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The anatomical substrates for language and hemispheric specialization

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Three main lines of investigation are discussed in this paper: (1) the comparison between the anatomical arrangement of the language areas and the large-scale neurocognitive cortical networks partly involved in active or working memory; (2) the relations between hemispheric specialization and the development of interhemispheric communication; and (3) the analysis of individual differences in brain organization for language. The hypothesis and evidence presented stem from work being performed in our laboratories.

Key terms: *anatomical asymmetries, brain lateralization, corpus callosum, Sylvian fissure.*

INTRODUCTION

The human brain is an organ that is evolutionarily specialized in social interactions or intraspecific communication. More specifically, in the human brain (cerebral cortex) there are two distinct areas (Broca's and Wernicke's) involved in linguistic performance, the most striking communication device of our species. Another unusual feature of our brain is that usually only one hemisphere –the left– has linguistic capabilities, the right hemisphere performing better in the so-called visuospatial tasks. Furthermore, we also face the problem of diversity: there seems to be an immense degree of interindividual variability in terms of brain organization for language (Geschwind, 1983).

This poses several problems for students of the neural bases of language: (1) how do the two hemispheres differ in terms of neuronal wiring and how did the language-specialized neural system arise in evolution?; (2) what kind of interaction is there between the linguistically specialized and the spatially specialized hemispheres?; and (3) is there individual variability in brain organization for language, and does it fit any structural or morphological patterns? In other words, are there any structural or anatomical correlates of individual differences in neurolinguistic organization? This latter question implies that morphology may reflect aspects of brain organization and thus may be used as an index for differences in function.

In this paper we will suggest partial answers to the four questions above. These do not intend to be comprehensive, but rather they correspond to some more specific problems we have been working on in the last few years. The first question, although being the most critical, is perhaps the most difficult to solve, largely due to the absence of appropriate techniques to study neural connections in humans. An answer may be sought in the

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evolutionary origin of the language areas (Broca's and Wernicke's) and their interconnections through the arcuate fasciculus, from some precursor in the non-human primate. The phylogenetic evolution of the language regions is proposed here to occur as a local specialization of a widespread neural system involved in tasks such as working memory (Goldman-Rakic, 1988) or active memory (Fuster, 1994) that is characteristic of the primate brain (Aboitiz, 1994). The second question mostly relates to work we performed at the University of California at Los Angeles (Aboitiz *et al*, 1992a, b, c), which has been recently summarized in this journal (Aboitiz, 1992). Finally, the fourth question concerns the development of a research line we have been working in our laboratory at the University of Chile, which for the moment relates to morphometrical studies of the variability in fissurization patterns in the human brain.

THE ORIGIN LANGUAGE AREAS IN THE CONTEXT OF A WIDESPREAD CORTICAL MEMORY NETWORK

(Aboitiz, 1994)

Human language has been considered by many as a unique character, not having any close parallel in the animal kingdom (for example, Chomsky, 1980). This condition is more striking considering that linguistic capacities are usually localized in the left hemisphere, and that in most people there are specific cortical regions involved in the generation of particular aspects of language. In very general terms, we have Wernicke's area, located in the posterior and superior aspect of the temporal lobe, which is more involved in perceptual aspects of language; and Broca's area, located in the pars opercularis and triangularis of the inferior frontal gyrus, and more related to language production. These two areas are interconnected by a system of long axons running in the arcuate fasciculus.

Homologues to these areas and their interconnections can be found in non-human primates (Galaburda and Pandya, 1982; Deacon, 1992), but obviously they do not have the same functions as in man. What was the original function of these cortical regions, and how did they acquire their new characteristics? In monkeys the homologues of Wernicke's and Broca's areas are not isolated from the rest of the cortex but are part of a large-scale system of temporoparietal-prefrontal connections (Petrides and Pandya, 1988; Pandya and Yeterian, 1990; Deacon, 1992). These connections are topographically organized, each temporoparietal area projecting to and receiving projections from a specific area of the frontal lobe. One of the functions of this system is to participate in what has been called working memory (Goldman-Rakic, 1988) or active memory (Fuster, 1994), that mainly consists in "keeping in mind" a past situation that will be relevant for future behavior (see also Mesulam, 1990). Furthermore, working memory of different kinds (for example, related to object shapes or to spatial location) is represented in anatomically separated subsystems of projections, corresponding to specific sets of cortical areas (Wilson *et al*, 1993). In this context, the connections between the homologues of Wernicke's and Broca's areas in monkeys may well correspond to a subsystem related to auditory working memory, that in the human lineage became more elaborated and sophisticated, originating the language areas (Aboitiz, 1994).

But why developing auditory working memory? A tentative answer is to retrieve names. Before the evolution of the language areas, a rudimentary capacity to name objects should have existed. Following Geschwind (1964), the ability to name objects depends on the establishment of non-limbic, cross-modal cortical associations that enable to associate, say, a visual image with the sound of a vocalization. These interactions largely take place in the posterior part of the brain (occipital, parietal and temporal lobes). This character may have been very primitive, since trained apes are perfectly able to name objects (Premack and Premack, 1983).

If some ability to name objects or situations was already present in the proto-human brain, an efficient working memory system (especially auditory, since social communication was mainly through vocalizations) would have permitted to recall and refer to past events by their names. This could be of great benefit to the social group, particularly in situations where the referred object or situation was not present anymore. In other words, this system permitted to retrieve names from Wernicke's area in the same way spatial and object information are retrieved from parietal and temporal areas (Wilson *et al*, 1993).

Syntax may have concomitantly developed in part through the progressive cortical control of vocal processes, and the consequent elaboration of complex motor sequences (see Lieberman, 1985; Deacon, 1989; Calvin, 1994). However, the origin of syntactic capacity may have also involved the further elaboration of reciprocal interactions between Wernicke's and Broca's areas, as well as between neighboring auditory and premotor areas that participated in aspects of phonation. As a result of this, individuals were not only able to generate their own mental images through working memory, but also to talk silently to themselves. This may have permitted the manipulation of both mental objects and the elements of phonation, thus combining them in creative ways and generating a primordial grammar (Aboitiz, 1994).

This scenario depicts the origin of the language areas in the context of an overall neural network in the primate brain. It implies that these regions are not an isolated innovation, but rather that they gradually evolved from a system organized in an extensive network of temporoparietal-prefrontal connections as is the primate cortex. This view also tackles the question of the modularity of language (Fodor, 1983), since although the language regions may be seen as anatomically delimitated, they are embedded in a larger-scale system of cortico-cortical networks and have emerged as a local specialization of these rather than as a de novo system, independent of its surroundings.

As a preliminary suggestion and working hypothesis, we propose that the temporo-frontal network related to language tended to localize in one hemisphere (the left) perhaps because it developed at the expense of other networks involved in spatial working memory and related processes. As a consequence, the other hemisphere (in this case the right) would have specialized in spatial-like working memory, perhaps developing to a larger extent the system of parieto-frontal connections. In this sense, the two cerebral hemispheres might be understood as two variants on the same theme, one that emphasizes temporo-frontal projections, while the other emphasizes parieto-frontal connections. Whether this proposal is correct or not will be determined by future research, very much like the one that is going on in our lab.

ANATOMICAL ASPECTS OF HEMISPHERIC SPECIALIZATION AND CONNECTIVITY

(Aboitiz *et al*, 1992a, b, c)

The functional differences between the hemispheres have a correlate at the gross morphological level, with the Sylvian fissure (especially its horizontal or middle portion) being larger on the left than on the right side. This reflects the asymmetric development of architectonic regions related to Wernicke's area (Galaburda *et al*, 1978). (However, the posteriormost part of the Sylvian fissure is larger on the right side; Ide *et al*, 1993). In fact, asymmetries in the size of specific cortical areas are now well documented in the *planum temporale* of the temporal lobe (Wernicke's area, Galaburda *et al*, 1978) and the pars triangularis of the frontal lobe (Broca's area, Galaburda, 1980; in both cases they are larger in the left and relate to left hemisphere specialization for language), and also in the parietal lobe (larger in the right and related to right hemisphere specialization for visuospatial skills; Eidelberg and Galaburda, 1984).

However, it has not been possible to determine hemispheric differences in connectional patterns, mainly because connectional studies in human brains are limited to post mortem degeneration analyses and some recent studies using carbocyanines (for example, Burkhalter and Bernardo, 1989). A system that is much easier to study is the corpus callosum, the fiber tract connecting both hemispheres. Interhemispheric connections are a good system to study connectivity in humans because: (1) most of these connections cross through the corpus callosum to the other hemisphere, and therefore they are anatomically delimitated; and (2) the corpus callosum has a topographic map of all the cortical areas projected to it (Pandya and

Seltzer, 1986), and hence regional variability in the number or type of fibers may reflect differences in connectivity between specific cortical regions. Some years ago, we (Aboitiz *et al*, 1992a, b, c) initiated an investigation of the variability in interhemispheric connectivity as a function of brain asymmetries in both males and females. If interhemispheric connections depend on hemisphere specialization, variability in the formers may offer some clues on intrahemispheric organization.

Following this rationale, we (Aboitiz *et al*, 1992a) underwent a morphometric study of the size and shape of the human corpus callosum and its relation to factors such as asymmetries in Sylvian fissure length and in the size of the closely related *planum temporale*. Interestingly, we found that the isthmus, a callosal region defined as the area between the posterior third and the posterior fifth of the corpus callosum (according to total straight length), showed a negative correlation with asymmetries in the Sylvian fissure and the *planum temporale*, but only in males, not in females.

These findings were confirmed when, instead of using callosal area, we counted the numbers of fibers crossing through these respective regions (Aboitiz *et al*, 1992c). However, we found that in females the number of fibers in a small callosal segment immediately posterior to the isthmus also showed a negative correlation with asymmetries. Therefore, in females there is also a relation between callosal fibers and Sylvian fissure asymmetries, although it is less striking (involves a smaller contingent of fibers), and relates to a different (although adjacent) callosal region than in males. These findings have been previously reviewed and discussed in this journal (Aboitiz, 1992).

It is of interest to consider that the isthmus and adjacent regions presumably contain fibers connecting perisylvian areas of the two hemispheres, indicating that the more asymmetric these areas are, the less interhemispheric connections they have, especially in males. This has been interpreted as the result of the differential stabilization of interhemispheric synapses in symmetrical versus asymmetrical cortical regions during neuronal development, and also indicates more interhemispheric isolation in asymmetric brains (Aboitiz, 1992; Aboitiz *et al*, 1992a, b).

Another sex-specific negative correlation was found between the average size of the two Sylvian fissures –and *planum temporales*– and the size of the region between the anterior half and the anterior third of the corpus callosum, only in males. This callosal region may include fibers connecting Broca's area with its counterpart in the right hemisphere (Pandya and Seltzer, 1986). A tentative explanation for this finding is that in males, growth in perisylvian areas implies increased projections to more anterior, ipsilateral cortical regions (such as Broca's area in the left hemisphere). Considering that long ipsilateral connections may compete with contralateral (callosal) connections for synaptic targets during development (Galaburda *et al*, 1990), the increase in ipsilateral connections may result in a decrease in callosal connections in more anterior regions. This would yield the negative correlation we found between the length of the Sylvian fissure and more anterior callosal regions. The fact that these relations between interhemispheric connections and hemispheric characteristics tend to hold in males more than in females suggests that in the formers there is a more intense process of competition between neuronal projections during development. This may perhaps be related to hormonal or neurochemical differences, and may result in an increased segregation of connections in males than in females. For example, highly lateralized females could perhaps tolerate better a high degree of interhemispheric transfer than similarly lateralized males.

Another relevant finding (Aboitiz *et al*, 1992b) is that histologically, the corpus callosum is not a homogeneous structure. Callosal regions that connect primary and secondary sensory and motor areas are characterized by a large proportion of fast-conducting, large-diameter fibers, while regions connecting the so-called association areas and prefrontal areas bear a high density of slow-conducting, lightly myelinated thin fibers. We suggested that fast-conducting fibers connecting sensory and motor areas contribute to fuse the two hemirepresentations in each hemisphere, a process that is in the early processing stages and thus is strongly time-constrained (Aboitiz, 1992; Aboitiz *et al*, 1992b).

Together, these results imply that in the cerebral cortex, callosal connections depend on the functional specialization of the two hemispheres, and that this dependency may be higher in males than in females. Although we still cannot precise the connectional differences that make the two hemispheres specialized in different ways, it seems clear that they have an effect in the development of connectivity between the two hemispheres.

INDIVIDUAL VARIABILITY

Another problem with studying the neural bases for language is their large degree of variability. Quoting Geschwind (1983), "there is enormous variation in the organisation of the speech areas, and we must be wary on the assumption that all brains are organised identically for language" (p. 66). This can be seen in the individual differences in size and asymmetries of specific architectonic areas (Galaburda *et al*, 1978). Our approach at this point is that the –highly variable– qualitative patterns of fissurization of the cerebral cortex in different subjects may yield some clues about the diversity in the arrangement of specific brain areas. It is known that fissures develop according to the expansion of specific cortical regions, and that alterations in the growth of certain brain areas may result in distinct convolutional patterns in the cerebral cortex (Welker, 1990). Our present research line consists in an analysis of the fissurization patterns in specific brain regions, and their correspondence with the arrangement of the respective cytoarchitectonic areas.

We have preliminary findings suggesting that the Sylvian fissure comes in several varieties. In its posterior region, it bifurcates into ascending and descending rami. Two main bifurcating patterns are the superior type (with the ascending ramus larger than the descending one), that is more common in males and the right hemisphere, and the inverted type (both rami being of approximately the same size, but the ascending ramus is directed forward instead of backwards as usual), which is more common in females and the left hemisphere (Ide *et al*, 1993). Curiously, this coincides with claims that females tend to have better left-hemisphere skills, while males tend to have better right-hemisphere skills (Kimura and Herschman, 1984). In addition, we (Peña *et al*, 1994) recently analyzed the fissurization patterns in the regions corresponding to Broca's area (the pars triangularis and opercularis of the inferior frontal gyrus). The pars triangularis consists of two fissures (F1 and F2) that merge at the level of the Sylvian fissure, forming a V-shaped gyrus. One or both of these fissures may be bifurcated, and they are more commonly bifurcated in the left hemisphere in females (66.6% *vs* 33.3%; $P < 0.05$), while the picture is somewhat more complicated in males.

We believe that these studies will allow to determine the specific location of cytoarchitectonic areas in the surface of the brain, and will be of great utility both as an index of hemisphere organization and as a guide for imaging studies in living subjects. These findings will give us clues as to whether or not there are correlations in the arrangement of cortical areas in Broca's and Wernicke's regions, and whether their relations show any differences with the right hemisphere. We will also investigate sex differences in the disposition of the relevant cortical areas. Since as said we may not have direct connectional data to study the anatomical basis of hemispheric specialization, this is perhaps the best (although very tedious) approach to the neurobiology of brain lateralization.

CONCLUSIONS

In the first part of the paper, we outlined some theoretical considerations of the language areas as seen in the context of large-scale neurocognitive networks in the human brain; then we suggested that in the left hemisphere the balance of these large-scale networks would be shifted towards temporo-frontal connectivity, while in the right hemisphere the balance would be in favor of parieto-frontal connections. Unfortunately, at the moment we do not have a direct access to these macroscopic neural networks in the human brain. Around this issue, we summarized data concerning the relations between hemispheric specialization (as seen in anatomical asymmetries) and interhemispheric connections, proposing that the latter ones are dependent on the intrahemispheric organization of connections. Perhaps at this point the best strategy to determine intrahemispheric organization is to study the tridimensional arrangement of the diverse language-related cortical areas in the temporal and frontal lobes, and determine if there are any correlations in the arrangement of posterior (temporal) versus anterior (frontal) regions, comparing possible differences between the two hemispheres and between sexes.

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