



0149-7634(95)00070-4

Lateral Asymmetries in Infancy: Implications for the Development of the Hemispheres

COLWYN TREVARTHEN

*Edinburgh Centre for Research in Child Development, Department of Psychology,
The University of Edinburgh, U.K.*

TREVARTHEN, C., *Lateral asymmetries in infancy: implications for the development of the hemispheres.* NEUROSCI BIOBEHAV REV 20 (4)571-586, 1996.—Cerebral asymmetry of cognitive processing of stimulus information is commonly viewed as a neocortical phenomenon. However, a number of lines of evidence give innate asymmetry of brainstem motivating systems, which anticipate experience, a key role.

Spontaneous asymmetries of gesture and emotion can be observed in infants, who entirely lack language and visuo-constructive skills. Motives for communication in early life may direct subsequent development of complementary cognitive systems in left and right hemispheres. In split-brain monkeys, lateralized motive sets, intentions for manipulation by one hand, can determine which hemisphere will see and learn. Evolutionary antecedents of cerebral asymmetry appear to affect motivation, social signalling and bimanual coordination, with secondary effects in perceptual processing and learning.

The hemispheres of adult humans differ in links with neurochemical systems that regulate motor initiatives, exploration and attention, and the approach/withdrawal balance in social encounters. Asymmetries in emotional and communicative behaviour in infancy support evidence that an Intrinsic Motive Formation emerging in the embryo human brain stem regulates asymmetries in development and in functioning of the cerebral cortex. Copyright © 1996 Elsevier Science Ltd.

Lateral asymmetries Motivation Emotions Communication Gestures of infants Embryology of human brain
Intrinsic Motive Formation

INTRODUCTION: WHAT ARE THE ORIGINS OF COGNITIVE ASYMMETRIES?

WE MAY not explain cerebral lateralization of cognitive functions unless we give attention to the generation, at all levels of the brain, of *motive impulses* that cause the subject's active motor involvement with the environment and selective attention. Understanding of cognition, i.e. the processing of environmental input, may not be enough.

Bilateral asymmetry of movement, in human expressive gestures and hand skills and in the locomotion of animals, has been known since ancient times. Brain asymmetry in humans was first demonstrated for a loss of movement, viz. speaking, resulting from a left frontal lesion. Nevertheless, the past century and more of neuropsychology has been predominantly concerned, not with acts, but with perceptual information processing in the posterior cortex, and with memory. The subject of neuropsychological tests is usually required to discriminate, scan, understand or remember stimuli. Contemporary neuropsychology presents a chart of higher psychological functioning defined by measured levels of performance in such experience-processing tasks (6).

Asymmetry characterizes core integrative processes of intelligence. Language is an acquired skill expressing symbolic thought, and visuo-constructive (eye-hand) abilities

depend upon imaginative construction of abstract images of spatial configurations outside the subject's body. Certain effects of unilateral lesions, such as perceptual neglect and prosopagnosia, indicative of anatomical lateralization for specialized kinds of motivation, or strategies in the attentional dynamics of consciousness for specific cognitive tasks, including interpersonal communication, have proved difficult to comprehend in the cognitivist theoretical frame, as have the influence on cerebral asymmetries of function of sex, handedness and mysterious correlations between these two.

We should remember that, in normal behaviour of intact subjects, it is gestures of communication, manipulative hand preferences, learned skills such as playing musical instruments, using tools, etc., as well as transitory orienting tendencies, that exhibit left-right asymmetries. Asymmetry in perceptual processing tests is measured in speaking, expressive gestures and voluntary motor co-ordination and in problem solving. It would seem reasonable to conclude that the origin of the asymmetry may be in the activities of the brain that precede and anticipate uptake of information from the environment, i.e. in motivation, attention and intention. With a change of theory that recognizes the priority of intrinsic motor planning and prospective motor imagery in cognition, and that also takes account of the expression of emotional states related to anticipatory self-regulation and

the subject's evaluation of the consequences of intended action, a different perspective on cerebral asymmetry of awareness and memory can be proposed, one that seeks the origins in cerebral activities that *anticipate* experience.

None of the functions of the neocortex is independent of reciprocal relations with the subcortex (22,131,133). Directed attention is mediated by an extensive system linking brainstem and cortex (77). Emotions arise as centrally generated states involving many levels of the brain, frontal cortex acting as the neocortical integrator of emotional expressions and emotional awareness (29,40,89). The neocortex is intimately linked to the basal ganglia, which communicate directly with hindbrain and midbrain motor structures, and to the limbic system, which has close anatomical links with the visceral, autonomic and endocrine parts of the brainstem reticular formation and hypothalamus (44,69,70,81,93). The cerebellum has massive two-way connections with the neocortex, notably between the prefrontal cortex and the neocerebellar vermis. All of the above are implicated in the interpersonal communication of dynamic emotions.

Integration of emotional displays, emotional states and regulation of emotional balance in relation to cognition and learning implicates limbic forebrain systems, the basal ganglia, and temporal and frontal cortex, especially the orbito-frontal cortex. A number of parallel systems linking prefrontal cortex with subcortical structures (caudate, nucleus accumbens, globus pallidus and ventral anterior and medial thalamus) are implicated in neuropsychiatric disorders (11). Two centres have been identified as essential for the relating of emotions to social experience and for the development of a reflective (cognitive) understanding and voluntary control of emotions; in the amygdala and temporal mesocortex (1,58,78,100), and in the orbito-frontal cortex (11,16,28,36,144). Orbito-frontal and temporal pole cortex develop extensively after birth and are presumed to modulate the activities of the infant's brainstem emotional system (109). Both regions are known to develop asymmetries, and particular attention has been given recently to asymmetries in frontal EEG activity in the final months of the first year of infancy (13). These correlate with cognitive developments, with different states of interpersonal contact and associated emotions, and with persistent temperamental characteristics (4,14,15,26).

Behaviour that is coordinated by the cognitively unsophisticated newborn brain, can offer conclusive evidence about what is asymmetric in the brain before cognitive development. If the motor patterns and responses of a newborn are already asymmetric, this would indicate that, indeed, laterally differentiated cerebral systems seeking experience are fundamental to later acquired cognitive processing asymmetries and memories. Furthermore, if newborn infants show asymmetry in communication and emotion, in expressions of emotion and in brain activity responding to emotive situations, this would carry the argument further, implicating subcortical core brain systems that are known to mediate emotional states, giving support to the hypothesis that cerebral asymmetry of perceptuo-cognitive functioning is founded on an embryogenic asymmetry of core regulatory and motor representational systems. Developmental studies into prenatal emergence of brain systems and the appearance of left-right asymmetries in body anatomy and movements of embryos and fetuses can bring direct

evidence on the epigenesis of cerebral mechanisms that become important in cognition after birth.

Given the old assumption that higher mental functions are acquired by a cortex that is uncommitted and in which functions are widely and stochastically distributed, the discovery of anatomical asymmetries in the auditory association cortex of the temporal planum posed a paradox, and at first von Economo's evidence was questioned or overlooked. Then it was demonstrated that this and other hemispheric asymmetries exist in foetal brains (114). In what form could the asymmetry of linguistic function be determined before there is any knowledge or use of language? What are the anatomical relations of the asymmetric areas with the rest of the brain that is formed before birth?

All considered, the asymmetries described in the behaviour of brain injured adults have been, in some degree, artefacts of prevailing psychophysical and psychometric theories and methods. These may not reveal the role of crucial intrinsic factors in development and evolution of brain systems, including intersubjective or social functions. Comparative studies of sub-human animals give rise to a similar suspicion. In lower vertebrates, cerebral asymmetry appears to affect autonomic control and sexual motivation; in rats, asymmetries are seen in brain systems for locomotor orienting (35); in birds, the cerebral control of singing is lateralized in the left half of the brain (83), and in monkeys and apes, social signalling and bimanual coordination are under asymmetric cerebral control (18,38,47,142). Lateralized effects in human perceptual processing, symbolic thought and categorical learning may turn out to be evolutionary derivatives of these older deep-seated asymmetries, especially as these may affect the extrapyramidal motor system which regulates expression of emotion in social encounters (93).

Here, I will first summarize evidence on the role of motives for one-handed activity in lateralization of visual learning in split-brain monkeys, and the results of experiments on the dynamics of consciousness in commissurotomy patients. Then, I will give an account of the development of lateral asymmetries in expressive behaviour and communication in infancy and early childhood. I will argue that asymmetries of perception and cognition reflect innate asymmetries in morphogenetic regulators and motivating systems for human communication that grow in the foetal brain, and that neocortical systems which perform perceptual categorization are products of post-natal selection processes, in which asymmetrically generated emotions transmitted in interpersonal encounters play a major regulatory role.

MOTIVES REGULATING AWARENESS AND LEARNING IN SPLIT BRAINS

In 30 years of research on hemispheric localization of learning, I investigated the relationship between subconscious processes that impel the subject to act, and the higher cognitive operations in which particular parts of the cerebral cortex take in different kinds of perceptual information. In 1958, in Sperry's laboratory at Caltech, I observed that what a chiasm-callosum sectioned (split-brain) monkey saw and remembered, i.e. in which hemisphere visual perception and learning occurred when both hemispheres were presented relevant stimuli, depended on which hand the animal chose for a response (119,120). I concluded that this was evidence

for a fundamental asymmetry in volition—that intention could instruct experience. In the 70s, I summarized work with split-brain monkeys and human commissurotomy patients, defending the claim that activities of the neocortex, whether it was split in two or not, were directed intrinsically by purposeful impulses generated in the brain as a whole, and not just processing the input of stimulus information at the cortical level (123,124).

The results of tests of interhemispheric transfer or cross-integration of visual inputs to the divided brain with certain kinds of stimuli led to the theory that, in primates, as in all vertebrates, visual systems are distributed in the brain in relation to a hierarchy of motor coordinative systems that direct the body into differing orientational relationship to the outside world, as well as impelling the sentient subject into differing prospects of commitment to objects identified as having life-relevant qualities. I specified two main active visual functions; ambient vision directing the body as a whole in locomotion and orientation, and focal vision for inspection of detail and exploration of the identities and structure of objects (121). I showed that ambient vision was not divided in human commissurotomy patients (138).

Later, I tried to interpret cerebral asymmetry of consciousness that was made evident in the tests of commissurotomy patients in terms of complementary varieties of motor initiative in looking, or in using the hands. This led to experiments in Paillard's Laboratoire de Psychophysiologie in Marseille in which I showed that a baboon built up asymmetric cerebral encoding of responses to visual stimuli and lateralized executive representations of how to deploy hand and finger movements to perform a skilled bimanual task rapidly (126). The location of the acquired skill depended on the spontaneous hand preference each animal already had for picking up food, pushing a pedal or performing careful manipulations.

Jerre Levy and I made studies of the dynamics of consciousness in commissurotomy patients, and the regulation of the different activities of the two hemispheres in relation to what the patient was intending to do, or to what he or she had been told to think about (60,61,64). We proposed that the specialized cognitions of the hemispheres were activated by cortico-subcortical motive sets that were capable of turning on or off one or other hemispheric cognitive mechanism, and that sometimes these directives acted independently of the different cognitive aptitudes on the two sides (60), an ability for directing consciousness by intention that we called "metacontrol". Later, Levy and colleagues (59,62) showed that normal subjects had habitual arousal biases that determined individual differences in the laterality of their hemispheric activity, and hence their differing effective cognitive aptitudes. Evidently lateralization of experiences could be determined by intrinsic motivating functions (131).

ASYMMETRIES OF COMMUNICATION IN INFANTS

If, as used to be believed, the newborn human has no complex psychological motives, then any asymmetries in behaviour will be attributed either to differences in peripheral anatomy that are impressing different reflex reactions on the two sides of the CNS, or to simple differences in strength of reflexes or orienting tendencies in left and right sides of the brain stem and spinal cord. Thus it has been assumed that the tendency of newborns to lie on the right side with the right hand raised is due to an asymmetry of the

"tonic neck reflex", possibly acquired by one-sided stimulation of the vestibular organs due to the lateralized position adopted by the late foetus (95), and that right-handedness is induced by the asymmetry in hand regard that is caused by the preference of most neonates to lie with head turned to the right (76). However, the tendency of foetuses to suck their right thumb more than the left from 15 weeks of gestation (42) occurs long before the foetus is lying predominantly on one side. A recent study of the Moro reflex, in which, following head drop, the arms of a newborn are extended and thrown back, has shown that movement of the right arm is faster (by 20 ms) in 82% of neonates; 12% being faster with the left arm (101). This effect is attributed to a fundamental spinal asymmetry which is evoked by input from the vestibular organs. However, observation of the spontaneous movements of alert newborns, and especially of their gestures in interaction with an attentive human partner shows that these movements are not simple reflexes. Foetuses have coordinated movements and hand preferences (8,94); there is more to newborns' laterality than postural bias or asymmetry in spinal systems. Moreover, foetuses possess integrated brain mechanisms of motor expression that are motivated for interaction with persons.

Newborn infants orient to the expressions of a sympathetic human partner and they are both sensitive to the motive states and emotions of human expression and capable themselves of expressing clear emotions (135). Within 6 weeks, an infant will focus gaze preferentially on the mother's eyes, orienting to her voice, which was remembered from experience in utero and identified at birth. When a mother speaks to a 2-month old affectionately, in a prosodically clear register called "intuitive motherese" (24), the infant becomes animated to produce cycles of expressiveness, in which smiles, vocalizations, lip and tongue movements of prespeech, movements of the limbs and gestures of the hands are coordinated. These expressions are clustered to produce emissions of phrases resembling utterances of adults in conversation (126,136). The infant is motivated to produce cycles of assertive expression alternating with apprehensive watching, and so mother and baby enter into a pattern of turn-taking called "protoconversation". The hand movements of the infant are complex and distinguishable from those made in orientation to objects that the infant is looking at or tracking (128). This difference, indicating a distinct motive process for communicative hand movements, can be seen in newborns (102). After microanalysis of many films of protoconversations and following the development through the first year, I concluded that infants' gestures are asymmetric in much the same way as those of adults in conversation. Most often, utterances of cooing and/or prespeech were accompanied by raised right hand gestures, and extending the hand and pointing with the fingers was frequently precisely synchronous with the oral gesture. At the same time, as well as in more reflective and observant phases, infants held their left hands toward their bodies and sometimes they actively touched or fingered their clothes (128).

Asymmetries observed in spontaneous expressive gestures of young infants lead to the conclusion that they reflect left-right differences in the brain systems that generate adaptive motives (128). There are also asymmetries in infants' perception of faces (108). Neonates imitate a wide range of expressions in communicative interaction with human partners (55,75). This proves not only that they possess

mechanisms that generate appropriate motor images, but also that these mechanisms are capable of taking in perceptual indices of the matching motor image in the partner. Neural "imitator" elements that are capable of making just this translation from observed action to matching motor image for hand actions have recently been identified in area F5 of the inferior premotor cortex of monkeys (19). Neurons in this area recognize motor acts; they are active when the monkey makes a movement, for example, to grasp a piece of food, *and* when a similar movement, to the same object, is made by the experimenter. There is a sympathetic response to the human being's activity in the motor cortex of the observer monkey. There appears to be a comparable substrate for recognition of facial expressions in the temporal cortex of monkeys (91,92), and systems that mediate imitation of vocalizations are also likely to be located in temporal auditory association cortex. An hemispheric asymmetry for discrimination of facial expressions and for responding to them that favours the right hemisphere has been found in split-brain monkeys (38,47,142).

In order to check the impression that infants' gestures showed consistent laterality biases, I made an analysis of asymmetries of gesture in three girls and three boys during the first five-and-a-half months after birth, using 1110 photographs taken in my laboratory in Edinburgh with a motor-driven Nikon camera while the infants were active and alert in a variety of contexts. They were supported in an infant seat in front of their mother or another partner while television recordings were made to trace the development of communication and acts directed to objects. The photographs, covering three kinds of interaction with persons, face-to-face play with the mother, facing an unresponsive mother, or confronting a stranger, were selected from a collection of 1972 as those which showed infants' hand positions clearly (128).

From these photographs taken during TV recording sessions, I obtained evidence confirming that expressive utterances in protoconversational play with the mother were accompanied most often by movements of raising and gesturing with the right hand. Furthermore, I observed a complementary bias favoring the left hand for self-touching movements. When the infants were mildly distressed, that is when they were with a stranger or confronted with an unresponsive mother (still-face situation), the pattern of gestures changed, and the left hand was more active and often moving free of the body, possibly signalling distress. This difference in asymmetries immediately suggests that different states of interpersonal motivation are associated with different activity in left and right halves of the infant's brain. It was clear that the asymmetries were highly labile and they varied from visit to visit, apparently at the mercy of intrinsic state changes in the infants' brains.

Tables 1 and 2 show that, while there were clear asymmetries in hand movements, each subject changed in the asymmetry of their gestures at different ages and that there were considerable individual differences. Table 1A shows that, in "chat" with the mother, the gestures of the girls were all weakly right-sided at 4-6 weeks, less so or left-sided at 8-12 weeks, and thereafter right-sided again. In contrast, the boys in the same situation were right-sided in their expressive gestures over the period 4-12 weeks and then less so or, in one case, strongly left-sided at 16-20 weeks (Fig. 1). This can be interpreted as possible evidence for an earlier passage through a transitory change of asymmetry in the females than

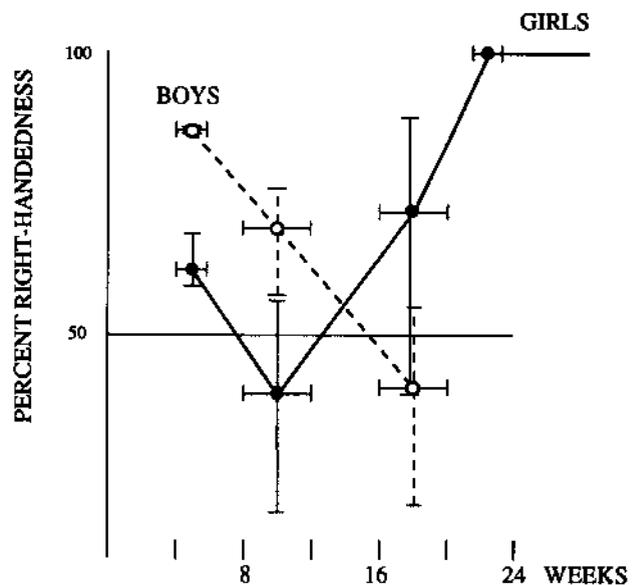


FIG. 1. Summary of handedness for gestures in communication with the mother (Table 1A). Mean values; bars show the full ranges of age and percent right-handedness scores. From this population we may tentatively conclude that both boys and girls show a decline in the frequency of right hand gestures between 8 and 20 weeks, that the boys appear to show this later than the girls, and that the laterality of hand gestures is more variable in this period (128).

in the males. On several criteria, notably in binocular stereopsis (41), auditory evoked responses (111), and in controlled reaching (46), boys tend to be developing a few weeks later than girls around 3-6 months. Our data are compatible with the interpretation that there is a loss of lateral asymmetry in gesture about the time that infants show marked development in ability to redirect or disengage visual attention (105) and when controlled reaching is developing. Regressive cycles in development are discussed below.

The counts of self-touching in communication with the mother shown in Table 1B are much more asymmetrical, and these show greater activity in the left limb. Self-touching in infants increases in tiredness and distress and it may be considered to be self-regulatory in the sense of pacifying and contributing to stabilization of state of emotion and arousal. All three girls and one boy were left-handed for self-touching at 4-6 weeks, and this bias persisted through to 24 weeks. One girl, who had the strongest left-sided self-touching at 4-6, 16-20 and 22-24 weeks, lost this bias at 8-12 weeks when she also lost her right preference for expressive gestures away from the body. That is, she was less strongly lateralized for both kinds of hand movement in the third month, just before she achieved controlled reaching. From this collection of pictures, we can conclude that, when infants are interacting with an attentive mother, self-regulating movements tend to be performed by the left hand, often at the same time as the right hand is raised in an expressive gesture.

An important correction must be made to the report I made of this data in 1990. An error in the labelling of the graphical representation of the above findings in my chapter on development of hemispheric asymmetries (134; figure 20.4, page 347) presented the left hand, self-touching, results in playful interaction with the mother as occurring when the

TABLE I
ASYMMETRIC HAND GESTURES OF INFANTS UNDER 24 WEEKS PROTO-CONVERSATIONAL PLAY
WITH MOTHER (662 photographs)

A - HAND RAISED

Age (weeks)	LP			Female SL			LO			AH			Male PL			MT		
	R/N	%	N	R/N	%	N	R/N	%	N	R/N	%	N	R/N	%	N	R/N	%	N
4-6	0.59	41	12	0.58	76	26	0.68	60	25	-	-	-	0.87	82	28	0.86	40	8
8-12	0.56	51	22	0.46	39	13	0.19	45	27	0.86	57	27	0.65	44	14	0.57	58	7
16-20	0.40	34	17	0.89	55	16	0.88	74	25	0.49	74	29	0.55	26	11	0.20	70	21
22-24	1.00	41	7	1.00	57	20	-	-	-	-	-	-	-	-	-	-	-	-
4-24	0.57	42	58	0.73	57	75	0.57	57	77	0.66	65	56	0.74	49	53	0.42	58	36
Total photos	139			131			136			86			108			62		

R/N = Proportion of photographs with right hand higher than left. % = Percent of photographs with one hand higher. N = Number of photographs with one hand higher.

B - SELF-TOUCHING (223 photographs = 34 % of 662)

Age (weeks)	LP			Female SL			LO			AH			Male PL			MT		
	R/N	%	N	R/N	%	N	R/N	%	N	R/N	%	N	R/N	%	N	R/N	%	N
4-6	0.00	86	6	0.00	88	7	0.00	67	8	-	-	-	0.00	100	7	0.39	63	5
8-12	0.25	100	4	0.67	38	6	0.50	75	6	0.10	71	10	0.24	20	4	0.00	100	2
16-20	0.00	13	2	0.00	43	10	0.16	46	6	0.44	47	7	0.22	29	5	1.00	100	1
22-24	0.00	33	4	0.17	57	12	-	-	-	-	-	-	-	-	-	-	-	-
4-24	0.06	42	16	0.17	51	35	0.20	61	20	0.24	59	17	0.13	36	16	0.38	73	8
Total photos touching	38			68			33			29			44			11		

R/N = Proportion of photographs with right hand only touching. % = Percent of photographs with one hand touching. N = Number of photographs with one hand touching. L = Left hand most active; R = Right hand most active. Significant asymmetry by one tailed Binomial Test, * = $p < 0.05$; † = $p < 0.01$

infant was distressed by confrontation with a still-faced mother or with a stranger. As is clear from the original report (128), the findings were as summarized here. They indicate that in most of the sessions self-regulating activity of the left hand (Table 1B) accompanied expressive movements away from the body with the right hand (Table 1A) while the baby was communicating playfully with the mother, *not in stressful situations*. The evidence favours the conclusion that assertive or demonstrative activity concentrates in the left side of the brain, moving the right arm and hand, often at the same time as apprehensive self-regulatory withdrawal is more active on the right side of the brain, moving the left limb.

When the same six infants were observed in the mildly stressful situations, either confronting an immobile and unresponsive mother or with a stranger who attempted conversation with the infant, expressive gestures are mixed in laterality and are variable between subjects (Table 2A and 2B). Age-related changes are known in the intensity of emotional reactions of infants to a still-faced mother, infants showing more distress at 2 months than after 3 months when they tend to avoid looking at the mother and explore surroundings. In spite of this variation, it is clear that for some of these infants, the proportion of left-sided gestures increased when interaction was more stressful.

TABLE II
ASYMMETRIC HAND GESTURES OF INFANTS: FIRST 24 WEEKS STRESSFUL SITUATIONS (448 photographs)

A - HAND RAISED

Age (weeks)	LP			Female SL			LO			AH			Male PL			MT		
	R/N	%	N	R/N	%	N	R/N	%	N	R/N	%	N	R/N	%	N	R/N	%	N
4-6	-	-	-	-	-	-	1.00	100	5	-	-	-	0.43	84	37	-	-	-
8-12	0.00	64	7	0.26	22	4	0.50	82	14	0.88	95	34	0.36	64	14	0.50	57	4
16-20	0.16	46	13	0.26	36	4	0.23	75	33	0.39	80	44	0.62	60	26	0.47	62	29
22-24	1.00	68	40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4-24	0.70	61	60	0.25	28	8	0.69	79	52	0.63	85	78	0.48	71	77	0.48	61	33
Total photos		98			29			66			92			109			54	

R/N = Proportion of photographs with right hand higher than left. % = Percent of photographs with one hand higher. N = Number of photographs with one hand higher.

B - SELF-TOUCHING (192 photographs = 43 % of 448)

Age (weeks)	LP			Female SL			LO			AH			Male PL			MT		
	R/N	%	N	R/N	%	N	R/N	%	N	R/N	%	N	R/N	%	N	R/N	%	N
4-6	-	-	-	-	-	-	0	0	0	-	-	-	-	-	0	-	-	-
8-12	0	0	0	0.00	50	5	0.17	67	6	0.00	100	13	0.50	17	2	0	0	0
16-20	0.11	59	10	0	0	0	0.30	57	13	0.85	68	13	1.00	47	9	0.50	40	6
22-24	0.02	74	31	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4-24	0.05	69	41	0.00	24	5	0.26	59	19	0.42	81	26	0.83	36	12	0.50	40	6
Total photos touching		59			21			32			32			33			15	

R/N = Proportion of photographs with right hand only touching. % = Percent of photographs with one hand touching. N = Number of photographs with one hand touching. L = Left hand most active; R = Right hand most active. Significant asymmetry by one tailed Binomial Test, * = $p < 0.05$; † = $p < 0.01$

Murray (79,80), in a detailed micro-analysis from films of movements of face, arm and hand, of eight 2-3-month-old infants in the still-face situation showed a significant increase in touching the clothes with the left or right hand, and an increased touching of the face with the right hand. The duration of right touches to the face also increased. The left arm was raised more, and the left palm was more often closed or clenched. In her original TV replay test with two subjects at 2 months of age, Murray (79) found that replay of the recording of the mother's communication to the baby, which disturbs the baby, led to increased touching of the clothes by both hands, and increased and longer face touching by the left hand, while expressive right arm raising decreased.

The evidence we have to date from the above preliminary studies supports the idea that the brains of infants have an

asymmetric motive system for assertive right hand gestures by which they regulate intersubjective contact with a mother in communication, and that there is an opposite or complementary asymmetry for self-regulating gestures to the infant's body or clothes by movements of the left hand when the baby is in a more receptive, or apprehensive, state (Fig. 2). Frightening or distressing situations favour withdrawal and self-touching, but a protesting baby's expression of anger or frustration may, alternatively, favour movement of the right limb, the same lateralization as for positive or happy gestures of communication. Mouth touching movements may also tend to involve the right hand more, at least in some states. There does not appear to be any simple correlation between positive versus negative emotions and asymmetries of hand gesture.

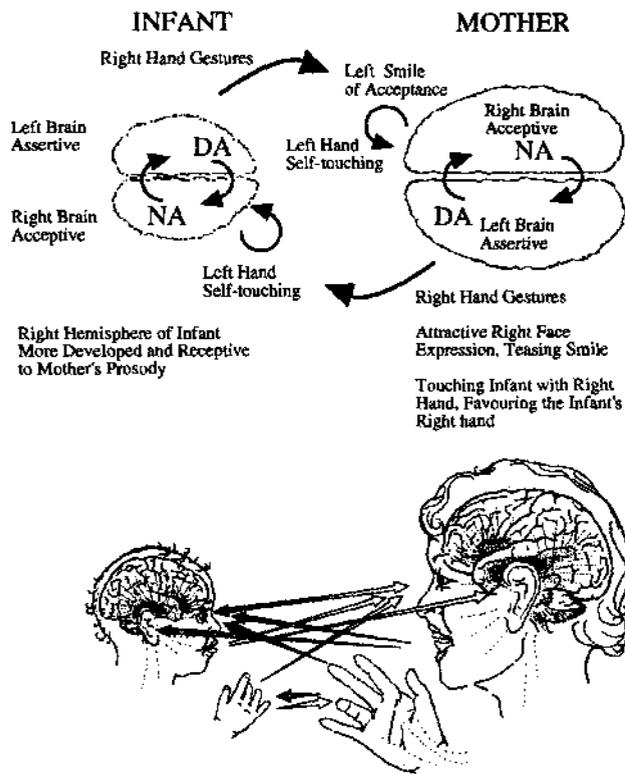


FIG. 2. Below: channels of communication that are active in proto-conversation, linking the motives of infant and mother. Above: hypothetical scheme to represent the coordination of asymmetric expressions between mother and infant, and hypothesised neurochemical asymmetries. Left hemispheres are more active in the generation of assertive initiatives. This produces the right hand gestures that accompany speech by the mother, and the baby's cooing vocalizations and "prespeech" mouth movements. The mother's teasing smile is more apparent on the right side of her face, but the left side of her face has a stronger expression of an attractive receptive smile (148). The right hemisphere is more receptive and self-regulatory (140). This leads to self-touching by the left hand. The infant's right hemisphere, which is more developed than the left (103), responds to the prosody of motherese (23, 24, 50, 104). Left hemispheres have greater dopaminergic activity (DA) associated with motor expression, while the right more attentive or more receptive hemisphere is predominantly noradrenergic (NA) (141).

Infants demonstrate these asymmetric expressions of communicative states in interaction with partners before they have acquired cognitive schemata for objects of manipulation and long before they acquire any linguistic semantic code from speaking companions. The asymmetries we have found in gestures match those made by adults in conversation (51,54). Right-handers make expressive gestures away from the body with the right hand while they make gestural movements directed to the body more with their left hands. Left-handers tend to have opposite movements.

It is highly unlikely that the asymmetries in young infants are taught by mothers, for two reasons. First, while infants are capable of imitating hand gestures from birth, mothers rarely raise their right or left hands to gesture to infants in protoconversation. In my photographs, mothers do touch the infant more with their dominant hands, and right-handed mothers show a preference for touching the right hands of their infants; but, secondly, this touching fails to influence the preferred handedness of a left-handed infant. We

observed older infants with strong left-hand preferences who have two right-handed parents and no left-handed siblings.

LATERALIZED EMOTIONS IN THE BRAIN AND THEIR DEVELOPMENT IN INFANTS

Tucker and colleagues (140,141) proposed that activation and arousal systems have lateral asymmetries. They suggest that the left hemisphere is more involved in dopaminergic action on the environment while noradrenergic regulation of attentive assimilation of experience is stronger in the right hemisphere. There is, indeed, increasing evidence that attentional regulations have a primitive asymmetry. Levy and colleagues (59,62) demonstrate the influence of lateralized arousal in the determination of individuals' habitual cognitive strategies.

The right hemisphere is evidently more active in the recognition of prosodic information that conveys emotion in the voice and in music, while the left is specialized for perception of the rapidly articulated sounds of speech (50,52,104). This asymmetry evidently is laid down prenatally. A right hemisphere advantage for hearing musical sounds develops by 2 months, and a left hemisphere advantage for speech may also be present at birth, but it develops efficiency later (74,111). Such asymmetries of auditory function are presumably mediated subcortically. They play a crucial role in the affective regulation of mother-child communication, and their development proceeds more rapidly in female infants (111).

Evidence that left and right halves of the face express different kinds of emotion or mood is conflicting and indicative of considerable individual differences. The methods of testing, which usually involve presentation of pictures of faces, including left-left and right-right composites, for appraisal by subjects who are not actively engaged in communication, have a number of problems, and there is conceptual confusion concerning the roles of experience, perception and expression in the asymmetries observed. Nevertheless, there is a consensus that the left side of the face is more often perceived as more expressive (63), and this appears to be true for monkeys as well (39). For both male and female faces, Zaidel and colleagues (148) report that left-left smiling composites appear to smile more strongly than right-right composites. The right side of the face appears to carry features for recognition of the whole face more strongly (34). Female, but not male, right-right composite pictures are judged the more attractive, and this is related to the judgement that portraits that have been painted of females over a long period of history are judged more attractive, by both male and female, if they emphasize the right half of the face of the subject (148). Infants have been shown to agree with young adults in judgements of "attractiveness" of faces (56), so it is not likely that attractiveness is entirely related to male choice of a desirable sexual partner. Schiff and Lamon (106,107) found that asking subjects to maintain contraction of one side of the face for 1 min produced emotional experiences. In most cases, right face contraction, presumed to activate the left hemisphere, led to euphoria and a feeling of "boldness", while left contraction, activating the right hemisphere, led to dysphoria or "gloominess". These findings implicate asymmetric brain activity in emotional processes that regulate approach versus avoidance or retreat in interpersonal contacts and relations, to feelings about oneself, and

to the perception of a pleasant and appealing personality in the other.

Electroencephalography and neuropsychiatry have accumulated evidence that the hemispheres differ in their relation to neurochemical systems that regulate motor initiatives, exploration and attention, self-regulation, and the approach/withdrawal balance in social encounters (140,141), and a similar neurochemical and physiological asymmetry is evident from birth (3,14,15,26,27,109). Asymmetries in emotional responses and developments in motivation in infants support the thesis that elaboration of complementary neocortical cognitive systems is directed from an asymmetric Intrinsic Motive Formation that emerges in the brain stem at the embryo stage before there are any neocortical neurons (132,137). This formation is, we claim, adapted in the human brain to regulate development of the cognitive systems of the child through communication of affects, interests and intentions.

MOTOR TIME IN THE CNS AND INFANT RESPONSES TO PROSODY

Infants have a remarkable sensitivity for the temporal patterns and intonational qualities or tensions of human expression, especially of affectionate maternal speech, playful vocalizations and singing (24,90,112,113,117,118). This indicates that babies are born with mechanisms that generate sympathetic kinematic motor representations that match the movements made by adults and that define the emotional quality of adult movements (129). There is a common code of feeling which an infant can share with the mother or any other individual who is prepared to behave with appropriate emotional and expressive involvement with the baby. Experiments using preferential orientation have demonstrated that infants can learn to recognize prosodic features of the mother's voice before birth, and that within a few months of birth, a baby has refined discrimination of many parameters and patterns of music that adults find pleasing or significant.

These findings demonstrate that the human sensitivity to kinematic features of movement, which has been charted by the classical researches of Michotte, Fraisse, Johanssen and Runeson, is part of the inborn structure of the brain. The innate structures produce both universal time-generating mechanisms and sensitivities, and individual differences in preferred tempi. Prosodic rhythms and intonational forms express innate constraints on generation of motor imagery, and these serve as detectors of expression of the same rhythms and forms in another individual's output.

Prosody carries expression of emotions on a basic parsing that is retained as the foundation of tempo and metre in poetry and music. Syllable, word and phrase units in infant's expression (66) may be related to the motor programming evident in movements of the hands, a programming that MacNeilage et al. (71) have claimed is the primary cause of cerebral asymmetry in the evolution of hemisphere functions in primates. They propose that the cerebral asymmetry of motor programming that evolved to control bimanual manipulative movements, allocating manipulations of intrusive foraging to the left hemisphere and right hand while the right hemisphere and left hand are primarily concerned with postural and visuo-spatial adaptations of limb use, was taken over in the evolution of speech, leading to the control of

rapid sequences of oral articulation by the left hemisphere while the right hemisphere retains greater responsibility for prosody. Kimura (52) has shown that the left frontal cortex is dominant in the programming of motor sequences. Arbib and Dominey (2) propose that sequential and non-sequential eye movements are mediated in primates by a system that integrates thalamocortical afference (visual corrective feedback) with internal motor command (efference copy) information mediated by basal ganglia. Rhythmic movements of the hands map easily onto the rhythmic movements of jaws, lips and tongue in speech and in conversation hand gestures often match and synchronize with speech. In newborns, rhythms of arm movement synchronize with saccadic eye movements. This coupling and visual-oral-manual equivalence in communication is evident in the ease with which a deaf toddler in a deaf family can learn to use sequences of hand gesture phrased in time with rhythmic arm movements for the expression of a sign language as competent for communication of ideas, feelings and intentions as is the ordinary speech of a hearing toddler in a hearing family. Humans have a faculty for "speaking to sight with their hands", something all of us are prone to do in conversation, unconsciously (73). Instrumental music is developed out of this multimodal rhythmic facility as a cultivated art form with dramatic narrative appeal.

Georgopoulos, recording from neurons of the motor cortex of monkeys while they are reaching for targets, has demonstrated that neural populations are tuned to the direction of movement and that different neural assemblies specify different directions of movement, and the duration of the movements (30,31). By measuring movement time and kinematics, he has shown that "neural population vectors" monitor in time the processing of directional information as the movement is being intended. In humans and monkeys, the durations of reaction times match the number of degrees of change when a reaching movement is reprogrammed to an off-target direction; that is, RT measures the transformation of the motor preparation or the "time of intention for the movement". The recorded neural population vectors track in time the rotation of mental representation, not the afferent effect in movement. In drawing, the relationship between speed and curvature of hand movements results from "central constraints", and not from biomechanical factors relative to the motion or inertial load of the arm (49). Changing the direction of an upcoming movement is a time-consuming process whose duration is proportional to the angle of directional change. These psychophysical and physiological findings prove that the brain generates internal temporo-spatial representations of arm and hand movements (49).

Such representations, in an immature but functioning form, may explain the innate abilities of infants to produce rhythmic and melodic forms of movement that match intrinsic kinematic features of adult movements, and to enter into synchronized, imitative or complementary interactions with an adult partner (10,129). They also explain the sensitivity that infants have to contingent stimulus effects of their own actions (143) and the distress that is caused by making a partner's movements non-contingent or uncorrelated with the cycles of expression that the infant is producing when making an attempt to communicate (80,136).

It is probable that intrinsic mechanisms of motor representation have a fundamental asymmetry of organisation. While musical and prosodic features of vocalization and

music are apprehended better by the right hemisphere (50,104), rapid sequencing and the articulation of speech are lateralized to the left hemisphere (52). Infants are more receptive to prosody by the left ear, but they develop a right ear preference for hearing speech (23).

ASYMMETRY OF MANUAL SKILL AND GESTURE AND THE DEVELOPMENT OF LANGUAGE

In the second 6 months of the first year, infants develop effective manipulation of objects and cooperative communication about shared topics of interest. The asymmetries of gesture seen in the first 6 months are consolidated and, at least in some individuals, the final hand dominance will be established by one year. When preferences for using the hands in communicative expression and in handling of objects are charted together, the two kinds of behaviour exhibit related or linked asymmetries, but the manipulative asymmetries, though they are the most studied, are neither primary nor the most marked. Indeed, preferences for manipulation develop later than preferences for gestural expression.

The above group of infants under 24 weeks of age was observed reaching when mothers presented objects (128). No lateral preferences were observed in reaching. In a test of imitation in which the mother protruded her tongue and waited for the infant to do likewise, some of the infants put a hand to their mouth instead of poking out their tongue. After 20 weeks, several attempted to touch their mother's tongue. Subjects SL, LO, PL and MT, all of whom were right-handed later as toddlers, showed right-hand preference for touching their own or their mother's tongue around 6 months. AH, who became left-handed by 2 years, raised his right hand at 12 weeks while watching his mother poke out her tongue, but touched his mouth with his left hand at 20 weeks.

Photographs of 10 infants in addition to those subjects discussed above were studied from recording sessions made in the laboratory when the infants were between 24 and 56 weeks of age. The infants were playing with their mothers with and without objects, and the pictures give evidence on asymmetries in both gestural and manipulative movements. Nine of these subjects, five girls and four boys were videoed playing with representational toys at 25–28 months, and their hand preferences were scored. Two girls were mixed but more left-handed, one used the two hands equally, one EB, was totally left-handed in her intended, meaningful movements and communicative gestures, and the fifth was right-handed. Three of the four boys were right-handed, and one showed equal use of left- and right hands. At 36–39 months, all children had become right-handed, except EB, who remained entirely left-handed, and one girl who had changed from being weakly left-handed to mixed in her handling of the meaningful objects. Before one year, nine of these infants preferred their right hands for touching their mother's mouth or tongue in the tongue protrusion test; EB, alone, preferred her left hand. She also clapped hands with her left palm above the right, while the others either held both hands up vertically or clapped right over left. Imitated displays of various other tricks with the hands, such as gesturing with an extended index finger or posing with thumb and index touching in a ring, and also holding objects up to show them to a partner, were performed most frequently with the right hand by all infants, except EB. Self-comforting movements when the infants were in front of a

stranger or protesting at being too long in the chair were frequently made with the left hand. No clear preferences were recorded in reaching and grasping for a suspended ball or manipulative play with wooden toys, but hand preferences have been reported for interception of moving objects by infants 18–36 weeks of age (45).

Infants, although they often make pointing gestures while vocalizing or making a prespeech utterance in early months, appear to follow mothers' pointing before they make pointing gestures themselves as deliberate messages to attract another's attention, which they begin to do at 7 or 8 months (147). After 9 months, infants combine gestures and vocalizations to express communicative messages that have a clear intersubjective intention or "illocutionary force". Studies of object manipulation generally have led to the conclusion that infants reach more with the left hand between 3 and 6 months, then increasingly prefer the right hand as visually directed manipulation improves. Early babblers also show lateral asymmetry of object prehension earlier (98). Rhythmic banging of objects, which infants do at the age they babble, has the same periodicity as babbling, which suggests a common cerebral time-keeper.

Young infants cannot accept and articulate with the different ego-center (origo) of a partner's acts and interests, but they watch movements, and by 6 months they pay attention to others' hands and try to follow. At 9 months, they deliberately point, and they begin to show signs of wanting to share the attentions and intentions that familiar partners give to objects by following their pointing or gaze. A one-year-old distributes attention systematically between multiple goals, a function now identified with the frontal lobes which are undergoing marked development at this age (20). The baby also willingly accepts gestural and vocal indications of how to share a task that involves selective manipulation of objects in novel combinations. Developments in motives for communication accompany cognitive advances demonstrated in "object permanence" tests, and tests of the infant's ability to inhibit motor impulses and to memorize one of two possible goals. These intellectual skills are guided by impulses of the child to identify and follow the feelings and interests of familiar companions (130). Thus, the entry to symbolic communication requires a step in the development of intersubjectivity or mental engagement. It requires the child to be adept at negotiation and interpretation of purposes and interests, abilities that the infant practised in the first year.

In the second year, infants becoming toddlers copy expressions, manners, actions, roles and imitate the use of tools and toys. They share this knowledge in communication and action before they make words or sign language. Vocal or gestural approximations to words in the maternal language emerge within this "acting to mean" (7,65). Names for objects and verbs for actions, are picked up by the toddler sharing the other person's foci of interest, and emotive descriptors and grammatical functors that regulate interpersonal initiative and locate agency are built upon a shared prosody of expression that requires matching or sympathetic emotional spectra in the learning child and teacher. Autism and other empathic disorders interfere with this process of access to meanings in communication and the codification of meanings in language (137). The "vocabulary explosion" at 20–30 months occurs when the child has a new compulsion to share items and narratives of experience, as well as a desire to identify things

that communication "needs" to name (65). Sign language is learned by deaf children in signing families at this age, and grammatical rules are acquired at the same rate in both speech and sign. Hand gestures are part of conversational expression from birth (73).

Infants who had been studied in the first year from both groups described above, 14 in all, were observed in videos at 19, 25–28 and 36–39 months. We recorded a strong link between the stabilization of hand preferences for using objects correctly in imaginative games and the development of speech. "Correct" use of objects increased greatly after 19 months. The left-hander EB was both early in exhibiting a strong and stable hand preference for employing objects with meaning and the earliest to achieve fluent multi-word sentences. Infants who were mixed in handedness through the third year were slow in speaking. All showed their hand preferences in complementary patterns. The dominant, more "intentional" hand manipulated significant objects while the other hand stabilized or stored other objects. This division of labour was seen in such tasks as scraping a plate, dealing cards, laying out cutlery, taking coins from a purse, cradling a doll to give the bottle, etc. The girl EB and the boy AH differed from the other 12 children observed in performing all such tasks with the left hand as principal actor, and the right hand in a supportive role.

As children begin to master conventions of regular grammatical forms, they start to think of explanations free of their own feelings and desires, or the feelings and desires they sympathetically attribute to others. At the same time, at 3–4 years, meta-representational "theory of mind" tasks are solved that require verbally taking the perspective of the other, or dealing with a "three-person" arena of meanings. The child learns how to think in and about language, and this is facilitated by school instruction in the use of text and narrative form, and how to avoid ambiguity in explanations and stories. These language skills make increasing demands on strategic or analytical use of memory, and on subtle expression of others' knowledge and states of mind. They are consolidated by the regular grammatical and phonological rules that have become customary in the language community over generations, and these become increasingly attractive to the child after three years. Communication in infants and toddlers shows that the emergence of language rests, not only on transfer of semantic category stores (reference) or on the activation of the innate syntactic processing logic peculiar to text when it is considered as an object of analysis, but on an empathic transfer of purposes, foci of interest and feelings about events and objects in the world shared with familiar and trusted companions (130). This development occurs in a brain that has already developed a clear asymmetry in expressive gestures of the hands. Lateralization of language appears as a developmental outcome in a brain already functioning differently on left and right sides (134).

BRAIN GROWTH CYCLES AND EMOTIONAL CHANGES: ROLE OF FRONTAL ASYMMETRIES

Dips in development, or regressive periods when developmental gains seem temporarily to be lost, and the infant acts with more unstable and defensive emotions, appear at many times in infancy and at the same ages in different infants (99). These will be related to unequal growth processes in the two hemispheres, changing laterality of function (Fig. 3).

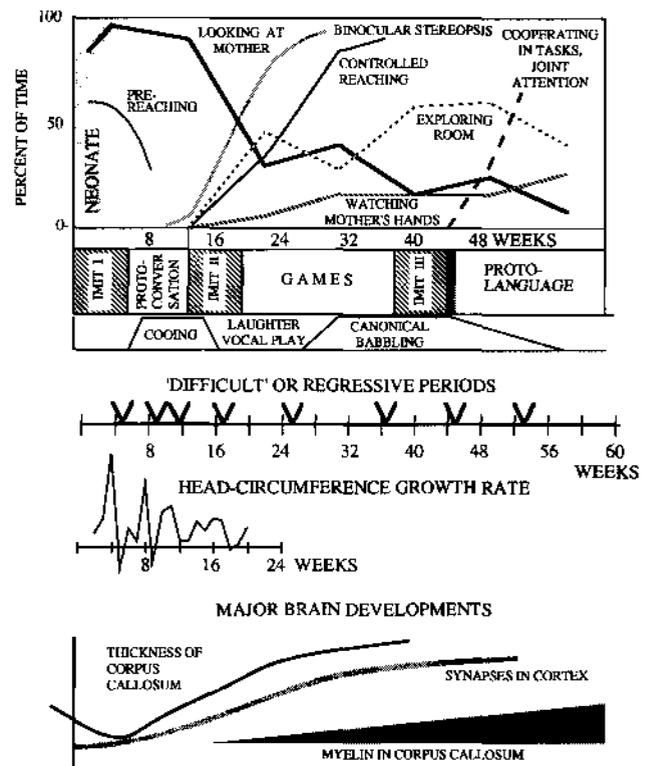


FIG. 3. In the first year infants show large changes in behaviour reflecting transformations in their motivation for communication, exploration of the environment and object prehension (132). Near the end of this year they become attracted to the focus of a partner's interest and more cooperative in joint tasks. Large changes occur in the brain (132), with frequent surges in head circumference (25), and the latter may be correlated with temperamental "difficult periods" (99), and changes in laterality of actions.

There is evidence from measurement of head circumference that brain growth spurts occur throughout the first year, notably at 3–4 weeks, 7–8 weeks and 10–11 weeks (25). Growth phases in cortical connections have been charted through childhood, and these developments take place at different ages and over different distances in the left and right cortices (Fig. 4). In a recent summary of his findings from studies of the growth of cortico-cortical connections by EEG coherence measurement, Thatcher (115) describes cycles of hemispheric development as follows, giving the frontal regions responsibility for regulating developments in more sensory parts, and cognitive stages: "one interpretation is that the frontal regions control or significantly influence the cycles of synaptic influence in posterior cortical regions. That is, frontal synaptic influence significantly determines which synapses will survive and which will be lost during the developmental sculpting process. ... This process is nonlinear in both space and time and is manifested behaviorally by relatively sudden changes in cognitive competence" (115, page 588). Given that the cerebral cortex has to undergo massive developments later in the first year and that the synaptic fields are very immature in the first few months, we can speculate that the asymmetries of expression before the 6-months stage are largely reflections of activity in subcortical regions. There is, unfortunately, no information on possible sex differences in these changes of developmental rate.

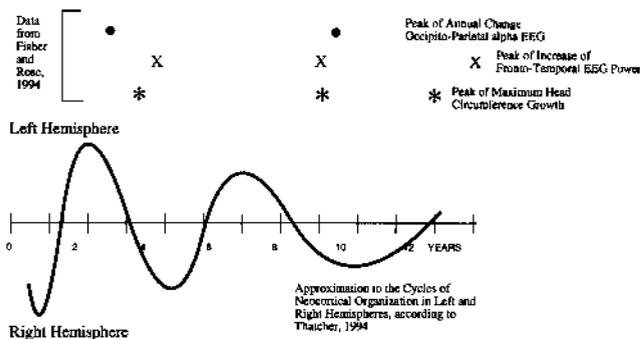


FIG. 4. Brain growth cycles continue asymmetrically throughout childhood, correlated with changes in the balance of functions in the two hemispheres (25, 115).

ASYMMETRIC FOUNDATIONS FOR TEMPERAMENT IN INFANTS

Evidence from recordings of frontal EEG activity in infants when they are in different social situations indicates that bold, confident assertiveness is associated with higher activity in the left frontal lobe, while timidity, shyness and withdrawal tend to be associated with right frontal activity. Both of these trends appear later as consistent dispositional or trait features of infants and toddlers. The individual asymmetries observed in infancy are predictive of tendencies to personality differences in later years.

Besides hand gestures, both the articulation of vocalizations and the distribution of eye movements are under frontal control. Infants have asymmetries in eye orientation related to communication by vocalization. Infants often look more often to the right when making an utterance or imitating vocalizations (67). In protoconversations, infants regulate contact with the partner by making and breaking eye contact. When protoconversation is perturbed, as in the "still face" experiment or in replay of a video of a live interaction, one of the most sensitive indices of breakdown in intersubjective contact is gaze avoidance and "paranoid glances" (80). It seems that transition between phases of positive assertive communication with a receptive partner and observant reception of the partner's expressions may be associated with a shift in the lateralization of activity in the brain (Fig. 2).

EMBRYOLOGY OF HUMAN BRAIN ASYMMETRIES

We have argued that human emotional asymmetries originate in gene-regulated processes of neurogenesis (137). Interneuron systems of the brain stem which mediate intermodal sensory integration, the coordination of motor patterns and motive states, appear in the human brain in the early embryo (85). They soon develop links with the diencephalic autonomic centre of the hypothalamus, the basal ganglia and the amygdala. These structures, constituting the Intrinsic Motive Formation (IMF), are well-developed before the cortical neurons appear (137).

Asymmetry may originate in the unfertilized ovum, and early embryos have an asymmetric spiral posture. Viscera, skeleton, skin features and hair arrangements have consistent, genetically regulated asymmetries. Photographs from

the Carnegie collection show that a majority of human embryos at 7 weeks have the right hand more developed and positioned above the left (84), and at 15 weeks, most fetuses suck their right hand in preference to the left (42). The human neocortex is visibly asymmetric in fetal stages (114,146) a feature which originates in the embryo (97). The migration and selective survival of cells round the Sylvian sulcus and in the frontal lobes, where important asymmetries appear (146), will be subject to influences projected from subhemispheric and palaeocortical parts of the brain known to have asymmetries in mammals (21,32,82,110,114), and the intrinsic genesis of asymmetry of brain function is also evident in brain chemistry (86).

In the mid-embryo stage, rudimentary nuclear masses in the basal (motor) plate of the brain propagate forwards from the spinal cord through the ventral hindbrain, midbrain tegmentum, ventral thalamus and subthalamus in the diencephalon, to the lamina terminalis and commissural plate in the forebrain. The dorsal alar (sensory) plate is less developed. In the hindbrain, a key reticular neuromodulator nucleus, the locus ceruleus, appears, which plays a commanding role in early brain development, and in the coordination of emotions postnatally. In week 5, monoamine transmission pathways grow from the brainstem into the primordial cerebral hemispheres.

Before week 8, the nervous system has no electrical activity and it generates no behaviour, but the basal ganglia (corpora striata) are relatively advanced, while the walls of the dorsal hemisphere rudiments above form an undifferentiated sheet or pallium. The first generalized movements occur in week 8 (17). The amygdala begins to differentiate from the basal nuclei, and integrating tracts appear in the midbrain connecting with the relatively large hypothalamus. Thus key components of the motor and emotional systems are in place when the neocortex is unformed.

The amygdala and hippocampus, key components of emotional and memory functions in the mature brain, begin rapid differentiation in the 7th week, with fibre connections through the lateral forebrain bundle, and the septum develops cholinergic nuclei that become of fundamental importance in the regulation of behavioural and cognitive functions. The neostriatum, caudate, substantia nigra and globus pallidus appear, establishing the mechanisms of basic instinctive motor functions linked to developments in the oculomotor nucleus, and the cerebellum, cochlear nucleus and the hindbrain sensory nuclei. In the 8th week, the beginning of the fetal period, the hippocampus enlarges and the first efferent fibres grow from neocortical cells to the epithalamus, dorsal thalamus and midbrain, which shows superior and inferior colliculi, and to the cerebellum. This may mark the beginning of neocortical involvement in sensory-motor and motivating integrations of the brainstem, but cortical processing of input from sense organs must be extremely rudimentary until dendritic fields begin to be elaborated in the neocortex in late fetal and infant periods.

The basic layout of the cerebral cortex is visible about week 6. In the primordial plexiform layer (PPL) of the hemispheres, which is the primitive nursery tissue in which the mammalian neocortex emerges (72), afferents from the brain stem (possibly monoaminergic from the midbrain) and the horizontal Cajal-Retzius cells form the first synapses seen in human embryos (57), and then the first radially migrating neurons appear in the hemisphere wall, splitting

the PPL and attaching themselves to the outer layer. The characteristic cell columns of the neocortex, which become the local units of functional integration, arise from stem cells in the proliferative zone (97). All cells in a column are produced by division of one germinal cell. Where cortical cell density will be high, the ventricular zone is active over a longer period, and the size of a functional cortical area depends on the number of proliferative units, which together form a 'proto-map' of the whole cortex in the ventricular zone. The total number of columns is about 200 million, with large individual variation. Rakic (97) proposes that the neocortex has expanded in evolution by inserting proliferative units, and this will have been the mode of origin for the perisylvian fissures that show the most pronounced asymmetry in the adult human brain. Afferents to the cortex are guided by position specific molecules before the neurons finished migrating. Inputs from the brainstem impose their influence right from the beginning of development of the cognitive mechanisms of the forebrain.

In weeks 7 and 8, neocortical neurons migrate radially in columns to lie in the cortical plate (97). Their differentiation is influenced by their passage through a dense cellular lattice and "sub-plate" of early neurons, axons, dendrites and glia fibres, which is larger in humans than in other primates and contains waiting afferents generated ahead of their neuronal targets in sequence from brainstem, basal forebrain, thalamus and ipse- and contra-lateral cortex (72). Earlier formed, deeper neuron layers in the cortex develop close relations with intrinsic limbic structures, while later formed layers receive sensory and intracortical, including commissural, connections (5,88,139). Subcortical systems have a role in deciding the distribution and laminar structure of cytoarchitectonic areas in the neocortex (96), including hemispheric asymmetries that later influence emotional and cognitive functions. Experiments with monkeys prove that the relative size of cortical areas depends on input from subcortical centers (97). Territories around the Sylvian sulcus, which show marked asymmetries in most individuals from their origins, are important in culture-related processes of the adult human brain, including language (103). They are particularly rich in callosal and intrahemispheric connections, and are also in close reciprocal relation with limbic cortex (48,87,88,109,139).

All principal neurons of the cerebral cortex are produced by week 17 of gestation, and cell death starts. Cell numbers are essentially stable from mid gestation. As the fetal cerebral wall grows and the cortical mantle folds due to neuron enlargement and separation with dendrite growth, anatomical asymmetries become visible, notably in the shape of the Sylvian sulcus, and by 29 weeks in the larger size of the dorsal surface of the left temporal lobe. The right hemisphere is more advanced than the left in surface features from about the 25th week (103) and this advance persists until the left hemisphere shows a post-natal growth spurt starting in the second year (116). These asymmetries will have been initiated earlier.

Brain development is linked with differentiation of the gonads and the appearance of secondary sexual features of the body in the late embryo (68), and sex differences in both brain anatomy and in the gonads appear to stem from differences in the organization of neurohumoral systems of the brainstem (33,145). Control of sexual differentiation involves a feedback loop between the hypothalamus and

medioventral reticular formation and the endocrine system of gonads and adrenals that regulate reproductive activities and development of the body and its secondary sexual features. This system, first evident in the early fetal stages, affects the postnatal growth of the mental abilities in children (68). Removal of the gonads at birth changes cortical growth and hemispheric asymmetry in rats (32). High levels of testosterone in newborn male monkeys, which slow cortical maturation, lead to sex differences in post-natal growth of the temporal neocortex involved in habit formation (37), and the orbito-frontal cortex of monkeys is affected by sex steroids in a critical period to produce male/female differentiation (9). This can be related to differences in cognitive functions, socio-emotional behavior and psychological sexuality of girls and boys that appear in the second year when the human orbito-frontal cortex is undergoing rapid differentiation (109). Sex differences in brain function affect many cognitive functions, and their cerebral asymmetry, in subtle ways (53).

EVOLUTIONARY SOURCES OF FUNCTIONAL BRAINSTEM ASYMMETRY

Comparative studies of lower vertebrates reveal that lateral asymmetries are frequently part of the makeup of primary motive systems of active animals. The asymmetries found in habenula nuclei and hypothalamus of amphibia and reptiles suggests that diencephalic centres mediating motivational processes, and coordinating CNS activity with the autonomic and endocrine systems, have, in the course of evolution, an early tendency to complementary specialization on the left and right side.

In his classical study of the brain of the tiger salamander, Herrick (43) identified the substrate of learning connections between inner motives and environmental affordances in the ventro-lateral peduncular neuropil at the anterior end of the reticular formation of the brain core on either side of the ventral diencephalon, and he pointed out that this was homologous with the tissue of origin for the neocortex in mammals. He described the midbrain tectum, which lies above the tegmental "head ganglion of the motor system" of Coghill, as a multisensorial field for specification of orientations to environmental events, and the midbrain, diencephalic transition as an area connected to evaluative/visceral systems of the hypothalamus and reticular core. From these functional anatomical principles, I worked out a description of the "behaviour field" in which experiences are assimilated to principles of action (or intentions) after their translocation, by means of orienting movements, into a central area in which decisions about consummatory behaviour are made (122, 125,127).

Whereas mirror symmetry of organization is adaptive for orienting trunk, limbs, head and sense organs of a bilaterally symmetrical body to chance encounters with environmental events, the location and timing of which is outside the organism's control, mechanisms that act for the organism as a whole regulating its inner state or commitment to take in or reject assimilation of an environmental object are likely to be either median and unpaired, or duplicated on the left and right. If duplicate, and if there are sufficient commissural connections, there will be an option for the evolution of complementary specializations on the two sides. Cerebral asymmetry of function will be associated with representations of motives

that determine what kind or quality of object the subject will seek to maintain an optimal adaptive state. Memories, the accumulation of new representations, will also be in territories that receive a convergence of afferent input from the senses and intrinsically generated output from the evaluative systems. They will be likely to become asymmetrical under the influence of laterally differentiated evaluative inputs.

Somatotopy, "body mapping" in neural fields, provides a frame for the specification of body centred "telotopic" (direction mapping) neural arrays for orienting the whole coordinated behavioural systems into the space surrounding the body (127). An integrated body-centred behaviour space, with pervasive anterior-posterior polarized bisymmetrical representations throughout the neuraxis, is specified in the mapping of receptors into the CNS and of the CNS to the effectors.

Commitment to action or reaction vis-à-vis the environment, which can be benign or hostile, beneficial or noxious, calm or tumultuous, etc., requires that intentions be qualified by emotions. These measure the risks or advantages that may come to the subject's state of health and well-being as a result of action. Emotions determine the level of energy put into acting, the vigilance, anxiety, analytical focussing, self-protectiveness, etc. of intentions. Physiological and behavioural research locates the mechanisms of emotion in ventromedial parts throughout the brain stem; in the reticular nuclei, hypothalamus, midline thalamus, septum, amygdala and limbic cortex, and in mesial pre-frontal cortex. The cognitive systems that exhibit pronounced functional asymmetry in humans are between receptor and motor fields and the limbic cortex. They are phylogenetically recent insertions of tissue (5). It may be proposed that their asymmetry is a reflection of left-right differences in the intrinsic, limbic, component.

CONCLUSIONS

As long as cerebral asymmetry of function is conceived only at the level of language and cognitive strategies (of information uptake, storing in memory or retrieval in the interests of problem solving), it will be difficult to identify its developmental, or evolutionary, origins. We need to find an explanation from the developmental process itself, either in anatomical terms, describing the sequence of structures that emerge in brain growth, or in terms of the adaptive motives that drive behaviour and its development.

Comparative studies that seek homologous asymmetries in the brains of different animal phyla indicate what asymmetries are the more primitive and suggest a sequence of elaborations of function. This kind of enquiry might also cast light on the origins of the higher cognitive functions of

human intelligence, including language. Another strategy is to look at the ontogenesis of human cerebral structures from embryo stages. Finally, evidence on precognitive functional asymmetries can be obtained by observation of left-right differences in the behaviour of infants and young children as they gain the abilities that manifest asymmetry in the adult brain.

In fact, information that we now possess from all three of these sources points in the same direction. Human cerebral asymmetry at the level of neocortical cognitive processes that take up and store experience develops from a deeper and more ancient asymmetry in regulatory motive structures that both control morphogenesis of the brain in the embryo and guide the infant into skilled action and an understanding of the motives and ideas of other members of the cooperative community.

Expression of motives and emotions between young children and their caregivers and companions regulates the acquisition of sense in the human world (12). Intersubjective mechanisms appear to have a primary asymmetry that may be interpreted in terms of the signals exchanged in face-to-face conversational exchanges, suggesting that, in the evolution of cultural learning, and the parenting and family structure on which it depends, the demands of several levels of interpersonal communication underlying language may have enhanced selection for cerebral asymmetry in humans.

Observations of behaviour to determine the initial state of the infant's mind, taken with evidence from physiological or brain scan observations of cortical neuronal activity in monkeys and infants when they are behaving in particular intentional ways, confirm that the brain can generate and give an aim to purposes in independence of peripheral circumstances, anticipating them. Furthermore, infant behaviour confirms that emotions are innate regulators of selective involvement with people and with objects. Neonatal imitation proves the primary efficacy of intersubjective systems, and their special adaptation for communication of both unconscious purposes and conscious experiences, the latter being identified as shared because they are acquired in a joint intersubjective field of action. Infants show asymmetrical expression of emotional states when interacting with partners in communication, before they have acquired cognitive schemata for objects of manipulation and long before they acquire any linguistic semantic code from communication with speaking companions.

The essential process by which human communication develops is one that makes alteroception ("other" awareness), and altero-centric purposes (what the "other" is intending) accessible from the outset of cognitive development. These processes have an intrinsic asymmetry of organization in the brain.

REFERENCES

1. Aggleton, J. P. The contribution of the amygdala to normal and abnormal emotional states. *Trends Neurosci.* 16:328-333; 1993.
2. Arbib, M. A.; Dominey, P. F. Modeling the roles of basal ganglia in timing and sequencing saccadic eye movements. In: Houk, J.; Davis, J. L.; Beiser, D. G., eds. *Models of information processing in the basal ganglia*. Cambridge, MA: MIT Press; 1995: 149-162.
3. Bell, M. A.; Fox, N. A. The relations between frontal brain electrical activity and cognitive development during infancy. *Child Devel.* 63:1142-1163; 1992.
4. Bell, M. A.; Fox, N. A. Brain development over the first year of life: Relations between electroencephalographic frequency and coherence and cognitive and affective behaviors. In: Dawson, G.; Fischer, K. W., eds. *Human behavior and the developing brain*. New York: The Guilford Press; 1994: 314-345.
5. Benes, F. M. Development of the corticolimbic system. In: Dawson, G.; Fischer, K. W., eds. *Human behavior and the developing brain*. New York: The Guilford Press; 1994: 176-206.
6. Bradshaw, J. L.; Nettleton, N. C. The nature of hemispheric specialization in man. *Behav. Brain Sci.* 4:51-91; 1983.

7. Bruner, J. S. *Child's talk. Learning to use language.* New York: Norton; 1983.
8. Butterworth, G.; Hopkins, B. Origins of handedness in human infants. *Devel. Med. Child Neurol.* 35:177-184; 1993.
9. Clark, A. S.; Goldman-Rakic, P. S. Gonadal hormones influence the emergence of cortical function in non-human primates. *Behav. Neurosci.* 103:1287-1295; 1989.
10. Condon, W. S.; Sander, L. W. Neonate movement is synchronized with adult speech: Interactional participation and language acquisition. *Science* 183:99-101; 1974.
11. Cummings, J. L. Frontal-subcortical circuits and human behavior. *Archs Neurol.* 50:873-880; 1993.
12. Darwin, C. *The expression of emotions in man and animals.* London: Methuen; 1872.
13. Davidson, R. J.; Fox, N. A. Asymmetric brain activity discriminates between positive and negative affective stimuli in human infants. *Science* 218:1235-1237; 1982.
14. Davidson, R. J. Temperament, affective style, and frontal lobe asymmetry. In: Dawson, G.; Fischer, K. W., eds. *Human behavior and the developing brain.* New York: The Guilford Press; 1994:518-536.
15. Dawson, G. Development of emotional expression and emotion regulation in infancy: Contributions of the frontal lobe. In: Dawson, G.; Fischer, K. W., eds. *Human behavior and the developing brain.* New York: The Guilford Press; 1994: 64-379.
16. Dawson, G.; Gofer Klinger, L.; Panagiotides, H.; Spieker, S.; Frey, K. Infants of mothers with depressive symptoms: Electroencephalic and behavioral findings related to attachment status. *Devel. Psychopathol.* 4:67-80; 1992.
17. de Vries, J. I. P.; Visser, G. H. A.; Prechtl, H. F. R. Fetal motility in the first half of pregnancy. In: Prechtl, H. F. R., ed. *Continuity of neural functions from prenatal to postnatal life.* Oxford: Blackwell; 1984:46-64.
18. Dawson, J. H., III. Preliminary evidence of hemispheric asymmetry of auditory function in monkeys. In: Harnad, S.; Doty, R. W.; Goldstein, L.; Jaynes, J.; Krauthamer, G., eds. *Lateralization in the nervous system.* New York: Academic Press; 1977:63-71.
19. Di Pelligrino, G.; Fadiga, L.; Fogassi, L.; Gallese, V.; Rizzolatti, G. Understanding motor events: A neurophysiological study. *Exp. Brain Res.* 91:176-180; 1992.
20. Diamond, A.; Goldman-Rakic, P. S. Evidence for involvement of prefrontal cortex in cognitive changes during the first year of life: comparison of human infants and rhesus monkeys on a detour task with transparent barrier. *Soc. Neurosci. Abstr. (Part II)* 11:832; 1985.
21. Diamond, M. C. Asymmetry in the cerebral cortex: Development, estrogen receptors, neuron/glia ratios, immune deficiency and enrichment/overcrowding. In: Ottoson, D., ed. *Duality and unity of the brain.* Wenner-Gren International Symposium Series, No. 47. London: Macmillan, London; 1987:37-52.
22. Diamond, S. J. The brain is not a simple see-saw. *Behav. Brain Sci.* 6:171-173; 1983.
23. Eimas, P. D.; Siqueland, E. R.; Jusczyk, P.; Vigorito, J. Speech perception in infants. *Science* 171:303-306; 1971.
24. Fernald, A. Intonation and communicative interest in mother's speech to infants: Is the melody the message? *Child Devel.* 60:1497-1510; 1989.
25. Fisher, K. W.; Rose, S. P. Dynamic development of coordination of components in brain and behavior: A framework for theory and research. In: Dawson, G.; Fischer, K. W., eds. *Human behavior and the developing brain.* New York: The Guilford Press; 1994:3-66.
26. Fox, N. A. If it's not left, it's right: Electroencephalograph asymmetry and the development of emotion. *Am. Psychol.* 46:863-872; 1991.
27. Fox, N. A.; Davidson, R. J. (eds) *The psychology of affective development.* Hillsdale, NJ: Erlbaum; 1984.
28. Franzen, E. A.; Myers, R. E. Neural control of social behavior: Prefrontal and anterior cortex lesions. *Neuropsychologia* 11:141-157; 1973.
29. Gainotti, G.; Caltagirone, C.; Zoccolotti, P. Left/right and cortical/subcortical dichotomies in the neuropsychological study of human emotions. *Cognition and Emotion*, 7:71-93; 1993.
30. Georgopoulos, A. P.; Lurito, J. T.; Petrides, M.; Schwartz, A. B.; Massey, J. T. Mental rotation of the neural population vector. *Science* 243: 234-236; 1989.
31. Georgopoulos, A. P.; Taira, M.; Lukashin, A. Cognitive neurophysiology of the motor cortex. *Science* 260:47-52; 1993.
32. Gerendai, I. Laterality and the neuroendocrine system. In: Ottoson, D., ed. *Duality and unity of the brain.* Wenner-Gren International Symposium Series, No. 47. London: Macmillan; 1987:17-28.
33. Geschwind, N.; Galaburda, A. M. *Cerebral lateralization. Biological mechanisms, associations and pathology. I. An hypothesis and a program for research.* *Archs Neurology* 42:428-59; 1985.
34. Gilbert, C.; Bakan, P. Visual asymmetry in perception of faces. *Neuropsychologia* 11:355-362; 1973.
35. Glic, S. D.; Ross, D. A. Lateralization of function in the rat brain: Basic mechanisms may be operative in humans. *Trends Neurosci.* 4:196-199; 1981.
36. Goldman-Rakic, P. Dopamine mediated mechanisms of the prefrontal cortex. *Sem. Neurosci.* 4:149-60; 1992.
37. Hager, C.; Bachevalier, J.; Bercu, B. B. The effects of perinatal testosterone on the development of habit formation in infant monkeys. *Soc. Neurosci. Abstr.* 12:23; 1986.
38. Hamilton, C. R.; Vermeire, B. A. Hemispheric differences in split-brain monkeys learning sequential comparisons. *Neuropsychologia* 20:691-698; 1985.
39. Hauser, M. D. Right hemisphere dominance for the production of facial expression in monkeys. *Science* 261:475-477; 1993.
40. Heilman, K. M.; Satz, P., eds. *Neuropsychology of human emotion.* London: Guildford Press; 1983.
41. Held, R.; Shimono, S.; Gwiazda, J. Gender differences in the early development of human visual resolution (Proceedings of the ARVO Meeting, April-May, 1984 Abstract No. 90). *Inv. Ophthalmol. Vis. Sci.* 25:220; 1984.
42. Hepper, P. G.; Shahidullah, S.; White, R. Origins of fetal handedness. *Nature* 347:431; 1990.
43. Herrick, C. J. *The brain of the tiger salamander.* Chicago: University of Chicago Press; 1948.
44. Hess, W. R. *Diencephalon: Autonomic and extrapyramidal functions.* Orlando, FL: Grune and Stratton; 1954.
45. Hofsten, C. von (1983) Catching skills in infancy. *J. Exp. Psychol. Human Percept. Perf.* 9:75-85; 1983.
46. Humphrey, D. E.; Humphrey, G. K. Sex differences in infant reaching. *Neuropsychologia* 25:971-975; 1987.
47. Ifune, C. K.; Vermeire, B. A.; Hamilton, C. R. Hemispheric differences in split-brain monkeys viewing and responding to videotaped recordings. *Behav. Neural Biol.* 41:231-235; 1984.
48. Innocenti, G. M. (1986) General organization of the callosal connections in the cerebral cortex. In: Jones, E. G.; Peters, A., eds. *Cerebral cortex*, vol. 5. New York: Plenum; 1986:291-353.
49. Jeannerod, M. The representing brain: Neural correlates of motor intention and imagery. *Behav. Brain Sci.* 17:187-245; 1994.
50. Joseph, R. The right cerebral hemisphere: Emotion, music, visuo-spatial skills, body-image, dreams and awareness. *J. Clin. Psychol.* 44:630-673; 1982.
51. Kimura, D. Manual activity during speaking. *Neuropsychologia* 11:45-50; 1973.
52. Kimura, D. Left-hemisphere control of oral and brachial movements and their relation to communication. *Phil. Trans. R. Soc. Lond. Series B* 298:135-149; 1982.
53. Kimura, D. Sex differences in the brain. *Sci. Am.* 267:119-125; 1992.
54. Kinsbourne, M. The mechanism of hemispheric control of the lateral gradient of attention. In: Rabbitt, P.; Dornic, M. A., eds. *Attention and performance, V.* London: Academic Press; 1975:81-97.
55. Kugiumutzakis, G. Intersubjective vocal imitation in early mother-infant interaction. In: Nadel, J.; Camaioni, L., eds. *New perspectives in early communicative development.* London: Routledge; 1993:23-47.
56. Langlois, J. H.; Roggman, L. A.; Rieser-Danner, L. A. Infant's differential social responses to attractive and unattractive faces. *Devel. Psychol.* 26:153-159; 1990.
57. Larroche, J.-C.; Privat, A.; Jardin, L. Some fine structures of the human fetal brain. In: Monset-Couchard, M.; Minkowski, A., eds. *Physiological and biochemical basis for perinatal medicine.* Basel: Karger; 1981:350-358.
58. LeDoux, J. E. Brain mechanisms of emotion and emotional learning. *Curr. Opin. Neurobiol.* 2:191-197; 1992.

59. Levy, J. Regulation and generation of perception in the asymmetric brain. In: Trevarthen, C., ed. *Brain circuits and functions of the mind: Essays in honour of Roger W. Sperry*. New York: Cambridge University Press; 1990:231-248.
60. Levy, J.; Trevarthen, C. Metacontrol of hemispheric function in human split-brain patients. *J. Exp. Psychol. Human Percept. Perf.* 2:299-312; 1976.
61. Levy, J.; Trevarthen, C. Perceptual, semantic and phonetic aspects of elementary language processes in split-brain patients. *Brain* 100:105-118; 1977.
62. Levy, J.; Heller, W.; Banich, M. T.; Burton, L. Are variations among right-handed individuals in perceptual asymmetries caused by characteristic arousal differences between the hemispheres? *J. Exp. Psychol. Human Percept. Perf.* 9:329-359; 1983.
63. Levy, J.; Heller, W.; Banich, M. T.; Burton, L. Asymmetry of perception in free viewing of chimeric faces. *Brain and Cognition* 2:404-419; 1983.
64. Levy, J.; Trevarthen, C.; Sperry, R. W. Perception of bilateral chimeric figures following hemispheric disconnection. *Brain* 95:61-78; 1972.
65. Locke, J. L. *The child's path to spoken language*. Harvard University Press, Cambridge MA and London; 1993.
66. Lynch, M. P.; Oller, D. K.; Steffens, M. L.; Buder, E. H. Phrasing in prelinguistic vocalizations. *Devel. Psychobiol.* 28:3-25; 1995.
67. MacKain, K. S.; Studdert-Kennedy, M.; Spieker, S.; Stern, D. N. Infant intermodal speech perception is a left hemisphere function. *Science* 219: 1347-1349; 1983.
68. MacKinnon, P. C. B.; Greenstein, B. Sexual differentiation of the brain. In: Falkner, F.; Tanner, J. M., eds. *Human growth. A comprehensive treatise*, vol. 2: Postnatal growth; neurobiology. New York: Plenum; 1985:437-468.
69. MacLean, P. D. The triune brain, emotion and scientific bias. In: Schmitt, F. O., ed. *The neurosciences: Second study program*. New York: Rockefeller University Press; 1970:336-349.
70. MacLean, P. D. Cerebral evolution and emotional processes: New findings on the striatal complex. *Ann. NY Acad. Sci.* 193:137-149; 1972.
71. MacNeilage, P. F.; Studdert-Kennedy, M. G.; Lindblom, B. Primate handedness reconsidered. *Behav. Brain Sci.* 10:247-303; 1987.
72. Marin-Padilla, M. (1987) Neocortex, mammalian, origins of. In: Adelman, G., ed. *Encyclopedia of neuroscience*, vol. 1. Boston, Basel, Stuttgart: Birkhauser; 1987:740-741.
73. McNeill, D. *Hand and mind: What gestures reveal about thought*. Chicago: University of Chicago Press; 1992.
74. Mehler, J. Language related dispositions in early infancy. In: Mehler, J.; Fox, R., eds. *Neonate cognition*. Hillsdale, NJ: Lawrence Erlbaum; 1985.
75. Meltzoff, A. N.; Moore, M. K. Early imitation within a functional framework: the importance of personal identity, movement and development. *Infant Behav. Devl.* 15:479-505; 1992.
76. Michel, G. F. Right-handedness: A consequence of infant supine head-orientation? *Science* 212:685-687; 1981.
77. Morecraft, R. J.; Geula, C.; Mesulam, M-M. Architecture of connectivity within a cingulo-fronto-parietal neurocognitive network for directed attention. *Archs Neurol.* 50:279-284; 1993.
78. Murray, E. A.; Mishkin, M. Amygdectomy impairs cross-modal association in monkeys. *Science* 228:604-606; 1985.
79. Murray, L. *The Sensitivities and Expressive Capacities of Young Infants in Communication with their Mothers*. Thesis for PhD. The University of Edinburgh; 1980.
80. Murray, L.; Trevarthen, C. Emotional regulation of interactions between two-month-olds and their mothers. In: Field, T. M.; Fox, N. A., eds. *Social perception in infants*. Norwood, NJ: Ablex; 1985:177-198.
81. Nauta, W. J. H.; Domesick, V. B. Neural associations of the limbic system. In: Beckman, A. L., ed. *The neural basis of behavior*. New York: SP Medical and Scientific Books; 1982:175-206.
82. Nordeen, D. J.; Yahr, P. Hemispheric asymmetries in the behavioral and sexual differentiation in the mammal brain. *Science* 218:391-394; 1982.
83. Nottebohm, F. Brain pathways for vocal learning in birds. A review of the first 10 years. *Progr. Psychobiol. Physiol. Psychol.* 9:85-124; 1980.
84. O'Rahilly, R.; Müller, F. *Developmental stages in human embryos*. Washington, D.C.: Carnegie Institute of Washington, Publication 637; 1987.
85. O'Rahilly, R.; Müller, F. *The embryonic human brain: An atlas of developmental stages*. New York: Wiley-Liss; 1994.
86. Oke, A.; Keller, R.; Mefford, I.; Adams, R. N. Lateralization of norepinephrine in human thalamus. *Science* 200:1411-1413; 1978.
87. Pandya, D. N.; Yeterian, E. H. Architecture and connections of the cortical association areas. In: Peters, A.; Jones, E. G., eds. *Cerebral cortex; vol. 4. Association and auditory cortices*. New York: Plenum; 1985:3-61.
88. Pandya, D. N.; Seltzer, B.; Barbas, H. Input-output organization of the primate cerebral cortex. In: *Comparative primate biology*, vol. IV: Neurosciences. New York: Allen Ardis; 1988:39-80.
89. Panksepp, J. A critical role for "Affective Neuroscience" in resolving what is basic about basic emotions. *Psychol. Rev.* 99:554-560; 1992.
90. Papousek, M.; Papousek, H. Musical elements in the infants vocalization: their significance for communication, cognition and creativity. In Lipsitt, L. P.; Rovee-Collier, C. K., eds. *Advances in Infancy Research*, Vol. 1. Norwood, New Jersey: Ablex; 1981:163-224.
91. Perett, D. I.; Rolls, E. T.; Caan, W. Visual neurons responsive to faces in the monkey temporal cortex. *Exp. Brain Res.* 47:329-342; 1982.
92. Perrett, D. I.; Harris, M. H.; Bevan, R.; Thomas, S.; Benson, P. J.; Mistlina, J.; et al. Framework of analysis for the neural representation of animate objects and actions. *J. Exp. Biol.* 146:87-113; 1989.
93. Ploog, D. Neuroethological perspectives on the human brain: From the expression of emotions to intentional signing and speech. In: Harrington, A., ed. *So human a brain*. Boston: Birkhäuser; 1992:3-13.
94. Prechtl, H. F. R. Continuity and change in early human development. In: Prechtl, H. F. R., ed. *Continuity of neural functions from prenatal to postnatal life*. Oxford: Blackwell; 1984.
95. Previc, F. H. A general theory concerning the prenatal origins of cerebral lateralization in humans. *Psychol. Rev.* 98:299-334; 1991.
96. Rakic, P. Specification of cerebral cortical areas. *Science* 241:170-176; 1988.
97. Rakic, P. Development of the primate cerebral cortex. In: Lewis, M., ed. *Child and adolescent psychiatry: A comprehensive textbook*. Baltimore: Williams and Wilkins; 1991:11-28.
98. Ramsay, D. S. Onset of unimanual handedness in infants. *Infant Behav. Devl.* 3:377-385; 1980.
99. Rijt-Plooi, H. H. C. van de; Plooi, F. X. Distinct periods of mother-infant conflict in normal development: sources of progress and germs of pathology. *J. Child Psychol. Psychiat.* 34:229-245; 1993.
100. Rolls, E. T. A theory of emotion, and its application to understanding the neural basis of emotion. *Cognition and Emotion* 4:161-190; 1990.
101. Rönnqvist, L. A critical examination of the Moro response in newborn infants—symmetry, state relation, underlying mechanisms. *Neuropsychologia* 33:713-726; 1995.
102. Rönnqvist, L.; Hofsten, C. von. Neonatal finger and arm movements as determined by a social and an object context. *Early Devel. Parenting* 3:81-94; 1994.
103. Rosen, G. D.; Galaburda, A. M. Development of language: A question of asymmetry and deviation. In: Mehler, J.; Fox, R., eds. *Neonate cognition: beyond the blooming, buzzing confusion*. Hillsdale NJ: Erlbaum; 1985:307-326.
104. Ross, E. D. Non-verbal aspects of language. *Neurol. Clinics* 11:9-23; 1993.
105. Rothbart, M. K.; Posner, M. I.; Rosicky, J. Orienting in normal and pathological development. *Devel. Psychopathol.* 6:635-652; 1994.
106. Schiff, B. B.; Lamon, M. Inducing emotions by the unilateral contraction of facial muscles: A new look at hemispheric specialization and the experience of emotion. *Neuropsychologia* 27:923-935; 1989.
107. Schiff, B. B.; Esses, V.; Lamon, M. Unilateral facial contractions produce mood effects on social cognitive judgements. *Cognition and Emotion* 6:357-368; 1992.
108. Schonen, S. de; Gild de Diaz, M.; Mathivet, E. Hemispheric asymmetry in face processing in infancy: A developmental

- study in 3-6 month old infants. In: Ellis, H. D.; Jeeves, M.; Newcombe, F.; Young, A. W., eds. *Aspects of face processing*. Dordrecht: Martinus Nijhoff; 1986.
109. Schore, A. N. *Affect regulation and the origin of the self: The neurobiology of emotional development*. Hillsdale, NJ: Erlbaum; 1994.
 110. Sherman, G. F.; Galaburda, A. M.; Geschwind, N. Neuroanatomical asymmetries in non-human species. *Trends Neurosci.* 2:429-431; 1982.
 111. Shucard, D. W.; Shucard, J. L.; Thomas, D. G. The development of cerebral specialization in infants; Electrophysiological and behavioral studies. In: Emde, R. N.; Harmon, R. J., eds. *Continuities and discontinuities in development*. New York: Plenum; 1984.
 112. Stern, D. N.; Beebe, B.; Jaffe, J.; Bennett, S. L. The infant's stimulus world during social interaction; a study of caregiver behaviors with particular reference to repetition and timing. In: Schaffer, H. R., ed. *Studies in mother-infant interaction*. New York: Academic Press; 1977:177-202.
 113. Stern, D. N.; Hofer, L.; Haft, W.; Dore, J. Affect attunement: The sharing of feeling states between mother and infant by means of inter-modal fluency. In: Field, T. M.; Fox, N.A., eds. *Social Perception in Infants*. Norwood, NJ: Ablex; 1985:249-268.
 114. Strauss, E.; Kosaka, B.; Wada, J. The neurobiological basis of lateralized cerebral function: A review. *Human Neurobiol.* 2:115-127; 1983.
 115. Thatcher, R. W. Cyclical cortical reorganization: Origins of human cognitive development. In: Dawson, G.; Fischer, K. W., eds. *Human behavior and the developing brain*. New York: The Guilford Press; 1994:232-266.
 116. Thatcher, R. W.; Walker, R. A.; Giudice, S. Human cerebral hemispheres develop at different rates and ages. *Science* 236:1110-1113; 1987.
 117. Trehub, S. E. The perception of musical patterns by human infants: The provision of similar patterns by their parents. In: Berkley, M. A.; Stebbins, W. C., eds. *Comparative perception; vol. 1, Mechanisms*. New York: Wiley; 1990:429-459.
 118. Trehub, S. E.; Trainor, L. J.; Nyck, A. M. Music and speech processing in the first year of life. *Adv. Child Devel. Behav.* 24:1-35; 1993.
 119. Trevarthen, C. Double visual learning in split-brain monkeys. *Science* 136:258-259; 1962.
 120. Trevarthen, C. Functional interactions between the cerebral hemispheres of the split-brain monkey. In: Ettlinger, E. G., ed. *Functions of the corpus callosum*. Ciba Foundation Study Group, No. 20. London: Churchill; 1965:24-40.
 121. Trevarthen, C. Two mechanisms of vision in primates. *Psychologische Forschung* 31:299-337; 1968.
 122. Trevarthen, C. Brain bisymmetry and the role of the corpus callosum in behaviour and conscious experience. In: Cernack, J.; Podovinsky, F., eds. *Cerebral interhemispheric relations*. Bratislava: Slovak Academy of Sciences; 1972:319-333.
 123. Trevarthen, C. Analysis of cerebral activities that generate and regulate consciousness in commissurotomy patients. In: Diamond, S. J.; Beaumont, J. G., eds. *Hemisphere function in the human brain*. London: Paul Elek (Scientific Books) Ltd.; 1974a; 235-263.
 124. Trevarthen, C. Functional relations of disconnected hemispheres with the brain stem and with each other: Monkey and Man. In: Kinsbourne, M.; Smith, W. L., eds. *Hemispheric disconnection and cerebral function*. Springfield, Illinois: Charles C. Thomas; 1974b:187-207.
 125. Trevarthen, C. Cerebral embryology and the split-brain. In: Kinsbourne, M.; Smith, W. L., eds. *Hemispheric disconnection and cerebral function*. Springfield, Illinois: Charles C. Thomas; 1974c:208-236.
 126. Trevarthen, C. Manipulative strategies of baboons and the origins of cerebral asymmetry. In: M. Kinsbourne, M., ed. *The asymmetrical functions of the brain*. New York and London: Cambridge University Press; 1978.
 126. Trevarthen, C. Communication and cooperation in early infancy. A description of primary intersubjectivity. In: Bullowa, M., ed. *Before speech: The beginnings of human communication*. London: Cambridge University Press; 1979:321-347.
 127. Trevarthen, C. Functional organization of the human brain. In: Wittrock, M. C., ed. *The brain and psychology*. New York: Academic Press; 1980:33-91.
 128. Trevarthen, C. Form, significance and psychological potential of hand gestures in infants. In: Nespoulos, J.-L.; Perron, P.; Lecours, A. R., eds. *The biological foundation of gestures: Motor and semiotic aspects*. Hillsdale, NJ: Erlbaum; 1986a:149-202.
 129. Trevarthen, C. Development of intersubjective motor control in infants. In: Wade, M. G.; Whiting, H. T. A., eds. *Motor development in children: Aspects of coordination and control*. Dordrecht, Martinus Nijhoff; 1986b:209-261.
 130. Trevarthen, C. Sharing makes sense: Intersubjectivity and the making of an infant's meaning. In: Steele, R.; Threadgold, T., eds. *Language topics: Essays in honour of Michael Halliday*. Amsterdam and Philadelphia: John Benjamins; 1987a:177-199.
 131. Trevarthen, C. Sub-cortical influences on cortical processing in 'split' brains. In: Ottoson, D., ed. *Duality and unity of the brain*. Wenner-Gren International Symposium Series, No. 47. London: Macmillan, London; 1987b:382-415.
 132. Trevarthen, C. Development of early social interactions and the affective regulation of brain growth. In: Euler, C. von; Forssberg, H.; Lagercrantz, H., eds. *Neurobiology of early infant behaviour (Wenner-Gren Center International Symposium Series, Vol. 55)*. Basingstoke, Hants: Macmillan/New York: Stockton Press; 1989:191-216.
 133. Trevarthen, C. Integrative functions of the cerebral commissures. In: Boller, F.; Grafman, J., eds. *Handbook of neuropsychology, vol. 4*. Amsterdam: Elsevier Science Publishers BV (Biomedical Division); 1990a:49-83.
 134. Trevarthen, C. Growth and education of the hemispheres. In: Trevarthen, C., ed. *Brain circuits and functions of the mind: Essays in honour of Roger W. Sperry*. New York: Cambridge University Press; 1990b:334-363.
 135. Trevarthen, C. The function of emotions in early infant communication and development. In: Nadel, J.; Camaioni, L., eds. *New perspectives in early communicative development*. London: Routledge; 1993:48-81.
 136. Trevarthen, C. The self born in intersubjectivity: An infant communicating. In: Neisser, U., ed. *The perceived self: Ecological and interpersonal sources of self-knowledge*. New York: Cambridge University Press; 1993:121-173.
 137. Trevarthen, C.; Aitken, K. J. Brain development, infant communication, and empathy disorders: Intrinsic factors in child mental health. *Devel. Psychopathol.* 6:599-635; 1994.
 138. Trevarthen, C.; Sperry, R. W. Perceptual unity of the ambient visual field in human commissurotomy patients. *Brain* 96:547-570; 1973.
 139. Tucker, D. M. Developing emotions and cortical networks. In: Gunnar, M. R.; Nelson, C. A., eds. *Minnesota symposium on child psychology, vol. 24: Developmental behavioral neuroscience*. Hillsdale, NJ: Erlbaum; 1992:75-128.
 140. Tucker, D. M.; Frederick, S. L. Emotion and brain lateralization. In: Wagner, H.; Manstead, T., eds. *Handbook of psychophysiology: Emotion and social behavior*. New York: Wiley; 1987.
 141. Tucker, D. M.; Williamson, P. A. Asymmetric neural control systems in human self-regulation. *Psychol. Rev.* 91:185-215; 1984.
 142. Vermeire, B. A.; Erdman, A. L.; Hamilton, C. R. Laterality in monkeys for discriminating facial expression and identity. *Soc. Neurosci. Abstr.* 9:651; 1983.
 143. Watson, J. S. Perception of contingency as determinant of social responsiveness. In: Thomin, E., ed. *The origins of social responsiveness*. Hillsdale, NJ: Erlbaum; 1979.
 144. Weddell, R. A.; Miller, J. D.; Trevarthen, C. Voluntary emotional facial expressions in patients with focal cerebral lesions. *Neuropsychologia* 28:49-60; 1990.
 145. Wierman, M. E.; Crowley, W. F. Neuroendocrine control of the onset of puberty. In: Falkner, F.; Tanner, J. M., eds. *Human growth: A comprehensive treatise; vol. 2: Postnatal growth; Neurobiology*. New York: Plenum; 1985:225-242.
 146. Witelson, S. F. Brain asymmetry, functional aspects. In: Adelman, G., ed. *Encyclopedia of neuroscience*. Cambridge MA: Birkhäuser Boston; 1987:14-18.
 147. Young, A.; Lock, A. J.; Service, V. Infant's hand preferences for actions and gestures. *Devl. Neuropsychol.* 1:17-21; 1985.
 148. Zaidel, D. W.; Chen, A. C.; German, C. She is not a beauty even when she smiles: Possible evolutionary basis for a relationship between facial attractiveness and hemispheric specialization. *Neuropsychologia* 33(5):649-655; 1995.