Broca's Area and the Origins of Human Vocal Skill

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Broca's area and the origins of human vocal skill

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Chimpanzees appear to be unable to learn to speak. It is usual to attribute their lack of vocal skill to limitations of their vocal tract, and to the absence in their neocortex of any area corresponding to Broca's area in the human brain. The first signs of Broca's area in hominid endocasts are therefore taken to represent an evolutionary development of great significance. There are two outstanding questions. First, what exactly does Broca's area do? Secondly, why does Broca's area in one hemisphere play a much greater role in controlling speech than does the corresponding area in the other hemisphere?

The following answers are proposed. (1) Broca's area seems to be concerned not with the production of individual sounds but with the regulation of sequences of sounds. Chimpanzees have no need for such an area because their natural calls are not made up by varying the sequential order of elementary units. (2) Cerebral dominance for speech may result from the fact that the vocal cords are innervated in the same way as other central organs, such as the tongue. Each hemisphere sends a projection, and the two projections overlap extensively so that either hemisphere can assume full control. It is argued that it is most efficient for a single hemisphere to dominate where a complex sequence of movements must be programmed. This reorganization has occurred for the production of song in some songbirds and for the control of the vocal cords in human speech.

Chimpanzees ape but they do not parrot. If a chimpanzee is brought up in a human household it copies some of the actions of its caretakers (Hayes & Hayes 1952); but it does not imitate their speech (Kellogg 1968). Even with extensive coaching the highest achievement of a chimpanzee has been to say 'mama', 'papa', 'cup' and 'up', and these with poor articulation (Hayes & Nissen 1971). The ape repeats what it sees but not what it hears.

The failure of apes to speak is partly accounted for by the limitations of their vocal tract. In man the back of the tongue forms the front wall of the superpharyngeal cavity, and the shape of this cavity can thus be altered by movements of the tongue. This is not so in the chimpanzee, and they are therefore able to produce only a restricted range of vowels (Lieberman 1975). But the ability of man to speak depends not only on the configuration of the vocal tract but also on the neurological mechanisms controlling the movements of the vocal cords. We may reasonably wonder whether similar mechanisms are lacking in the brains of apes.

In man speech is partly under the control of 'Broca's area', which lies on the opercular surface of the third frontal convolution (Bailey & von Bonin 1951). Damage to this region leads to a poverty of speech and a loss of fluency (Benson 1967; Mohr 1976). It is understandable that there should have been great interest in whether this region can be identified on the endocasts of early hominids, because its presence might be taken to be a mark of the advent of the ability to speak (Holloway 1972, 1978).

Whereas we have no access to the actual brains of the early hominids the brains of monkeys and apes are there for us to examine. But the microscopic study of the cell layers of frontal cortex has not yet settled the issue. In the human brain Broca's area can be differentiated on cytoarchitectonic criteria and it has been labelled area FCBm (von Economo 1929). In their early studies von Bonin & Bailey believed that they could identify an area with a similar microscopic structure in the brains of the rhesus monkey and chimpanzee (von Bonin & Bailey 1947; von Bonin 1948; Bailey *et al.* 1950). But on reconsidering the material they were less confident that they could make out a special subregion of area FC that they could reasonably label FCBm (von Bonin & Bailey 1961). There the matter must rest until further studies are undertaken, perhaps with the newer pigment stain that has proved valuable in distinguishing between the superior temporal cortex of man and monkey (Braak 1978).

There are other ways of attacking the question (Passingham 1979). The area of the neocortex that directly controls the vocal cords can be identified in patients during surgical operations. Vowel sounds can be evoked by electrically stimulating the inferior part of frontal motor cortex, and movements of the lips and jaws can be elicited from much the same area (Penfield & Rasmussen 1950; Penfield & Roberts 1959). In chimpanzees stimulation of this same region of motor cortex produces movements of the larynx (Bailey *et al.* 1950). That movements of the vocal cords themselves can be elicited in this way has been directly demonstrated in rhesus monkeys (Hast *et al.* 1974). By recording from the muscles of the larynx it was shown that the intrinsic muscles are controlled by sites anterior to those directing the extrinsic muscles, as in swallowing, and that both sites lie within the area tentatively designated FCBm (von Bonin & Bailey 1947). But this very demonstration casts doubt on the suggestion that this area in the rhesus monkey is functionally similar to Broca's area in man, for electrical stimulation of Broca's area does not give rise to movements of the vocal cords as indicated by vocalization; in the human brain Broca's area lies anterior to the region of frontal cortex that directly controls the vocal cords (Penfield & Roberts 1959). In other words if there is an area analogous to Broca's area in the chimpanzee or monkey brain it must lie in front of the region initially proposed and labelled FCBm (Jürgens 1979).

Whether there is in fact such a region is best judged from the effects of cortical damage on vocalization. Incomplete removals of the area directly controlling the larynx in monkeys have no discernible effect on the animals' spontaneous calls, and the monkeys can still make a call when given a signal as they have been taught to do before the operation (Sutton *et al.* 1974; Sutton 1979). More complete removals, including the area representing the face, do impair the monkey's ability to call; the voice is feeble and low-pitched (Green & Walker 1938). But it is not clear to what extent the general facial paralysis contributes to the animal's problem.

Even if we could be confident that the effect was the direct result of interference with the mechanisms controlling the vocal cords it would be analogous to the syndrome produced in patients by damage to the motor mechanisms of vocalization rather than the speech mechanisms of Broca's area. The speech disorder of patients with lesions of Broca's area alone is not to be accounted for by an elementary problem with articulation or phonation (Mohr 1976). A better parallel for the loss of fluency in such cases is provided by the marked decrease in spontaneous calling that follows the removal of prefrontal cortex in monkeys, that is of the area in front of premotor cortex (Myers 1976). But the symptom is most effectively produced in monkeys by damage to the orbital prefrontal cortex (Ervin *et al.* 1975), which also changes them emotionally (Butter & Snyder 1972; Kling & Mass 1974). It is possible that the change in vocalization is secondary to an alteration in temperament. For the moment, then, we can find no very promising candidate for the role of Broca's area in the monkey brain. The brain of apes has yet to be explored.

Let us suppose that Broca's area is indeed uniquely human. We are left with two outstanding questions. First, what exactly does Broca's area do, and how did an area with this function evolve? Secondly, why does Broca's area in one hemisphere play a much greater role in directing speech than does the same part of the brain in the other hemisphere?

Function

To answer the first question we must consider the functional organization of motor and premotor cortex in monkeys. In the primary motor area, MI, the body is represented in an inverted position; if a stimulating electrode is moved up the cortex in front of the central sulcus, movements will be elicited first of the face, then of the arm, the leg and finally the tail (Woolsey *et al.* 1952). This somatotopic map is crudely preserved in premotor cortex. The face area of MI is reciprocally connected via fibres to the larynx area of ventral premotor cortex; and the arm and face areas are reciprocally connected to the central and dorsal premotor cortex, the leg being represented above the arm (Kunzle 1978*a*; Matsumara & Kubota 1979; Muakkassa & Strick 1979). We may assume, without knowing it to be true, that in the human brain Broca's area is reciprocally connected to the larynx area.

We have supposed that the monkey brain lacks a region analogous to Broca's area, that is a higher centre directing the larynx area. But there are mechanisms in premotor cortex for the higher regulation of actions as carried out by the limbs. If we understood the influence of these areas on the movements of the limbs we might be in a better position to appreciate the nature of the influence of Broca's area on the movements of the vocal cords.

The motor area is particularly concerned with the production of the discrete and independent movements that are essential for skilled performance. It influences the muscles most directly through the fibres of the pyramidal tract. In primates this tract contains over 1½ times as many fibres as in carnivores and rodents, after allowance is made for differences in body size, and over 3½ times as many as in ungulates (Passingham 1981). In other words the size of the tract correlates with the degree of independence with which the digits can be moved, being greatest in animals with a hand, less in those with a paw, and least in animals with hooves.

The importance of motor cortex for skilled movements is more directly demonstrated by examining monkeys in which the pyramidal tract has been sectioned or in which motor cortex has been removed. In either case rhesus monkeys can still climb and leap, and can reach out and grasp objects with the whole hand; but they are unable to pick up small objects between thumb and forefinger in a fine precision grip (Lawrence & Kuypers 1968; Passingham *et al.* 1978). That the animal is unable to make discrete finger movements can be shown by requiring it to put its forefinger through a small hole so as to push a piece of food off a shelf. After removal of motor cortex and somatosensory cortex on one side rhesus monkeys are unable to do this with the affected hand (Passingham & Perry 1981).

Just as the sensory areas of the neocortex are primarily concerned with the analysis of fine detail, so the motor area appears to have an especial interest in the generation of refined movements. We might expect to find the larynx area to share a similar concern. As we have already noted we know nothing of the contribution of this area in monkeys and apes. In the squirrel monkey the repertoire of cackles, chirps, shrieks and so on can be elicited by electrically stimulating structures other than the neocortex (Jürgens & Ploog 1970). The chimpanzee vocabulary consists essentially of variations on a series of grunts, barks, screams and hoots (Marler 1969), and one might wonder whether the neocortex would be necessary for the production of such poorly articulated vowel sounds. In man, by comparison, the larynx area clearly contributes to the production and articulation of the very many discrete sounds used in human speech. Electrical stimulation of this area disrupts articulation (Penfield & Roberts 1959), and damage disrupts the execution of the many refined movements involved in vocal skill (Mohr 1976).

To return to the control of the limbs, we have now to consider the influence exerted by higher centres in premotor cortex. A monkey's ability to perform acts in a correct sequence can be tested by requiring it to carry out a series of manipulations. For example it can be arranged that a box containing food can only be opened if three catches are operated in the correct order. Monkeys in which an area including dorsal premotor cortex has been removed are poor at this task (Deuel 1977). Yet they have no problems in operating each of the latches on its own. Their problem lies in the ordering of the three movements.

The brain must programme not only the order in which a series of acts must be performed but also how many there are to be in the sequence. Monkeys can be trained to count by requiring them to press a button once or five times depending on some previous instruction. They are poor at this task if dorsal prefrontal cortex is removed (Passingham 1978). This area lies in front of dorsal premotor cortex and is linked to it by anatomical connections (Kunzle 1978*b*).

By analogy with dorsal premotor cortex it is tempting to suggest that the primary function of Broca's area is to direct the sequencing of the basic movements, in this case the movements of the vocal cords. Meaning is conveyed in speech by the serial ordering of the phonemes and morphemes, and a high order of vocal skill is demanded (MacNeilage 1970). Patients with large anterior cerebral lesions may suffer some loss of verbal fluency (Benson 1967); but they also have difficulties in sequencing sounds. In one study such patients were found to be able to say 'ba-ba-ba', but unable to repeat the sequence 'ba-da-ga' (Mateer & Kimura 1977). The lesions encroach on tissue controlling movements of the face, since the same patients have difficulties with copying simple facial movements or with repeating sequences such as retracting the lips, putting out the tongue and biting the lower lip (Mateer & Kimura 1977). It is possible to demonstrate a defect in reproducing the sequence without a corresponding difficulty in copying each oral movement on its own. This has been done by electrically stimulating anterior points in the left cerebral hemisphere of patients undergoing neurosurgery under local anaesthesia. On three occasions stimulation of inferior frontal sites well forward of the motor area has rendered the patient unable to copy a sequence of oral movements although the ability to copy each one on its own was preserved (Ojemann & Mateer 1979).

If it is accepted that Broca's area plays some role in the sequencing of speech sounds then the apparent lack of such an area in the brains of other primates may have a simple explanation. The calls of these animals are not constructed by the sequencing of elements to form the message; they can be treated rather as single elements, the equivalent of the basic phoneme. These primates have no need of a cortical area regulating the serial order of sounds.

Birds compose their songs in a quite different way. The basic elements are the notes and glissandi, and these are ordered into syllables and then into phrases. Some birds have relatively simple stereotyped songs, but others, such as the robin, rock wren and canary, sing long songs and possess a very large repertoire of song variants (Bremond 1968; Kroodsma 1975; Nottebohm 1977; Jellis 1977). In their structure, though not in their content, these songs are more like human speech than are the calls of other primates.

DOMINANCE

The brains of some song birds also offer a clue as to the answer to the second question that we posed. Why is Broca's area in the left hemisphere more important for speech than the corresponding area in the right hemisphere? Speech is controlled by the left hemisphere in 96% of right-handed but only 70% of left-handed or ambidextrous subjects, by the right hemisphere in 15% of non-right-handed but only 4% of right-handed people, and by both hemispheres in 15% of non-right-handed people but in none of those who are right-handed (Milner 1975). The link with handedness makes it tempting to suggest that the left hemisphere is specialized for both manual and vocal skills, and that handedness may hold the key to the evolutionary origin of cerebral dominance for speech (Kimura 1976, 1979).

But cerebral dominance for vocalization can be present without handedness, as is shown by the existence of some birds in which there is an asymmetry in the neural control of song. In canaries, chaffinches and white-crowned sparrows, section of the nerve innervating the left syrinx markedly impairs singing, whereas section of the nerve innervating the right syrinx has little or no effect (Nottebohm 1977). Left dominance has also been demonstrated in canaries for the central controlling area, the hyperstriatum ventrale pars caudale; the number of syllables of song that the bird loses is much greater if lesions are made on the left rather than on the right (Nottebohm 1977).

This example suggests that there may be reasons why cerebral dominance is of advantage for the production of sounds. Perhaps the key to dominance lies not in handedness but in the way in which the brain innervates the vocal cords. The hand is controlled mainly by the contralateral hemisphere. If the motor area of that hemisphere is damaged the ipsilateral motor cortex is unable to direct the normal range of movements of that hand. This is true in monkeys even if the damage occurs very early in life (Passingham *et al.* 1978). The arrangement is quite different for central organs of the body, such as the tongue and jaw. If the motor cortex is electrically stimulated in man the limb that moves is always the one opposite the hemisphere stimulated; but movements of the tongue and jaw can be elicited from either hemisphere (Penfield & Roberts 1959). If the hypoglossal nerve, which innervates the tongue, is cut on one side in the monkey, stimulation of the motor area on the other side still elicits most tongue movements (Walker & Green 1938). This indicates that there are paths from each hemisphere to both sides of the tongue. If, therefore, the motor area is removed in one hemisphere, a monkey can still rotate and deviate its tongue to either side; and it remains able to rotate its tongue either way even if the hypoglossal nerve is sectioned ipsilateral to the cortical lesion (Green & Walker 1938).

It has been demonstrated in monkeys that the vocal cords also receive a bilateral innervation from the neocortex; the cords can be excited by electrical stimulation of either cortical larynx area (Hast *et al.* 1974). Vocalization can be induced in patients by stimulating the left or the right hemisphere (Penfield & Roberts 1959). This bilateral organization permits considerable recovery of function. It has traditionally been believed that lesions of Broca's area in people give rise to a long-lasting aphasia, but more careful analysis indicates that where the lesion can be shown to be confined to Broca's area and the adjacent larynx area the patients recover their speech remarkably well (Mohr 1976; Mohr *et al.* 1978). It is reasonable to suppose that this improvement occurs in part because the corresponding areas in the contralateral hemisphere can take over the relevant function.

It does not necessarily follow that because an organ can be controlled by either hemisphere it would be most efficient for one hemisphere to assume the dominant role. The movements of the tongue, for example, are relatively simple, and there is no reason why the relevant cortical areas cannot coordinate their instructions without loss of proficiency. But such an arrangement would not be optimal for the execution of complex sequences of movement, as in the production of speech. In such a case we would surely expect the highest skill to be achieved if the sequence was directed by one central programme, located in a single hemisphere, rather than by two separate programmes which must use the long commissural pathways to coordinate their instructions. The same reasoning applies to the production of intricate songs by those birds that, like canaries, learn a new song each season (Nottebohm 1977, 1979).

This is not to say that the right hemisphere normally makes no contribution to speech, even in people who are fully right-handed. This can be shown by using the amount of blood flowing to any cortical area as a measure of the metabolic requirements and therefore of the activity of that region. When a person talks there is an increase in the blood supply to Broca's area, but there is also a similar increase to the corresponding region of the right frontal lobe (Lassen *et al.* 1978). But, whatever the contribution of the right hemisphere under normal circumstances, the left hemisphere can direct speech efficiently on its own. In right-handed people damage to the inferior frontal region of the right hemisphere only rarely gives rise to the gross symptoms of aphasia (Hécaen & Albert 1978).

If there is an advantage in programming speech from one area rather than two it follows that those people in whom speech is controlled by both hemispheres should be at a disadvantage. There is suggestive evidence that this may be so, in particular that cerebral lateralization of speech may be less firmly established in some people who stutter. One method for investigating cerebral dominance for language is the dichotic listening technique. Different digits or words are played simultaneously to the two ears; the subject reports the words he hears, and if he gives mainly the words played to the right ear it is assumed that his left hemisphere is dominant for speech. In one study stutterers were found to differ from other subjects in reporting fewer of the words played to their right ear and more of those to the left; 55 % of the stutterers actually reported more words presented to their left than to their right ear (Curry & Gregory 1969). The most plausible interpretation of these results is that in these stutterers speech was less firmly represented in the left hemisphere, even though they were all right-handed.

The diagnosis of dominance made on the basis of the dichotic listening test usually agrees well with the results obtained by a more direct procedure, the sodium amytal test (Milner 1975). Sodium amytal is injected into the blood supply of one hemisphere; in this way the activity of a hemisphere can be temporarily inhibited. If speech is controlled only by the left hemisphere it will be disrupted by left-sided but not by right-sided injections. If injections into the blood supply of either hemisphere produce dysphasic symptoms we know that speech is represented in both hemispheres.

The sodium amytal test has been performed on very few stutterers. Of the seven right-handed tested two have shown evidence of bilateral representation of speech (Jones 1966; Andrews *et al.* 1972; Luessenhop *et al.* 1973). Speech was found to be controlled by both hemispheres in three of the four subjects who were ambidextrous or left-handed, and there was a suggestion that this might also be so in the fourth (Jones 1966; Luessenhop *et al.* 1973). The sample is small, but the results are as expected from the data on dichotic listening.

An objection immediately presents itself. On the sodium amytal test speech has been shown to be bilaterally represented in 18 out of the 122 patients who were ambidextrous or left-handed, and had not suffered any early brain injury (Milner 1975). We are not told whether any of these patients stuttered, but we may assume that they did not all do so, as the fact would surely have been noted. But the objection rests on an assumption: this is that in these patients the sequencing of speech was carried out by both hemispheres, and without a penalty. This assumption is not justified. Certainly speech was disrupted by injection of sodium amytal into the blood supply of either hemisphere, but the type of speech problem often differed for the two hemispheres (Rasmussen & Milner 1975). In 43 % of the patients with bilateral representation, errors of sequencing followed injection on one side and errors of naming the other. Errors of programming a sequence were detected on simple tasks requiring counting, enumerating the days of the week or the months of the year, and going through the alphabet. At least in these patients the production of such series was controlled by only one hemisphere.

For the moment we may reasonably entertain the notion that where complex sequences must be programmed it will be more efficient to set up one programme rather than two. We do not know whether it is the learning or the production of such sequences that imposes the constraint. The general view proposed here is distinct from the idea put forward by Levy (1977) to account for cerebral dominance. Her suggestion is not that any function will be carried out more effectively if it is controlled by a single hemisphere. Instead she points out that the capacity of the brain might be better used if particular functions are carried out by only one hemisphere instead of two. She argues that to duplicate programmes would be needless; it is argued here that to do so would be counter-productive.

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