Asymmetrical Function of the Brain

Edited by Marcel Kinsbourne

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CAMBRIDGE UNIVERSITY PRESS

CAMBRIDGE
LONDON-NEW YORK-MELBOURNE

Published by the Syndics of the Cambridge University Press
The Pitt Building, Trumpington Street, Cambridge CB2 1RP
Bentley House, 200 Euston Road, London NW1 2DB
32 East 57th Street, New York, NY 10022, USA
296 Beaconsfield Parade, Middle Park, Melbourne 3206, Australia

© Cambridge University Press 1978

First published 1978 Reprinted 1979

Printed in the United States of America
Typeset by Automated Composition Service, Inc., Lancaster, Pa.
Printed by Hamilton Printing Co., Rensselaer, N.Y.
Bound by Payne Edition Bindery, Inc., Chester, N.Y.

Library of Congress Cataloging in Publication Data

Main entry under title:

Asymmetrical function of the brain.

Includes index

1. Cerebral dominance. 2. Laterality.

3. Brain - Localization of functions. 4. Cognition.

I. Kinsbourne, Marcel.

[DNLM: 1. Laterality. 2. Brain - Physiology. 3. Behavior. 4. Cognition. W1335 A861]

QP385.5,A85 612'.825 77-8633

ISBN 0 521 21481 5

Editorial preface

In principle, the fact that some cognitive functions are asymmetrically represented in the human brain has been accepted by neuropsychologists for more than a century. But only recently has it become apparent how pervasive a property of higher mental functions is their asymmetrical representation at the cerebral and even the thalamic level. The left lateralization of verbal processes had long been regarded as a curious exception to the generally bisymmetrical organization of the vertebrate central nervous system. As an increasing number of different left-lateralized processes came to light, an increasingly strained effort was made to write them all off as verbal or at any rate verbally mediated. This conservatism finally succumbed to the clear demonstration of complementary specialization of the two hemispheres. Now that we know both hemispheres exhibit specialization, the question is the reverse: Are there any cognitive functions that are not asymmetrically represented? It cannot, as yet, be asserted that there are.

This book illustrates the types of investigations that have led to this upheaval in neuropsychology. In Part II, productive clinical neuropsychology programs are summarized that bear on double dissociation of cerebral representation of cognitive function. In Part III, the early discovery and modern interpretations of asymmetries in normal human behavior are considered. In Part IV, light cast by behavioral asymmetries on species-, age-, sex-, and handedness-related differences in cerebral organization are considered. Parts I and V place these issues in a biological framework.

The editor respectfully dedicates this book to Professor Oliver Zangwill, who pioneered the concept of complementary specialization of the cerebral hemispheres and has had fruitful influence on generations of neuropsychologists. We are all much in his debt.

Marcel Kinsbourne

Toronto, November 1977

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Contents

	Editorial preface vii Contributors ix	
	I. Biological origins: preamble	
1	Biological determinants of functional bisymmetry and asymmetry Marcel Kinsbourne	3
	II. Studies of lateralized lesions	
2	Functional cerebral hemispheric asymmetry Sidney Weinstein	17
3	Hemispheric asymmetry as evidenced by spatial disorders Ennio De Renzi	49
4	Spatial and temporal factors in visual perception of patients with unilateral cerebral lesions Amiram Carmon	86
5	Direct examination of cognitive function in the right and left hemispheres Robert D. Nebes	99
	III. Studies of behavioral asymmetry	
6	Lateral dominance as a determinant of temporal order of responding E. Rae Harcum	141
7		267
8	Lateral asymmetries revealed by simple reaction time James Swanson, Alexa Ledlow, and Marcel Kinsbourne	274
9	Asymmetry of electrophysiological phenomena and its relation to behavior in humans Gail R. Marsh	292
10	Weber on sensory asymmetry	-,-
	I.D. Mallon	318

	IV. Comparative studies	
11	Manipulative strategies of baboons and origins of cerebral asymmetry Colwyn Trevarthen	329
12	Dichotic listening and the development of linguistic processes M. P. Bryden and F. Allard	392
13	Sex differences in spatial ability: possible environmental, genetic, and neurological factors Lauren Julius Harris	405
14	Human handedness Robert E. Hicks and Marcel Kinsbourne	523
	V. Biological origins: perspectives	
15	Evolution of language in relation to lateral action Marcel Kinsbourne	553
	Name index	567
	Subject index	578

PART I BIOLOGICAL ORIGINS: PREAMBLE



1

Biological determinants of functional bisymmetry and asymmetry

MARCEL KINSBOURNE

At times progress in an area of research encounters technological limitations, and at times the limitations are conceptual. At present, progress in the area of brain organization as it relates to behavior is limited for the most part by the use of inadequate theoretical models. The switchboard model (Kimura, 1961; Geschwind, 1965) conceives of brain function as an exercise in information flow and ignores the possibility of dynamic interactions between areas of brain. It is concerned with the time required for a message to travel from one point in the brain to another and the extent to which its intelligibility is impaired by the journey. Although it has served a useful purpose, this model underestimates the capabilities of the brain and our ability to understand them. Switchboard theorists also exaggerate the range of behavioral phenomena that lend themselves to this passive type of modeling. After all, connections between any two points in the nervous system not only may transmit information, they also may mediate either excitation or inhibition (Sherrington, 1906; Kinsbourne, 1974a). The switchboard model is based on the notion of passive stimulus-response relationships. Rather than adopt this pretence that it is natural for animals to be passively exposed to input and to jerk lawfully in response, we acknowledge that normally an animal searches actively for information. Here follows an idealized minimal account of the behavior common to all active bisymmetrical organisms (Bilateria).

THE SEARCH CYCLE

Begin observing the individual while he is in an inert, vegetative state (parasympatheticotonus). After a time, under the influence

of some drive, he enters an alert or sympatheticotonic state. This is a state of search (or of problem-solving thought, its internal equivalent). Both external search and problem-solving thought are characterized by specific mental sets that in themselves are fashioned from expectancies and their relative payoffs.

Orientation

The beginnings of search are anticipatory receptor orientations, exploratory in various directions and by means of various sense modalities. In the course of these orientations, if they are external, the individual may happen upon an event, which he then experiences. If they are internal, he may remember an event. That event then generates further (reactive) orientations for the purpose of data acquisition (the data being events or memorandums). Each orientation is followed by data analysis. Reactive orientation continues until there is enough information to satisfy a preset decision criterion. That decision, however elaborate it is, must incorporate a choice between approach and withdrawal (Schneirla, 1959). If the decision is to withdraw, then the search continues and subsequently resumes the above-mentioned sequence. If the decision is to approach, there follow locomotion (if the object is at a distance), grasp, and consummation. The proceeds of consummation restore the inert parasympatheticotonic state, which later is the point of departure for a repeat of the search-initiated cycle. With respect to this sequence, search through consummation, we can now consider which component steps must for adaptive purposes be bisymmetrically represented and which can plausibly depart from bisymmetry without detriment to their adaptive usefulness.

Bisymmetry is an improbable state of affairs. For any biological system to be exactly counterpoised could hardly occur by chance. Bisymmetry must be the outcome of natural selection based on adaptive advantage. It was first developed for purposes of efficient locomotion and swift turning to either side and is not necessarily perpetuated if the organism evolves to a sedentary mode. Even when it occurs, bisymmetry is presumably approximate rather than perfect, as is the rule with biological systems (in contrast to engineering systems). So there must be further fine controls to correct inequalities inherent in the primary balances (between right and left turning; Kinsbourne, 1974a).

To illustrate these principles, consider turning behavior from the point of view of the most ancient bisymmetrical organism, a wormlike creature (Hyman, 1940). Being elongated and terrestrial, the worm must be able to turn right or left. As worms do not have special senses, we can relate the origin of bisymmetry primarily to this motoric requirement: to be able to turn with equal effectiveness and speed either to the left or to the right in relation to external events that with equal probability could occur on either side. So, right orienting and left orienting in terrestrial animals are the basic behaviors that make bisymmetry necessary, and whatever control center encodes such turning in a particular animal must therefore be represented in both halves of the nervous system. These opposing tendencies are in mutual inhibitory balance, and the organism travels along the vector that results from their interaction (Kinsbourne, 1974a). In such turning behavior we see directional biases only if we set up artificial conditions specially designed to make manifest any inherent lack of complete equality in the balance between these opposing tendencies. Suppose an animal has more tendency to turn to the right than to turn to the left, although adaptively it is most useful to be able to turn with equal facility to either side. Such an innate bias to one side can be corrected in two ways: by external stabilization using the spatial framework provided by sensory input to hold the animal on its course, or by "voluntarily" deciding to turn more to the weakly represented side than the other. For instance, a lower animal that normally travels in a straight line might, when deprived of its distance receptor information, travel in a trajectory with a systematic bias in one direction (Kinsbourne, 1974b). Analogously, if a human being is asked to divide his attention between an auditory message to the right ear and another to the left, without knowledge of results or preconceptions about how he is doing, he might reveal an otherwise compensated bias to one side. But, if he knew he had missed some trials on one side, he could readily compensate by shifting his attention to that side (at the expense of the other), thereby masking the basic imbalance. A special case in which a turning bias goes uncorrected is when the subject is preoccupied with some other task and the axis of attention is not relevant to that main task. This reveals a bias which, had the subject been aware of it, could have easily been overcome. This conceptualization applies to experiments on task-specific lateral direction of gaze while thinking. When righthanded people are asked to solve verbal problems, they usually look to the right while thinking about them; if they are asked to solve spatial problems, they look up and to the left while doing so (Kinsbourne, 1972, 1974c). However, they could easily think in these modes without deviating gaze in these ways and, indeed, do so once they become self-conscious about where they are looking while thinking.

Coding

When the orienting is completed and data analysis proceeds at a more abstract level without further need to refer to external stimuli, bisymmetry becomes less necessary. Abstracting or coding the information need not be done equally on the two sides. So the adaptive pressure toward bilateral symmetry relaxes with respect to that stage of information processing, and as bisymmetry occurs only when there is need for it, there is, in fact, asymmetry when that need is absent. Therefore, higher mental functions would be expected not to be symmetrically represented, there being no reason why they should be; and, in fact, they are not.

Locomotion

Orienting is the first step in the approach sequence. Given the decision to proceed, it acts as point of departure for locomotion to the target (unless an approach decision is made for a target that happens already to be within reach, in which case grasp supervenes at once). Basic to any decision to act is the choice between approach and withdrawal (Schneirla, 1959). That, too, must be bisymmetrical, because where one goes is determined by external circumstances not under his control that are distributed unpredictably to the right and left in space. So the locomotor apparatus is bisymmetrical; but even there minor wrinkles can be demonstrated. For example, in order to help them locomote, fish have fins that steer them in various ways like rudders, and these fins are not equally thick and muscular on both sides (Hubbs & Hubbs, 1944). In most species they are more muscular on the right. But for actively mobile species, the somatic asymmetry is not so severe as to impair the streamlining that makes for mechanical advantage in movement.

Consummation

Having approached its target, the animal exhibits consummatory behavior. For instance, it manipulates and chews. Here the need for symmetry depends on what is done, which in turn is limited by what the species is capable of. Most species act bimanually with the forelimbs in coordination, and for them bisymmetry is advantageous and therefore expected. So we would not expect paw preference to be a good indicator of brain organization in those species that do not normally use one paw in isolation for biologically important functions. Nor do laboratory tasks that call for single-limb response necessarily tap limb preferences even if they exist. With species that do practice unimanual activities in the natural environment, there is not necessarily any biological pressure to use each hand equally well, because once the object is apprehended one can, at leisure, so position himself that one and the same hand will do in virtually any situation. Because there is no adaptive need for bisymmetry, the scene is set for asymmetry. So at this behavioral stage one would expect asymmetry, and (in the human) it is there.

Thus, there are two functional locuses for major asymmetry in some species; at orienting and at consummating. One example of asymmetrical turning in humans is the spontaneous turning of newborns, four times more often to right than to the left (Turkewitz et al., 1965; Siqueland & Lipsitt, 1966). Another is the tendency to show a performance differential in hemifield presentation and dichotic listening in favor of stimuli emanating from one side of space rather than the other (e.g., Kimura, 1961, 1967). Both are basically elaborations of asymmetry: turning sideways, scanning sideways (Kinsbourne, 1970a, 1973, 1975). There is either physically obvious turning - of the eyes, the head, the body, singly or in combination - or a premotor attentional shift based on the same mechanism, though of shorter latency. These orienting operations are quite distinct from the consummatory acts, typically the grasp. Because hand preference as usually estimated relates to the use of the limb in manipulation, not in pointing, there is no particular reason why hand preference and side of attentional preference should be perfectly correlated. Nor are they (see Chapter 14). The asymmetries at the consummatory stage include paw preference, unequal dexterity between the two hands that usually favors the

right (Provins, 1967; Annett, 1972;), and the observation that 3-month-old babies maintain grasp far longer with the right hand than with the left hand (Caplan & Kinsbourne, 1976).

In summary, asymmetry represents a relaxation of the need for symmetry. Asymmetry occurs in inverse degree to the biological advantage of bisymmetrical representation. That advantage depends on the particular stage in behavior catered to by the control mechanism under scrutiny. Advantage may, of course, also accrue from the asymmetry itself, but this is not a necessary condition for its appearance in phylogeny.

DEMONSTRATIONS OF BEHAVIORAL ASYMMETRIES

One can demonstrate behavioral asymmetries caused by innate or preprogrammed inequalities, which normally are functionally compensated for, by experimentally observing the effect of strategically located damange or by disposing of stabilizing factors.

Lateralized brain damage

Take the phenomenon of unilateral neglect of space. When people are damaged in certain parts of one or other cerebral hemisphere, they show a striking lack of orienting turns to the side opposite to the damage. They tend not to look over to that side, but instead unduly frequently look to the same side as the damage. Unilateral neglect is an imbalance in orienting tendencies made manifest by brain damage (Kinsbourne, 1970b, 1977). It is a pathological exaggeration of the imbalance we have drawn attention to in newborn babies. An interesting finding that has been in search of an explanation is that in humans lesions of the right hemisphere of the brain cause much unilateral neglect of space in many cases, whereas left hemisphere lesions cause a little neglect in only a few cases. Why? Right and left turning in the intact human being has to be equilibrated by corrective mechanisms; there is an innate propensity to turn to the right more than to the left. Right hemisphere damage releases the overpowering right-turning tendency programmed by the left hemisphere. The effect of damage to the left side on the distribution of attention across space is not as serious, because the left-turning tendency programmed by the right hemi-

sphere is not as great. A supplementary explanation is a takeoff point in introducing the principles controlling the effect of functional proximity of control mechanisms. In the left half of the brain are located not only the facility that turns attention to the right (in all persons) but also the verbal processor (in some 96% of persons). When the verbal processor is activated because a person is anticipating speaking, listening to speech, or speaking, then that activation overlaps the adjacent right-turning control center and the verbal activity biases attention to the right. The left-turning center, in the right hemisphere, is far removed from the site of activation and is overpowered by its activated opponent. Consider the patient with brain damage and the clinician approaching him. The patient's right hemisphere is damaged, his left is in control, so he tends to turn to the right. The clinician addresses the patient. This activates the patient's left hemisphere and attention swings to the right. So the verbal interchange exacerbates the attentional imbalance, which thus becomes more observable clinically. Take the opposite case. The left hemisphere is damaged. The clinician approaches and makes verbal overtures as before. Again, the verbal processor in the patient's left hemisphere is activated. But this time it minimizes the imbalance. It is as if a "behavioral electrode" were applied to the left hemisphere to strengthen its opposition to the left-turning bias of the intact right hemisphere. This proposed mechanism is an instance of a more general principle with respect to the manner in which the functional distance between control centers affects their interaction. Any two control centers can be ranked on a continuum of how closely they approximate to each other. The degree of proximity is operationally defined as follows: The closer control centers are to each other, the more effectively they collaborate on concordant tasks and the less effectively they time share on discordant tasks. Conversely, the further apart they are functionally, the less effectively they collaborate on concordant tasks, but the more effectively they time share on discordant tasks.

Dual-task interaction studies

We have demonstrated the effect of functional distance in intact humans in two main ways: by showing how two processors in one hemisphere interact and by showing how a processor in one hemisphere interacts with the orientor in the same hemisphere. Inciden-