The anatomy of language revisited

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The language areas have been classically viewed as a posterior, perceptual Wernicke's region connected with an anterior, motor Broca's area via a tract of long fibers denominated the arcuate fasciculus. Recent connectional studies in the monkey indicate that there may be few direct connections between the regions strictly corresponding to Broca's or Wernicke's areas, and that inferior parietal areas may serve as a link between them. The proposed connectional pattern of the language regions fits the network of parietotemporal-prefrontal connections that participate in working memory, a type of memory used in immediate cognitive processing. Supporting this concept, brain activation studies in the human during linguistic working memory tasks have determined a close relation between the supramarginal gyrus (parietal area 40) and Broca's area. We suggest that language processing is closely related to working memory networks, and that the language regions in fact originated in evolution from a working memory network for linguistic utterances.

Key terms: *aphasia, arcuate fasciculus, Broca's area, cortico-cortical connections, language, Wernicke's area, working memory*

INTRODUCTION

The anatomical delimitation of the language areas and their main connections have been considered to be well established for nearly a century (Galaburda *et al*, 1978). There are two main, relatively well-defined "language areas" located in the left hemisphere of most right-handed people, but perhaps more bilaterally in non-consistent right handed and left handed individuals (Damasio, 1992; Zaidel, 1985). These are Broca's and Wernicke's areas, which –broadly speaking– process respectively motor and perceptual aspects of language. These two areas have been considered to be interconnected through the arcuate fasciculus, a large tract of fibers that curves behind the bottom of the Sylvian fissure and extends from the superior temporal region to the inferior frontal gyrus. Damage to Broca's area (usually designated as Brodmann's regions 44, 45 and sometimes 46) and neighboring frontal and prefrontal regions produces a non-fluent aphasic deficit, in which one key aspect is the inability to handle grammatical items (agrammatism), although it is known that comprehension deficits also occur in this type of aphasia (Damasio, 1992; Alexander, 1997). On the other hand, damage to Wernicke's area (in the posterior aspect of the superior temporal lobe and neighboring regions of the parieto-occipital junction) results in a fluent aphasic disorder, in which the intonation and prosody of language are normal, but –depending on the severity and location of the lesion– the

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patient's speech is difficult to comprehend because of shifting of phonemes (paraphasia) and incapacity to find the proper names of objects. Finally, conduction aphasia involves lesions of the arcuate fasciculus and related areas, especially area 40 in the supramarginal gyrus (Alexander, 1997). This type of aphasia is characterized by the incapacity to repeat sentences presented to the patient, a characteristic that is shared by Broca's and Wernicke's aphasics, but –in the case of conduction aphasia– there is relative preservation of speech production and comprehension (Damasio, 1992). There are other cortical and subcortical regions that are also involved in language (Damasio, 1992), but in this paper we will only deal with the so-called classical areas of language, because our main concern is the connectivity between these two regions.

We will contrast the classical anatomical model of the language areas with more modern evidence concerning the connectivity of homologue regions to Broca's and Wernicke's areas in the monkey, and recent results of brain activation studies during linguistic tasks. It will be suggested that the connectivity between Wernicke's and Broca's areas is more complex than implied by the classical model, and that the language cortex can be conceived as part of a large-scale system of cortico-cortical connections between the temporo-parietal and frontal lobes. This network serves to organize behavior in time, and especially participates in a form of short-term memory referred to as working memory (Fuster, 1995; Goldman-Rakic, 1996), that consists in maintaining "on line" cognitive information that is relevant for current behavior. Based on these considerations, we will propose a hypothesis for the evolutionary origin of the language regions in the human brain, starting from a working memory network involved in the learning and rehearsal of complex vocalizations (Aboitiz, 1995).

THE MAIN LANGUAGE REGIONS

Connectional studies are impossible to perform in humans. Therefore, the most practical strategy has been to use the macaque as a model of cortico-cortical connectivity of the human brain. Nevertheless, the macaque brain is much simpler than that of the human, and finding homologues of the human language areas in the monkey has been a difficult task (see Fig 1). It is clear that areas performing the exact functions of language areas will not be found in monkeys, but it is our premise that these areas evolved from some less differentiated cortical sectors that can be identified in the macaque (see also Preuss & Goldman-Rakic, 1991a, b, c).

Homologues to Broca's area in the monkey and its connections

Brodmann's areas 44 and 45 –located in the pars triangularis and pars opercularis of the inferior frontal lobe– are the minimal sectors in which damage can produce Broca's aphasia (Alexander, 1997). Of these areas composing Broca's region, only area 45 has been confirmed by Preuss and Goldman-Rakic (1991a) inside the macaque's inferior arcuate sulcus, between areas 6 and 8, while neither area 44 or 45 seems to exist in prosimians. Barbas and Pandya (1989) do not describe area 45 in the macaque, perhaps considering that the corresponding region is part of premotor areas 6 or 8. It is quite possible that the latter authors were actually not searching for architectonic homologues of area 45. In the human, the ventral part of premotor areas 6 and 8 are adjacent to areas 44-45, and therefore Broca's region can be conceived as a differentiation of the ventral premotor region (ventral area 6 of the monkey) representing orofacial movements (Lieberman, 1985; Deacon, 1989, 1992; Preuss, 1995). Furthermore, it has been considered that Broca's area is a premotor region specialized in the generation of complex rhythmic-hierarchic routines that permit the complex motor coordination required for speech (Greenfield, 1991; Givón, 1995). According to Preuss and Goldman-Rakic (1991c), area 45 of the macaque receives projections from parietal area 7b. This latter area (7b) also projects to frontal granular cortex, in the intermediate
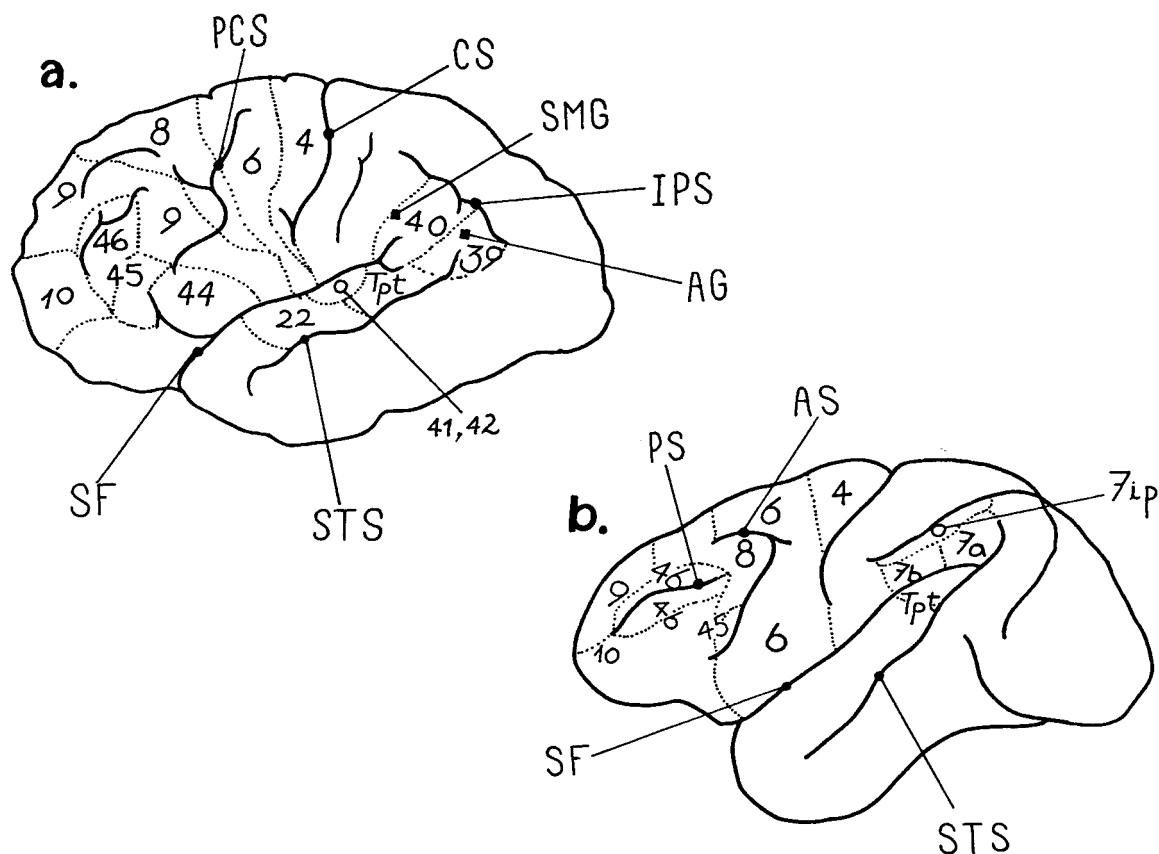
Fig 1. Some architectonic areas of relevance to the present paper in the human (a) and in the macaque (b). AG, angular gyrus; AS, arcuate sulcus; CS, central sulcus; IPS, intraparietal sulcus; PCS, precentral sulcus; PS, principal sulcus; SF, Sylvian fissure; SMG, supramarginal gyrus; STS, superior temporal sulcus.

principal sulcus of the frontal lobe (area 46). Another interesting parietal area is 7ip within the intraparietal sulcus, that projects to the dorsal and ventral aspects of the anterior arcuate sulcus (area 8) and to the posterior principal sulcus in frontal granular cortex (area 46) (Preuss & Goldman-Rakic, 1991a, b, c; Cavada and Goldman-Rakic, 1989b). The other components of parietal area 7 (7m and 7a) have abundant connections with frontal granular cortex, but a relatively weak projection to the inferior bank of the arcuate sulcus.

Homologues to Wernicke's area.

The most likely candidate for Wernicke's region is area Tpt in the superior temporal lobe, as described by Galaburda and Sanides (1980) and by Galaburda *et al* (1978). Damage to the posterior aspect of the superior temporal lobe, that corresponds to area Tpt, is the minimal lesion necessary to produce Wernicke's aphasia (Alexander, 1997). Surprisingly, area Tpt has been described in prosimians, indicating that it may represent an ancestral character of primates, more ancient than Broca's area. Area Tpt of the macaque receives projections from auditory association areas that surround it (Pandya & Yeterian, 1985; Pandya, 1995). The possibility of visual association regions projecting to this area has not been reported, but it is not clear if this has been extensively investigated. In the monkey, this area probably has a role in head-turning movements oriented to localize sound sources (Pandya & Yeterian, 1985; Preuss & Goldman-Rakic, 1991b). Considering that the superior temporal lobe —especially on the left side– is related to the processing of species-specific calls in the macaque (Heffner & Heffner, 1984;

Rauschecker & Hauser, 1995), it is possible that area Tpt may be involved in the spatial localization of conspecific calls.

Some frontal connections of area Tpt and inferoparietal regions

In the macaque, area Tpt projects to the frontal lobe but its terminals do not seem to reach the region corresponding to Broca's area in the inferior arcuate sulcus (Petrides & Pandya, 1988; Bullier *et al*, 1996). Its axons end in dorsal area 8 (dorsal prearcuate region) and area 46 in the lateral frontal lobe, and in areas 8, 46 of the lateral frontal cortex and also area 6 in the dorsal frontal lobe. In fact, although there are some projections from the postero-superior temporal lobe (more specifically, the secondary auditory area) to the equivalent to Broca's region in the inferior arcuate sulcus, according to Petrides and Pandya (1988) these are minor and their origin does not correspond to the equivalent to Wernicke's area.

Evolutionary trends

Considering what is known about the connectivity of the equivalent to the language regions in the monkey, the best candidates to Wernicke's area seem not to be directly connected with the candidates for Broca's area (Fig 2). The connectional studies of Petrides and Pandya (1988) indicate that most of the frontal connections
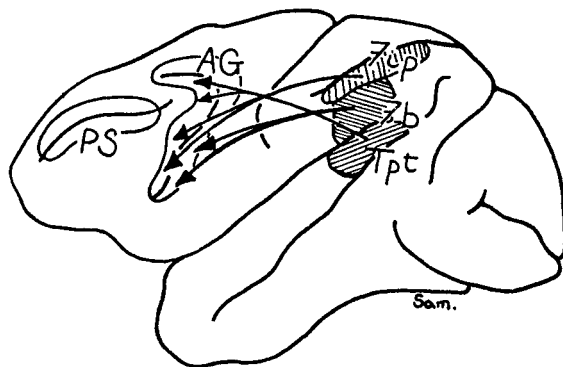

Fig 2. Frontal projections of areas 7 a, b and Tpt in the arcuate sulcus of the macaque. For further details, see text. Abbreviations as in Fig 2. Data from Petrides and Pandya (1984, 1988) and Cavada and Goldman-Rakic (1989).

of Tpt and related cortices (representing Wernicke's area) are with frontal granular cortex and with dorsal rather than ventral area 8 (anterior bank of the superior arcuate sulcus). Neither of these areas is considered to be related to Broca's language area, in so far as the latter has been homologized to a premotor region representing orofacial movements, located in the inferior arcuate sulcus. In the macaque, area 45 –corresponding to Broca's area– receives projections from parietal area 7b, and –more generally– the inferior parietal lobule projects to cortical sectors related to the inferior part of the anterior and posterior arcuate sulcus, which respectively correspond to ventral premotor areas 8 and 6. Recall that inferior parietal regions also have important projections to granular frontal cortex.

Given the above evidence, it is possible that part of the macaque inferior parietal region partly corresponds to human parietal areas 40 and 39, which are similarly located; no equivalent areas to the latter having been described in the macaque. If this is correct, we should expect human areas 40 and 39 to have important connections with Broca's area. The latter makes functional sense, as it provides the basis for a somatosensory-motor circuit of coordination for orofacial movements.

Pandya and Yeterian (1985) indicate that area Tpt is connected with somatosensory parietal regions in the macaque. However, in a detailed and more recent study of the monkey, Cavada and Goldman-Rakic (1989a) did not report inferoparietal projections to area Tpt, indicating that perhaps such connectivity is not well developed in this species. Considering that the vast majority of cortico-cortical connections are reciprocal, a connection from areas 7b or 7ip to area Tpt should be expected if the latter projects to inferoparietal regions. There are abundant projections from area 7ip to the posterior aspect of the superior temporal sulcus (superior and inferior banks) and some, very scarce, from areas 7b and 7a to the superior bank of the superior temporal sulcus (Cavada & Goldman-Rakic, 1989a). Retrograde tracing studies (Seltzer &

Pandya, 1994) indicate some connections between inferoparietal regions and the posteriormost aspect of the superior temporal sulcus, which may be adjacent to area Tpt.

In human evolution, two tendencies in the development of cortical connections may have occurred that resulted in the origin of the language areas. First, and perhaps more important, the superior temporal region (area Tpt) became increasingly connected with inferoparietal regions. This may have been achieved indirectly via regions in the superior temporal sulcus (Cavada & Goldman-Rakic, 1989a; Seltzer & Pandya, 1994) or the posterior insula –which is interposed between temporal and parietal cortices (Aggleton, 1993)–, or through newly established direct connections between area Tpt and the inferior parietal lobe. This contributed to produce a link between the auditory system and a parieto-premotor loop involved in the generation of complex vocalizations (recall the parietal projections to area 45). The development of inferoparietal sectors in the human brain (areas 39-40) may partly relate to the establishment and strengthening of this temporo-parietal link. The second process may have been the development of direct connections between the precursor of Wernicke's region and areas 44-45 and prefrontal sectors such as area 46, which served as a parallel pathway to send auditory information to the prefrontal and orofacial premotor regions.

We postulate that the first, indirect pathway relates to working memory circuits for linguistic and protolinguistic utterances, and must have been fundamental both in the evolutionary origin of language and in the acquisition of language during ontogeny. If, as we claim, language initially evolved mainly by imitation, in a similar way as songbirds learn their song (Doupe, 1993), working memory must have been fundamental for the internal rehearsal and incorporation of auditory templates. The second, direct pathway may have evolved as a pathway for acquired, automatic phonological routines and as part of a circuit to maintain auditory information "on line" while

linguistic behavior is being generated. In the rest of the paper we will extend on these points.

FRONTAL GRANULAR CORTEX, WORKING MEMORY AND LANGUAGE

In the context of the present paper, the most important prefrontal regions are some granular frontal regions (like areas 9 and 46) that have undergone an extensive growth in the anthropoid lineage, apparently having no equivalents in prosimians and participating in the high-level organization of planned behavior (Preuss & Goldman-Rakic, 1991a,c; Preuss, 1995; Fuster, 1993, 1995). Additionally, regions in the posterior superior temporal region and inferior parietal lobe project to granular frontal cortex, and have been shown to be involved in a sort of short-term memory referred to as active (Fuster, 1995) or working (Baddeley, 1986; Goldman-Rakic, 1987a, b; 1995a) memory (see Petrides, 1996). We will now argue that there is a series of interconnected parallel channels between temporo-parietal and frontal regions, that is involved in several aspects of the organization of behavior. The anatomical arrangement of the language areas fits this large scale cortico-cortical network and can be described as part of it. In this sense, the neural architecture involved in language is embedded in a complex system of cortico-cortical connectivity that may be the hallmark of the primate brain, and therefore should not be considered as an isolated system working with rules independent of the neural substrate for other cognitive phenomena.

The pattern of temporoparietal-prefrontal connections in the primate brain

Although a common, very general plan of cortical organization may exist in different mammals, there are also important species and evolutionary differences in the pattern of cortico-cortical connectivity and in the arrangement of specific cortical areas. For example, a gross morphological examination

of a primate brain indicates that higher-order cortical regions in the frontal, temporal and parietal lobes have undergone a notable increase in relation to other mammals; this is associated with a brain that is on the average about two times larger than that of another mammal of the same size (Aboitiz, 1996). We mentioned that area 44 (part of Broca's area) of the pars opercularis in the human frontal lobe is not present in the macaque, and the related area 45 of the human pars triangularis has been described in the macaque but is not found in prosimians. We also mentioned that parietal area 7 in the macaque has several subdivisions that make it more complex than in prosimians (Preuss & Goldman-Rakic, 1991b), and suggested that area 40 (and perhaps also area 39) of the human parietal lobe may have arisen as a consequence of subdivision (parcellation) of the inferior moiety of area 7 in the monkey. Interestingly, despite the gross anatomical development of the temporal lobe, higher-order areas in the superior temporal gyrus –such as Tpt and related ones– have been described as somewhat conservative in all primates, including humans (Galaburda & Sanides, 1980; Preuss & Goldman-Rakic, 1991c).

Perhaps more than the differentiation of specific cortical regions, the development of the system of long cortico-cortical connections between the sensory association areas of the parietal and temporal lobes and the frontal regions –including frontal granular cortex– may better represent the modifications of the primate brain in regard to other mammals. This is not to say that long, ipsilateral cortico-cortical connections are not to be found in non-primates, but rather that these connections may be especially well developed in primates. In the posterior cortex of primates, the different sensory areas are interconnected in such a way that "streams" of information processing can be described along specific sensory modalities (Pandya & Yeterian, 1985; Pandya, 1995). In addition, the different sensory areas are connected with frontal and motor regions via long, ipsilateral axons. In the macaque, Pandya and Yeterian (1985) have described a

massive system of temporoparietal-prefrontal connections, that are organized topographically and reciprocally in such a way that the frontal cortex has a map of the temporoparietal regions projecting to it, and vice-versa. In this projection system, an important rule is that areas with a given level of architectonic differentiation tend to project to regions of similar architectonic characteristics in the other side of the hemisphere. Since anatomical gradients of increasing architectonic granularity can be described in the temporal, parietal and frontal lobes, the result is a large matrix in which sites of a similar degree of granularity tend to be interconnected in the frontal, temporal and parietal lobes. As a consequence and as Fuster (1993, 1995) describes it, there are parallel motor and sensory hierarchies of neural processing for each modality, which are highly interconnected at equivalent points in the hierarchy: high-level sensory areas connect with high-level motor areas and lower-level sensory areas do so with lower-level motor ones.

Working or active memory

In general terms, the functions of this system are to integrate sensory and mnemonic information of the temporo-parietal lobes with the frontal systems involved in the organization of behavior, both at the short– and the long-term. It may be described as a conscious interface between incoming sensory information (or recently retrieved information from memory stores) and the frontal system related to the execution of long– and short-term behavior. To serve such a role, this system needs to keep on line information about the environment that is to be used in contingent behavior. Fuster (1995) has described this system as of "active memory", indicating that it is a sort of short-term memory that is currently being used to perform specific behavioral actions. Other authors (Baddeley, 1986; Goldman-Rakic, 1987a, b; 1995a, 1996; Tovée & Cohen-Tovée, 1996) refer to this sort of memory as "working memory", whose main feature is that the subject or the animal does not have any immediate clue to solve the problem that is required –as in the

case of classical associative memory– but rather it must "keep in mind" an object or event for some time before executing whatever action is necessary for the memory task.

Neurons in the prefrontal cortex that are specific for certain stimuli have been found to become activated during the period in which the monkey is rehearsing the short-term memory of an event related to such stimuli. Some of these neurons tend to extinguish their activity as the response time approaches, while others tend to increase their firing as the interval before the response comes to an end (Fuster, 1993, 1995). This has been interpreted by Fuster as a transition from perceptually-related neuronal populations to behaviorally-related populations in the frontal lobe. Furthermore, recent experiments by Wilson et al (1993) indicate that working memory for the spatial location of objects involves a network that includes the posterior parietal cortex (where spatial vision is processed) and its connections with the dorsolateral prefrontal cortex (perhaps corresponding to dorsal area 46), while working memory for object characteristics relies on connections between the inferior temporal lobe (where object features are processed) and the inferior convexity of the prefrontal cortex, that may correspond to ventral area 46. Thus, working memory for different features seems to be segregated in different regions of the prefrontal and temporo-parietal lobes and their respective connections.

Working memory operates in concert with other cognitive systems in the brain. It utilizes other types of memory –such as declarative or associative memory– and holds these in line while making decisions about appropriate responses in specific environmental contexts (Goldman-Rakic, 1987a, b, 1995a, 1996). Furthermore, Goldman-Rakic claims that working memory is the underlying neurobiological mechanism for most prefrontal functions, including tasks such as the Wisconsin Card Sorting Test. This type of memory is essential for the organization of behavior, as it guides it through representations of the outside world instead of relying directly

on external or sensory cues. For this reason, it is strongly related to the formation of concepts and ideas, and to our capacity to think. The permanence of objects in our minds relies in large part on working memory, which is fundamental for the formation of abstract concepts. In this sense, working memory is a pivotal element in the establishment of models or representations of reality.

Working memory and the language areas

Working memory has been proposed to consist of two main components: slave systems involving working memory of the specific sensorimotor circuits involved in particular behaviors, and a generalized, central executive that controls and distributes attention according to the contingencies (Baddeley, 1986; Baddeley & Della Sala, 1996). On the other hand, Goldman-Rakic (1995b) asserts that there may be multiple special-purpose working memory systems organized in parallel, rather than a central, panmodal executive controlling several modality-specific slave systems. This possibility will be discussed below.

In the human, some imaging studies have been performed in order to determine the localization of the so-called central executive and slave systems, especially for verbal working memory (Frackowiak, 1994; Awh et al, 1995; Habib & Demonet, 1996). One issue with these studies is that, since they are based on the method of subtraction, precise knowledge of the control task is fundamental for correctly interpreting the results. Using this methodology, a "slave" linguistic phonological-rehearsal working memory system has been allocated to the supramarginal gyrus (parietal area 40) and Broca's area 44 –the former more involved in the phonological store and the latter in the subvocal rehearsal that takes place during verbal working memory (Paulesu et al, 1993; Salmon et al, 1996). Paulesu et al (1993) used two different tasks, one requiring short-term memorization of letters –involving both a phonological store and a subvocal rehearsing system– and the other requiring rhyming judgement for

letters –involving only the subvocal rehearsing system. These tasks were compared to non–verbal working memory reference tasks. In this experiment, both the control and the experimental tasks involved working memory, while only the experimental situation required linguistic processing. The results indicated predominant activation of the supramarginal gyrus in the parietal lobe (area 40) in relation to the phonological store, and activation of Broca's area in relation to the subvocal rehearsal. Salmon *et al* (1996) also detected involvement of area 6 in the subvocal rehearsal component. It is of the highest interest that the regions involved in the phonological loop correspond to the connections above proposed between the inferior parietal lobe and Broca's area. Paulesu *et al* (1993) also found activation in Wernicke's area, which is consistent with the concept of these regions connecting to inferoparietal regions. We discussed above that lesions in area 40 produce conduction aphasia, which may be considered as a deficit in verbal working memory (Habib & Demonet, 1996; Alexander, 1997). More recent studies have also identified the supramarginal gyrus as an important element in linguistic working memory (Cohen *et al*, 1997; see also commentary by Goldman-Rakic, 1997). Using functional magnetic resonance imaging, Binder *et al* (1997) found activation of several cortical areas beside the classical ones, which included some inferoparietal sectors such as the angular gyrus (area 39), although area 40 was apparently silent. Note, however, that these authors did not use a working memory paradigm in their studies.

From the studies in the monkey reviewed before, frontal projections from the classical Wernicke's area (area Tpt) terminate mainly in the prefrontal cortex rather than in Broca's area, which receives its main projections from inferoparietal sectors (see Fig 3). It is therefore possible that the posterior superior temporal region represents in the human a transition zone in which concepts progressively acquire a phonological correlate, while the (parietal) supramarginal gyrus stores this phonological representation for some time. Neurons in human area 40 (and perhaps also area 39) may
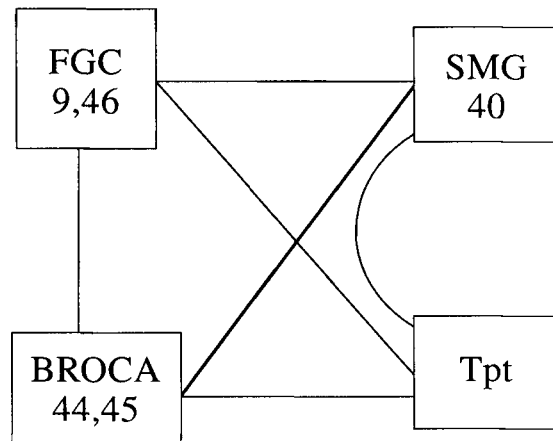

Fig 3. Proposed network of connectivity for linguistic working memory. Other cortical components may also participate in this system. Connections between area 40 and Tpt, and between Tpt and Broca's area have not been confirmed in the macaque, but we propose they have developed during human evolution. We consider especially important the projections from area 40 (and/or 39) to Broca's area. FGC, frontal granular cortex. Other abbreviations as in Fig 2.

then project to Broca's region (areas 44 and 45), thus establishing a neuronal circuit for the phonological-rehearsal system for linguistic working memory. This circuit requires a connection between superior temporal and inferoparietal areas that has not been described in the monkey, but we postulate that has developed in the human lineage.

On the other hand, frontal granular areas (area 9 and especially area 46) seem to relate with more general aspects of working memory, perhaps associated with the central executive (Petrides *et al*, 1993a, b; Salmon *et al*, 1996; Petrides, 1996). For example, in the study by Petrides *et al* (1993b), the experimental tasks involved verbal working memory processes (*i.e.*, saying aloud the numbers 1 to 10 but in random order and without repeating each other) while the control task consisted of just counting from 1 to 10, which minimizes the component of working memory as it is an automatic procedure. In this experiment, both the experimental and the control tasks were linguistic, while working memory was required only for the experimental task. Therefore, in the latter only the central executive system was expected to be activated, since this should be specific for working memory tasks and not depend on particular sensorimotor circuits. The result was

a bilaterally increased blood flow in the mid dorsolateral frontal cortex, which corresponds to the anatomical location of areas 9 and 46.

There is, however, some controversy as to the existence of an anatomically delimited central executive in the prefrontal cortex (Goldman-Rakic, 1995a, b, 1996; Petrides, 1996; Wickelgren, 1997). As mentioned, Goldman-Rakic (1995b) claims that the prefrontal cortex is subdivided into a mosaic of areas that are specialized in working memory for different modalities, there being no specific anatomical location for a multimodal central executive that coordinates attention. Thus, in the human, visuo-spatial working memory might involve connections between parietal area 7 and prefrontal areas 46 and 8; while working memory for object features might depend on inferotemporal area TE and its connections with frontal areas 45 and 12 (see Wilson et al, 1993); finally, linguistic working memory would involve connections between inferoparietal areas 39-40 and frontal areas 44-47, which roughly correspond to the above proposed phonological-rehearsal loop. Based on data from brain lesions indicating that damage in frontal granular areas contributes to Broca's aphasia (Damasio, 1992) and on the connectional information discussed above, we propose that beside areas 44/45 (and 47), frontal granular areas such as 9 and 46 also participate in language processing, especially in aspects related to working memory tasks. As mentioned, these frontal granular areas may not only relate to the distribution of attention, but may also handle cognitive information that is relevant for language processing. For example, when recalling the objects observed in a room, one might say "there is a lamp in the corner (visuo-spatial working memory) with four light bulbs (object feature working memory)". Tasks such as this probably require the coordinated activity of the respective working memory circuits that are located in frontal granular cortex. In this sense, although the so-called central executive may in fact be a mosaic of different areas subserving different modalities, these areas probably cooperate with the circuit for linguistic processing in

order to feed cognitive information and distribute attention between the different modalities. The central executive may perhaps be conceived as a mosaic of closely interconnected but functionally diverse prefrontal regions, that become tightly coordinated during working memory tasks. For example, direct projections from area Tpt to area 46 can participate by feeding auditory information to frontal granular cortex. Therefore, we should expect activation of several frontal granular areas in many types of relatively complex working memory paradigms, but perhaps especially in the case of linguistic working memory as it requires handling several and varied items of cognitive information (Petrides et al, 1993b).

DISCUSSION

Based on the reviewed evidence, we propose that the language areas may be connected in several ways (Fig 3). There is an indirect pathway connecting Wernicke's area to Broca's area in three steps. The first step corresponds to Wernicke's area in the superior temporal lobe (area Tpt). This area has been classically viewed as the center for "language perception". Nowadays, more than a speech processing center, Wernicke's area is considered a place of convergence for cortico-cortical interactions in which sounds are mapped into words and associations occur with other sensory regions that convey meaning to these words (Damasio, 1992). This is a region in which phonemes and morphemes are perceived, and sounds are associated with multimodal concepts. The second step may consist in the projection from area Tpt to inferoparietal area 40 (and perhaps also 39), in which the phonological representation is maintained for a while, permitting the transient storage of vocalizations. Finally, the third step consists in the projection from inferoparietal areas to Broca's region, where linguistic rehearsal takes place. It is of the highest interest that the connectional evidence from the macaque is consistent with the findings of brain activation for linguistic working memory tasks in humans, indicating that

some aspects of language processing are closely related to working memory performance. In fact, conduction aphasia –consisting of the incapacity to repeat verbal sequences– can be interpreted as a deficit in working memory that results from the disruption of the connections between the inferior parietal lobe and Broca's area. We postulate that the working memory circuit for linguistic utterances has been fundamental in the evolutionary origin of language and is essential for language acquisition in children, as it provides a circuit for imitative learning of phonological sequences.

An alternative pathway may consist in direct connections from Wernicke's region to Broca's area and prefrontal regions, establishing a sort of short-cut between the anterior and posterior language regions that permits the execution of certain automatic linguistic routines that do not require rehearsal anymore, and the "on line" maintenance of auditory information while linguistic behavior is being generated. There are other possible subcortical pathways, including for example the basal ganglia, but these are not considered here.

The evolutionary origin of the language areas

The above evidence also suggests to us a scenario for the origin and evolution of the language areas in the human brain. Geschwind (1964) originally postulated a theory of the origin of language that was based on the development of non-limbic, cross-modal cortico-cortical interactions, which –according to him– were especially well developed in humans and allowed associations to be readily established between the sound of a vocalization and the image of an object. These associations permitted the generation of a lexicon, in which arbitrary sounds (vocalizations) represented objects identified through the visual or the tactile system. Cross-modal auditory-visual associations are perhaps the best example for the origin of names, but Geschwind's hypothesis was that –in general– all sorts of cross-modal (and also unimodal) associations were facilitated in the human brain, permitting the origin of

denotation through vocal or gestural modes of communication. According to Geschwind's hypothesis, cross-modal sensory associations need an intact limbic system to develop in the monkey, while these associations become established via a sort of short-cut of cortico-cortical interactions in the human. In fact, cross-modal associations can be performed much faster in humans than in monkeys and apes (Davenport, 1976). More recent experiments in monkeys support Geschwind's contention that non-limbic, cortico-cortical associations are better developed in humans than in monkeys: the amygdala, a complex closely related to the limbic system and located in the anterior temporal lobe, is essential for establishing cross-modal associations in the macaque, although lesions in the amygdala have much less effect in associative learning in the human (Murray & Mishkin, 1985; Nahm et al, 1993, Aggleton, 1993).

Behavioral experiments performed during the seventies and eighties showed clearly that if trained from an early age, chimpanzees and gorillas were capable of learning some aspects of sign language and developed a reasonably sized lexicon, although no hints of grammar could be observed (Premack, 1983). This indicated that at least apes were able to establish cross-modal associations such as those required to generate a limited lexicon. Furthermore, there is evidence that some primates –such as vervet monkeys– naturally develop different cries specifying distinct predators, and that the association between these cries and specific animals is learned, not genetical (Cheney & Seyfarth, 1990; Seyfarth & Cheney, 1992). Therefore, non-human primates have the potential to develop a naming system under appropriate circumstances. One possibility is that the neural substrate for the development for a lexicon (say, relatively well-developed cross-modal cortico-cortical interactions) existed in an incipient form in higher primates before the origin of language and humans, and was part of an adaptation for a different function (Wilkins & Wakefield, 1995).

In early hominids, Wernicke's area may have developed as a place of convergence

for cortico-cortical associations that in addition acquired a phonological correlate. This probably facilitated the generation of slightly more complex linguistic utterances, and also permitted the expansion of the lexicon. Concomitantly, a phonological-rehearsal circuit including inferoparietal areas and Broca's region started to differentiate, that served as a sensorimotor loop for the internal rehearsal of complex vocalizations that needed to be learned. In analogy with other accurate sensorimotor systems where sensory feedback is of great relevance for the performance of complex, learned tasks (Doupe, 1993), it is likely that projections from parietal somatosensory areas to the motor orofacial region corresponding to Broca's area were important in the development of learned, socially relevant vocalizations. In this sense, the language circuit may have originally developed as a system for learning complex vocalizations, that was mainly based on working memory (Aboitiz, 1995). As mentioned above, it has been proposed that the elementary aspects of syntax arose as a consequence of the differentiation of the premotor regions related to Broca's area (Lieberman, 1985; Givón, 1995; Deacon, 1989, 1992; Greenfield, 1991; Preuss, 1995), in which these regions specialized in controlling complex, high-frequency sequences of movements such as those involved in articulate speech. Our view is that this sophisticated device originated in the context of a working memory system for the generation of complex, meaningful vocalizations that evolved into the phonological-rehearsal neural circuit proposed above.

One further, and perhaps fundamental, step was probably the increased coordination and coupling of this primordial language device and granular frontal areas, that kept "on line" relevant cognitive information to be used during language. We postulate that higher levels of syntax -such as those required for the organization of discourse- were achieved at this level, through the integration of the prefrontal system of working memory for nonlinguistic events and the language-related working memory circuit. Note that in transcortical

motor aphasia, which is usually caused by extensive prefrontal damage, the patients have very limited capacity to generate complex syntax (Alexander, 1997). Some cases of transcortical motor aphasia with exclusively subcortical lesions have been reported, but in these -as in the examples of cortical lesion- there is pronounced hypoactivity in the prefrontal lobes.

The considerations about connectivity presented here have the drawback of being based on a model animal that does not speak, and therefore they may not correspond precisely to the connectivity in the human language areas. Further anatomical and functional studies may determine that the language circuits include some different cortical regions and connections than those specified at this moment. Ours is intended to be a starting model, in which the connectivity of the language regions (*i*) is considered to be more complex than only a direct connection from Wernicke's region in the temporal lobe to Broca's area through the arcuate fasciculus, as it includes at least the inferoparietal system; and (*ii*) is tightly related to circuits for working memory in the prefrontal cortex.

Language lateralization

Another critical issue in the evolution of the language regions is that they tend to be localized in the left hemisphere. The explanation for this asymmetry is beyond the scope of this paper, but it may perhaps be a consequence of previously established asymmetries for sequential (left hemisphere) *versus* spatial (right hemisphere) skills. Perhaps, the manufacturing of tools imposed a left-hemisphere tendency for sequential movements, to which the language system turned out to fit (Bradshaw & Rogers, 1992). Whatever the reason for language lateralization, we propose that it mainly consisted in the specialization of two different types of working memory systems: the left hemisphere emphasized working memory for sequential and linguistic (and perhaps also object identification) tasks, while the right hemisphere emphasized working memory

for spatially-related tasks. In other words, more than resulting from the specialization of specific areas in the temporal (left hemisphere) or the parietal (right hemisphere) lobes, brain lateralization may perhaps be viewed as a consequence of asymmetries in the organization of temporoparietal-prefrontal networks in the two hemispheres, the left emphasizing temporal and inferoparietal connections with the frontal lobe, while the right might emphasize projections from posterior parietal areas involved in spatial vision. This perhaps explains the relatively modest differences in anatomical arrangement between the language regions in the left hemisphere and their right hemisphere equivalents (Aboitiz & Ide, 1997), as compared to the functional laterality of the two hemispheres. Perhaps the structural basis for hemispheric asymmetry fundamentally lies in the anatomical arrangement of temporoparietal-frontal projections in the two hemispheres rather than on the development of specific cortical areas. Unfortunately, this might make the issue even less tractable since there is as yet no method to study such large-scale connections in the human.

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