A Systems Approach to the Cerebral Hemispheres

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ABSTRACT

There is evidence that the two cerebral hemispheres are at birth equally capable of acquiring language. There is also evidence that control over linguistic function becomes, in due course, the domain of only one hemisphere, usually the left. We are thus confronted with the paradox that a neurological system (the right hemisphere), though fully equipped to control a particular function, normally develops in such a way that it fails to do so. Cerebral dominance theory has recently been revised by several theorists, partly in order to resolve this discrepancy between the linguistic potential and the linguistic achievement of the right hemisphere under normal conditions of development. The resolution is affected by expanding the concept of cerebral dominance to include the notion of active control, through inhibition, of one hemisphere by the other. The language-dominant left hemisphere is thus considered to inhibit the right. However, rather than resolve a paradox by modifying theory, a more satisfactory solution is to remove it. This may be accomplished by adopting a novel perspective on the apparently discrepant observations, so that they lose their paradoxical appearance. The present paper argues that such a perspective is provided by a theory of dominance modeled after the tenets of General Systems Theory.

The concept of cerebral dominance has been radically revised in the last several years. In 1962, Zangwill described the then accepted view of dominance as the asymmetric representation of function in the human cerebral hemispheres. This view might be called "static," since it merely locates a particular function in a particular hemisphere and says nothing about the functional relations between hemispheres. The static view may be contrasted with a second perspective on dominance that conforms more to the usual meaning of the word. Dominance, according to the second view, refers to the active control of one hemisphere by the other. Zangwill considered this dynamic interpretation, but rejected it on grounds of parsimony: although the dynamic view was compatible with the static, he saw nothing in the available evidence to demand it.

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Recently, several investigators have seen the matter differently and have therefore incorporated the dynamic perspective into their accounts of cerebral dominance (Geschwind, 1969; Gazzaniga, 1970; Gazzaniga and Hillyard, 1973; Kinsbourne, 1973, 1974; Moscovitch, 1973; Selnes, 1974). One impetus for augmenting the concept of dominance was the recognition of a paradox deriving from the following observations. First, there is convincing evidence that the human cerebral hemispheres at birth are more or less equipotential in their capacity to become the language dominant hemisphere (Lenneberg, 1967). Second, the right hemisphere only realizes its potential under unusual conditions. The paradox, then, is that a "language center" develops in only one hemisphere, even though the capacity to develop language is present in both. Recent qualifications of the equipotentiality of the hemispheres—provided by evidence that the left hemisphere is both structurally (Witelson and Pallie, 1973) and functionally (Molfese, 1972; Entus, 1975) specialized before language acquisition begins—do not resolve the paradox, since the fact remains that, under conditions of early left-hemisphere removal, the right hemisphere does acquire language.

Indeed, the paradox cannot be resolved within the static dominance scheme, for it holds that dominance is total: a particular function is the exclusive domain of a particular hemisphere. Hemispheric specialization is thus a fait accompli; there is no provision within the scheme for the gradual establishment of asymmetric representation in initially equipotential hemispheres. Therefore, the evidence that hemispheric representation of function is not deterministically asymmetric from birth demands either a modification of the static view or its rejection.

There are two ways in which a scientific paradox may be handled. Theory may be modified expressly to resolve it. Or the paradox may be dissolved by adopting a new perspective from which the discrepant observations lose their paradoxical appearance. The first tack has been taken in two recent accounts of development of cerebral dominance, namely those of Selnes (1974) and of Gazzaniga (1970). Both investigators modify the static view by incorporating within it the dynamic notion of dominance as control over one hemisphere by the other. The second tack will be taken here. We shall argue that neither Selnes nor Gazzaniga provides a satisfactory account. More importantly, we shall argue that total rejection and replacement of the static view with a Systems Theoretical view of dominance development provides a simpler solution to the problem. Before characterizing these two attempted resolutions of the paradox, and their consequences for the theory of hemispheric specialization, let us lay out in more detail the specific observations that require explanation.

HEMISPHERIC EQUIPOTENTIALITY IN EARLY CHILDHOOD

The literature on cerebral dominance provides information about language acquisition and hemispheric specialization for language in a variety of neural contexts. Studies of language acquisition in cases of callosal agenesis and of early hemispherectomy reveal the linguistic capacities of the isolated left and right hemispheres. These capacities may be compared with those of left and right hemispheres that were connected during language acquisition. The latter evidence comes from normal individuals and from individuals who underwent commissurotomy or hemispherectomy as adults.

Differences in the neural contexts of language acquisition give rise to apparent differences in the locus of language representation. In no case does
language acquisition fail to occur. In the normal individual, language function comes to be controlled primarily by a single hemisphere, usually the left, while the right hemisphere demonstrates very limited linguistic skills if examined during left-hemisphere anesthetization (Milner, Branch, and Rasmussen, 1964), after commissurotomy (see, for example, Gazzaniga, 1970) or after hemispherectomy (Smith and Burklund, 1966). We might therefore adopt an extreme view of dominance, and say that language is normally represented in the left hemisphere, but not in the right.

However, if one hemisphere is removed early in life, language develops in the remaining hemisphere regardless of which has been removed (see, for example, Basser, 1962). Thus if the left hemisphere is removed, language is acquired by the remaining right hemisphere. In cases of callosal agenesis, the evidence is less clear, though not incompatible with the interpretation that "language centers" are established in both hemispheres (Bryden and Zurif, 1970; Sperry, 1970; Saul and Scott, 1973).

In any event, we have clear evidence that the right hemisphere has the capacity to acquire and represent language, and the paradox is that this capacity is not realized under normal conditions of development. The resolutions of the paradox offered by Gazzaniga (1970) and by Selnes (1974) take as their starting point the above descriptions of the conditions under which right-hemisphere language acquisition occurs or fails to occur. The systems approach advocated in the present paper will argue that the conditions are both inappropriately characterized and inappropriately interpreted by the proposed resolution.

MODIFICATIONS OF THE STATIC DOMINANCE VIEW: PARADOX RESOLUTION

The observations of the preceding section suggest an obvious solution to the paradox. Since the right hemisphere, under normal developmental conditions, fails to realize its demonstrated potential to acquire language, something must prevent it from doing so. The nature of the conditions under which it does realize its language acquisition potential—for example, early left hemispherectomy—suggests that the source of right-hemisphere suppression lies in the left hemisphere. This is the reasoning of Selnes and of Gazzaniga. The mechanism of right-hemisphere suppression they both propose is inhibition, initiated by the left hemisphere and mediated by the corpus callosum (Gazzaniga, 1970; Gazzaniga and Hillyard, 1973; Selnes, 1974).

The inhibition hypotheses proposed by Gazzaniga and Selnes are not identical; in fact they are complementary. Gazzaniga (1970), elaborating on Hewitt's (1962) evidence that the corpus callosum is not fully developed at birth, argues that the infant is functionally split-brained for the first two years of its life. During this period, before the onset of suppression, the right hemisphere acquires those minimal linguistic skills that can be demonstrated in the isolated adult right hemisphere. As the corpus callosum matures, the left hemisphere begins to suppress the right, and further right-hemisphere language acquisition is prevented. For Gazzaniga then, the term dominance has a dual reference: it refers both to the permanent active control of one hemisphere by another, and simultaneously to the consequence of that control—the asymmetric representation of function in the hemispheres.

Selnes (1974), on the other hand, recognizes some of the fairly strong evidence against the inhibition hypothesis, at least as applied to adult hemispheres.
(see next section). Therefore, since the facts of dominance development appear
to demand an inhibition interpretation, he proposes that the period of right-
hemisphere inhibition by the left is restricted to infancy and early childhood.
For Selnes, that is, dominance has two phases: an initial dynamic phase of ac-
tive left-hemisphere control of the right, and a subsequent static phase of dom-
inance as asymmetric respresentation of function.

The development of asymmetric representation in the initially equipotential
hemispheres can now be explained. Both hemispheres have the potential to acquire
language. But the left hemisphere is additionally equipped to inhibit the right,
to prevent it from acquiring language during infancy, and, according to Gazzani-
aga (1970), to prevent the interference of any primitive right-hemisphere linguistic
activity with left-hemisphere processing in the mature brain. However, if the
source of inhibition is removed while the brain is still immature, or if the
pathway mediating the inhibitory influence fails to develop, the right hemi-
sphere's capacities are realized.

In sum, both the above resolutions of the dominance development paradox in-
volve the addition of a very powerful construct—that of active inhibition—to
the theory of cerebral dominance. As we have seen, this construct appears to be
required by the facts of cerebral dominance development. Moreover, its addition
can be justified on grounds independent of those facts (Geschwind, 1969;
ever, strong objections can be raised to the inhibition hypothesis, even within
the static dominance view, and some of these will now be considered.

INHIBITION HYPOTHESES

The inhibition hypothesis takes several different forms, each largely shaped
by the facts it is supposed to explain. First, both Kinsbourne (1973) and
Gazzaniga and Hillyard (1973) have postulated a bidirectional reciprocal inhibi-
tory relation between the hemispheres. Kinsbourne does so in order to complement
a proposed mechanism for focusing attention on operations taking place in one or
the other hemisphere; Gazzaniga and Hillyard (1973), in order to account for the
observed increase in total processing capacity of the brain following commissur-
otomy. Second, Geschwind (1969) and Moscovitch (1973) have argued for a uni-
directional, focalized, and tonic inhibition of right-hemisphere language centers
by language centers in the left hemisphere. The grounds for this hypothesis are
comparisons of right-hemisphere linguistic abilities among normals, commissur-
atomies, adult and child aphasics, and left-hemispherectomized individuals.
Finally, as we have seen, Selnes (1974) has proposed unidirectional inhibition of
the right hemisphere by the left during infancy, largely to resolve the develop-
mental paradox described above.

We will consider each of these hypotheses in turn.

Inhibition as Reciprocal Inhibition

Gazzaniga and Hillyard (1973) offer the following description of the pro-
posed interhemispheric inhibitory operation:

...the role of the forebrain commissures in integrating the atten-
tional processes of the two cerebral hemispheres is revealed by the
increases of total processing capacity upon the removal of the corpus
callosum. It is as if in the normally interconnected brain the callosum is involved in inhibiting the transmission of information undergoing processing extraneous to the dominant cognitive activity under consideration. The brain cannot consider all things at all times, and perhaps order only is brought about by what amounts to a cognitive counterpart of a reciprocal inhibition kind of mechanism. (p. 237)

Kinsbourne's (1970) proposal is similar in form although he derives it from a different set of observations. He describes his attentional model as follows:

Each hemisphere serves the contralateral half of space.... Thus, as a matter of course, orientation to one side of space coincided with preparatory activation within the contralateral hemisphere. If the principle of reciprocal innervation holds not only at spinal cord level (Sherrington, 1906),¹ but also between the cerebral hemispheres (Kinsbourne, 1970),² then as one hemisphere actively subserves its orienting function, the other is inhibited as regards the contrary tendency it subserves. (pp. 195-196)

There are five main objections to the reciprocal inhibition hypothesis.

(1) The analogy made by Kinsbourne (1973) and by Gazzaniga and Hillyard (1973) between spinal reciprocal inhibition and the proposed inhibitory effect is not a close one. In the spinal cord, reciprocal inhibition works to offset the tendency of a muscle antagonist to counteract agonist activity. When an agonist contracts, antagonist muscle spindle's are stretched and their spindle afferents are excited. If uninhibited, the spindle afferents elicit (via their connections to the α motorneurons innervating the antagonist) antagonist contraction that counteracts the effect of agonist activity. Therefore, if voluntary movements are to occur, antagonists must be prevented from counteracting agonist activity, and this appears to be the role of spinal reciprocal inhibition.

Notice that the neural system innervating an agonist does not inhibit the motorneurons of every muscle that might interfere if activated simultaneously. Rather it specifically inhibits those motorneurons innervating the muscle that is structurally designed to counteract its effects. Unless we assume that, like agonist and antagonist, the left and right hemispheres are designed so that activities in one hemisphere are countered by subsequent activities in the other, the reciprocal inhibition analogy would seem to be inappropriate to a description of interhemispheric relations.

(2) The reciprocal inhibition hypothesis is inconsistent with data demonstrating a much greater degree of suppression in commissurotomized individuals than in normals. These data suggest that the normal corpus callosum may mediate


arousal rather than suppression. The split-brain suppression effect is reported quite frequently in the literature, and three examples follow.

(i) Trevarthen (1970) reports that callosalized human subjects, asked to fixate the center of a table on which an irregular shape, cut out of white card, had been placed and to mark the center of the card, experienced a fading or disappearance of the shape, if it was located in the visual field contralateral to the responding hand. If the responding hand was the left hand, and the shape was in the right visual field, the subject reported that he could not see the object. Trevarthen notes that this perceptual "neglect" was not typically observed when the required response was less skilled and more automatic than the marking response.

(ii) Trevarthen and Sperry (1973) report similar perceptual neglect effects among callosalized subjects who were asked to compare stimuli presented in different visual fields. Unilateral neglect occurred when the subject was asked to describe the stimuli or when manual responses were required. For example, subjects often neglected the left visual field stimuli when responding verbally, or, if they tried to express what they had apparently perceived, suffered an arrest of speech. In at least one subject, unilateral neglect declined in frequency as a session progressed—as the subject, according to Trevarthen and Sperry, "developed sufficient concentration of his attention on the task."

(iii) Teng and Sperry (1973, 1974) report that under conditions in which digits or dots were presented for identification in both visual fields (subjects held out a number of fingers corresponding to the digit or to the number of dots displayed), callosalized subjects tended to neglect one visual field. Neglect was not observed under conditions of unilateral presentation of digits or dots.

Since these suppression effects are peculiar to individuals lacking a corpus callosum, it is unlikely that the role of the callosum in normal individuals is to suppress functioning. The evidence suggests rather that it may mediate arousal.

(3) Callosal anatomy and physiology suggest that the callosum functions to permit communication between split sensory fields rather than to suppress functioning. Selnes (1974) reviews literature showing that callosal fibers between corresponding projection areas in the hemispheres only connect those parts of the projection areas representing the midlines of the sensory fields. There are no striate-striate callosal connections in the visual system. Callosal fibers only connect the extrastriate areas, which represent the midline of the visual field. Similarly in the somesthetic and motor areas, fibers interconnect primary projection areas representing axial body structures, but not the hand, finger, or foot areas. "Association areas" show a similar duality—that is, well-defined areas that are interconnected across the callosum and others that are not. At least with respect to the projection areas, the specificity of callosal connections to areas representing sensory or motor midlines suggests that the role of the callosum is to permit communication between areas of the brain representing neighboring areas of space that are split between the hemispheres.

(4) Measurements of left- and right-hemisphere-evoked potentials during the performance of linguistic and nonlinguistic tasks provide evidence incompatible with reciprocal interhemispheric inhibition. Wood, Goff, and Day (1971) found that the right hemisphere responded identically to syllables presented auditorily,
regardless of the linguistic or nonlinguistic nature of the subject's task. The left-hemisphere-evoked potential, on the other hand, varied with the nature of the task. Although it is not clear what the evoked potential represents, one might reasonably expect that, if the right hemisphere was inhibited in one case and not in the other, its evoked potential would vary accordingly.

(5) A final objection to the reciprocal inhibition hypothesis is simply that it is unnecessary. We do not need it to explain either the failure of the hemispheres to interfere with one another under normal conditions or the occurrence of interference effects during the simultaneous performance of two tasks by the hemispheres (Geffen, Bradshaw, and Nettleton, 1973; Hicks, 1975; Kinsbourne and Cook, 1971). These effects can be satisfactorily accounted for by attentional mechanisms similar to those proposed by Kinsbourne (1973) and by Trevarthen (1974) to explain perceptual neglect effects among callosalized subjects.

Inhibition as Focalized Unilateral Suppression of Right-Hemisphere Language Centers

Most of the arguments marshaled against the notion that the corpus callosum mediates reciprocal inhibition apply, of course, to this inhibition hypothesis as well. However, Moscovitch (1973) suggests that some part of the inhibition effect must be assumed to be subcortical if the continued inability of the right hemisphere to initiate speech following commissurotomy is to be explained. Consequently, the focalized inhibition hypothesis cannot be rejected on the grounds that inhibition is not mediated callosally.

The observations explained by an inhibition hypothesis are, according to Moscovitch:

1. the apparent inability of the right hemisphere in normal adults to process verbal information,

2. improved right-hemisphere linguistic abilities following commissurotomy,

3. the inferior right-hemisphere linguistic abilities of some aphasics relative to split-brain subjects.

There appear to be two grounds for the claim that the normal right hemisphere cannot process verbal information. First, individuals are typically unable to initiate speech during left-hemisphere anesthetization. We should note, however, that according to Milner, Branch, and Rasmussen (1964) this effect gives way, after a few minutes, to a transient aphasia. If the aphasia is symptomatic of left-hemisphere recovery from the anesthesia, then the claim that the right hemisphere is mute is based merely on its performance in the very few minutes before left-hemisphere recovery. We cannot justifiably conclude from this that the right hemisphere's muteness would persist indefinitely if the period of left-hemisphere suppression were extended.

The second ground for Moscovitch's assessment of normal right-hemisphere linguistic abilities comes from his own work on visual field effects (Moscovitch, 1973). Subjects in these experiments listened binaurally over earphones to
either one or six letter names (such as "bee," "cee," "dee," etc.) and were then presented with a letter in either right or left visual field. Subjects indicated whether or not the visually presented letter had been among those presented auditorily. A left visual field reaction time advantage was obtained for the single letter memory set, while a right visual field advantage was obtained for the six item set. When the single letter memory set condition was made "more linguistic" by requiring subjects to respond to letters that were rhymes of the auditorily presented letter as well as to the letter itself, a right visual field advantage was obtained. The evidence indicated to Moscovitch that the right hemisphere among normals is unable to process verbal information.

He then argues that, since right-hemisphere speech perception has been demonstrated among split-brain subjects, these speech abilities must be inhibited in the normal right hemisphere. We should note, however, that the stimuli used by Moscovitch were letter names, while those used to test callosalized subjects had, until recently, been real words. Consonant-vowel (CV) nonsense syllables were used, both monaurally and dichotically, by Zaidel (1974) to test right-hemisphere perception in split-brain subjects. He found that the subjects were unable to identify the syllables presented to the right hemisphere by pointing to their letter representations. Thus, split-brain subjects fail to demonstrate linguistic skills superior to those of the normal right hemisphere when the stimuli are nonsense syllables, and Moscovitch may have unwittingly chosen the wrong stimuli to test his hypothesis. On the other hand, Dimond (1971) has shown that visually presented letter sets are better reported by normals if the letter sets are divided over both hemispheres than if they are sent to a single hemisphere. This indicates that some part of the letter sets was processed by the right hemisphere. Hence Moscovitch's claim that the normal right hemisphere cannot process verbal stimuli may be incorrect. In fact, his reaction time technique may not establish which hemisphere is uniquely able to process verbal stimuli, but merely which hemisphere processes them faster.

Moscovitch's first two claims, therefore, that the normal right hemisphere is unable to process verbal information and that the right hemispheres of callosalized individuals exhibit improved linguistic abilities relative to the normal right hemisphere, may be unjustified. His final claim, that some aphasics demonstrate less comprehension of speech than does the right hemisphere of callosalized individuals, may well be true. However, as we shall see below, it may be attributed as readily to interference by a malfunctioning left hemisphere as to inhibition.

Inhibition in Infancy

Selnes's (1974) proposal that inhibition of the right hemisphere by the left is restricted to infancy purports to explain first, as noted above, the more or less unilateral development of language despite apparent left- and right-hemisphere equipotentiality during infancy, and second, the rapid improvement of linguistic skills following dominant hemispherectomy for infantile hemiplegia (see, for example, Basser, 1962).

Although inhibition of the right hemisphere by the left (and its release following left hemispherectomy) could account for these phenomena, inhibition cannot be the simplest explanation, nor is it a very likely one. We have already reviewed evidence suggesting that the role of the corpus callosum is to transmit
information between the hemispheres, and Selnes (1974) himself rejects the notion that the corpus callosum mediates inhibition in the mature brain. The hypothesis that it mediates inhibition in infancy therefore requires the unlikely assumption that there exists some inhibition mechanism that disappears or changes its character as the organism matures.

Beyond this, and more generally, the reasoning of Selnes's proposal [like that of Gazzaniga (1970)] is specious. Briefly, the reasoning was this: if the right hemisphere has the potential to acquire language, but only does so when it is isolated from the left, then the left hemisphere must normally prevent the right from developing its potential. A plausible neurological mechanism for this process is inhibition.

But does logic compel us to conclude that the left hemisphere "prevents" the right from developing, and how plausible, in fact, is the inhibition hypothesis? A radio damaged by a hammer blow may emit a continuous howl; after a stroke, a person may walk with a limp or may only be able to produce jargon when he tries to speak. Yet we would not be inclined to claim that the novel behaviors following injury were "released" because their inhibitors were damaged (cf. Gregory, 1961). The radio does not emit a howl because its howl inhibitor was damaged by the hammer blow; nor does the aphasic produce jargon because his jargon inhibitor has been destroyed. The novel responses arise because the injured system—the radio or the brain—is different both structurally and functionally from the system that it was before injury. Some of its components have been destroyed, and the interrelations among the remaining intact components have been altered as a consequence.

Of course, the right hemisphere's "response" to isolation is not entirely comparable to the radio's howl or even to the aphasic's jargon. Whereas the latter are pathological and maladaptive, the acquisition of language is highly adaptive. Nonetheless, we may account for right-hemisphere language acquisition after hemispherectomy in the same general way that we account for the emergence of the howl and the jargon following accident or injury. In the intact brain the two hemispheres comprise a single system of interdependent components. When a subset of these components is removed, the functioning of the rest changes in consequence. By this account, the isolated right hemisphere is not functionally the same system as the intact connected right hemisphere.

In short, the development of language in the right hemisphere following its isolation from the left does not necessarily imply that it has been freed from a language-center inhibitor. There is at least one alternative view: that isolating the right hemisphere from the left effects a change in the right hemisphere's mode of functioning. A new system then emerges with the capacity to acquire language. It is this alternative view that we consider in the following sections, and that we will elaborate in relation to the dominance development paradox and the theory of cerebral dominance.

ADOPTION OF THE SYSTEMS APPROACH: PARADOX DISSOLUTION

Systems Theory (Bertalanffy, 1968; Weiss, 1969, 1971) provides a perspective on hemispheric specialization from which the observations on cerebral dominance development lose their paradoxical appearance. Indeed, the observations are closely analogous to certain characteristics of developing biological
organisms that are frequently cited to illustrate fundamental systems properties. Many of these properties can be derived from the following preliminary definition of a system: a system is a whole or a unit composed of hierarchically organized and functionally highly interdependent subunits that may themselves be systems. The following are examples of systems: an atom, a cell, a person, a factory, a society. The systems-theoretical perspective on these instances of "organized complexity" reveals that they share certain fundamental properties. Moreover, despite the diversity of the organizations properly described as systems, these properties are not so general as to be trivial or useless. Some of them will be described below.

Weiss (1969, 1971) characterizes the functional interdependence of the systems subunits in terms of the following inequality: \( V_s < (V_a + V_b + \ldots + V_n) \), where \( V_s \), \( s \), and \( a-n \) stand for "variance," "system," and "subunits a to n," respectively. According to the inequality, the variance in the states of the system as a whole is less than the sum of the variances of the individual subunits. To illustrate how this property manifests itself, let us look at an example of a system in which it is clearly revealed. The system is the speech production system, and we will examine its output, the spoken word. Lehiste (1971) described an experiment in which a talker is asked to repeat a word 50 times. The duration of each repetition is measured and its variance across repetitions is computed. Additionally, the durations of the component acoustic segments are measured on each repetition and variances are computed for each. The sum of the variances of the component segment durations consistently exceeds the variance of the total word duration, in Lehiste's experiment by a factor of 3 to 5. What this implies, as Lehiste points out, is that on a repetition in which some segments are unusually long in duration the others must be correspondingly short. That is, in order for the variance of a whole to be small relative to the sum of the variances of its parts, the parts must be compensating for deviations in each other's behavior.

That the durations of the individual acoustic segments vary at all across repetitions of a word of relatively fixed duration indicates that they are not or cannot be rigidly controlled by the speaker. Weiss (1969) terms the corresponding systems property "microindeterminancy." Nonetheless, although the subparts are not rigidly controlled as individuals, their collective behavior is relatively controlled; the speech production system consistently reaches a (relatively) fixed goal, despite the microindeterminancy of its component subparts. More generally, a system is an organization whose overall state is stable relative to the states of its components. These observations suggest an important conclusion: temporal compensation may occur among the acoustic segments of a word because the talker establishes or plans the total word duration from the outset. The target-word-duration then exerts a regulatory influence throughout the course of each word's production. We can think of the duration specification as the fixing of a potential and crucial degree of freedom in the system—the endpoint that the system is then constrained to reach. The established endpoint exerts a regulatory influence on the subsequent behavior of the system. The influence must be regulatory rather than controlling because only the endpoint is set, not the route by which the endpoint is reached.

Generalizing the conclusion to systems of all kinds, we can say that a system whose goal state has been set is constrained to reach that state, and that the goal specification regulates the course of goal attainment. However, since
the influence is not microdeterministic, the system can reach the goal by a variety of routes. This tendency for a system to reach a constant endpoint from a variety of starting points and by a variety of routes is called "equifinality." It is characteristic of any organization that, as a whole, has functional properties that do not inhere in any of the subparts individually. (In the speech production system, for instance, word duration is not a functional property of any of the system subparts responsible for producing the different acoustic segments.) These functional properties or systems dynamics constitute an equilibrium state of the system. They define the configuration or endpoint toward which the system will tend; they do not, however, define the precise way in which it will attain that configuration.

Examples of the diverse kinds of organizations that exhibit the equifinality characteristic (and do so for the reasons described above) are the speech production system, the joint-muscle system responsible for setting a joint angle (Asatryan and Fel'dman, 1965), the developing embryo, and, we will argue, the developing cerebral hemispheres.

So far, two closely related systems properties have been described: the stability of the system as a whole relative to variations in the states of its component parts (microindeterminacy), and the regulation of changes in the system's states by means of preset goals (equifinality). A final systems characteristic can be derived from the information already compiled. We have noted the existence of functional systems properties that do not inhere in any of the subparts. The existence of such properties implies a certain degree of independence of the systems dynamics from the structural units over which they operate. This independence provides the system with a corresponding degree of resistance to destruction due to the loss of individual subunits. To cite an example given by Weiss (1971), the death of a cell does not destroy the systems dynamics in a biological organism. It does not, because the functional properties of the system do not depend for their realization on the performances of particular cells. Functions are not coded in terms of individual subunit behaviors.

Experiments performed on the developing embryo are frequently cited by systems theorists, in part, because they clearly demonstrate this last systems characteristic. Here is Weiss's (1971:22-23) description of the experiments:

It was only consistent on the part of performanceists, who adhered strictly to a machine-like concept of development, that upon seeing a whole embryo develop from each half of a bisected egg, they would presume each blastomere of the 2-cell stage to be endowed with a spare mechanism for the formation of a whole embryo, to be activated in just such an emergency as accidental blastomeral separation. What neither they nor evolution could have foreseen was that enterprising human experimenters would move on in the opposite direction and fuse two whole eggs, with the result that a single harmonious giant embryo would form from the fused mass.... Since contrary to splitting, the natural occurrence of such a merger would be impossible, among other reasons because of the barrier of the enveloping egg membranes, it would have been absurd to postulate the providential inclusion by evolution of a spare mechanism for half an embryo in a whole egg. This once and for all disposed of the notion of spare mechanisms pre-designed for developmental correctives, and by the same token, also
of wholly rigid preformed mechanisms for the normal course of development as such.

We are thus compelled to fall back on pure and unreducible system behavior as an indispensable principle of developmental dynamics.

Weiss was, of course, mistaken in his claim that the experiments "once and for all disposed of the notion of spare mechanisms predesigned for developmental correctives," since that notion is manifest in the inhibition hypotheses of hemispheric equifinality described above.

There are two possible analogies between embryo development and the development of cerebral dominance for language: (1) Each half of a bisected egg develops into a whole functioning organism. Similarly, each hemisphere of an immature acallosal (bisected) brain develops a language function, as does the remaining half-brain after early left or right hemispherectomy. (2) Two fused eggs develop into a single organism. Analogously, the two normally connected hemispheres develop a single language function. The similarities between the two sets of observations suggest that the "spare mechanism" account of right-hemisphere language potential is not correct, and that the hemispheres might profitably be viewed as instances of a system.

The hemispherectomy and callosal agenesis data constitute a demonstration of the systems properties of equifinality and of the partial independence of systems dynamics from the structural units over which they operate. Because, on the systems view, the developmental sequence leading to dominance is not coded in terms of particular kinds of changes in particular systems subunits (because it is, in fact, a set of possible sequences sharing a common endpoint), it is resistant to destruction due to the loss of individual subunits. It is apparently resistant even to the loss of an entire cerebral hemisphere. Hence, when a hemisphere is removed, or when the fiber tract connecting the hemispheres fails to develop, the systems dynamics remain intact. However, the domain over which they operate becomes a single hemisphere instead of two. (Two independent sets of systems dynamics are considered to operate in the acallosal brain.) The endpoint or goal that the dynamics define is attained in the remaining whole.

Clearly, if we adopt the systems view, interhemispheric inhibition is not required to "prevent" the right hemisphere from realizing its potential to acquire language. Indeed, the right hemisphere has no "spare mechanism" for language development that might require inhibition. The development of dominance is not the realization of some potential inherent in the individual subunits themselves. Rather it is the product of systems dynamics that, in the normal hemispheres, regulate the whole brain. Nor are the hemispheres considered to be independent units competing for functional prepotency; they are interdependent systems subunits tending toward the same goal or equilibrium state.

There is a final case in the hemispheres literature that has no analogue in the series of experiments briefly described by Weiss (1971). Language functions in the adult or child may be impaired more seriously before than after surgical removal of a damaged left hemisphere. This observation is considered by some theorists (see, for example, Geschwind, 1969; Moscovitch, 1973) to constitute evidence that the left hemisphere inhibits the right even following damage. However, an analogous observation, again provided by experiments performed on the developing embryo, suggests an alternative explanation. Needham (1968) describes
an experiment performed by Roux in 1888 in which one cell of a two-cell frog embryo was killed by cautery. A half-embryo developed from the remaining still-living cell. This result contrasts with those of the later experiments cited by Weiss in which whole embryos developed from the isolated blastomeres of embryos at the two-cell stage. The crucial difference between the two sets of experiments may be that Roux did not isolate the cell he had killed from the living cell that remained. Clearly, the dead cell did not inhibit the living cell. Yet, by its propinquity to that cell, it constrained the living cell's course of development. The contrast between the results of the Roux experiments and those of the Driesch experiments described in the extract above is analogous to the contrast between observations of language functions in the whole brain with left-hemisphere damage, and observations of language functions in the isolated right hemisphere. Thus, it may not be the case that the damaged hemisphere inhibits the intact hemisphere. Rather, the damaged left hemisphere together with the intact right hemisphere may constitute a single system whose "equilibrium state" is incompatible with right-hemisphere control of language functions.

From the systems theoretical vantage point, the facts of cerebral dominance development are no longer paradoxical. In fact, the development of a "language center" in the right hemisphere only when it is isolated from the left is almost an expected dominance characteristic given the systems property of equipifinality and given our knowledge of its operation in the developing embryo. The dissolution of the dominance development paradox within a systems theoretical framework is more satisfactory on at least three grounds than its resolution as provided by a revision of the static dominance view. Two of the grounds have already been discussed: the inadequacy of the inhibition hypotheses and the fact that the proposed resolution invokes a construct that has been disconfirmed in the biological realm. Additionally, and perhaps most importantly, the systems description of dominance development is preferred because it is the simpler of the two descriptions. That is, it explains dominance development using principles that have already been proposed in other areas of scientific knowledge to account for properties of other systems.

The Equilibrium State Leading to Dominance Development

Adopting the systems view requires us to revise not only our account of cerebral dominance development, but also the concept of dominance itself. In this and the following section, a first approximation to a systems theoretical view of dominance will be described.

We can begin by taking stock of what has already been said about systems dynamics. The dynamics constitute the equilibrium state of the system; that is, they define the goal toward which the system tends. Being an equilibrium state, the goal exerts a regulatory influence on the current activities of the system. Again, the dynamics only establish the endpoint or the target state toward which the system works. They do not fix the route by which it will attain that state. Functions are not coded in terms of changes in particular subunits.

Therefore, although dominance typically appears to develop "in" the left hemisphere, the equilibrium state for the developing hemispheres cannot be a "left-hemisphere representation of language." The goal state must rather be one that allows for equipifinality, or more generally, that allows for goal attainment despite the loss of some systems subunits—including those in the left
hemisphere. Systems theory provides a clue to the form that this developmental goal specification might take. According to Bertalanffy (1968), increasing degrees of differentiation or of hierarchical complexity is a general phylogenetic trend. One instance of the phylogenetic trend toward hierarchical complexity may be the evolution of hemispheric specialization. Differentiation is advantageous to a system because it permits more refined or reliable control of particular systems subunits. However, it also leads to a loss of flexibility. The functions that were performed by a subpart before it was damaged are not so readily compensated for if the remaining intact subunits are specialized for other functions. Therefore, according to Bertalanffy, differentiation or mechanization is never complete in a biological organism. Rather, organisms reach some compromise between the advantages of specialization and those of flexibility. Since there is no apparent reason to suppose that the human cerebral hemispheres should constitute an exception to the rule, we assume that differentiation of function in the hemispheres is likewise incomplete.

The form that the specialization/flexibility compromise often takes in biological systems is the establishment of a "leading part" (Bertalanffy, 1968). The leading part is a subunit in a system whose activities are highly influential with respect to the state of the whole system. Although each subunit in a system influences and is influenced by changes in every other subunit, they may differ in their degree of influence. A leading part is a subunit whose influence is large relative to that of other subunits. Organizers or inductors in the developing embryo are examples of leading parts.

The leading part is not considered to control the systems operations. Rather, it contributes more influentially to the character or organization of the systems dynamics than do other subunits (we recall that mechanization or differentiation is not complete). Therefore, the reactions between the leading part and other subunits are still those of mutual influence and interaction, not of cause and effect.

We might guess then that the goal state defined by the systems dynamics of language development is the establishment of a mode of cerebral function for which some subunit becomes a leading part. Under normal conditions, because of its relation to the rest of the systems subunits, some left-hemisphere subunit emerges as a leading part. If the left hemisphere is removed, a right-hemisphere subunit, with a new relation to the remaining whole, emerges as a leading part. In short, cerebral dominance provides an instance of the general rule formulated by Pattee (1970) in a discussion of biochemical structure and function: "Function is never determined by a particular structure itself, but only by the context of the organization and the environment in which this structure is embedded" (p. 119).

**Dominance in the Mature Brain**

In the mature brain, some hemispheric leading part acts to organize each mode of cerebral function. For instance, the left-hemisphere leading part organizes linguistic processing. However, the left-hemisphere leading part is probably not the only hemispheric leading part, nor is linguistic processing the only functional mode that a lateralized leading part acts to organize. The claim is often made that the right hemisphere is dominant for a class of tasks that, loosely stated, demand gestalt-like processing modes. If we accepted this
view, we would also assume that a right-hemisphere leading part develops ontogenetically to serve as the organizer of global or gestalt processing. The brain could then be said to engage in two broadly defined modes of processing, one organized by a left-hemisphere leading part, and one organized by a right-hemisphere leading part.

Of course, we do not want to claim that the brain has only two modes of function. The techniques used to identify these processing modes are only sensitive to lateralized modes. In systems theoretical terms, they are sensitive only to modes of function for which there is a lateralized leading part. When a subject performs a verbal task, for instance, we infer a distinct mode of processing because that mode has certain observable consequences: the subject is sensitized to visual information presented in the field contralateral to his dominant hemisphere (Kinsbourne, 1970), and to verbal information presented to his right ear (see, for example, Kimura, 1967). Furthermore, he tends to move his eyes to the right while engaging in verbal activities (Kinsbourne, 1972), and if he is speaking, he makes more movements of the right side of his body than of his left (Condon and Ogston, 1971; Kimura, 1973). Other kinds of activities, however, do not provide evidence of lateralization, or they provide evidence of a lesser degree of lateralization. These activities, we might then infer, involve processing modes for which there is no lateralized leading part, or they evoke some balance between two lateralized processing modes.

In any case, in adopting a systems view of lateralized functions, we hypothesize that such functions are whole-brain modes and that the modifier "lateralized" simply means that one hemisphere contributes more influentially than the other to the character of the processing. Since there are at least two differently lateralized processing modes, the term "dominance" can only be ascribed to a hemisphere with reference to a particular mode of functioning. Furthermore, in contrast to the static dominance view, dominance must be considered a temporary hemispheric characteristic evident only when the mode of processing with which it is associated is evoked.

Possible Tests of, and Empirical Evidence for, the Systems Hypothesis

The systems theoretical perspective on dominance in the mature brain does make testable claims to distinguish it from current views. Specifically, it claims that differentiation of function is incomplete and that the term "dominance" must therefore refer to the temporary emergence of a leading part. From this, at least two predictions follow. First, both hemispheres in the normal brain must contribute to all processing modes, even if in different degrees. Second, a nondominant hemisphere in the normal brain should contribute even to tasks it is unable to perform in isolation; a whole normal brain will therefore perform a given lateralized task more efficiently than the isolated dominant hemisphere of a callosalized individual.

If the first prediction is correct, then the right hemisphere of an intact brain must contribute to phonetic processing, even though it demonstrably cannot do so in the callosalized brain (Zaidel, 1974). Dimond's technique for assessing left- and right-hemisphere contributions to word recognition (Dimond, 1971) might be adapted to test this prediction. Dimond presents pairs of words, one each to two of the four hemiretinae, such that the words are transmitted, directly, both to the left hemisphere, both to the right hemisphere, or one to each
hemisphere. Subjects report the items more accurately, if the words are transmitted to different hemispheres than if both are transmitted to either hemisphere alone. These results suggest that the right hemisphere contributes to the processing of those words that are presented in the left visual field. If it did not so contribute, then the best condition in the experiment should be that in which both words are presented to the left, language-dominant, hemisphere.

Dimond's paradigm might be altered so that the occurrence of phonetic coding could be observed and measured. One technique for demonstrating the occurrence of phonetic coding in reading 3 involves tachistoscopic presentation of word pairs. The words are either totally unrelated or phonetically related. One of the words is marked to its left with a star, and the subject's task is to read the starred word as quickly as he can. The finding is that vocal reaction times in reading the starred word are significantly longer if members of the word pair are phonetically related than if they are unrelated. The difference in mean reaction time between the phonetically related and unrelated word pairs is a measure of phonetic interference. Merging this paradigm with Dimond's, the word pairs presented to the different hemiretinas might be phonetically related or unrelated. If the right hemisphere contributes to the phonetic processing of words transmitted directly to it, then the phonetic interference effect should be less if items are presented to different hemispheres than if both are presented to the left hemisphere. If the right hemisphere does not contribute to phonetic processing, then the interference effect should be the same in all conditions.

The second prediction has already been tested by Milner and Taylor (1972) for a mode of processing generally attributed to the right hemisphere. They showed that commissurotomized subjects are inferior to controls (with intact commissures, but comparable extracallosal brain damage) in their performance on a tactile memory task. This result obtained even when the left-hand (right-hemisphere) performances of the two groups were compared. An analogous experiment, intended to generalize the claim to left-hemisphere modes of processing, would assess the left hemisphere of a callosalized individual on some linguistic task in comparison with the whole brain of an appropriate control subject.

Finally, the systems view is compatible with, and is able to incorporate, current evidence on lateralization and on attentional effects in normal subjects. Thus, it already has a firm empirical base. However, the strongest argument for the systems view is neither its testability nor its compatibility with current evidence on dominance. It is, rather, that the view provides a perspective on dominance that effaces an anomaly in hemispheres theory—the failure of language to develop in a hemisphere with the capacity to acquire it.

REFERENCES


3 Carol Fowler and William Fischer, 1975: unpublished data.


