Bihemispheric Language: How the Two Hemispheres Collaborate in the Processing of Language

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Summary. Speech production in most people is strongly lateralised to the left hemisphere (LH), but language understanding is generally a bilateral activity. At every level of linguistic processing that has been investigated experimentally, the right hemisphere (RH) has been found to make characteristic contributions, from the processing of the affective aspects of intonation, through the appreciation of word connotations, the decoding of the meaning of metaphors and figures of speech, to the understanding of the overall coherency of verbal humour, paragraphs and short stories. If both hemispheres are indeed engaged in linguistic decoding and both processes are required to achieve a normal level of understanding, a central question concerns how the separate language functions on the left and right are integrated. Relevant studies on the hemispheric contributions to language processing are reviewed, and the role of interhemispheric communications in cognition is discussed.
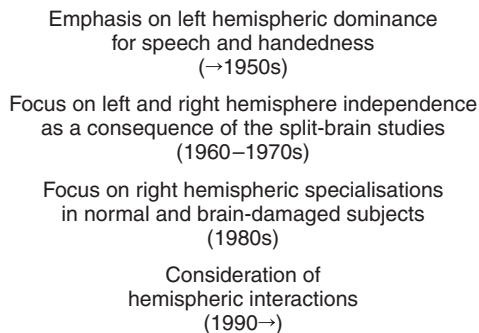
INTRODUCTION

THE LONG-TERM GOAL of psychology is an understanding of the human brain such that psychological disorders can be treated at the appropriate level of intervention. Although psychological medicine is still a young science, already there are clear distinctions between organic brain diseases requiring surgical therapy, metabolic disorders that can be treated pharmaceutically, personality abnormalities that can be dealt with psychotherapeutically, and other brain problems caused by genetic defects that might some day be amenable to genetic engineering therapy. The psychological disorder that has proven most difficult to treat is schizophrenia, in which bizarre and paranoid ideation is found, often

associated with excessive and disordered speech, the schizophrenic 'word salad'. It is a disease that has no clear analogue in the animal world, but affects about 1% of the human population, regardless of cultural or racial background. For this reason, Crow (1997) has argued that schizophrenia may be as old as the divergence of *Homo sapiens* from other primate lines, is as characteristic of humans as the potential for learning and using language, and can be considered as the 'price' that we, as a species, pay for having language capabilities. Because functional hemispheric specialisation is one of the most unusual characteristics of the human brain, relative to other primates, and various abnormalities of cerebral dominance have been implicated in schizophrenia (e.g. Crow, 1998; Gur, 1999), a proper understanding of the mechanisms underlying cerebral lateralisation is arguably a prerequisite for understanding the psychopathology of schizophrenia.

Since the 1960s, the lateralised functions of the cerebral hemispheres have been the focus of much research that has led gradually to a more comprehensive understanding of hemispheric differences, if not yet a full understanding of hemispheric interactions. The changing emphasis on various laterality themes can be briefly outlined, as in Figure 1.

Following reports on the sometimes very different cognition of the two hemispheres in patients who had undergone severance of the corpus callosum (Sperry, 1968; Sperry *et al.*, 1969), the fact that all people contain two potentially independent 'brains' in one skull became widely known, and attention was focused on precisely how these 'two brains', and possibly these 'two personalities', differ. While some of the speculation prompted by the split-brain research was perhaps excessive, the core findings on the split-brain patients have stood the test of time: such patients do show signs of internal

Emphasis on left hemispheric dominance
for speech and handedness
(→1950s)

Focus on left and right hemisphere independence
as a consequence of the split-brain studies
(1960−1970s)

Focus on right hemispheric specialisations
in normal and brain-damaged subjects
(1980s)

Consideration of
hemispheric interactions
(1990→)

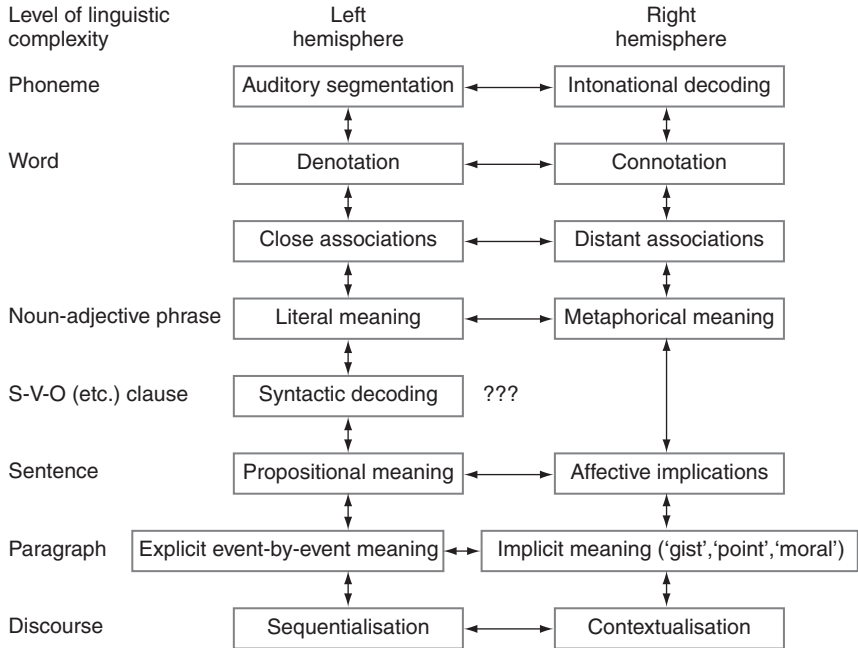**Figure 1.** The recent evolution of the main themes concerning human laterality.

contradictions that can be traced to the loss of corticocortical connections between the cerebral hemispheres. It can therefore be inferred that the corpus callosum in the intact brain acts to resolve contradictions between the hemispheres and integrate the cognition of the left and right to produce a more or less unified self.

Subsequent to the initial split-brain work, neuropsychological studies on brain-damaged patients provided numerous examples of hemispheric specialisation. Related, if generally much weaker, results in normal subjects using tachistoscopic and dichotic techniques were also reported, and gradually a host of methodological issues have been addressed. There has even been a resurgence in interest in the 'two personalities' of the cerebral hemispheres and the implications for psychotherapy (Schiffer, 1998). Most recently, brain-imaging techniques have made it possible to measure directly the cortical activity in normal subjects, and these new methodologies have again invigorated laterality research.

Many of the bold dichotomies of hemisphere function proposed in the 1960s and 1970s have found their way into the textbooks, but virtually none has survived the harsh glare of empirical research. 'Verbal and visuospatial' remains the single most popular summary of left and right hemispheric specialisations, but studies of unilateral brain damage, continued investigation of the split-brain patients, behavioural studies of normal subjects, and the brain-imaging work of the 1990s are unanimous in showing that both hemispheres process both verbal and visuospatial information in their own ways. Since the earliest PET studies, a consistent finding has been approximately bilateral activation of the cerebral hemispheres during language processing. Given the rapid changes in regions of cortical activation (as found in EEG studies) and the extreme localisation of functions (as seen in fMRI studies), it can be said that if any consensus has been provided by recent brain imaging it lies in the idea that hemispheric functional asymmetries need to be considered as dynamic, rather than as static, processes. Evidence indicating that both hemispheres are actively engaged in language processing is reviewed below.

COMPLEMENTARY LANGUAGE PROCESSING

The analysis of language processes in normal subjects and brain-damaged patients has been undertaken from the level of the smallest segments (morphemes, graphemes and phonemes) through small units (words and phrases) to complete utterances and coherent messages (sentences, jokes, short-stories, etc.). As summarised below, at each level a fairly consistent pattern of hemispheric functional asymmetry has been found and indicates the active involvement of both hemispheres at multiple levels of language processing (Figure 2).

Level of linguistic complexity	Left hemisphere	Right hemisphere
Phoneme	Auditory segmentation	Intonational decoding
Word	Denotation	Connotation
	Close associations	Distant associations
Noun-adjective phrase	Literal meaning	Metaphorical meaning
S-V-O (etc.) clause	Syntactic decoding ???	
Sentence	Propositional meaning	Affective implications
Paragraph	Explicit event-by-event meaning	Implicit meaning ('gist', 'point', 'moral')
Discourse	Sequentialisation	Contextualisation

Figure 2. A schema of the multiple levels of bilateral language processing. The horizontal arrows indicate levels at which the cerebral hemispheres may interact via the corpus callosum. The vertical arrows indicate the bottom-up sequential processing from smaller to larger linguistic units, as well as the top-down effects from larger to smaller units. Whether or not there are RH functions comparable to and interacting with the syntactic decoding of the LH is uncertain.

The loss of the affective prosody of speech following RH damage is well-known clinically (Weniger, 1984). As in music perception/production, the two principal dimensions of the prosody of speech concern the temporal dimension, i.e. the rhythm and timing of speech output, particularly consonant stops, and the pitch dimension, i.e. the fluctuation in auditory frequency of particularly vowel sounds. Abnormalities of timing and fine temporal discrimination are found following LH damage, and may be a key factor responsible for dyslexia (Tallal *et al.*, 1996). Following RH damage, the pitch dimension appears to be most disturbed (Behrens, 1989; Ross *et al.*, 1997); callosal damage has similar effects (Klouda *et al.*, 1988). The range of pitch fluctuations is reduced, the frequency of changes in the direction of pitch intervals (melodiousness) decreases (Schirmer *et al.*, 2001), and what prosody there is often seems inappropriate to the linguistic content. Although sometimes dismissed as 'para' linguistic, the production and understanding of prosody is clearly important for normal verbal communication and is a function for which the RH is dominant.

In dichotic listening experiments on normal subjects, Bulman-Fleming & Bryden (1994) and Grimshaw (1998) have studied intonation using a design that allows the measurement of affective and linguistic understanding simultaneously. They demonstrated the superiority of the RH in detecting emotional prosody (happy, sad, etc.) and the LH in detecting linguistic meaning. In studies on patients with unilateral brain lesions, Van Lancker & Sidtis (1992) showed a double dissociation between pitch and rhythm perception, and Alcock *et al.* (2000) reported similar effects (unrelated to speech) that suggest LH specialisation for rhythm and RH specialisation for pitch. Ross *et al.* (1981, 1997) have defended the idea that there are types of aprosodia due to focal lesions of the RH that are as specific as the varieties of aphasia that occur with focal lesions of the LH. Most importantly, they present clinical evidence for a distinction between two forms of aprosodia related to the understanding and to the production of prosody, a distinction that mirrors sensory and motor aphasia. Finally, Zatorre *et al.* (1994, 2002) have repeatedly reported evidence of RH involvement in pitch perception and have emphasised the role of the RH in both speech prosody and music.

In line with the idea that the LH and RH functions can be summarised as verbal and visuospatial, respectively, the possibility that concrete, easily visualised, words might be more competently processed in the RH, and abstract, less easily visualised, words by the LH, has often been studied. Results have been mixed, probably reflecting differences in stimulus materials. In a recent fMRI study designed to examine specifically the abstract/concrete aspects of hemispheric processing, Kiehl *et al.* (1999) found (1) bilateral activation in temporal, parietal and frontal regions during all verbal processing, with (2) more activation of right temporal cortex for abstract words, and (3) more activation of left temporal cortex for concrete words. This pattern is the exact opposite of what many would predict, and is an indication that the concrete/abstract dimension is problematical for distinguishing between LH and RH processing.

With the notable exception of the so-called function words, most nouns, adjectives and verbs have connotative meanings, in addition to their dictionary denotations. The connotation is related to the affective state and the larger cognitive context within which the words are typically used, and normally has implications beyond the literal meaning of the phrase or sentence. As both cerebral hemispheres in most individuals will be exposed to the same words in the same contexts for an entire lifetime, it is of extreme interest that unilateral brain damage can lead to deficits of linguistic processing at either the denotative or the connotative level. In a classic study by Brownell *et al.* (1984), the understanding of words by the LH and RH was compared by having patients with unilateral brain damage group words according to their similarity. The dimension along which 'similarity' was to be determined was not specified, but the test design forced a choice between denotative and connotative grouping.

Patients with an intact RH but a damaged LH preferred metaphoric or connotative pairings, whereas patients with an intact LH but a damaged RH preferred antonymic or denotative pairings. Gainotti *et al.* (1983) also found specific lexical semantic deficits in patients with RH damage. More recently, Taylor *et al.* (1999) showed qualitative hemispheric differences in semantic category matching in normal subjects. The dimensions of RH semantic processing appear to be complex and may reflect individual differences rather than neuropsychological universals, but it cannot be said that semantics is exclusively a LH function.

The idea of a semantic network within which the words known to an individual are organised along various semantic dimensions has a long history in both psychology and artificial intelligence, and the possibility that the two hemispheres contain similar lexicons, but are organised differently, has frequently been studied. Particularly in light of the demonstration of the independence of the hemispheres in simple word recognition tasks in both normal subjects (Iacoboni & Zaidel, 1996) and split-brain patients (Zaidel, 1985), it is of interest to know if the semantic organisation of the LH and RH differs. In a split-visual field study, Rodel *et al.* (1994) found the LH to favour close associations, and the RH to favour distant associations. Using an ERP technique, Kiefer *et al.* (1998) examined the hemispheric response to closely related words, distantly related words and unrelated words. Both hemispheres responded to closely related words, but only the RH responded to distantly related words. Such findings are viewed as support of the idea that the RH maintains more associations than the LH, with the latter focusing on one of several possible trains of thought.

Judgements of metaphoric meaning show a similar laterality, with the RH preferring the metaphoric over the literal and the LH preferring the reverse. In a study by Winner & Gardner (1977), patients were asked to select one of four pictures that depicts the meaning of a phrase, such as 'lending a hand'. With one picture depicting a literal loaning of a disembodied hand and another picture depicting an individual giving help to another, the LH-damaged patients more often chose the metaphoric meaning, and the RH-damaged patients more often the literal meaning. Similar results were obtained by Van Lancker & Kempler (1987) and Anaki *et al.* (1998). Bottini *et al.* (1994) compared literal and metaphoric sentences in a PET study using normal subjects. The relevant comparison revealed right-sided frontal, temporal and parietal activations during the metaphoric sentences and left-sided activations during the literal sentences. Finally, Burgess & Chiarello (1996) have provided evidence indicating that an intact RH is essential for metaphor comprehension.

The construction of a coherent paragraph consisting of several, individually coherent (grammatically and semantically), sentences necessitates the sequencing of the sentences in the semantically correct order. In a comparison

of the abilities of brain-damaged patients to do so, Gardner *et al.* (1983) found the RH-damaged patients to perform more poorly. Schneiderman *et al.* (1992) found that RH damage significantly disrupts patients' ability to arrange sentences into coherent paragraphs. The understanding of short stories requires one to grasp not only the individual actions of story participants, but also the consistency, overall coherence and sequence of events. Wapner *et al.* (1984) presented short stories to groups of brain-damaged subjects and had them retell the stories immediately upon completion of presentation. The stories were constructed with various logical anomalies, including temporally or causally anomalous events, and counter-intuitive actions. Regardless of the type of anomaly, RH-damaged patients were generally capable of retelling the story including its main elements, but failed to detect the nature of the anomaly. In contrast, the LH-damaged patients with intact RH, despite more diverse language problems, were capable of detecting the unusualness of the stories. These and related results have led Gardner *et al.* (1983) to consider the RH as an 'anomaly detector'. In related work on the understanding of jokes, Winner *et al.* (1998) have reported deficits in understanding following RH damage, and have argued that it represents a loss of second-order mental states.

In one of Geschwind's (1982) most neglected papers, he noted that the single most common consequence of diffuse RH damage, as seen in the neurological clinic, is the 'confusional state'. He defined this condition as one in which the ability for speech production is normal, but the coherence of verbal output is degraded, leading to unwitting humour, paramnesias and an inability to carry a train of thought to its logical conclusion. Being based on clinical observations, Geschwind's (1982) argument that the RH normally prevents 'confusion' must be considered anecdotal, but raises the interesting question of what state we are in when we are 'not confused'. Whether in conversation or in a monologue of speaking or writing, when ideas fall into place and lead to coherent conclusions, it might be said that each word, thought or statement is 'in context', and that cognition as a whole is contextually grounded. If such coherency is a function of the RH, it may be that the highest level contribution of the RH to language functions is the construction or maintenance of cognitive contexts. [Note, however, that Leonard *et al.* (1997) have failed to demonstrate a contextual role of the RH in brain-damaged patients. This might be attributable to the syntactic nature of the task (the resolution of ambiguous pronouns) but, in any case, highlights the need for a more precise definition of 'context'.]

What is significant about the above findings is that they indicate that, within the linguistic realm, both cerebral hemispheres are engaged in information processing at approximately the same level of complexity, but with apparently different strategies. Unlike hemispheric dichotomies in which very unlike processes are contrasted (verbal/visuospatial, etc.), the multiple levels of bilateral

language processing summarised in Figure 1 suggest a complementary compe-
tence of the 'two brains'. Both hemispheres process linguistic information but
manage *not* to duplicate their processing, despite the fact that their life-long
experience of all language input is identical. The complementarity, as distinct
from dissimilarity, of the two modes of cognition has been a recurring theme in
the laterality literature (Landis *et al.*, 1979; Kinsbourne, 1982). Bogen (1997),
in particular, has been a persistent defender of the idea that the RH is capable
of high-level cognition, and has shown convincingly that both hemispheres in
most split-brain patients have linguistic competence, provided only that one
does not insist on a definition of 'linguistic competence' that is syntax-based.

For further discussion of individual experiments and laterality models that
focus on the bilaterality of language, two edited volumes can be recommended:
Right Hemisphere Language Comprehension (Beeman & Chiarello, 1998) and
Language and the Brain: Representation and Processing (Grodzinsky *et al.*,
2000). An older review by Code (1987), *Language, Aphasia and the Right
Hemisphere*, and a more recent discussion of metaphoric and figural under-
standing by Burgess & Chiarello (1996), are also noteworthy.

EFFECTS OF CALLOSOTOMY ON LANGUAGE FUNCTIONS

The results concerning the language specialisations listed in Figure 2 have come
predominantly from patients with unilateral brain damage, but a remarkable
fact is that callosal damage alone can produce effects similar to those following
RH damage [for example the loss of affective intonation (Klouda *et al.*, 1988;
Ross *et al.*, 1997) and infrequent use of affect-related words following callosal
section (TenHouten *et al.*, 1985)]. In general, the language abnormalities of
split-brain patients are mild when tested in a non-lateralised fashion, but
already in the earliest discussions of these patients, Sperry (1968; Sperry *et al.*,
1969) noted that their spontaneous speech was affectively flat or inappropriate,
and unusually concrete with a tendency toward literalism. These comments are
particularly noteworthy as they were made before most of the neuropsycho-
logical studies on the affective, contextual and higher-order contributions of
the RH to language understanding.

Another remarkable acute effect of callosal section is mutism. Cutting the
corpus callosum results in the complete loss of speech for days, weeks or
months in most callosotomy patients (Ross *et al.*, 1984). The effect is not per-
manent, but remains unexplained. Why would the speech-competent LH
require input from the RH to initiate speech? RH damage itself does not nor-
mally produce mutism, indicating that, when the integrity of the RH is com-
promised, the LH is *not* prevented from acting on its own. Paradoxically,
following severance of the corpus callosum when the RH is intact and capable

of normal information processing, the presence of two functioning cerebral hemispheres that have been suddenly disconnected means that the LH can no longer undertake its most usual and perhaps least effortful behaviour, speech. The implication is that the LH, prior to callosotomy, normally *awaits* cognitive input from the RH before initiating verbal behaviour.

The phenomenon of mutism is perhaps not so surprising in light of the effects summarised in Figure 2. That is, if the multilevel hemispheric division of labour shown in the figure is typical of the normal brain, then mutism can be understood as a consequence of the loss of the cognitive—connotative, metaphorical, contextual—input that motivates most *normal* speech behaviour. It is relevant to note that, in response to perceived speech, even when the literal meaning is entirely clear, normal people do not necessarily respond if the 'point' of the speech is not perceived. When contextual information, implications and underlying meaning are missing, many normal people are *not* talkative and are reticent about engaging in 'meaningless' verbal discourse except for reasons of social politeness. Such an argument concerning post-callosotomy mutism remains speculative, but a loss of spontaneous speech would not be paradoxical if the various 'meanings' that normally drive verbal behaviour reside in the RH and are disconnected from their normal outlet through the LH.

In so far as callosal damage produces linguistic deficits similar to those of RH damage, the obvious inference is that, even with both hemispheres fully functional, RH cognition does not affect behaviour if information is not sent across the corpus callosum for use by the talkative 'dominant' LH. In other words, for the purposes of motor utilisation of the 'para-linguistic' information of the RH, callosal connections are essential (or, if not essential, at least the most efficient route over which information can flow between the left and right cerebral cortices). Less clear is the influence that an intact corpus callosum has on RH language understanding. That is, does the RH need the syntactical decoding of the LH to understand correctly even propositional speech? 'The boy kissed the girl', 'The girl kissed the boy' and 'The boy was kissed by the girl' (etc.) might sometimes be construed as providing the same affective 'young love' message, but these sentences might also be understood as emotionally quite different, depending on the situation. In the 'young love' context, precisely who was kissed by whom is not important, but consider a situation where the boy had been chasing the girl relentlessly for weeks, and at some point the relationship developed into a kiss! The syntactic information available from the verb form could provide the key information to distinguish between an act of unwanted harassment or one of reciprocated love. Clearly two distinct types of RH affect might be the result, depending crucially on syntactic information. In that case, does the syntactic information of the active/passive verb form, presumably processed in the LH, play a role in determining

the polarity of the RH affect? If so, the processing of the RH would make use of input from the LH to deduce the actual affective state, whereas, if the RH is a 'coarse processor' (Beeman *et al.*, 1994), the summation of the connotations of the three words, 'boy', 'girl' and 'kiss', tells the entire 'young love' story; in that case, the information contained in the verb form would presumably not play a decisive role in determining the affect perceived by the RH, and the flow of information from left to right would not be an important aspect of RH language processing.

Whatever the case may be with regard to hemispheric co-operation during language understanding, what is known about language *expression* is that the RH does *not* act as a language processor capable of independent action. It relies on the LH for verbal expression, and when its access to the LH is prevented by callosal section, RH information is simply not expressed verbally. The affective state of the RH may be 'leaked' through limbic mechanisms (blushing and giggling) or somatically through gestures or facial expressions, but the RH remains verbally silent if direct transfer to the LH is not possible. The only apparent exception to this rule is verbal expression through singing. Although brain-damage studies support the idea that the RH is capable of singing but incapable of normal speech, the clearest demonstration of this effect comes from unilateral anaesthesia (the Wada test). Following left carotid artery injection of sodium amytal, the LH is temporarily incapacitated, but singing is not disrupted. Contrarily, right-sided anaesthesia has little effect on language production but disrupts singing. The capability of the RH to sing provides an interesting insight into the nature of RH language capabilities. While it seems likely that the prosody and pitch contour of the song aids the RH in its verbal expression, what is most remarkable about RH singing is that, with the help of the melody, the RH is capable of correct pronunciation, correct syntax and appropriate timing of speech output. Propositional speech may not be its strength, but the RH is *not* non-verbal!

INTEGRATION

While the ability to respond literally to simple questions and to produce syntactically coherent propositional statements is a prerequisite to more complex language usage, verbal exchanges among normal people rarely remain at the literal level. If you don't laugh at my jokes, don't respond appropriately to my metaphors, don't pick up on the 'gist' of my argument or if you giggle in response to my unhappy news, we do not 'understand' one another in the sense that we normally use the word 'understand'. It may be the case that literal language use and non-metaphoric information exchanges constitute the foundation on which metaphoric language is built, but the syntactic and literal

semantic issues that have been the primary topic of traditional linguistics, and are the linguistic strengths of the LH, are closer to the starting point than the completion of an understanding of characteristically human communications. In an extensive review of the cognitive psychology of non-literal language use, Gibbs (1994) has argued that:

> Metaphor, metonymy [part-whole metaphors], irony and other tropes [figures of speech] are not linguistic distortions of literal mental thought but constitute basic schemes by which people conceptualize. (Gibbs, 1994: 1)

> Metaphor is a fundamental mental capacity by which people understand themselves and the world through the conceptual mapping of knowledge from one domain onto another. (Gibbs, 1994: 207)

Clearly, in so far as we are engaged in verbal communication more complex than asking directions to the nearest bus stop, the understanding of language requires the contributions of both literal and metaphoric/connotative/affective processes. As linguistic and paralinguistic information must be brought together to obtain the benefits of literal and non-literal modes, the question of 'integration' is an important issue still facing cognitive psychology. This general point has been understood for many years, and felt acutely by researchers in artificial intelligence who have been able to implement a variety of literal language-understanding processes and logical inference mechanisms, but have utterly failed to build intelligent machines. Given the nature of psychological research and the underlying assumptions of a scientific methodology, it is inevitable that definition of the identifiable components of cognition should precede discussion of the integration of those components, but the gap between robotic language processing and the level of normal human language use is as great as ever. From a neuropsychological perspective, the bridging of the gap between the realm of literal language and that of non-literal language means addressing questions of the relationship between the language functions of the LH and RH. Unfortunately, most neuropsychological arguments about LH and RH 'capabilities', 'specialisations' and 'information-processing modules' still conclude with statements concerning the nature of the differences or unilateral superiorities, and fail to address the next issue, that of interaction.

A recent example is the remarkable book by Ivry & Robertson (1998), *The Two Sides of Perception*. They defended the idea that the LH and RH are specialised for, respectively, high and low frequency information-processing in both the auditory and visual domains. The book constitutes a coherent, reductionist, argument about laterality and, if not the final word, it is certainly a worthy attempt to delineate a core mechanism that might account for a host of hemispheric functional differences, including language capabilities. On the penultimate page of the monograph, however, the authors note explicitly that the possibility of hemispheric interaction has not been dealt with:

> In our current development of the … theory we have emphasized how processing within each of the hemispheres considered in isolation can account for laterality effects in a variety of task domains. Our current lack of consideration of inter-hemispheric communication is an obvious weakness of the theory … (Ivry & Robertson, 1998: 276)

When dealing with 'low-level' psychophysical phenomena, the omission of callosal effects may be justified (although some would challenge the very notion of low-level), but when the discussion turns to 'high-level' language processing and the functions of association cortex where the density of callosal fibres is greatest, it is far from obvious that a 'hemispheres in isolation' perspective will have any validity. Callosally connected cortical regions are *not* isolated, and it remains an open question whether or not specialised functions are influenced by contralateral input.

Despite the continuing preference for treating the cerebral hemispheres as if they were disconnected brains, there are clear indications that hemispheric interaction does occur at various levels in the normal brain, and indeed that a failure of integration of functioning components is one possible clinical syndrome following brain damage. The clearest example of such failure of integration is the disconnection syndrome seen in the split-brain patients. Each hemisphere actively processes information, but, with the corpus callosum absent, each is ignorant of what the other hemisphere knows. Unfortunately, the split-brain studies have had the unintended effect of emphasising the independence of the LH and RH. Without a corpus callosum, *independent* and somewhat different information-processing can occur in the split-brain patients, but, however important that insight might be concerning the possibility for radically different modes of hemispheric processing in such patients, the intact brain necessarily has, in addition, the opportunity for collaboration, interaction and integration across the corpus callosum. While perhaps no one any longer advocates the idea that the corpus callosum does nothing of interest psychologically, the bulk of current theorising about the cerebral hemispheres still emphasises dominance and potential independence, rather than what it may mean to have two somewhat different hemispheric processes communicating with one another in the normal condition. Final answers may not yet be possible, but the general question of hemispheric interaction clearly requires some attention.

HERA

Starting in 1993, several laboratories reported a consistent, but unexpected, prefrontal asymmetry of activation in various short-term memory tasks; Tulving *et al.* (1994) labelled this phenomenon 'the hemispheric

encoding/retrieval asymmetry' (HERA). The basic effect is that LH prefrontal regions are relatively active during the encoding phase of stimulus memorisation, whereas RH prefrontal regions are activated in the recall or retrieval phase. This was found using various brain-imaging techniques, including EEG, ERP, PET and fMRI, and reported by diverse groups. Debate continues regarding the influence of the nature of the stimuli and whether or not recall success and/or effortfulness are important factors (Nyberg, 1998), but the reality of the effect using meaningful verbal stimuli is not in doubt (Fletcher *et al.*, 1998a, b; Heun *et al.*, 1999). Many issues remain unsettled, but the asymmetry of cortical activation during verbal information-processing in short-term memory tasks is an unambiguous indication of some form of hemispheric collaboration.

In a typical HERA experiment, word-pairs, such as category–exemplar combinations (for example, furniture–bookcase, tool–hammer, fruit–papaya), are presented during the encoding phase, and retrieval of the exemplars in response to the category label is demanded in the retrieval phase. The familiarity of the words, their concreteness and ease of visualisation are factors that might influence the strength of activation, but the most robust effects have been found in tasks requiring a verbal response to a verbal stimulus (notably, the use of semantically 'empty' stimuli, i.e. pronounceable non-words do not elicit the HERA effect; Lee *et al.*, 2000). Although activation of the LH during the encoding of verbal material is unremarkable and expected solely on the basis of LH dominance for language, the activation of the RH during recall to produce a verbal response is a nonsensical, inexplicable effect if the possibility of inter-hemispheric communication is not considered. That is to say, in an extreme 'independent-hemispheres' model, HERA simply cannot be explained: if the information is initially encoded in the LH, recall should not involve RH activation at all, much less activation more robust than that of the LH regions involved in encoding. Presumably, the prefrontal RH activation during recall is indicative of retrieval of information in response to the verbal (category) stimulus, and transfer of that information to the LH to initiate the appropriate speech response. That the corpus callosum (CC) may be involved in this inter-hemispheric communication is the obvious first consideration, so that a working hypothesis might be summarised as follows.

The encoding phase:

> **sensory organs** ($\rightarrow$ posterior LH) $\rightarrow$ **prefrontal LH** ($\rightarrow$ CC $\rightarrow$ prefrontal RH)

Followed by the retrieval phase:

> **sensory organs** ($\rightarrow$ posterior LH $\rightarrow$ prefrontal LH $\rightarrow$CC) $\rightarrow$ **prefrontal RH** ($\rightarrow$ CC $\rightarrow$ prefrontal LH) $\rightarrow$ **speech organs**

The structures in bold type are known to be involved, while the involvement of the structures in parentheses is empirically uncertain, but theoretically necessary, whenever the basic HERA effect is obtained. That is, if retrieval occurs from structures to which encoding must necessarily have first taken place, then we must postulate a relatively 'silent' (or delayed) involvement of the RH subsequent to LH encoding. Similarly, the involvement of the LH during retrieval must be assumed, even if not evident in brain images, initially to register the category to which an exemplar must be matched, and subsequently to provide the exemplar speech response. Interhemispheric communication is thus a *necessary* component of any viable explanation of the HERA phenomenon. This prefrontal asymmetry is found in the normal adult brain with intact corpus callosum in response to bilateral (auditory or visual) stimulus presentation, thus making an 'independent-hemisphere' model extremely unlikely. As the LH is clearly dominant for speech output in most individuals and notably superior at syntactic functions, its importance for both decoding input and encoding output seems clear. Despite the fact that the RH is remarkably *unable* to control the organs of speech for normal propositional speech output, it is known to be involved in various language processes, but that fact alone does not explain the HERA effect. The most obvious possibility is that the RH contributes to language processing by communicating with the LH across the corpus callosum, rather than using its information for direct control over the relevant somatic musculature. While the more difficult questions of neuronal mechanisms remain to be explored, this first-order understanding of the flow of language information in the human brain can be summarised in what I refer to as a 'central dogma' (Cook, 1986, 1989, 2002) for human neuropsychology:

$$RH \leftrightarrow LH \rightarrow \text{striate musculature}$$

The 'dominance' of the LH is due to its role in, particularly, speech output. Of course, both cerebral hemispheres are heavily connected to sensory and motor organs, but, at least with regard to language processing, the RH does *not* actively control the midline organs of speech. Moreover, in the absence of the LH, the RH is incapable of understanding even mildly complex propositional speech, despite its rich lexicon. In other words, although the RH contributes in characteristic ways to language understanding and production, it is not 'independent'. Instead, a large part of the flow of linguistic information from the RH seems to go through the LH. This fact about the neuropsychology of language is as frequently misunderstood as it is widely acknowledged. On the one hand, the cerebral hemispheres are each virtually complete information-processing neural structures: if either hemisphere is removed at a young age, the other hemisphere alone is capable of a nearly normal range of sensory, cognitive, affective and motor processing, including language. On the other hand, in the normal intact brain, the hemispheres become specialised during

the developmental process to such an extent that, subsequent to acute brain damage in adulthood, the undamaged RH often cannot take over lost LH functions, and vice versa. It is this paradox of equipotentiality, but functional specialisation (and consequent asymmetry of information flow), that lies at the heart of the 'central dogma.'

Analogous to the central dogma of molecular biology, this psychological dogma does *not* address the important issues of mechanisms, i.e. the neuro-physiology of intracerebral information flow (i.e. a 'brain code' with a scientific clarity comparable to the nucleotide base-pairing of the genetic code), and is essentially nothing more than a highly simplified flow chart. For focusing on the most important processes in language input and output, however, it is a valid summary of the division of labour that the human brain appears to employ. That there may be other flow charts for non-linguistic processes or for the cognitive processes of other species is likely, but for the all-important usage of language (and possibly tools) the human brain has evolved a functional asymmetry that entails not only functional differences, but a specific pattern of asymmetrical information flow (Figure 3).

Regardless of the label given to this pattern of hemispheric interaction, its general validity with regard to linguistic processing has been partially known since the mid-1800s, when the dominance of the LH for speech became established. Precisely what the RH does during language processing has remained more of a puzzle, but most of the confusion about hemispheric specialisation has come from attempts to summarise all types of hemispheric functions with a single dichotomy of a psychological nature: verbal/non-verbal, logical/emotional, or whatever. Unfortunately, even when there is strong empirical support for a given dichotomy in a given context, the dichotomy is defined by the nature
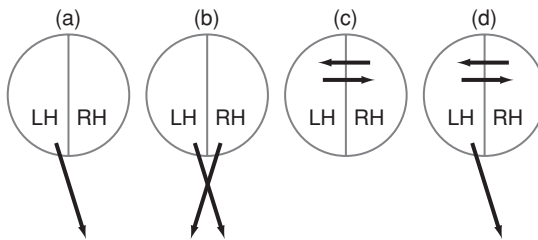
Figure 3. The evolution of ideas on human laterality. An emphasis on LH 'dominance' for speech and handedness was the main theme of early (pre-1950) laterality studies (a), while hemispheric independence and the distinct modes of LH and RH cognition were the focus of most split-brain and split-brain-motivated studies (1960s–1980s) (b). Hemispheric interaction has more recently (1990s) been researched and debated (c), but hemispheric interaction models still need to be reconciled with traditional ideas of dominance, particularly with regard to language (d).

of stimulus materials and does not necessarily generalise to other modalities. What is needed, therefore, is not the perfect set of philosophical or psychological adjectives, but a neuronal mechanism, or a small set of neuronal mechanisms, that can be understood to operate on various kinds of cortical information.

The establishment of mechanisms to replace (and explain) a host of psychological dichotomies may seem unachievable at the present time, but the relative simplicity of callosal anatomy (largely homotopic connections between cortical areas that process information of the same modality or modalities) and the two-dimensional organisation of the cortical surface greatly constrain the types of callosal mechanisms that must be considered (Reggia *et al.*, 1998; Cook, 1999; Shkuro *et al.*, 2000). Already prior to 1986, all four of the most obvious possibilities (i.e. assuming predominantly excitatory or inhibitory synaptic effects, and predominantly diffuse or focal callosal fibre termination) had been defended in the laterality literature as 'the crucial mechanism' underlying human laterality (reviewed in Cook, 1986). Since then several variations on the basic excitatory and inhibitory models have been advocated (for a review see Burgess & Lund, 1998; for discussion of the relative merits of the models see Querné *et al.*, 2000; for some clarity on the various versions of interhemispheric inhibition see Chiarello & Maxfield, 1996). When taken as the-one-and-only mechanism of hemispheric interaction, however, no single hypothesis alone can account for the diverse nature of interhemispheric information flow, but the validity of each model taken on a cortical module-by-module basis may well be demonstrable both behaviourally and in brain-imaging studies. Final answers are not at hand, but the HERA pattern of cortical activation provides an indication that something as simple as the 'central dogma' flow chart for interhemispheric communications may be a useful framework into which the neuronal mechanisms (specific cortical circuitry, neurotransmitters, etc.) will eventually need to be plugged.

NEURONAL MECHANISMS

From the point of view of cognitive psychology, neurones are rather simple things: as far as is known, they have significance for cognition only when they generate an action potential that leads to the release of neurotransmitters at synapses. The strength of the synaptic effect and the frequency of firing can vary continuously from small to large values, but the synaptic polarity is fixed as either excitatory or inhibitory (Dale's law). The complexity of neuronal 'information-processing' therefore lies in (1) the spatial configuration of neurones (numbers of neurones, numbers of synapses and pattern of connectivity) and (2) the temporal structure of neuronal firing. Arguably the single most

important addition to the basic concepts of neurophysiology in general since the 1950s has been the realisation that the temporal dimension, i.e. synchronisation of neuronal firing, may be important for information processing (Singer, 1993; Crick, 1994; Singer & Gray, 1995). That is to say, not only does the frequency of neuronal firing have influence on cognition, but the temporal relationships are also relevant as a means for 'binding' cognitive operations that occur in diverse locations in the nervous system. Synchronisation thus adds an important *temporal* dimension to the basic concepts of neurophysiology that were established in the first half of the twentieth century, and promises to play a central role in the elucidation of so-called higher cognitive activity.

The dimensions along which information is organised in early sensory and late motor cortex are known and give rise to the retinotopic, somatomotor, etc., topographical mapping of large portions of the neocortex. Despite some indication of the semantic organisation of association cortex obtained by direct stimulation (Penfield, 1959), the simplicity of sensory and motor cortex mapping is not found, and individual differences in the organisation of association cortex may be large. Assuming only that the association cortex also has some sort of meaningful two-dimensional organisation, it can be concluded that the interaction between homologous regions in the LH and RH will be influenced primarily by the anatomical connectivity between them, and the nature of the synaptic effects. As mentioned above, the main classes of interaction are easily summarised and simulated (Reggia *et al.*, 1998; Cook, 1999; Shkuro *et al.*, 2000). If a relatively fine-grained topographic connectivity between cortical regions is assumed, then the transfer of information (either excitatory or inhibitory) from one hemisphere to the other is possible. In contrast, if callosal effects are relatively diffuse, the possibilities for the transmission of detailed information decrease, and the corpus callosum will act to alter the hemispheric balance of arousal and attention.

Attentional models of hemispheric functions have been advanced by Kinsbourne (1970, 1982), Heilman & Van Dan Abell (1979) and Guiard (1980), and more recently by Banich (1998) and Liederman (1998). These attempts to explain laterality effects on the basis of asymmetrical 'arousal' or 'attention' are psychologically plausible, but suffer from terminological problems. Commonly used phrases such as 'the dynamic allocation of attentional resources' have no obvious physiological meaning and thus lack the specificity to bridge the gap between psychological phenomena and neuronal mechanisms. Interestingly, recent advances in explaining arousal, attention and awareness on the basis of the synchronisation of neuronal firing mean that the psychological concepts of the attention theories, such as 'resources,' 'spotlights' and 'bottlenecks', might be translatable into the language of neuronal activity (Singer, 1993; Crick, 1994).

The importance of the synchronisation hypothesis for the issue of human laterality is that it has the potential to replace a host of plausible, but inherently fuzzy, descriptions of hemispheric relations with an explicit neuronal mechanism that allows distant (including bihemispheric) cortical modules to collaborate without requiring a cortical region at which all cognitive 'results' are integrated. While explanation of bilateral cognition on the basis of synchronisation has not yet been achieved, progress has been made in defining the relationship between synchronisation and arousal, attention and awareness, the relevant frequencies of oscillation have been studied in various animal species, and possible neuronal mechanisms have been explored in artificial neural nets (Engel & Singer, 2001). Hypotheses concerning the synchronisation of LH and RH neuronal activity during language processing might eventually replace or augment ideas of topographical information transfer.

As mentioned in the introduction, the paradox of the duality of the nervous system and yet the unity of subjective consciousness remains unsolved. It remains a paradox primarily because the problem of subjective feeling itself is one of the so-called 'hard problems' in consciousness studies (Searle, 1997; Shear, 1998). That is, why do we have subjective feeling at all? Why, in addition to the 'information-processing' of neurones, do we feel that there is something like direct 'experience' that is fundamentally different from cognition? Here, as well, the synchronisation hypothesis provides an essential connection between the realm of cognition and the various issues of subjective consciousness.

Briefly, the argument concerning the relationship between synchronised neuronal firing and subjective consciousness (Cook, 2000, 2002) is as follows. The neuronal membrane is normally closed to the diffusion of ions, but at the time of the action potential there occurs (1) a localised, transient permeability of the membrane, (2) several hundred thousand ion channels are opened, and (3) about 10^8 ions per channel per second flow between the intra- and extracellular fluids as a consequence of the transmembrane potential gradient (Koch, 1999). The action potential is in effect a means by which the neurone directly 'experiences' the electrotonic state of its environment and re-equilibrates its own ionic concentrations to concentrations more similar to those of the extracellular fluid. Synchronisation of the firing of neurones is essentially the temporal correlation of many action potentials, such that there occurs a coordinated pattern of the inflow of ions to many neurones at diverse locations throughout the nervous system.

The behaviour of neurones is well understood and not controversial. What is unusual in this account is only the emphasis placed on the membrane dynamics of the action potential. Instead of seeing the action potential simply as a means of impulse discharge (the mechanism by which the neuronal cell body sends a message to its axonal terminals), I maintain that it is the very fact of

opening ion channels and allowing the physiochemical diffusion of ions across the normally closed cell membrane that is the key phenomenon (Figure 4).

The philosophical argument is therefore that the momentary opening of the cell membrane at the time of the action potential is the single-cell proto-phenomenon (MacLennan, 1998) underlying 'subjectivity', literally, the opening up of the cell to the surrounding biochemical solution and a brief, controlled, breakdown of the barrier between cellular 'self' and the external world. The synchronisation of the action potentials of many neurones produces a pattern of 'openness' of the nervous system as a whole, arguably a simple by-product of the temporal co-ordination of neuronal firing that is *needed* for feature 'binding' in cognition. In this view, the normal ebb and flow in the strength of subjective feeling is real, and a direct consequence of the variable number of neurones participating in synchronous firing. When synchronisation occurs interhemispherically, not only is there a co-ordinated activation of the information in both hemispheres, and simultaneous participation in the cognition of the organism as a whole, but there occurs an associated simultaneous 'feeling' of awareness in both hemispheres (Cook, 1999, 2000).
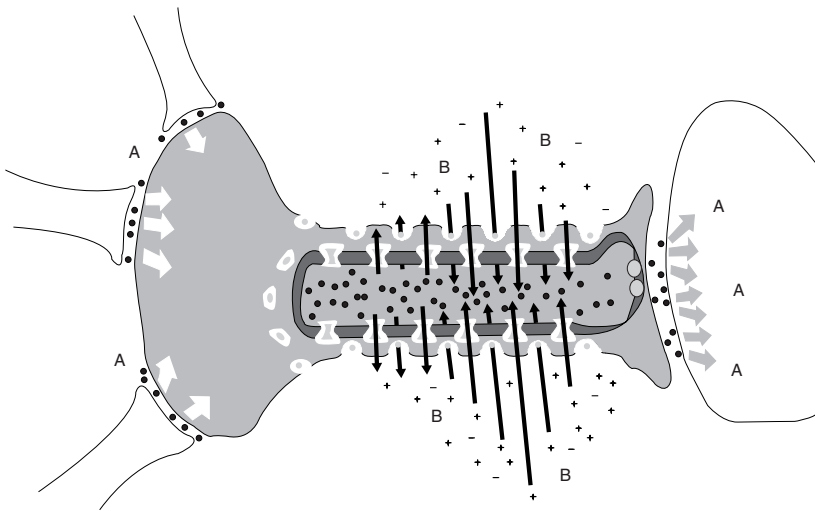
Figure 4. A cartoon of the two modes of contact between a neurone and its environment: (A) synaptic transmission and (B) ion exchange. Synaptic transmission is the functional unit of cognition, whereas ion-exchange during the action potential is the means by which the neurone makes direct contact with the extracellular fluid and, as such, is the functional unit of subjective consciousness (Cook, 2002). Both functions attain significance for the organism as a whole only when many neurones are active within synchronised neuronal networks. Synchronisation itself must occur through appropriate neuronal circuitry (i.e. synaptic effects), but means that neurones distributed throughout the nervous system can contribute to the same cognitive and conscious phenomena.

If the synchronised opening of the neuronal membrane is the basis for a feeling of openness to the external world, then the only thing 'illusory' about subjective awareness is that we tend to think mistakenly that we feel the 'outer world' directly, a world that, in fact, exists millimetres or miles outside our own skin. In contrast, it is *not* an illusion that individual nerve cells are momentarily in direct contact with their extracellular environments, with each cell briefly sampling the electrostatic state of the surrounding ion solution. This is to say that the dilemma of the hard problem is real (Searle, 1997) and not merely a linguistic trick of armchair philosophers! Already at the cellular level, there is indeed an explanatory gap between computational cognition and incomputable consciousness, between quantifiable synaptic communications that lead to behaviour and diffuse membrane dynamics that result in an unquantifiable 'feeling' with no direct behavioural implications. The gap is real, but not inexplicable, and the problem is perhaps not so hard, if it can be understood as a direct consequence of the two modes of neuronal interaction with the 'external' biochemical world (Cook, 2002) (Figure 4).

Synaptic transmission is widely believed to be the functional unit of cognition: in the act of neurotransmitter release and the exertion of inhibitory or excitatory effects on other neurones, a neurone participates in small-network logical functions, the sum of which is cognition, but a single neurone does not 'think' anything beyond its own function of inhibition or facilitation. Similarly, at the moment of the action potential, the neurone exchanges ions with its environment and participates in the organism's overall feeling of the external world, but a single neurone is not 'aware' of anything other than its own relative activation or quiescence. Of course, the action potential is the causal trigger leading to neurotransmitter release at the synapse, but transmembrane ion flow and neurotransmitter release are distinct phenomena and contribute to two different types of organism-level psychology: in addition to whatever small role the neurone may play in the cognition of the whole organism, it also makes a small contribution to the overall subjective feeling of openness of the organism through contact with its extracellular environment.

By focusing on the temporal synchronisation of neurones, solutions to two fundamental problems in consciousness studies come into view: the binding problem of cognition (including the binding of simultaneous LH and RH cognitive activity) and the subjective feeling problem of consciousness. Both of these core topics can be understood in relation to protophenomena *at the neuronal level.* Synaptic communications lead ultimately to the cognition of multicellular nervous systems, and the transmembrane flow of ions leads ultimately to the feeling of awareness of an 'external' world, i.e. subjective consciousness. Questions about subtypes of consciousness and cognition that depend on the connectivity of the multineurone networks are not addressed by this synchronisation argument, but by identifying the relevant cellular

mechanisms the construction of strictly *neuronal* theories of both conscious-
ness and cognition may be possible, and obviate the need for introducing other-
worldly philosophical or quantum mechanical postulates.

CONCLUSION

The pattern of results concerning the contributions of the cerebral hemi-
spheres in language processing clearly points away from the old ideas of 'uni-
lateral dominance' and towards the conclusion that both hemispheres are
involved in multiple subtasks during most language functions. Because the LH
is essential for the motor functions underlying speech, it may be appropriate to
refer to it as 'language dominant', but most findings over the past 20 years indi-
cate that the RH is far from irrelevant, and is actively involved in processing
linguistic information in ways that are distinct from those of the LH.

In addition to proposals concerning the flow of information between the
cerebral hemispheres, recent work on neuronal synchronisation provides a
'non-information flow' means of interhemispheric communication. In effect,
the synchronisation argument provides a mechanism for interhemispheric
'binding' and thus gives an explicit neuronal mechanism for one variety of
attentional model. So doing, the need for the verbal gymnastics of most previ-
ous attentional models can be avoided and the relevant psychological phenom-
ena can be translated into the terminology of neurophysiology. Details of the
neuronal mechanisms and the important oscillatory frequencies (by species
and by task) still need to be clarified, but the concept of synchronisation may
achieve, in one bold step, a neurone-level elucidation of cognition, conscious-
ness, attention and hemispheric interactions.

Modelling of hemispheric interactions across the corpus callosum remains
of fundamental interest for human psychology in general, not only for clarifi-
cation of the nature of hemispheric specialisation, but more importantly for
answering the question why functional asymmetry is associated with the three
quintessentially human forms of behaviour, language, tool usage and music.

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DISCUSSION

Crow: Your model does not seem to depend on the anterior/posterior torque? Also, Is it unidirectional?

Cook: No, the direction is not one way, it is mutual. I am only talking about a small portion of the torque, the frontal association cortex. In particular, transfer of sensory information, auditory, visual, etc., would probably be excitatory. The inhibitory function is the most interesting cognitively and that is what I was trying to focus on there.

Questioner: Do you have any information about corpus callosal agenesis?

Cook: Most of these individuals are actually subnormal. They are often detected because of headaches. The brain is quite plastic and so they manage to compensate somehow. Even some of the split-brain patients have developed language in the right hemisphere.

Questioner: Do acallosal subjects develop schizophrenia?

Cook: Yes, they turn up more than would be expected in the brain scan literature.

Questioner: There are aspects of language which are located in the right hemisphere, like understanding metaphors or understanding jokes. These aspects of language are important in terms of being able to trust an individual. If someone doesn't share a set of jokes with you, these are essentially warning signals. So I wonder whether there isn't a right hemisphere aspect of language that is present in primates, and then a left hemisphere set of syntactical functions that are subject to sexual selection.

Comment: We can't do metaphor unless we have syntactic rules to do it by, so the two interact.

McManus: 10% of the population have language on the right side of the brain. If you look at the pattern of brain organisation, we actually have a brain polymorphism here. To try and give information about the mean is misleading when it is actually the variance that we ought to be looking at. Means are going to mislead us. There are always simple stories if we want to say, this is left and this is right, but half of the data are based on patients with lesions.

Cook: I agree that we are talking here about population means and we can not ignore population differences. Nevertheless, lateralisation is an issue and it keeps coming up.

Comment: We have to realise that evolution is working on the entire distribution. It is the whole 'lot' that is selected, not just the mean of the population.

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