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Issue: *The Year in Cognitive Neuroscience***What's left in language? Beyond the classical model**

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Until recently it was widely held that language, and its left-hemispheric representation in the brain, were uniquely human, emerging abruptly after the emergence of *Homo sapiens*. Changing views of language suggest that it was not a recent and sudden development in human evolution, but was adapted from dual-stream circuitry long predating hominins, including a system in nonhuman primates specialized for intentional grasping. This system was gradually tailored for skilled manual operations (praxis) and communication. As processing requirements grew more demanding, the neural circuits were increasingly lateralized, with the left hemisphere assuming dominance, at least in the majority of individuals. The trend toward complexity and lateralization was probably accelerated in hominins when bipedalism freed the hands for more complex manufacture and tool use, and more expressive communication. The incorporation of facial and vocal gestures led to the emergence of speech as the dominant mode of language, although gestural communication may have led to generative language before speech became dominant. This scenario provides a more Darwinian perspective on language and its lateralization than has been commonly assumed.

**Keywords:** evolution; gesture; language; lateralization; primates; speech

**Introduction**

... a chimpanzee is very smart and has all kinds of sensorimotor constructions (causality, representational functions, semiotic functions, and so forth), but one thing is missing, that little part of the left hemisphere that is responsible for the very specific functions of human language.<sup>1</sup>

This quotation reveals two widespread assumptions that were prevalent until fairly recently. One is that language is an encapsulated system that is entirely unique to human, and the other is that left-hemispheric dominance for language is also unique to our species, and indeed dependent on a dedicated left-hemispheric system. I myself once subscribed, albeit with a foreboding that things were about to change,<sup>2</sup> to the view that cerebral asymmetry, and particularly the left-hemispheric specialization for language, was unique to humans. And change they did, in part through the emergence of brain-imaging techniques that revealed new information about the nature and extent of cerebral asymmetries, and

partly through growing understanding that cerebral asymmetry was far from unique to humans.<sup>3</sup>

Chomsky has long proposed that human language is profoundly different from any other form of animal communication. This view was modified by Hauser *et al.*<sup>4</sup> who distinguish between the *faculty of language in the broad sense* (FLB), which includes aspects of language shared with other species, and the *faculty of language in the narrow sense* (FLN), which is unique to humans. The main property of FLN is recursion, which allows humans to generate an infinity of possible sentences, in theory if not in practice. Hauser *et al.* make no assertions as to when FLN evolved, and even allow that it may have evolved for reasons other than language. Although Chomsky was himself a coauthor on this paper, he has since made more specific claims as to the sudden emergence of language as a distinct faculty.

In a chapter published in 2010, Chomsky asserts that there were no languages before 100,000 years ago,<sup>5</sup> so that language, presumably in the distinctive form of FLN, evolved well after humans actually emerged as a distinct species. In this view, language is a symbolic mode of thought, known as *internal*

*language* (or I-language), and only secondarily involved in communication, whether through speaking or sign language. Internal symbols are combined by a process of *unbounded merge*, the recursive process in FLN that creates potentially an infinity of possible constructions, explaining the generative character of thought as well as of language. Chomsky goes on to write:

Within some small group from which we are all descended, a rewiring of the brain took place in some individual, call him *Prometheus*, yielding the operation of unbounded Merge, applying to concepts with intricate (and little understood) properties (p. 59).

Precisely what that rewiring was is uncertain. Elsewhere Chomsky<sup>6</sup> writes “Perhaps it was an automatic consequence of absolute brain size . . . or perhaps some minor chance mutation” (p. 18).

The paleoanthropologist Ian Tattersall<sup>7</sup> adds support to the idea that the properties of language and thought distinctive to our species emerged suddenly and recently in human evolution:

Our ancestors made an almost unimaginable transition from a nonsymbolic, nonlinguistic way of processing information and communicating information about the world to the symbolic and linguistic condition we enjoy today. It is a qualitative leap in cognitive state unparalleled in history. Indeed, as I've said, the only reason we have for believing that such a leap could ever have been made, is that it *was* made. And it seems to have been made well *after* the acquisition by our species of its distinctive modern form (p. 199).

As Pinker and Bloom once pointed out,<sup>8</sup> such views are contrary to Darwin's theory of evolution, according to which a faculty as complex as language, and indeed thought itself, should have evolved through small, successive increments. In this paper, I set language in an evolutionary context that links it with manual functions, including simple grasping and more complex manual skills, setting it in a context more compatible with Darwin's theory of natural selection (see also Ref. 9). This is elaborated below.

Our understanding of the brain mechanisms for language has also been enriched, if not radically altered, by the emergence of brain imaging, as the now-dominant method of study. This has also given further insight into the likely precursors of language

and its lateralization, taking us well beyond the view expressed by Chomsky in the quotation that opened this paper. To set the stage, I begin with the classic findings on hemispheric specializations for language.

## Classical findings

The discovery that the left hemisphere is dominant for language in most people can be attributed to Marc Dax. In a paper delivered at a medical society meeting in Montpellier, France in 1836, he inferred from observations of patients with signs of unilateral brain damage that speech was controlled by the left hemisphere. The paper was not published until his son Gustav Dax located the text and arranged for it to be published in 1865. This appeared shortly after Paul Broca<sup>10</sup> published his account of a patient rendered unable to talk by a lesion in the left inferior frontal gyrus, an area since known as Broca's area. In 1874, Carl Wernicke documented a deficit in verbal comprehension associated with damage in the upper posterior region of the temporal lobe, the area since known as Wernicke's area.<sup>11</sup> Based essentially on the work of Broca and Wernicke, but supplemented by succeeding observation of the various deficits of language associated with unilateral brain injury, Geschwind<sup>12</sup> formulated what came to be known as the Wernicke–Geschwind model of language processing, involving interconnections between Broca's area, Wernicke's area, the angular gyrus (for reading), and corresponding sensory and motor areas for input and output.

Cerebral asymmetry for language was largely confirmed, but with some qualification, in split-brain studies, beginning in the late 1960s, and initiated by Michael S. Gazzaniga and Roger W. Sperry. Patients who had undergone section of the forebrain commissures for the relief of intractable epilepsy were shown to be able to name objects or read words aloud only when they were projected to the left hemisphere.<sup>13</sup>

Rather surprisingly, though, the mute right hemisphere of the split brain proved capable of understanding language. The patients could generally identify objects or words projected to the right hemisphere by pointing to the corresponding name or object, respectively, and were generally capable of following instructions as to how to respond to information presented to the right hemisphere. Zaidel developed a contact-lens apparatus that enabled

prolonged viewing while restricting visual input to a single hemisphere, and found that the isolated right hemispheres of two adult split-brained patients had comprehension scores equivalent to those of the average 16-year-old and 11-year-old.<sup>14</sup> These findings ran counter to evidence that left-hemisphere damage can result in profound deficits in both the production and comprehension of language; more specifically, damage to the superior temporal lobe has long been associated with deficits in comprehension (Wernicke's aphasia). Gazzaniga has suggested that because the patients sampled by Zaidel were not representative of the totality of operated patients they overestimated normal right-hemisphere function.<sup>15</sup> Sperry himself suggested that it was the evidence from unilateral brain damage that was misleading, arguing that right-hemisphere function is suppressed when the left hemisphere is damaged.<sup>16</sup> The extent of right-hemispheric comprehension, and the conditions under which it does or does not occur, are still not fully understood.

In any event, cerebral asymmetries were largely confirmed by behavioral studies of normal individuals. The most common procedures were through dichotic listening and tachistoscopic presentations, which became cottage industries in experimental psychology laboratories in the 1960s and 1970s, continuing, although somewhat abated, to this day. Dichotic listening involves presentation of material simultaneously to the two ears, and if the material is verbal the right-ear information is reported more accurately than the left-ear information, which is taken to imply a left-hemisphere dominance.<sup>17</sup> Tachistoscopic studies involve responses to brief presentations of visual input, with a right-visual-field superiority for letters or words and, less reliably, a left-visual-field superiority for nonverbal material.<sup>18,19</sup> These techniques provide no information as to the actual brain regions involved, and asymmetries at the behavioral level are dampened by interhemispheric transfer. Nevertheless, they provide broad confirmation of left-hemispheric dominance for language, at least at the group level.

As documented below, the emergence of brain imaging has altered our understanding of the brain circuits involved in language, but asymmetries in the regions of the classic areas have been largely confirmed. For example, Bethmann *et al.*<sup>20</sup> showed strong left-hemispheric activation induced

by a semantic task requiring subjects to determine whether pairs of words were synonyms. This occurred across regions in the prefrontal cortex, superior temporal sulcus, and angular gyrus, again largely as expected from earlier lesion-based work. Indices of cerebral asymmetry based on asymmetrical functional magnetic resonance imaging (fMRI) activity correlated poorly with indices on the basis of a dichotic-listening test and identified 26 of the 30 participants (four left-handers) as left cerebrally dominant, compared with only 14 so identified from the dichotic-listening test. Hugdahl *et al.* similarly found that asymmetry assessed from dichotic listening correlated only weakly with that based on positron emission tomography (PET).<sup>21</sup> In a later review, Hugdahl<sup>22</sup> notes that auditory asymmetries are modulated by top-down processes, such as shifts of attention, and in any case different measures of asymmetry are seldom in perfect agreement. Handedness also correlates only weakly with fMRI indices of cerebral asymmetry, and there is often disagreement between fMRI indices computed in different brain regions, such as frontal and temporal areas.<sup>23</sup>

Functional magnetic resonance imaging has also revealed a strong left-hemispheric dominance in activation induced by the production of speech. In one study, subjects were asked to silently generate words beginning with designated letters, revealing pronounced activation in the left prefrontal cortex in an area that included Broca's area.<sup>24</sup> Indices of laterality showed significant leftward activation in both left- and right-handers, although it was more pronounced in right-handers. The percentages showing left cerebral dominance were 95.3% for right-handers and 81.3% for left-handers. Similar percentages were obtained in other brain-imaging studies (e.g., Refs. 25 and 26) and are in line with those previously calculated from earlier studies based on the effects of unilateral lesions,<sup>27</sup> on the sodium amytal test administered prior to surgery,<sup>28</sup> and on the effects of unilateral electroconvulsive therapy (ECT).<sup>29,30</sup> In these respects, then, brain imaging supports evidence based on lesion studies and provides especially strong affirmation since it is based on individuals without preexisting neurological conditions.

Although there is still broad support for the Wernicke–Geschwind model, the advent of brain imaging, along with more detailed study of neurological cases and altered understanding of the nature

of language itself, has led to a deeper understanding of the circuitry involved. This in turn has led to a better understanding of the nature of cerebral asymmetry.

### The dual-stream model

While brain imaging shows marked functional asymmetry in the classic language areas, they also reveal networks that are more complex than that described by the Wernicke–Geschwind model. Poeppel *et al.*<sup>31</sup> (p. 14125) go so far as to remark that “the era of the classical model is over.” In the study by Badzakova-Trajkov *et al.*,<sup>24</sup> for example, word generation induced significant left-hemispheric activation in a number of areas outside Broca’s area, including the supplementary motor area, insula, and cerebellum. In the study by Bethmann *et al.*,<sup>20</sup> the synonym task also yielded activation outside the classic language areas, notably in the left medial prefrontal gyrus, the left anterior cingulate, and the left thalamus. The right cerebellum was also activated, reflecting its contralateral connections with cortical areas.

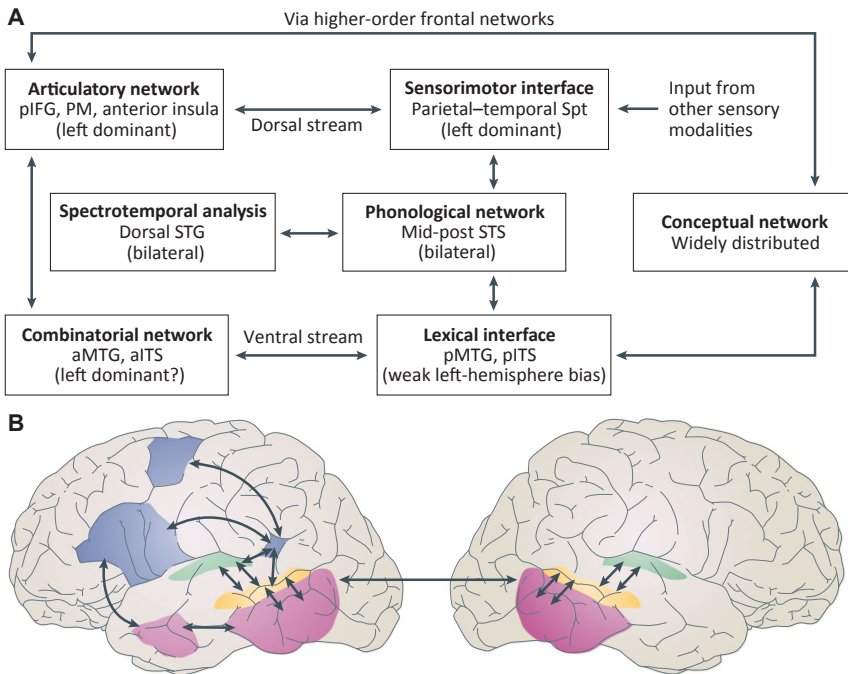
Integrating findings across a range of studies, Hickok and Poeppel<sup>32</sup> propose that there are two neural streams connecting posterior and anterior regions involved in the processing of speech (see Fig. 1). A ventral stream processes speech for comprehension, and a dorsal stream maps acoustic speech signals to articulatory networks in the frontal lobes. The main connecting tract in the dorsal stream is the superior longitudinal fasciculus, while the inferior longitudinal fasciculus is at least one of the routes underlying the ventral stream (e.g., Ref. 33). Although it applies to speech, the circuits involved in sign languages are strikingly similar, despite the obvious differences in both input and output. The parallels include a phonological structure, left-hemispheric lateralization, and fronto-temporal circuitry for both production and comprehension.<sup>34–36</sup>

Van der Lely and Pinker<sup>37</sup> suggest a further elaboration of the dual-stream model. They draw attention to a subtype of specific language impairment (SLI) in which the primary deficit is grammatical. Children with this subtype, known as Grammatical-SLI, are especially deficient in processing complex grammatical constructions. To account for this deficiency, van der Lely and Pinker distinguish between basic and extended syntax. Basic syntax connects words to meanings, and deals with short-range

syntax, as in words in which tense is conveyed in the word as a whole, such as the English irregular past-tense forms “ate” or “bought.” Basic syntax is represented in the ventral system, and may be sufficient for what has been termed *protolanguage*—language without combinatorial syntax. Extended syntax is combinatorial, as in the merging of morphemes to represent past tense (“jumped,” “climbed”), or in more complex cases where understanding may depend upon integrating across different words, as in sentences where subject and verb are separated by intervening clauses. Extended syntax depends on the dorsal system—left-hemispheric in most people—and involves interaction between the lateral frontal cortex and the basal ganglia.<sup>38</sup>

Friederici *et al.*<sup>39</sup> proposed a similar division within the left frontal cortex itself, with Broca’s area responsible for the processing of phrase-structure grammar, involving long-range dependencies, and the frontal operculum responsible for local transitions. Although their test of phrase-structure grammar was questionable<sup>40</sup> the distinction does map onto the notions of extended and basic syntax, respectively; Friederici *et al.* suggested that the phylogenetically older opercular system may account for the limited grammars of nonhuman communications. It is the recursive processing enabled by Broca’s area, they suggest, that makes human language unique, although Broca’s area itself probably derives from area F5 in primates.<sup>41</sup>

Dual-stream organization itself is not confined to language, nor is it restricted to humans. In their work on vision in monkeys, Mishkin *et al.*<sup>42</sup> proposed a dorsal stream specialized for location in space (the “where” system) and a ventral system dedicated to the recognition of objects (the “what” system). Goodale and Milner,<sup>43,44</sup> on the basis of neuropsychological work in humans, gave the distinction a different emphasis, characterizing the dorsal stream as mapping onto action and the ventral stream as mapping to perception. Similar streams specialized for auditory perception have been identified in nonhuman primates, and are said to “illuminate human speech processing”<sup>45</sup> (p. 718). Petrides and Pandya<sup>46</sup> identified dorsal and ventral streams anatomically in the macaque, linking parietal and temporal areas to the homologue of Broca’s area. In accord with Goodale and Milner, they suggest that the ventral stream in the monkey has to do with the retrieval of mnemonic information from the posterior association areas, and the



**Figure 1.** Dual-stream model of language processing. (A) Schematic diagram. (B) Approximate anatomical locations of dual-stream components. aITS, anterior inferior temporal sulcus; pITS, posterior inferior temporal sulcus; aMTG, anterior middle temporal gyrus; pIFG, posterior inferior frontal gyrus; PM, premotor cortex; STS, superior temporal sulcus; STG, superior temporal gyrus. Reproduced from Hickok and Poeppel, with permission.<sup>32</sup>

dorsal stream has to do with the programming of action. They also write that their findings “are consistent with suggestions that specialization for the control of action and gesture may have preceded specialization for language” (p. 13)—a theme developed in more detail below.

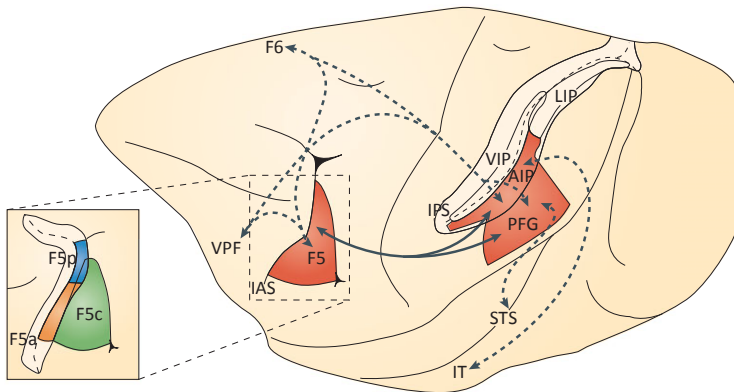
Adding their support for the dual-stream model, Saur *et al.*<sup>47</sup> remark “that language, for all its human uniqueness and sophistication, adheres to the same anatomical principles that govern brain functions in other domains” (p. 18035). By the same token, though, the dual-stream model can be taken as evidence against the idea that language is *special*, requiring dedicated neural wiring. Rather, it emerged through the modification, whether through learning or natural selection, of structures that long predate human evolution.

### *The mirror neuron system*

Another aspect of the dual-stream system emerged from the discovery of mirror neurons in monkeys. These neurons respond both when the monkey makes a grasping movement with the hand and when it observes the same movement made by

another individual. These were first discovered in area F5, the homologue of Broca’s area,<sup>48</sup> but later shown to be part of a broader mirror neuron system (MNS), which includes not only area F5 but also two areas in the parietal lobe containing neurons with mirror properties. The parietofrontal circuit also receives higher-order visual information from the superior temporal sulcus (STS) and inferior temporal lobe, but the neurons in these areas do not have motor properties, and the circuit is under the control of two further areas in the frontal lobes, the presupplementary motor area, and the ventral prefrontal cortex.<sup>49</sup> As shown in Figure 2, the MNS conforms to the two-stream organization, dedicated to the integration of perceived manual action with its production, although with some added connections.

The MNS is now well documented in the human brain. A meta-analysis of 125 studies using fMRI revealed 14 clusters of neurons with mirror properties. These were located in areas homologous to those identified in the monkey brain, including the inferior parietal lobule, inferior frontal gyrus, and ventral prefrontal cortex, but also included regions in the primary visual cortex, cerebellum, and the



**Figure 2.** The parietofrontal mirror network in the macaque. AIP, anterior intraparietal area; F5a, F5p, F5c, subsections of Area F5; IAS, inferior limb of arcuate sulcus; IPS, intraparietal sulcus; IT, inferior temporal lobe; LIP, lateral intraparietal area; PFG, area between parietal areas PF and PG; VIP, ventral intraparietal area; VPF, ventral prefrontal cortex; STS, superior temporal sulcus. Reproduced from Rizzolatti and Sinigaglia, with permission.<sup>49</sup>

limbic system.<sup>50</sup> Evidence for individual mirror neurons was also obtained from multiple electrode implanted in patients to monitor epileptic activity. The patients were asked to execute or observe grasping movements of the hand or facial expressions of emotion, and neurons with mirror properties were identified in areas homologous to the MNS identified in monkeys, as well as in the hippocampus and the supplementary motor area.<sup>51</sup> It appears that the human brain is indeed well endowed with mirror neurons, perhaps more so than the monkey brain. Although it embraces areas involved in language, the MNS in humans also seems to be involved in wider social and emotional function.<sup>52,53</sup>

With respect to language, the importance of the MNS is that it suggests that language evolved from a system largely devoted to manual grasping in primates, and extended to manual gesturing, pantomime, and ultimately to human speech. The conjecture that language originated in manual gesture has a long history, going back at least to Condillac<sup>54</sup> and Vico,<sup>56</sup> but more recently attributed to Hewes,<sup>56</sup> and developed from remarkably different perspectives in books by a number of authors.<sup>57–61</sup> It is an idea that is partially captured in terms applied to language itself. The word *grasp* is often used to mean “understand.” *Comprehend* and *apprehend* derive from Latin *prehendere*, “to grasp;” *intend*, *contend* and *pretend* derive from Latin *tendere*, “to reach with the hand;” we may *press* a point, and *expression* and *impression* also suggest pressing. We *hold* conversations, *point* things out, *seize upon* ideas, *grope*

for words, *get* ideas. It works visually, too, as when you *see* what somebody means. Fonagy and Target<sup>62</sup> (p. 437) suggest that such examples are indeed “a residue of gestural language”—although, to continue the theme, some may consider this a stretch too far.

As Rizzolatti and Arbib<sup>63</sup> recognized, mirror neurons seem to operate according to the same principles as postulated earlier by the motor theory of speech perception,<sup>64</sup> which holds that speech sounds are perceived by how they are produced, rather than as acoustic elements. As Galantucci *et al.*<sup>65</sup> put it in a review of the motor theory, “perceiving speech is perceiving gestures” (p. 361). But the role of mirror neurons in perception is controversial. Hickok *et al.*<sup>66</sup> point out that perception of speech has been demonstrated in individuals with severely impeded speech production due to brain injury, or even congenital disease preventing speech entirely. Chimpanzees<sup>67,68</sup> and even dogs<sup>69,70</sup> seem able to understand simple spoken requests, and respond accordingly. What is lacking in both species, however, is the ability to produce anything resembling human speech, although great apes have shown some proficiency in the use of a simplified form of sign language,<sup>71,72</sup> or in pointing to arbitrary symbols on a large tablet-like display.<sup>67</sup>

Hickok *et al.* propose that sensorimotor interaction occurs within the dorsal system, in which forward sensory prediction provides a modulatory influence on perception, but this influence is not necessary for perception itself. They propose an

integrative model of the speech-related dorsal stream that essentially reverses the motor theory of speech perception. Instead of speech perception depending on production, they propose a model in which production is supported and molded by perceptual feedback. The system involves forward sensory prediction, which provides a natural mechanism for a limited motor influence on perception, but the influence is modulatory; speech can be perceived without it. In a more general critique of mirror neurons, Hickok<sup>73</sup> gives the example of observing a person playing the saxophone. A nonsaxophone player may well have adequate perception of the player's performance, but a fellow saxophonist is likely to have an enriched perception and understanding by relating her perception to her own expertise.

The role of mirror neurons remains controversial, but the important point is that the mirror circuit in primates is primarily concerned with visuo-manual action. Its anatomical homology with the language circuit<sup>46</sup> provides strong supporting evidence for the manual origins of language, at least with respect to its perception and production.

## Cerebral asymmetry

The dual-stream model offers new perspectives on the brain circuits involved in language, and on their asymmetries. Noting conflicting evidence from brain imaging, Hickok and Poeppel<sup>32</sup> proposed that in the case of speech processing, the dorsal stream strongly favors left hemispheric processing, while the ventral stream is bilaterally organized. The asymmetry of the dorsal stream is anatomical, with evidence from diffusion tensor imaging (DTI) showing stronger connectivity in the left than in the right arcuate fasciculus, which forms part of the superior longitudinal fasciculus, the major connecting fiber tract in the dorsal stream. The asymmetry was reversed, though, in monozygotic twins with opposite functional asymmetries for word generation; the twin with left cerebral dominance showed stronger connectivity on the left, while the twin with right dominance showed stronger connectivity on the right. This implies a strong nongenetic component in the structural asymmetry of the arcuate fasciculus.<sup>74</sup>

Van der Lely and Pinker<sup>37</sup> endorse the idea that the ventral system underlying basic syntax is

bilaterally organized, though there is evidence to the contrary. In the study by Friederici *et al.*<sup>39</sup> the two grammatical systems, phrase structure and local, activated the left frontal cortex, in Broca's area and the frontal operculum, respectively. Functional magnetic resonance imaging tracking shows increasing leftward lateralization as one proceeds from posterior to anterior regions, and correspondingly from auditory-phonetic to lexico-semantic processing.<sup>75</sup> The synonym task employed by Bethmann *et al.*<sup>20</sup> also showed strong leftward asymmetry in the superior temporal lobe, as well as in the angular gyrus. Although the stimuli were presented visually rather than as speech, the study illustrates a leftward advantage in comprehension. Bemis and Pyllkänen<sup>76</sup> similarly found that matching word-pair combination to pictures activates the left angular gyrus and the left anterior temporal lobe, whether the subjects listened to the words or read them.

Nevertheless, as suggested by the split-brain findings described earlier, there does seem good reason to suppose that left-cerebral dominance is more pronounced for production than for the comprehension of language. Hickok and Poeppel<sup>32</sup> write that "... the finding that the right hemisphere can comprehend words reasonably well suggests that there is some degree of bilateral capability in lexical and semantic access, but that there are perhaps some differences in the computations that are carried out in each hemisphere" (p. 398).

With reference to anatomy and physiology, cerebral lateralization was almost certainly established well before the emergence of *Homo sapiens*, and probably before the emergence of true language. Broca's area was enlarged on the left in *Homo erectus* (albeit in a single specimen)<sup>77</sup> and great apes show enlargements of the homolog of Broca's area<sup>78</sup> and the temporal planum, which encompasses the homolog of Wernicke's area.<sup>79</sup> A PET study showed greater activity in the left than the right superior temporal gyrus in monkeys as they listened to calls made by conspecifics.<sup>80</sup> Even mice seem to have asymmetrical brains. Shipton *et al.*<sup>81</sup> reported that optogenetic silencing of the left hippocampus produces a deficit in long-term spatial memory, whereas silencing of the right hippocampus does not. Although this might appear the reverse of the asymmetry in humans, Shipton *et al.* suggest that the asymmetry depends on processing demands,

which in humans might be greater for verbal than for nonverbal memory. Cerebral asymmetry might have ancient origins in nonlinguistic mnemonic and communicative functions, and might adapt to processing demands.

### Praxis

It has long been known that damage to the left cerebral hemisphere in humans can lead to apraxia, an impairment of learned skills that cannot be attributed to difficulties in language or in sensory or motor weakness.<sup>82,83</sup> Brain imaging reveals a left-hemispheric network for the planning of tool use, pantomimes, and familiar gestures, a network that, at least within the limits of resolution supplied by neuroimaging, seems largely to coincide with the language network.<sup>84</sup> This network is also largely independent of handedness. Vingerhoets *et al.*<sup>85</sup> selected 10 volunteers with left- and 10 with right-hemispheric representation of language, and found that the same areas were activated when generating words and when miming actions. The actions were either unimanual, such as aligning one egg with another, or bimanual, such as sharpening a pencil or threading a needle. Regardless of the handedness of the subjects or the hand used, the asymmetry of activation for praxis matched that of word generation. The authors write:

The finding that every individual showed asymmetry for praxis and language in the same direction is a powerful argument for a functional and topographic link between the two, and supports models that link gestures and speech in an effort to explain the evolution of language (p. 10).

Indeed, one might go further and conclude that language itself is simply an example of skilled action, predominantly lateralized to the left hemisphere in most people. According to Roy and Arbib,<sup>86</sup> this may even include syntax; they describe the common brain areas activated during language, pantomime, and praxis as the “syntactic motor system.”

The use of tools may also have roots in primate evolution. The MNS in monkeys responds both to grasping with the hand and grasping with pliers.<sup>87</sup> Chimpanzees make and use tools.<sup>88,89</sup> Evidence as to whether the brain mechanisms involved are left-lateralized is sparse, but, as noted earlier, chimpanzees show enlargements in Broca's and Wernicke's areas on the left. Great apes,

with the apparent exception of orangutans, are predominantly right-handed,<sup>90</sup> and the leftward enlargement of Wernicke's area in the chimpanzee is correlated with a right-hand bias in gestural communication.<sup>91</sup> As discussed above, though, handedness in humans is only weakly correlated with cerebral dominance for either praxis or language.

As manual action progressed from grasping to more complex function, lateralization may itself have been emerged. Grasping things, as in plucking fruit or simply maneuvering through tree branches, is better served by a bilateral system providing equivalent reach on either side of the body. With added specialization, however, there may be advantages to asymmetry, especially with respect to internal programming. One advantage of hemispheric specialization is that it avoids duplication, and this may be especially important in complex functions—like language—that require large amounts of neural circuitry. Duplication may therefore be too wasteful of neural space, and may also lead to interhemispheric conflict.<sup>2</sup> Another possible advantage is that lateralization is not constrained by the relatively slow conduction time between hemispheres, so that computations can be carried out with greater speed.<sup>92</sup> A related notion is that the left hemisphere is itself specialized for rapid sequential processing, which is why it is favored for speech.<sup>93</sup> Yet, the dominance of the left hemisphere applies to sign language as well as to speech,<sup>35,93</sup> suggesting that complexity, rather than speed per se, may be the critical element.

Llorente *et al.*<sup>94</sup> document population-level right handedness in chimpanzees across a wide range of studies, including their own, but note that the incidence increases with complexity of task. Introducing a communicative aspect may also increase the right-hand preference. Meunier *et al.*<sup>95</sup> tested human infants and nonhuman primates on two manual actions. When reaching to grasp, all used the hand closest to the reached-for item. But when pointing to where an item was hidden so that an experimenter could fetch the items for them, human infants, baboons, and macaques showed strong overall preference for the right hand (tufted capuchins did not).

The emergence of more complex praxis, and perhaps more pronounced cerebral asymmetry, may perhaps date from the emergence of the Acheulian

tool industry beginning some 1.6 Ma. Unlike the earlier Oldowan industry, which comprises simple flake tools, Acheulian hand-axes required more complex planning; and PET imaging of modern people making these hand-axes elicited activation of brain areas overlapping those activated by language.<sup>96</sup> From this time, gestural communication may have begun to incorporate combinatorial structure, perhaps a precursor to syntax, although whether this preceded or followed manufacture of more complex tools is a matter of conjecture. Brain size increased dramatically during the Pleistocene, perhaps correlated not only with the emergence of manufacture but also with the increasing complexity of social structures and the emergence of what has been termed the *cognitive niche*.<sup>97</sup> Language, even including recursive syntax, may well have emerged out of this mix.

Language itself retains a strong manual connection. Sign languages activate the left-hemispheric language areas and are predominantly manual, though with facial accompaniment.<sup>98</sup> All humans gesture with their hands while they speak<sup>99–101</sup> and manual gesture may lurk not far below the surface as a substitute for speech. When asked to communicate without speaking, hearing adults spontaneously develop a form of sign language, in which grammatical components are introduced.<sup>102</sup> Manual gestures also play an important role in the development of speech in children (e.g., see Bates and Dick<sup>103</sup>). Word comprehension in children between 8 and 10 months and word productions between 11 and 13 months are accompanied by gestures of pointing and showing, and by gestures indicating recognition, respectively.<sup>103</sup> Manual gestures predate early development of speech in children, and predict later success even up to the two-word level.<sup>104</sup>

### And so to speak

Despite the strong affiliations of language with manual action, primate behavior and neurophysiology provide little information as to the origins of speech, the dominant mode of language. The putative shift from manual to vocal shift has proven one of the stumbling blocks for the gestural theory of language evolution. The linguist Robbins Burling,<sup>105</sup> for example, writes, “[T]he gestural theory has one nearly fatal flaw. Its sticking point has always been the switch that would have been needed to move from a visual language to an audible one” (p. 123). MacNeilage<sup>106</sup> expresses similar concerns.

The MNS in primates is strongly linked to manual action, with little sense of how it might have been adapted to vocal control. In the monkey, some mirror neurons are responsive to the sounds produced by manual actions, such as the noise of a stick being dropped, or the cracking of peanut shells, but they are conspicuously unresponsive to vocal calls.<sup>107</sup> Nonhuman primates also appear to be largely incapable of voluntary vocalization. Some counter-evidence, though, has been claimed by Coudé *et al.*,<sup>108</sup> who trained two macaques, pre-selected for a high frequency of spontaneous “coo” calls, to emit coos in order to receive food; electrophysiological recordings from an area of the prefrontal cortex known to be involved in orofacial movements revealed a small proportion of neurons that discharged during the calls. This evidence, yet to be replicated, provides weak support (at best) for a system that might lead to complex vocal learning and control. In a broad review of the neurophysiology of vocalization in primates, Jürgens<sup>109</sup> concluded that “primate calls can be used as models for nonverbal emotional vocal utterances of humans, but not for speech and song” (p. 247). He also cites evidence that direct connections from the motor cortex to the nucleus ambiguus, which innervates the muscles involved in speaking and swallowing, is present only in humans.

Even chimpanzees, our closest nonhuman relatives, appear to be deficient in voluntary vocal control. Jane Goodall, famous for her studies of wild chimpanzees in Gombe National Park in Tanzania, once wrote that “(t)he production of sound in the absence of the appropriate emotional state seems to be an almost impossible task for a chimpanzee”<sup>110</sup> (p. 125). David Premack, another pioneer in the study of chimpanzee behavior, states that chimpanzees, our closest nonhuman relatives “lack voluntary control of their voice”<sup>111</sup> (p. 13866). In a review of vocal learning in animals and birds, Petkov and Jarvis<sup>112</sup> note evidence for limited vocal learning in some nonhuman primates but suggest that this is often based on movements of the lips, such as the “raspberry” sound emitted by chimpanzees,<sup>113</sup> rather than of the larynx.

The switch from a manual to vocal medium for intentional communication, then, must have occurred after the split, some 5 or 6 Ma, of the hominins from the great apes. Vocal language is not in fact a denial of gestural origins, since

speech is itself a gestural system made up of movements produced by six articulatory organs: the lips, velum, larynx, and the blade, body, and root of the tongue.<sup>114,115</sup> The evolution of speech may therefore be regarded as the inclusion of vocal gestures along with manual ones into the dual-stream system. The dual-stream organization was already present in a multimodal guises, including vision, audition, and manual grasping, and the primary change needed was the incorporation of cortical control of voicing, alongside the already well-established systems of manual control.

A natural bridge from manual gesture to vocalization is provided by the face itself. Independently of vocalization, manual and facial gestures are closely linked neurophysiologically, as well as behaviorally—a connection derived from integration of hand and mouth in eating. Some neurons recorded in area F5 in the monkey fire when the animal makes movements to grasp an object with either the hand or the mouth.<sup>116</sup> Petrides *et al.*<sup>117</sup> have identified an area in the monkey brain just rostral to premotor area 6, also considered a homologue of part of Broca's area, which is involved in control of the orofacial musculature, though not of vocalization itself. Gentilucci and colleagues have shown that the extent to which people open their mouths while speaking is influenced by manual grasping. When articulating the syllable /ba/, for instance, they open their mouths wider when grasping an apple than when grasping a cherry, and do so even when watching another individual grasping these objects. Reviewing some of this work, Gentilucci and Corballis<sup>118</sup> argue that it strongly supports the gestural theory of language evolution. Subsequent work has revealed similar effects in 11- to 13-month-old infants.<sup>119</sup> Facial gestures also play a significant role in sign languages. Mouth gestures are especially important, to the point that some linguists identify a system of phonology underlying mouth movements. Explicit schemes for mouthed “phonemes” have been proposed for a number of European Sign Languages, including Swedish, English, and Italian.<sup>120</sup>

Cerebral asymmetry may also be evident in facial movements themselves, especially during speech or communication. Graves and Potter<sup>121</sup> showed that the right side of the mouth moved more than the left during speech, but this was reversed during emotional expressions. These asymmetries are

also evident in 5- to 12-month-old human babies, who open the right side of the mouth wider when babbling, the left side when smiling.<sup>121</sup> In adults, the asymmetry of the mouth when speaking also influences the McGurk effect, in which the perception of spoken syllables depends on movements of the mouth as much as on the actual sounds emitted.<sup>122</sup> This effect depends on movements of the right side of the mouth, not the left.<sup>123</sup> Again, the asymmetry may have prehuman origins; Hook-Costigan and Rogers<sup>124</sup> found that marmosets opened the right side of the mouth wider when making social contact calls, implying left cerebral dominance, but the right side of the mouth wider when expressing fear, implying right cerebral dominance for emotion.

The face, then, is a natural adjunct to the hands with regard to intentional control, manipulation, and expressivity. The mouth, in particular, is well adapted to complex movement, whether in biting, chewing, and even grasping—and of course in vocalizations, whether learned or instinctive. The extension of intentional control to include voicing may therefore have been a fairly small step in the evolution of productive language. Many facial movements are internal to the mouth, and the addition of voicing may then have been selected as a means of rendering invisible movement accessible to the perceiver. Movements of the larynx, tongue, and velum are perceived through their influence on the pattern of sound—the lips, of course, remain visible, enabling some deaf individuals, in particular, to become skilled at lip-reading; but lip movements also strongly influence sound patterns in speech.

In hearing people, speech gradually assumed dominance, although manual and facial gestures were still important accompaniments. But the evolution of speech was not without its perils. It led to other anatomical changes, including the shaping of the vocal tract to sharpen phonemic discrimination, and this was accomplished in part by the lowering of the larynx. This in turn removed some of the separation between the trachea (windpipe) and esophagus (foodpipe), increasing the chances of choking. According to the National Safety Council, as cited by Lieberman,<sup>125</sup> choking on food is the fourth leading cause of accidental death in the United States, around a tenth of the incidence of deaths caused by motor vehicles. The advantages of speech over manual and facial gesture for evolutionary

fitness must therefore have been strong enough to overcome the risk of choking. What were these advantages?

First, the retreat of facial movement into the mouth may have proven adaptive for the saving of energy, and might be regarded as an early example of miniaturization. Speech is driven partly by the outgoing breath, which requires very little energy<sup>126</sup> and humans must breathe anyway to sustain life. Second, speech allows communication in the dark or when obstacles intervene between sender and receiver. Pinker and Bloom<sup>8</sup> suggest that vocal oratory (especially at night, one is tempted to conjecture) might have been subject to sexual selection, citing Symons's<sup>127</sup> observation that tribal chiefs are often both gifted orators and highly polygynous. Third, speech would have freed the hands for other activities. In a species that increasingly made use of the hands and arms for manufacture, and probably also for carrying things,<sup>128</sup> there were surely advantages to shifting the communicative load to the face, and ultimately to the vocal channel. Carrying would presumably have been important in an increasingly peripatetic existence, as exemplified in migrations from Africa well before the emergence of *H. sapiens*, beginning a little under 2 Ma.<sup>7</sup> perhaps leading to the pressure to add voicing. Speech and the freeing of the hands may have enhanced the development of technologies, enabling manual crafts to be at once demonstrated and verbally explained.<sup>59</sup> Moreover, the products of manufacture are cumulative, so that a slight initial advantage may have multiplied to the point that our African forebears dominated and eventually replaced all other hominins. Technology has continued to advance in exponential fashion, allowing humans unprecedented dominion over and beyond the planet, but it may have been seeded by a simple change to cortical control that enabled speech.

Speech may have evolved emerged after language itself. Tomasello<sup>60</sup> notes that sign languages show full grammatical structure, and can emerge within a few generations in deaf communities. He writes that

... it is [also] possible that the human capacity for language evolved quite a long way in the service of gestural communication alone, and the vocal modality is actually a very recent overlay. If humans were actually adapted for communication in

complex ways gesturally, with voluntary controlled articulate speech being a recent evolutionary modification, this would go a long way toward explaining the naturalness of complex human communication in the gestural modality (p. 246).

## Conclusions

The modern understanding of language has shifted from the notion of language as special, involving the addition of neural circuitry unique to humans—a sort of dedicated “app” downloaded onto the primate brain. Instead, language is now better viewed as evolving through brain circuits common to other animals, and probably to birds as well. The dual-stream organization of these circuits underlies visual and auditory perception, the integration of memory into perception and action, and the mapping of perception onto motor outputs. It was adapted through evolution to manipulation of the environment, communicative gesture, and eventually to human language. Even the recursive structure of language—Chomsky's unbounded merge—may have origins in nonlinguistic functions such as social understanding, mental time travel, and manufacture<sup>129</sup> and perhaps navigation.<sup>4</sup>

Against this background, not only language itself but also its cerebral asymmetry probably has roots in nonlinguistic functions. If language evolved from systems initially dedicate to the grasping of objects, its lateralization may have derived in part from manual preference. Humans are predominantly right-handed when picking up objects or reaching for them, and great apes also show preference for the right hand, although it is less extreme than in humans. One problem, though, is that handedness is only weakly correlated with cerebral asymmetry for language, perhaps because it is more labile. There are advantages to maintaining a degree of bimanual control in a world where access to things is needed on either side of the body, and even in brain function there may be a trade-off between bilateral symmetry and asymmetry.<sup>130–132</sup>

That trade-off might explain why neither right-handedness nor left-cerebral control of language is universal. Some 12% of the human population are left-handed, or in a few instances ambidextrous, while the proportions with left-cerebral dominance for speech may be as high as 94%.<sup>133</sup> Given that those who depart from the “normal” pattern appear to show no major deficiencies in sensory, cognitive,

or motor function—except perhaps in cases where handedness and cerebral asymmetry are due to injury or disease—the pressure for asymmetry may not be overwhelming. Attempts to locate a genetic source for asymmetry have been largely inconclusive (and are beyond the scope of this paper), but most agree that departures from the normal pattern are due to the cancellation of a genetic source rather than its reversal, and a recent report suggests that there may be as many as 40 genes involved.<sup>134</sup>

The pressure to lateralization may have increased as manipulative action became more highly programmed and complex, and at the same time less governed by the layout of the natural world and indeed by the fundamental bilateral symmetry of the body itself. This process would have been enhanced in hominins by bipedalism, freeing the hands for more complex action. Language itself, whether manual or vocal, can be considered a process of manipulation, a means of manipulating the minds and behaviors of others. Cerebral dominance for praxis also appears to be poorly correlated with handedness itself, and more highly correlated with cerebral asymmetry for speech. Although bipedal humans are especially proficient at manual skill, and especially in communication, the ability of great apes to make and use tools and to communicate manually suggests precursors in their common ancestry. With respect to both the degree of complexity and its lateralization, Darwin's<sup>135</sup> view, "The difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind" (p. 126), rings true.

Historically, cerebral asymmetry has been regarded as unidimensional, and indeed one of subjugation. The 19th-century neurologists referred to the left hemisphere as "dominant" or "major," and the right hemisphere as "nondominant" or "minor," although they also recognized that in some people this was reversed. Gazzaniga<sup>15</sup> once wrote that "it could well be argued that the cognitive skills of a normal disconnected right hemisphere without language are vastly inferior to the cognitive skills of a chimpanzee" (p. 536). LeDoux *et al.*<sup>136</sup> earlier suggested that right-hemispheric specializations were simply a secondary consequence of left-hemispheric dominance for language, an idea also noted by Bradshaw and Nettleton.<sup>137</sup> I once wrote that "the left hemisphere has forfeited some of its capacity for perceptual functioning because a lot of its neural

circuitry is taken up with the invading presence of language . . ." <sup>59</sup> (p. 124).

These characterizations are in marked contrast to the view that emerged in the 1970s as a result of the split-brain studies, which earned Sperry the Nobel Prize in 1981, and popularized by Ornstein's 1972 book *The Psychology of Consciousness*.<sup>138</sup> The left hemisphere was depicted as logical, linear, propositional, the right as intuitive, emotional, creative. It was probably also fuelled by political and social divisions of the 1960s, such as the feminist debate and protests against the Vietnam War, with the left hemisphere associated with the military West and the right with the supposedly pacifist East.<sup>139</sup> A dichotomy between "left-brain" and "right-brain" thinking became well established in folklore, and persists in a wide range of contexts. A recent example is McGilchrist's 2009 book, *The Master and His Emissary*, which documents cultural trends in Western civilization regarding putative struggles between left and right brains.<sup>140</sup> McGilchrist reverses the traditional view in that it is the right hemisphere that is the master, the left hemisphere merely the emissary.

Neither the notion of hemispheric dominance nor the romantic view of complementary function is supported by the evidence. The brain retains a fundamental symmetry despite the well documented asymmetries. But right-brain specializations do appear to be more than a consequence of the invasion of the left hemisphere by language and praxic function. Indices of right-brain dominance for spatial processing, for instance, are only weakly correlated with those for left-brain dominance for speech, and not at all correlated with handedness.<sup>24</sup> A factor analysis of asymmetries in human brain activity suggests that there may be as many as four independent dimensions of asymmetry, two favoring the left and two the right,<sup>141</sup> throwing doubt on the idea that cerebral asymmetry has some unitary and universal import. There is much still to unravel in our understanding of the brain's asymmetry.

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## Conflicts of interest

The author declares no conflicts of interest.

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