontal hierarchy is not entirely unique. A number of posterior regions have multimodal input, specifically those at the far centripetal extreme of the hierarchy including inferior parietal cortex and superior temporal sulcus cortex in the monkey (Pandya & Yeterian, 1985). In general, the centrifugal development proceeds from multimodal to unimodal areas. These posterior multimodal areas send centripetal projections to prefrontal areas as do supplementary cortex and some premotor areas, and these are reciprocated. These findings suggest that the prefrontal cortex represents a stage prior to the centrifugal differentiation of muscular from perceptual components of action. All the centripetal inputs to prefrontal cortex likely play a role in the differentiation of the intention to act, and the centrifugal efferents from prefrontal cortex to all modalities influence the centrifugal development within each. The differentiation of action must be thought of as beginning with the coordinated and undifferentiated activation of all modalities. The developing intentional "motor" response is more than just a muscular output. It is comprised of the coordinated parallel activation of all centrifugal pathways. Here we have returned full circle to describe the motorlike function of sensory areas.

Not all mental processes developing through the cortical hierarchies are microgenetic in their time scale. There is reason to suspect that many aspects of learning may be described in the same terms as momentary actions or perceptions. The process of acquiring a skilled movement pattern is in many ways analogous to learning to distinguish between different complex sensory stimuli. The earliest stages of both processes lack peripheral specificity and both require considerable volitional control and mental exertion. The early stages of a developing skill are characterized by only crude similarity of the motor patterns from trial to trial with considerable variety in the details of movement, and the early stages of a developing sensory discrimination are characterized by distractibility and attention to irrelevant sensory details. As each is learned, they become progressively unconscious, automatic, and constrained in the variance between different performances. This is clearly a centrifugal progression, not on a microgenetic time scale, but on a protracted time scale that may be measured in hours, days, or years. The fact that the final "overlearned" discrimination or behavior can become automatic and nearly unconscious suggests that at this stage centrifugal processes play a minimal role. Thus, the nearly automatic reflexlike response or sensory discrimination might well approach at its extreme limit the classic connectionist model.

The Counter-Current Analogy

By using the logic of connectionist theory to describe processes proceeding along centripetal pathways, and using the logic of microgenetic theory to describe the processes proceeding along centrifugal pathways a more comprehensive view of cortical processes has emerged. The constraint of having to consistently apply one model to a single type of projection pattern wherever it occurs has also helped to uncover hidden problems in both theories. For example, where connectionist interpretations appropriately describe the function of long sensory–frontal projections they probably do not appropriately describe the frontal centrifugal motor hierarchy. Where microgenetic interpretations appropriately describe the frontal centrifugal motor hierarchy they probably do not appropriately describe the function of long sensory–frontal projections. By the same logic it has been possible to describe the functional organization of two major neglected pathways: frontal centripetal projections and prefrontal–sensory projections. Finally, this synthesis has provided a more unified view of all cortical processes, by emphasizing the motor-like functions of sensory areas and sensory-like functions of motor areas. It is fair to say, then, that the synthesis of these two views, according to this anatomical constraint, has provided a result that is far more than just the sum of the two theories.

Despite these contributions there is still something missing in this synthesis. By treating the two processes in isolation there is no real theoretical integration. The result may be an enhancement of descriptive power over either theory alone, but it does not address the underlying problem of explaining why the brain is laid out this way in the first place. More importantly, it does not provide an explanation for the cognitive process itself—the mechanism responsible for the transformation of information from one stage to the next and from one area to another.

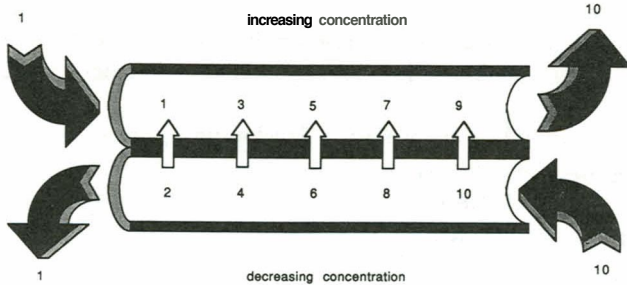
I think that the centripetal/centrifugal geometry itself holds the key to this question. The precisely opposed juxtaposition of these two pathways in all cortical systems indicates that the two corresponding developmental processes are also in some way interdependent. Every cortical area intermediate between primary and limbic regions receives and sends both centrifugal and centripetal projections, and signals from both pathways likely converge upon the same pyramidal cells within each cortical column. Presumably both pathways are often (if not usually) simultaneously active, and so their interaction within an area undoubtedly alters what is relayed to efferent areas in both directions. In other words, the secret of the transformation of the signal from one level of processing to the next may lie in this interaction. Peripheral information may be necessary to differentiate a developing perceptual object or motor envelope (as it develops

centrifugally), and the activation of attentional constraints and preperceptual images may be necessary to selectively abstract certain local features and global spatial relationships from peripheral information (developing centripetally).

The means by which information developing in one direction can alter the development of information in the other direction is not immediately obvious. However; there are other systems that have a similar organization and may provide the essential clues to an answer: The first general feature of this connectional relationship is the precise complementarity of oppositely directed pathways. The second is the gradient that these pathways span, each in opposite directions. This gradient is defined by a number of polar attributes: from local independence of spatially segregated features to global integration of spatially distributed features; from highly differentiated representation of the periphery to diffuse representation of the periphery; from minimal influence of autonomic arousal state to central representation of autonomic arousal; from highly facile processes with minimal integration across time to processes that exhibit patterns that are predictable over relatively long periods (in neurological terms).

The combination of oppositely directed pathways and a gradient across which they extend has suggested to me an analogy with counter-current fluid diffusion systems (see Fig. 1.8). Counter-current flow, as it is also called, describes a general feature found in many biological as well as engineering systems. Examples of counter-current diffusion processes can be found in the flow of water and blood through a fish gill or the flow of coolants within a nuclear reactor. There are many different ways to describe the same basic principle. What they all share in common is an opposed flow of two separated but interacting media (e.g., water in a heat exchanger) such that their region of interaction forms a gradient along which some parameter (e.g., heat) of one decreases while the corresponding parameter in the other increases, as a result of their interaction (e.g., diffusion). The logic of the opposed direction of flow is that it enables the gradient of difference between the two media to be distributed equally along the interface, even when the values are far from the static equilibrium point for the two sources of the flow. Figure 1.8 demonstrates this in a schematic fashion. Because of the opposed flow each fluid only comes in contact with the other at points where their concentration values are closest and so one can be increased or decreased to very nearly the concentration of the other. As a result the exchange medium (e.g., a membrane) can function far more efficiently than if interposed between the two fluid media in a passive state. This is why counter-current flow is so widespread in biological adaptations and engineering applications.

The analogy between fluid systems and information transformation systems derives both from the geometric similarity between



COUNTER-CURRENT DIFFUSION

FIGURE 1.8. Diagram of the principle of counter-current diffusion. The flow of **two** different fluids in opposite directions through adjacent **tubes** is indicated by the large shaded arrows. The concentration (or other parameter **such as heat, etc.**) of some component of each fluid is indicated by numbers, and the small white arrows depict the diffusion of **this** component from one fluid to the other across the permeable interface that separates them. Notice **that** the lower half of the system **begins** with a high concentration (10) and is reduced to a low **value**, whereas the upper half **begins** with a low concentration (1) and is increased to a high **value** by the diffusion process. **Because** the equilibrium **value** for static diffusion would be 5, the diffusion process is pushed well **beyond** static equilibrium in the vicinity of the **tubes**. Notice also **that** the gradient **between** any **two** adjacent **regions** of the **two** fluids in the **tubes** is the same. To compare **this** to an information diffusion system reinterpret the numbers to represent measures of some informational parameter **such as** the spatial complexity or temporal variety of a signal.

counter-directed neural pathways and oppositely flowing fluid diffusion systems, and from the similar alignment of both along some gradient. The concept of *diffusion* of some energetic or material quantity such as heat or dissolved oxygen across a permeable boundary between two fluids **can** be **given** more general formulation *as follows*: *Two media interact such that there is a decrease in some parameter describing one medium and a complementary increase in that parameter for the other medium*. In these general terms we **can** also describe the "diffusion" of information between two information carrying channels: *Two information carrying channels interact such that the information in each is used to transform the information in the other with the result that some parameter describing the information of one is increased while the corresponding parameter in the other is decreased in the process*. Appropriate informational parameters might be some measure of total **variety**/redundancy or **spatial/temporal** complexity, or some measure of other pattern parameters of the signal. A counter-current information processing system **can** formally be described *as a set of interactions between channels*

whose inputs are from two sources of information with opposite extreme values of some parameter, in which the first stage in the series of diffusion-interactions involving that parameter for one is the last stage in the series for the other and vice versa.

Once we recognize the formal correspondence of these two analogous processes (diffusion in the chemical-thermodynamic and informational senses, respectively), it is possible to see the corresponding enhancement that counter-current organization can provide for an informational diffusion system such as the brain. As in fluid systems, counter-current organization maximizes diffusion (i.e., total assimilation of information) and distributes the gradient of difference between centrally generated information and peripherally originating information uniformly throughout the system. Relatively stable, integrated information representing internal states and central programs, enters the network from one end, directed centrifugally, whereas highly complex, fragmented and rapidly changing information representing the sensory environment enters the network from the opposite end, directed centripetally. As sensory information passes by stages centripetally it progressively loses local complexity but gains in global integration, and as limbic information passes by stages centrifugally it progressively differentiates and decreases in integration with other systems as well as becoming less constrained by internal states. At each stage the two pathways bring together centripetal and centrifugal patterns of information that have been transformed by preceding stages so as to converge towards the same level of differentiation. The brain might thus be described as being arranged so as to generate the closest possible match to peripherally captured pattern information at every level of central-peripheral interaction.

The incompleteness of both microgenetic and associationist models of cortical processes is a consequence of their assumption of unidirectionality. The arguments presented here suggest that centrifugal processes *require* centripetal processes and that centripetal processes *require* centrifugal processes in order to function. There can be no development in one direction without a complementary development in the other. Centrifugally developing perceptual images require centripetally flowing peripheral information to progressively differentiate them, and centripetally progressing sensory stimulation patterns require centrifugally developing perceptual images in order to organize sensory features and abstract their integrated relationships. In this way it can be said that the developing *perceptual object* (to use Brown's term) assimilates sensory information in order to differentiate. By a parallel process centrifugally elaborating motor programs require centripetally directed peripheral motor-programming and somatosensory information to bias and gate the progressively differentiating behavior sequence. Each stage in a sensory or motor process represents a

completed image (more generally, an attentional envelope) or action (more generally, an intentional envelope) at a particular level of differentiation and a completed registration and assimilation of peripheral features at the corresponding level of detail. The processes of "recognition" and "decision" are not localized to the "highest" cognitive centers (whatever this might mean) but are distributed throughout all levels.

Fundamental to this hierarchic interdependence between globally organized processes at one extreme and locally differentiated processes at the other is the fact that these processes also reflect different temporal scales (see also Brown, 1982). The primary sensory and motor areas are engaged in processing information that is both spatially complex and extremely short lived. The immediately previous pattern of activity must instantly make way for the next. There is no room for a long lasting stable pattern of activity. At the other extreme, limbic and association areas sustain activities whose duration may extend from many seconds to minutes. The more general or global attributes that guide perceptual attention or guide the execution of a skilled behavior are also highly redundant in time. Centrifugal projections, then, are conveying information from a slower more redundant process to a faster more variable one, whereas centripetal projections are conveying information from a more rapidly fluctuating process to a slower one. The time scales for the basic units of analysis at the two extremes of the cortical hierarchy may differ by as much as two to three orders of magnitude. This is not to say that neurons fire at a different rate at the two extremes, only that there is a great difference in the time period over which redundancy in neural activity patterns should be observed (analogous to cycle length in some rhythmic process; see Brown, 1982). This may help explain why association areas and limbic structures appear so involved in mnemonic processes: not because they are the locus of memory, or because they have some specialized mnemonic function, but because of their position at the slow end of cortical processes. They provide the stable centrifugal constraint that enables systems with far more facile and easily perturbed processes to achieve the level of redundancy necessary to consolidate memories.

This simple counter-current analogy needs to be augmented in a number of ways before it is adequate. With respect to anatomical details I have tended to downplay subcortical relationships, particularly the multiple thalamic inputs to and parallel subcortical outputs from each stage of cortical processing. These both link across modalities and provide independent sources of peripheral information (in addition to that entering the network from either the limbic or specialized cortex ends). It is interesting that thalamocortical projections also exhibit an internal/external termination pattern dichotomy (Frost & Caviness, 1980; Rausell & Avendano, 1985; Friedman, Bachevalier, Ungerlieder & Mishkin, 1987; Herkenham,

1980). These appear to have a similar centrifugal/centripetal relationship as well. Projections with internal patterns (e.g. principal projection nuclei) generally relay spatially organized peripherally specialized information, whereas those with external patterns (e.g. intralaminar and limbic nuclei) generally relay information from deep midbrain or limbic structures that are more centrally organized. As indicated in figure 6 (and discussed in the last section), cortical-subcortical efferents too must be considered in the total centrifugal scheme. So it appears that the logic of centripetal/centrifugal organization is probably not limited to cortical circuits. For these reasons the simple analogy of input at one end and output at the other of each pathway is insufficient. The basic logic of counter-current organization must be complicated to deal with a system with multiple inputs and outputs.

The counter-current concept provides a useful framework to help conceive of an information processing system laid out as are the circuits of the human cerebral cortex. But it also goes further than previous models. It provides a model, not just of the relationships between cognitive and neural stages, but of the mechanism underlying the transformations of information from one stage to another in the process of cognition. It is an attempt to outline the means by which processes of the brain are capable of assimilating information about the world and of differentiating actions with respect to it. As with any analogy, this model reflects only certain general features of this pattern of cortical organization. However, I believe it provides the first alternative to the one-directional, hierarchic models or undifferentiated parallel models of brain processes that we have explicitly or implicitly relied upon for insights, hypotheses, and explanations regarding the function of the brain and mind.

CONCLUSIONS

In hindsight it seems that associationist and holist theories of mental processes were not so much alternative theories of mind as descriptions of complementary aspects of a single process. The failure of each to provide more than just a descriptive account of the movement or change of information in cortical systems derives from a failure to recognize this complementarity. The reformulation of neuropsychological theory in terms of the interaction between centrifugal and centripetal processes breaks down many preconceptions about hierarchic organization that have been the source of contention and confusion since the beginnings of neuropsychology. Because the centrifugal/centripetal logic is reflected both in cortical organization and in cortical-subcortical relationships, attention to this pattern may well lead the way to a more comprehensive general model of brain function.

During the last century the evolution of associationist and holist theories of brain function has been powerfully influenced by neuroanatomy and neurophysiology as much as by the findings of neurologists. During different periods, experimental findings have been crucial to the rise or fall of one or the other paradigm. It now appears that new neuroanatomical findings may force a rapprochement between these two major paradigms of neuropsychology. The model presented here in answer to the contradictions between theories, and between theory and anatomy, shares much in common with the original connectionists' models. Like its 19th-century predecessors, the counter-current theory of cortical information processing has grown out of anatomical considerations, is based on a simple analogy, and suggests a wide range of new predictions concerning brain functions. However, the neurosciences have become unimaginably more complex since Wemicke's time, and it is likely true that any simple model will quickly be found to be inadequate in a number of ways. On the other hand, the survivability of this particular model is not as important as its capacity for generating new questions and providing new perspectives on old questions. In this regard, I feel that some version of a complementary, bidirectional model of cortical information processing will ultimately provide the best model of cortical processes.

The neurosciences are only just emerging from a long pretheoretical slumber. Up to this point in time theories of brain function have been little more than adaptations of philosophical arguments. Their elaboration has been limited by the complexity and relative inaccessibility of brain processes. The rapid growth of new information to fill this void has radically changed the scientific context in which our classic conceptions of brain function evolved. As a result many of the most basic assumptions we bring to the clinic and laboratory—what functions ought to be "higher" or "lower," what constitutes "input" or "output," and which direction is "forward" and which is "backward"—will all need to be reexamined.

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