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difficulties in the recognition of vocalizations with retained ability to discriminate between different sounds. Monaural discrimination experiments in intact monkeys, furthermore, suggest that there is a left hemisphere (right ear) advantage for the recognition of species-specific (but not other) sounds. The principal neural prerequisites for decoding speech sounds thus seem to be already present in the monkey. This fits in with the fact that the specific meaning of many monkey calls, similar to human words, has to be learned. It also is in harmony with the observation that, in human infants, language comprehension matures before language production which, in HaeckePs sense, can be taken as an indication that the physiological mechanisms underlying language comprehension are phylogenetically older than those underlying speech production. This assumption is also supported by recent studies in the bonobo, *Pan paniscus*, which document a highly developed capacity to understand spoken language on the one hand, and a complete inability to imitate speech on the other.

The acquisition of voluntary articulation and pitch control is a necessary but not sufficient condition for speech development. This is well documented in the chimpanzee who has voluntary control of his arms and hands and can be trained to use specific arm/hand movements, derived from American sign language, for designation of specific situations, but nevertheless is unable to develop a gestural sign language on his own. It is unclear which brain mechanisms must come into play for the capacity of voluntary muscle control to lead to imitation of movements or sounds and from there to spontaneous production of arbitrary motor patterns as symbols (that is. self-generated conditioned stimuli relating to objective states).

Without hard data, conclusions about the form of early languages must be speculative. In the transcultural approach, present-day languages spoken by societies representing early cultural stages, such as the hunter-gatherer societies of bushmen and Australian aborigines, are compared with languages representing more advanced cultural stages. In the ontogenetic approach, the vocal utterances of one- to two-year-old children are compared to stages of more advanced language competence. From this material it may be hypothesized that language evolution began with one- and two-word sentences. There was a lack of differentiation between noun, verb, and object; that is, words designated complex situations in a rather generalized way. The number of words (lexicon) was small; many of them had an onomatopoeic character and showed reduplication of syllables. Vocal utterances and accompanying gesture often formed inseparable components of semantic units ("words"). Phoneme differentiation was done to a large extent laryngeally (tonal modulations, relaxed/strained vowel distinctions).

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See also Evolution of vertebrate brains; Language development; Speech development; Language, gestural; Language, nonhuman

Language in the disconnected right hemisphere

Eran Zaidel

1. Disconnection syndrome

In about 98% of normal right-handed individuals the left cerebral hemisphere (LH) is specialized for controlling speech and other language functions, especially phonetics, phonology and syntax. However, converging evidence suggests that the right hemisphere (RH) plays a supportive role in communicative functions, ranging from lexical semantics to discourse processing, with selective contributions to social pragmatics. The evidence comes from recovery in aphasia following LH lesions, from language deficits following RH lesions, from patients with dominant left hemispherectomy following adult lesions, and from brain monitoring and behavioral laterality effects in normal subjects. In this entry I will focus on evidence for RH language in the disconnected RH of patients with complete cerebral commissurotomy.

Beginning about 1940, the neurologist Akelaitis tested patients of the Rochester neurosurgeon Van Wagenen who had various degrees of commissural section for medically intractable epilepsy. He found few linguistic or cognitive deficits. However, beginning in 1961, Sperry et al. (1969) applied rigorous experimental techniques, originally developed in split brain cats and monkeys, for stimulus lateralization to one sensory field (visual hemifield or hand) in patients who had a single-stage complete cerebral commissurotomy, including the corpus callosum, anterior commissure, and hippocampal commissure. They demonstrated a loss of normal communication between the two cerebral hemispheres. The patients could not verbally identify objects palpated out of view by the left hand or pictures flashed briefly in the left visual hemifield (LVF). At the same time, these patients demonstrated nonverbally good perception and awareness of the meaning of stimuli restricted to the RH, by appropriate manipulation of the stimuli and reliable retrieval from a collection. A similar pattern was observed by Geschwind and Kaplan in a patient with a natural callosal lesion due to a stroke. In both situations, surgical and vascular, the disconnected RH had no speech, thus confirming the long-standing neurological doctrine from lesion studies of exclusive LH specialization for speech in most right-handers.

It is customary to distinguish the acute syndrome immediately following disconnection from the more stable, chronic syndrome. The acute disconnection of a right-handed, left hemisphere dominant patient whose surgical approach involves retraction of the RH, often includes mutism of variable duration and severe left-hand apraxia to verbal command (Bogen, 1993). Mutism may be persistent in patients discordant for speech and manual dominance. The reason for the mutism is unknown. It may reflect temporary diaschistic effects of the surgery which perturb a complex cortical-subcortical network regulating speech and subsuming supplementary motor cortex and the basal ganglia. Indeed, the corpus callosum itself may be part of such a system (see *The Split-brain).*

Within a few months after the operation, patients appear normal in casual social situations. They perform normally in clinical language tests although they tend to exhibit some pragmatic deficits in conversation, including inappropriate or exaggerated politeness, an occasional tendency to confabulate, and alexithymia, an impoverished verbal description of strong emotional personal experiences (Hoppe and Bogen[1]). The patients fail to sustain reading of extended texts and do not read for enjoyment. It is assumed that normal linguistic interaction with complete commissurotomy patients reflects engagement of the disconnected LH and that observable deficits are attributed to absence of the usual RH contribution.

2. Psycholinguistic analysis

2. /. *Functional systems*

The disconnected RHs of patients in the Los Angeles series have substantial auditory language comprehension, more limited reading, little or no spontaneous speech and no writing. Auditory comprehension in the disconnected RH was assessed by providing free-field auditory stimuli, requiring left-hand pointing responses to multiple choice picture arrays, and restricting the visual choices to the left hemifield while permitting ocular scanning of the array using a contact lens technique. The RHs had surprisingly rich vocabularies, as large as a normal adult in one case, and ranging over diverse parts of speech and semantic-fields. It recognizes some abstract nouns, many verbs, and spatial prepositions. Comprehension of sentences is restricted to short phrases. It has a severely limited short-term verbal memory of 3 ± 1 items, as against 7 ± 2 in the disconnected LH or in the normal brain.

Reading comprehension in the disconnected RH is consistently worse than auditory comprehension, and the reading lexicon is a proper subpart of the auditory lexicon. The RH can read words in different cases and typefaces. It can point to a picture depicting an action among multiple choices and it can imitate manual actions when vision and feedback are restricted to the RH, but it fails to execute a printed command flashed in the LVF, presumably because then the LH maintains control over the motor system. Unlike LB and NG, the RHs of JW and DR from the Dartmouth series are said to possess equal auditory and visual lexicons (Tramo et al., 1995).

The disconnected RHs of four patients with complete commissurotomy from the Los Angeles series (LB, NG, RY and AA) could perform above chance lateralized lexical decision of concrete nouns and orthographically regular nonwords (Zaidel, 1983, 1990). The LHs were superior in accuracy but not in sensitivity and the pattern of bias suggested that there are independent modules for word decisions and for nonword decisions in each hemisphere. Subsequent experiments with LB showed LH superiority in sensitivity and no hemispheric difference in bias (lacoboni and Zaidel[1]) but a dramatic hemispheric bias in NG (lacoboni, Rayman and Zaidel'). Other studies confirm that there is receptive language competence in the disconnected RHs of all six patients from the California series who were tested regularly at Caltech. Those include auditory language comprehension by AA (Nebes and Sperry[1]), execution of verbal commands by RY (Gordon[1]), phonological encoding in CC (Levy and Trevarthen[1]), auditory comprehension and lexical reading in NG. LB, AA and RY (Hamilton et al.[1]), and auditory comprehension in NW (Bogen[1]). Similar abilities have been demonstrated by the RHs of four commissurotomy patients from the Dartmouth (PS, JW, DR) and Toledo (VP) series (Baynes et al., 1992. cited in Tramo et al., 1995).

2.2. *Linguistic systems*

The disconnected RH has a rich lexical and pictorial *semantics.* It recognizes linguistic and nonlinguistic references to people and events and it has access to episodic (personal) and semantic knowledge (about the world). D.W. Zaidel has shown that the RH but not the LH exhibits a typicality effect in category membership decisions ("Is this (lateralized) picture an exemplar of the (named) category 'vehicle'?") and that the LH is superior in remembering pictorial scenes in which semantic organization violates physical, logical or social conventions (D.W. Zaidel, 1994). The disconnected RH can recognize diverse relations between words and pictures, ranging from reference (to objects), and part-whole, to functional relations and abstract associations (E. Zaidel. 1978). It is facile in recognizing a variety of semantic relations among words, including synonymy, hyponymy (class membership), and antonymy. The semantic "network" in the RH is apparently connotative rather than denotative; it is denser than in the LH, the arcs are longer (connect more distant concepts) and the semantic relationships among concepts are more loosely associative and dependent on experience.

The disconnected RH can comprehend not only nouns, verbs and adjectives but also a variety of *grammatical* and some simple syntactic structures, ranging from functors and te'nse markers to transformations such as the passive or the negative. Uninflected morphological constructions (free morphemes) are easier than inflected ones (bound morphemes). Constructions that place a premium on word order and make a heavy demand on memory, such as subject-object or direct object-indirect object, are particularly difficult. The RH finds syntactic structures (predication, complementation, etc.) more difficult than grammatical categories (case, number, gender, tense, etc.), which are in turn more difficult than morphological constructions (suffixes), with lexical items (nouns, verbs, adjectives, adverbs and prepositions) being relatively easiest (Carrow's Test, Zaidel, 1978).

It is not clear whether the disconnected RH has input *phonolog* or whether it understands spoken words as abstract acoustic templates. It performs poorly in auditory discrimination tests where the monosyllabic target differs from the decoy in one phoneme. It is especially poor at distinguishing nonsense consonant-vowel syllables with initial stop consonants (ba, da, ga, pa, ta, ka) deemed phonetically complex because of their fast formant transitions. The RH performs poorly on the Token Test, probably because it has a very limited short-term verbal memory.

In spite of the *pragmatic* lacunae already mentioned, LB, NG. AA and RY all showed varying degrees of consistent and frequent use of humor in conversation. They also used idioms and proverbs appropriately and frequently and their gestures, prosody and intonation .seem normal. However, on formal unlateraltzed testing with Gardner and Brownell's Right Hemi-

To facilitate literature searches without encumbering the reference list I often include the names of investigators responsible for particular findings in parentheses.

sphere Communication Battery the patients showed consistent deficits in appreciating prosody, understanding familiar pictorial metaphors, and retelling stories, suggesting selective if subtle RH contribution to these functions (Zaidel, 1990).

None of the split brain patients in the Los Angeles series read fiction for pleasure and they avoid extended texts. Formal reading tests (Davis) disclose poor comprehension and speed (Zaidel, 1990). However, poor scores on tests of *discourse* comprehension may be confounded with poor memory.

2.3. Dual mute variables in word recognition

The hemispheric version of the dual route model posits that during word recognition and naming each hemisphere has access to a lexical route ("sight reading"), characterized by frequency, concreteness and part-of-speech effects (better reading of frequent, concrete nouns than infrequent, abstract function words, respectively), but only the LH has access to a nonlexical route ("phonic reading"), characterized by a regularity effect (better reading of words that follow regular rules of translating orthography to sound than of exception words). That is, each hemisphere has its own visual input lexicon that can access its semantic system, but only the LH has a grapheme-phoneme translator and a phonological output lexicon.

The disconnected RH can recognize letters and words that differ in size, font, case and handwriting styles, suggesting that its visual input lexicon stores abstract letter representations.

Data from three lateralized lexical decision experiments suggest that a length effect in the disconnected, as in the normal hemispheres, only occurs when resources are limited. It can occur in both VFs for both words and nonwords but is more likely to occur in the LVF than in the RVF and for nonwords than for words (Eviatar and Zaidel. 1991).

Early experiments showed that the disconnected RHs of patients LB and NG could not match words (or orthographically regular nonwords) with different end spellings for rhyming, suggesting that they cannot translate graphemes into phonemes (Zaidel and Peters, 1981). More recent lateralized lexical decision experiments showed a regularity effect only in the RVF of LB, or (using simpler words) no regularity effect in either of his VFs. Semantic effects are similarly variable. Frequency effects can either occur in both VFs of LB (Zaidel and Kaiser[1]) or in neither (lacoboni and Zaidel'). A concreteness effect was also observed in both VFs of LB (Eviatar, Menu and Zaidel[1]). These data together are consistent with a hemispheric dual route model in which frequency and regularity effects in lexical decision occur only when resources are taxed.

Patient JW of the Dartmouth series showed better recognition of a letter mismatch when embedded in a word than in a nonword in both VFs, but RVF errors predominated in midstring target positions whereas LVF errors increased with distance from the beginning of the string (Reuter-Lorenz and Baynes, 1990, cited in Tramo et al, 1995). The authors concluded that both hemispheres have access to visual word forms (input lexicons), but that RVF strings are processed in parallel whereas LVF strings are processed serially. However, this task may not generalize to reading.

An unexpected result was obtained with a lateralized Stroop task using unimanual responses, spatially separate color words and color patches which could be presented to the same or opposite VFs. Commissurotomy patients LB and NG showed significant Stroop effects predominantly in interhemispheric conditions, suggesting that the effect may be inherently interhemispheric and can be mediated subcallosally (E. Zaidel, 1994).

In a lexical decision experiment with unilateral targets and contralateral distractors, patient NG showed a strong word bias for RVF targets and a strong nonword bias for LVF targets, regardless of the responding hand. Bilateral displays yielded decisions reflecting control by the hemisphere opposite the responding hand. Thus, identical displays yield dramatically different strategies depending on which hemisphere is in control, reflecting parallel and opposite conscious linguistic decisions by the two disconnected hemispheres (lacoboni, Rayman and Zaidel[1]).

3. Interhemispheric relations

3.1. Dynamic RH language competence

Faure and Blanc-Garin (1994) describe a provocative case of a patient with a large fronto-occipital white matter lesion and a posterior (half) callosal lesion, resulting in temporary global aphasia and a persistent disconnection syndrome. Hemifield tachistoscopic semantic decisions (Is this word an animal name?) following language recovery disclosed better LVF performance with prior RH priming and with concurrent LH loading, suggesting that the linguistic competence of the RH varies with the balance of interhemispheric activation. However, the roles of prior aphasia and of partial callosal section in these data remain unclear. We failed to show comparable priming or loading in either the normal or commissurotomized brains (lacoboni, Rayman and Zaidel[1]). suggesting (1) that the anterior callosum mediates inhibitory channels which can be modulated by attention, and (2) that posterior channels permit the LH to automatically share resources with the normal (and independent)RH.

3.2. Implicit transfer

We may distinguish between explicit and implicit transfer of linguistic information between the disconnected hemispheres. As mentioned, LB and NG differ dramatically in their ability to name LVF stimuli, including letters and words, and to compare (linguistic) stimuli in the two VFs. LB's ability to name LVF words includes instances where the disconnected RH relays subcallosally a semantic address to the LH, resulting in a semanticparalexia.

Define interhemispheric transfer in the split brain as implicit if both verbalization of LVF stimuli and cross-matching on demand fail, but there is nonetheless some automatic influence of the unattended stimulus in one VF on a decision in the other. Reuter-Lorenz and Baynes (1992") found no evidence for letter priming across the disconnected VFs of callosotomy patient JW, and E. Zaidel (1983) found no evidence of associative interhemispheric priming of lexical decision in patients LB, NG, RY and AA. Similarly, LB failed to show the normal word-selective bilateral gain in lexical decision from redundant bilateral presentations of words in the two VFs (Mohr, Pulvermuller, Rayman and Zaidel[1]).

However, Lambert' showed presumed negative priming of an RVF target by an LVF prime in a lexical categorization task in LB. Further, lacoboni, Rayman and Zaidel[1] presented bilateral letter strings with cued unilateral targets for lexical decision by LB and NG and found interhemispheric lexicality priming only in LB. The lexicality priming effects were largely symmetric for word and nonword targets and in the left and right VFs. Response programming variables affected the facilitation of congruent pairs (word-word or nonword-nonword) but not the interference of incongruent pairs (word-nonword or nonword-word). This suggests that the split brain has separate subcallosal channels for facilitation and for interference. Facilitation is likely mediated by response programming, whereas interference is likely mediated by an earlier, lexical access stage.

[2] Cited in E. Zaidel, 1994.

In sum, in spite of persistent "hints", evidence is still lacking for a systematic, consistent and theoretically coherent lexical priming effect across the disconnected commissures (E. Zaidel, 1994).

4. Relationship to acquired aphasia and alexia

Although the linguistic profile of the disconnected or isolated right hemisphere does not correspond to any classic aphasic syndrome, there is some agreement between this profile and the pattern of breakdown and preserved abilities in a majority of aphasics. For example, auditory comprehension is more resistant to damage and recovers sooner than reading and speech. There is a vast literature on RH contribution to recovery of language competence following aphasia due to LH lesions (e.g.. Code, 1987). However, some aphasics with lesions restricted to the LH, such as word-deaf, word-blind and global aphasic patients, show devastating deficits inconsistent with residual language in the intact RH. Most likely, these syndromes represent maladaptive maintenance of control in the diseased LH with pathological inhibition of RH competence. They may also reflect individual differences in degree of language competence in the RH. Similarly, selective discourse deficits observed following some RH lesions (Brownell and Joanette[1]) would predict more severe pragmatic deficits in the disconnected LH than one actually observes (Zaidel. 1990). Acquired alexia illustrates the range of possible consequences of LH damage.

4.1. *Deep dyslexia (DD)*

These patients have large LH lesions and show three prominent symptoms in reading aloud: (i) a prevalence of semantic paralexias; (ii) a concreteness effect (concrete words better than abstract words) and a part-of-speech effect (nouns better than function words); and (iii) failure of grapheme-phoneme translation (reading nonsense words aloud or matching rhyming strings). This profile is consistent with the language of the disconnected RH. Moreover, a DD patient with intact VFs (RW) had many more semantic paralexias in the LVF than in the RVF (Schweiger, Field, Dobkin and Zaidel, cited in Zaidel, 1990). However, the patient had a much greater overall reading competence than the disconnected RHs (e.g., reading sentences aloud), suggesting that her RH contributed to lexical access selectively and adaptively when LH access failed, by providing a semantic address to the intact output phonology of the LH. RW's performance on a lateralized lexical decision task manipulating the dual route variables was consistent with a failure of the nonlexical route in the LH. Ten years later, RW evolved into a phonological dyslexic (no semantic paralexias). At this time an associatively primed lateralized lexical decision task with RW's original semantic paralexias as targets (and their triggers as primes) revealed significant priming only in the RVF, suggesting that the semantic paralexias did not reflect the unique semantic organization in her RH (Langley and Zaidel[1]).

4.2. *Pure alexia*

These patients (i) have a selective inability to read words visually, except (ii) by laboriously spelling out the letters one at a time, while (iii) having intact speech and auditory language comprehension. Occasionally, (iv) they demonstrate "covert reading" during quick presentations that circumvent letter-by-letter reading, consisting of correct forced choice pointing to related pictures even while verbally denying awareness of the word. The received anatomical account of pure alexia is that it reflects a lesion to primary visual cortex in the LH (usually resulting in R homonymous hemianopsia) together with a splenial interhemispheric disconnection. There is evidence from magnetic coil stimulation that covert reading reflects temporary RH contribution. Pure alexia then generally reflects a maladaptive maintenance of control in the diseased LH and inhibition of language in the intact RH, leading to letter-by-letter reading.

An opposite view is maintained by Arguin and Bub who believe that (i) overt letter-by-letter reading in pure alexia reflects RH processing, and that (ii) covert reading in pure alexia reflects LH processing. These claims presuppose that the LH does and the RH does not represent abstract letter identities, an assumption which our own data dispute.

4.3. *Optic aphasia*

These patients have primary left visual cortex lesions together with disruption of the splenium and more anterior portions of the corpus callosum. They cannot name visual objects or words but can demonstrate their use by miming, and they can name auditory or tactile stimuli. Recent accounts of optic aphasia emphasize interhemispheric visual and semantic disconnection together with a RH contribution to semantic interpretation of the visual input without verbal output (e.g., Coslett and Saffran[1]).

Converging direct behavioral, anatomical and physiological evidence for extent of RH contribution to deep dyslexia, pure alexia and optic aphasia remain to be assembled.

5. Developmental analysis

In order to compare linguistic performance across tests, patients, and hemispheres, developmental age norms on standardized tests for language acquisition can be used. The resulting profile does not correspond uniformly to any stage in the ontogenesis of first language (Figure 1). For example, the RH has well-developed auditory comprehension but little or no speech. Its comprehension of single words can reach that of an 18 year old, whereas its understanding of nonredundant (e.g., token test) phrases is as poor as that of a normal 4 year old. This means that the RH is not arrested uniformly at some stage of language when LH specialization sets in, as hypothesized by Lenneberg (1967[1]). Moreover, RH recovery of language in aphasia, if it occurs, would not respect the regression hypothesis, according to which functions that are acquired last are lost first.

For most components of language, however, RH competence falls between that of 3 to 6 year olds, signaling some early interhemispheric interaction in language processing. Thereafter, some components are suppressed whereas others continue to develop in the RH into adulthood. In short, different components of language specialize in the LH to differing degrees.

There is no evidence that word recognition in immature readers, normal or dyslexic, relies selectively on their RHs and that their reading profiles parallel that of the disconnected RH (Bloch and Zaidel[1]).

Right hemisphere language deficits cannot be accounted for in terms of the immaturity of putative prerequisite cognitive operations. A Piagetian analysis of spatial concepts in the disconnected hemispheres (Zaidel, 1978, cited in Zaidel, 1990) showed that neither hemisphere corresponds to a consistent developmental cognitive stage and that there was no correlation between the syntactic competence of either hemisphere and its developmental stage in acquiring the concrete operational structures of reversibility, coordination and conservation.

6. Generalizability

The Los Angeles series of commissurotomy patients is unique. (1) They are all relatively high functioning and permit testing of both hemispheres on diverse language tests. (2) They exhibit relatively minor extracallosal damage and nothing

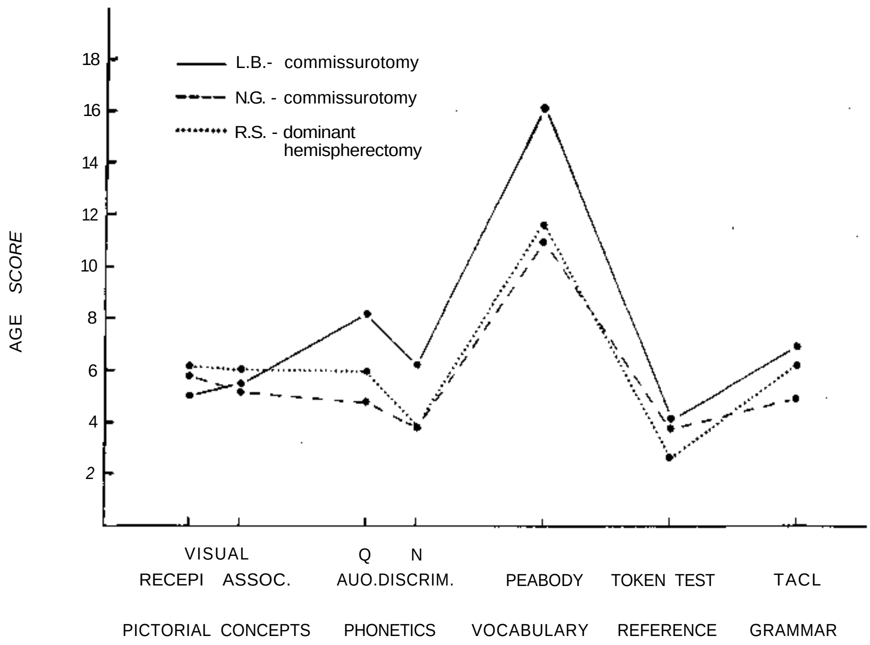

Figure 1. The psycholinguistic mental age profile of the disconnected right hemispheres of two patients, 20 years-old LB and 40 years-old NG. who had complete cerebral commissurotomy at ages 13 and 30, respectively, and of the isolated right hemisphere of a 13-year-old girl, RS. following left, dominant hemispherectomy for a tumor at age 10. Scores are expressed as equivalent mental ages in years. The Visual Reception and Visual Association are subtests of the Illinois Test of Psycholinguistic Abilities. The Auditory Discrimination test of Goldman, Fristoe and Woodcock presents words in quiet (Q) and in noise (N). The Peabody Picture Vocabulary Test measures auditory vocabulary, the Token Test measures auditory comprehension of increasingly long phrases, and Carrow's Test of Auditory Comprehension of Language (TACL) measures grammar and syntax.

to suggest linguistic hemispheric reorganization. (3) These patients have diverse neurological histories yet show generally similar profiles. (4) In general, the predominant hemisphericity of pre- and post-surgical extracallosal damage in these patients does not correlate with behavioral laterality effects. Thus, the language profile of the disconnected RH is likely to represent a normal state of cerebral dominance.

Gazzaniga and colleagues emphasized the variability and plasticity found in their patient pool, arguing against a unique RH language profile (Sidtis et al.. 1981). However, the profile observed in the disconnected RHs of the Los Angeles series is generally consistent in pattern, if not in absolute level of ability, with that observed in aphasia following LH lesions, following dominant hemispherectomy for lesions in adulthood, and in behavioral laterality effects in normal subjects. What varies across these preparations is the amount of resources and control available to the intact RH. In addition, normal RH language must be subject to considerable individual differences.

Long-term disconnection does exhibit some individual variations. Patient LB from the California series can sometimes name pictures and words in the LVF but cannot match such stimuli across the two VFs. This could reflect (i) cross-cueing between the disconnected RH and the verbalizing LH; (ii) subcallosal semantic/phonological but not sensory visual transfer from the RH to the LH; or (iii) RH speech. We compared LB's ability to name LVF words with and without visual figural and verbal distractors in the RVF in order to decide between RH and LH control of LVF naming. The results showed occasional RH control of speech. Baynes et al. (1995) observed a similar partial LVF naming in callosotomy patient JW from the Dartmouth series, conducted a series of naming and matching experiments and concluded that JW demonstrates RH speech. But their data are equally consistent with subcallosal transfer.

By contrast, 20 years after surgery, patient NG from the California series could make same/different judgments about visual stimuli in the two visual hemifields (VFs), without being able to name stimuli in the left visual hemifield (LVF). She could match nonsense shapes and she could match upper and lower case letters for shape but not for name across the vertical meridian. This probably reflects "ipsilateral" visual transfer from the LVF to the LH via a particularly effective superior collicular extra-geniculo-striate system (LVF —* R superior colliculus —* intercollicular commissure -» L superior colliculus —» LH). The collicular visual information thus transferred appears limited to the level of initial representation, or Marr's primal sketch, allowing figure-ground and contour discrimination without specifying the identity of the stimulus.

Since the disconnected RH is generally free of some dramatic language deficits commonly seen after LH damage (such as word deafness, word blindness or global aphasia), evidence from aphasia appears to underestimate the language competence of the disconnected RH. At the same time, the disconnected RH underestimates the language competence of the normal RH inferred from behavioral laterality paradigms. Even when the two normal hemispheres draw on separate lexical representations and exhibit independent strategies, there occur dynamic sharing of resources and variable automatic priming effects across the commissures, which effectively increase RH language competence and range. Even the split brain permits some subcallosal linguistic interhemispheric interaction, including transfer of resources from the disconnected LH to the RH, so that the disconnected RH may overestimate the linguistic competence of the RH following surgical removal or anesthesia of the LH in adulthood.

7. Conclusion

When the LH is separated from the RH there emerges a distinct profile of language in the remaining RH. This profile is characterized by much better language comprehension than speech, better auditory comprehension than reading, no access to grapheme-phoneme translation for rhyming judgments and a rich lexical semantic system but poor phonology and an impoverished syntax. The failure of some aphasics to attain the same profile must reflect complex interhemispheric facilitatory and inhibitory influences, both normal and pathologic. The precise role and extent of participation of the RH in natural language processing by the intact brain need further clarification.

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Zaidel E (1982): Reading in the disconnected right hemisphere: An aphasiological perspective. In: *Dyslexia: Neuronal, Cognitive and Linguistic Aspects.* Zotterman Y, ed. Oxford: Pergamon Press, pp. 67-91

Zaidel E (in press): Language in the right hemisphere following callosal disconnection. In: *Handbook of Neurolinguistics.* Whitaker H, Stemmer B. eds. San Diego: Academic Press

See also Split brain; Aphasia, acquired; Dyslexia: Language development: Language, neurology of; Hemispheric specialization; Alexia; Brainlateralization:dichoticlisteningstudies

Lateral line system *(Historical Paper}*

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The lateral line system consists of water-movement-sensitive sensory organs in the epidermis of cyclostomes, fishes (Chondrichthyes, Osteichthyes), and aquatic stages of all three orders of amphibians. The phylogenetic origin of this system is not known. Already the oldest known ancestors of the modern fishes, the ostracoderms, probably possessed a lateral line system. At least twice during evolution part of this system evolved to an electrosensitive system, possibly by reduction of mechanical sensitivity and enhancement of electrical sensitivity of the sense organs. Like the labyrinth, the lateral line system derives from dorsolateral placodes.

1. Morphology

In cartilaginous and bony fishes parts of the sense organs are submerged in subepidermal canals or grooves on the head and trunk (lateral line). A lateral line organ consists of one neuromast (canal organs, some epidermal organs) or several neuromasts (most epidermal organs), arranged singly or in groups or rows (stitches, Figure 1). Epidermal neuromasts may also lie in slits or pits (pit organs in elasmobranchs or auricles in catfish). On the dorsal and ventral surface of the rostral part of electric rays, three neuromasts (one central, two lateral) form a Savi vesicle, 100 to 200 of which are arranged in a row. The typical budlike neuromast is composed of elongated mantle cells enveloping a core of supporting cells and several shorter cylindrical or flask-shaped sensory cells (hair cells). On the apex of the hair cell one long stiff cilium (kinocilium) with a typical 9 + 2 arrangement of the filaments is inserted excentrically, and about 50 considerably shorter stiff stereovilli (stereocilia) arise and decrease in length with increasing distance from the kinocilium. There are two sets of hair cells with respect to the insertion of the kinocilium. In approximately half the hair cells, the cilium, inserting near the rim of the cell apex, is positioned toward one end of the oval sensory epithelium of a neuromast; in the other half of the hair cells the cilium is positioned toward the opposite end. The neuromast is covered by a jelly-like cylindrical or more or less flattened cupula. The cupula is composed of two layers, a central core secreted by the supporting cells, and a surrounding sheath secreted by the mantle cells. The cupula continuously grows proximally (15 to 30 jitrn per day in *Necturus)* and erodes distally. It is nearly critically damped and most probably determines the mechanical frequency characteristic of the hair cells within the neuromast.