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Research report

Cortico-cortical projections of the motorcortical larynx area in the rhesus monkey

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Abstract

The efferent cortico-cortical projections of the motorcortical larynx area were studied in three rhesus monkeys (*Macaca mulatta*), using biotin dextranamine as anterograde tracer. Identification of the larynx area was made with the help of electrical brain stimulation and indirect laryngoscopy. Heavy projections were found into the surrounding ventral and dorsal premotor cortex (areas 6V and D), primary motor cortex (area 4), the homolog of Broca's area (mainly area 44), fronto- and parieto-opercular cortex (including secondary somatosensory cortex), agranular, dysgranular and granular insula, rostral-most primary somatosensory cortex (area 3a), supplementary motor area (area 6M), anterior cingulate gyrus (area 24c) and dorsal postarcuate cortex (area 8A). Medium projections could be traced to the ventrolateral prefrontal and lateral orbital cortex (areas 47L and O), the primary somatosensory areas 3b and 2, the agranular and dysgranular insula, and the posteroinferior parietal cortex (area 7; PFG, PG). Minor projections ended in the lateral and dorsolateral prefrontal cortex (areas 46V and 8B), primary somatosensory area 1 and cortex within the intraparietal sulcus (PEa) and posterior sulcus temporalis superior (TPO). Due to its close spatial relationship to the insula on the one hand and the premotor cortex on the other, the larynx area shows projections which, in some respects, are not typical for classical primary motor cortex.

Theme: Motor systems and sensorimotor integration

Topic: Cortex

Keywords: Motor cortex; Larynx area; Phonation; Rhesus monkey

1. Introduction

Electrical stimulation of the inferior precentral cortex has been reported to produce vocal fold adduction in man [10], chimpanzee [31], rhesus monkey [16,59,63] and squirrel monkey [15,20]. In man, in contrast to monkey and ape, it was also possible to elicit phonation from this area [10,45]. In non-primate mammals, such as the cat and dog, the existence of an area specialized for isolated vocal fold movements has been questioned [38]. The primate cortical larynx area borders the precentral tongue, lip and masticatory muscle representation and, therefore, can be considered as part of the primary motor cortex. Cyto-architectonically, however, similar to other parts of the facial motor cortex, it does not represent area 4, but area 6, according to Brodmann [6] or area 6bα, FCBm and F5, according to Vogt and Vogt [62], von Bonin and Bailey [3] and Matelli et al. [36], respectively.

Bilateral lesions in the cortical larynx area in humans cause a complete loss of voluntary control over phonation [2,11,12,35]. The cortical larynx area thus represents an indispensable structure for the production of speech and song. For a better understanding of speech and song control, it is essential to have a detailed knowledge of the anatomical connections of this area. Up-to-now, there is only a single study that has investigated the efferent projections of the cortical larynx area [21]. This study was carried out with a tracer (^{3}H-leucine) which does not allow to distinguish terminals from by-passing fibers (due to the fact that the autoradiographic method has a too low resolution to depict details of the neuronal structure). The study, furthermore, was made in the squirrel monkey

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(*Saimiri sciureus*). This species belongs to a group of primates (New World monkeys) that has separated from the branch leading to man and modern Old World monkeys about 40 million years ago. The aim of the present study, therefore, is to reinvestigate the efferent projections of the cortical larynx area in a species (rhesus monkey) more closely related to man than the squirrel monkey and with a tracer (biotin dextranamine) without the shortcomings of ^{3}H-leucine. As a first step towards a comprehensive description of the complete efferent and afferent projection system of the cortical larynx area, we concentrate in the present study on the anterograde cortico-cortical connections.

2. Materials and methods

The experiments were carried out in three rhesus monkeys, *Macaca mulatta*. The animals were narcotized with a mixture of 10 mg ketamine, 2 mg xylazine and 0.02 mg atropine sulfate in 0.2 ml sterile water per kg body weight. This dose was renewed every 30 min until the end of the operation which took about 2.5 h. The head was fixed in a stereotaxic apparatus (David Kopf Instruments, Tujunga, USA). The skin was incised in the temporal region and the bone removed above the inferior motor cortex in a diameter of 15–20 mm. By the aid of a monopolar stainless steel electrode (shaft diameter 250 μm), the cortex was explored for sites yielding vocal fold adduction when electrically stimulated. All animals were tested on the same (left) side for better comparability. The exploration area was limited by the inferior branch of the arcuate sulcus rostrally, the anterior subcentral dimple caudally, the Sylvian fissure ventrally and a dorsal border 12 mm above the Sylvian fissure, making up altogether ca. 100 mm^2. This area has been shown by Hast et al. [16] to produce contractions of the thyroarytenoid and/or cricothyroid muscle in the rhesus monkey when electrically stimulated. In order to reduce cortical damage to a minimum, we did not explore the whole area systematically, but limited our stimulations, depending upon the stimulation effects, to 6–12 probing sites. Stimulation was carried out transdurally in the case of animals 2 and 3; animal 1 was stimulated with the dura removed above the stimulation area. The stimulation parameters used were monophasic rectangular pulse trains of 1 ms pulse width, 70 Hz repetition rate and 3 s train duration. During exploration, a current intensity of 500 μA was used (impedance: 14 k Ohm). If a site yielding vocal fold movement was found, threshold was determined. Thresholds ranged between 320 and 410 μA. A repetition rate of 70 Hz was chosen as, with the macroelectrodes used, this was the lowest rate with which a smooth (non-quavery) vocal fold movement was obtained; at the same time, the area yielding such a movement was smaller than when higher repetition rates were used. The type of vocal fold movement obtained was in all cases a bilateral symmetrical adduction. Vocal fold movements were observed by indirect laryngoscopy.

When a site producing vocal fold adduction was found, a drawing was made indicating the position of the stimulation site in relation to nearby blood vessels. In the animals with the intact dura, the site of electrode penetration was marked with ink. Then, the electrode was withdrawn, and an anterograde tracer was injected into that site. Injection was carried out by the aid of a micromanipulator-driven Hamilton microsyringe with a cannula diameter of 0.47 mm. One microliter of 20% biotin dextranamine (BDA; Molecular Probes, Eugene, USA) in 2% dimethyl sulfoxide was injected in animal 1. Animals 2 and 3 received two injections of 1 μl each. In the latter two animals, the injection sites were about 1.0 mm apart and both yielded vocal fold movements when electrically stimulated. Injection duration was 10 min; there were another 10 min waiting time, before the cannula was slowly withdrawn. After the injection, the dura defect in animal 1 was covered with human dura (Lyodura, Braun, Melsungen, Germany) glued to the bone rim with Histoacryl (Braun, Melsungen, Germany). In all three animals, the wound was closed by sewing up muscle fascia and skin in two layers. The animals were returned to their home cage. After a survival period of 7 weeks (a period suggested by Brandt and Apkarian [5] to be optimal for primates of the size of the squirrel monkey and above), the animals received an overdose of 16% pentobarbital sodium and were perfused with 2 l of physiological saline (37 °C), followed by 4 l of 4% paraformaldehyde in 0.1 M phosphate buffer (pH 7.2) at room temperature.

Brains were removed from the skull, postfixed in phosphate-buffered 4% paraformaldehyde for 2 days and then stored in 20% sucrose in 0.1 M phosphate buffer for cryoprotection at 4 °C for 4 days. The brains then were cut from the frontal pole to the caudal medulla in the stereotaxic frontal plane at 45 μm on a freezing microtome (Frigocut, 2800, Reichert–Jung, Nussloch, Germany). The sections were collected in 10 mM phosphate buffer (pH 7.4). Immunohistochemical tracer identification was carried out according to a modification of the procedures described by Veenman et al. [61] and Brandt and Apkarian [5]. Briefly, after several washings in 10 mM phosphate buffer, the sections were incubated in 1% H_2O_2 in 10 mM phosphate buffer (pH 7.4) for 10 min at room temperature to block endogenous peroxidase. The sections then were rinsed 10 times in 10 mM phosphate buffer (pH 7.4) and incubated with avidin–biotin–peroxidase complex (Vectastain Standard Kit, Vector Laboratories, Burlingame, USA) in 0.5% Triton X-100 for 60 min at 37 °C. After another washing in 10 mM phosphate buffer (pH 7.4) and 0.2 M sodium acetate (pH 6.0), the sections were pre-incubated for 30 min in a solution of 100 mg 3,3′-diaminobenzidine dihydrochloride, 2.5 g nickel ammonium sulfate, 40 mg ammonium chloride and 40 mg cobalt (II) chloride hexa-

hydrate in 100 ml 0.2 M sodium acetate. After adding 1% H_2O_2 to a final concentration of 0.003%, a post-incubation period of 15 min followed. The sections then were rinsed in 0.2 M sodium acetate and mounted onto gelatine-coated slides from 10 mM phosphate buffer (pH 7.4). After drying overnight, half of the sections were counterstained with Cresyl Violet. All sections were dehydrated through an ascending alcohol series and xylene, and finally cover-slipped with DePeX.

Light microscopic evaluation was done in bright- and dark-field. Identification of brain areas followed the stereotaxic atlas of Paxinos et al. [44]. Terminals were distinguished from by-passing fibers by their bouton-like specializations, irregular course, small diameter and rich ramification (Fig. 1).

The experiments were approved by the animal ethics committee of the district government Braunschweig, Lower Saxony, Germany.

3. Results

All injection sites were located in a small region lying between the inferior ramus of the arcuate sulcus and the subcentral dimple just above the Sylvian fissure. Cyto-architectonically, the region corresponds to area 6VR and

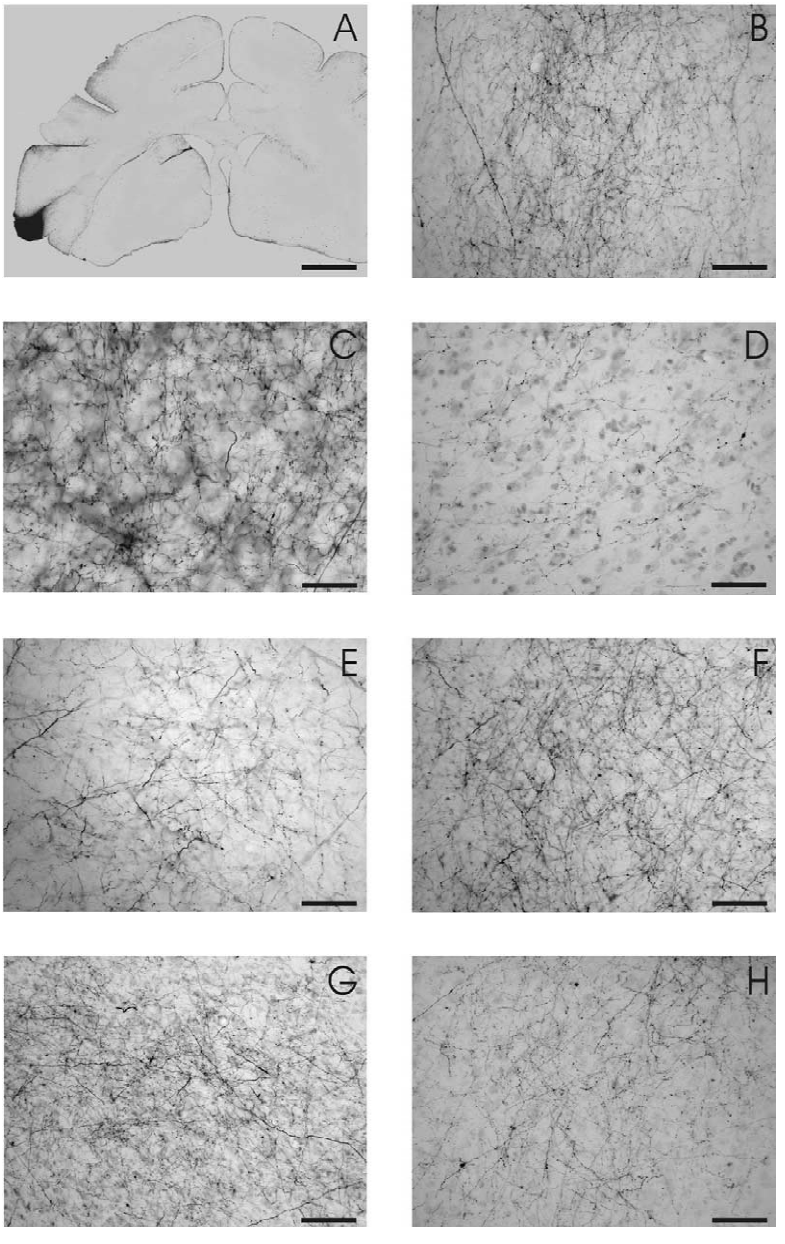

Fig. 1. Photographs of the injection site (A) and terminal labeling in the promotor area (B), area 6VC (C), area 24c (D), parieto-opercular cortex (E), fronto-opercular cortex (F), area 3a (G) and area 44 (H). All photographs are from animal 2. Scale bars: (A)= 7 mm; (B, G, H)=100 μm; (C–F)=50 μm.

ProM, according to Paxinos et al. [44]. The injection site of animal 1 had a diameter of about 2 mm. In animals 2 and 3, the two injection sites merged into each other and formed an injection area of about 2 by 3 mm. The injection areas were characterized by an even distribution of dense, granular reaction product and numerous intensely labeled neurons with their somata and dendrites completely filled.

Altogether, 88 cytoarchitectonically distinguishable projection areas were found, 34 of which were shared by all three animals. These areas are listed in Table 1 and depicted in Fig. 2 (except those buried in the depth of the sulci).

In all three animals, there was a projection from the injection site into large parts of the surrounding premotor and motor cortex, including areas 6VR, 6VC, 6DR, 6DC, ProM and 4. More rostrally, terminal fields were found in areas 44, 45A, 46V, 47 and 8, with the area 47 field extending on the lateral orbital cortex. In the dorsomedial cortex, extensive projections could be traced to the supplementary motor area proper (area 6M) and the cortex within the anterior cingulate sulcus (area 24c), but not the pre-supplementary motor area. Within the Sylvian fissure, labeling was found in the fronto- and parieto-opercular cortex, including gustatory and secondary somatosensory cortex, as well as in the insular proisocortex, agranular, dysgranular and granular insula. Parietal projections could be traced into the lower primary somatosensory areas 3a, 3b, 1 and 2, and, to a smaller extent, into the inferoparietal cortex (area 7; PFG, PG) and the cortex within the intraparietal sulcus (area 5; PEa). Finally, a very weak projection into the cortex within the posterior sulcus temporalis superior, more specifically, into its upper lip

Table 1
Brain structures with input from the cortical larynx area

Brain structures	Animal 1		Animal 2		Animal 3	
	Ipsi	Contra	Ipsi	Contra	Ipsi	Contra
Cortex within superior arcuate sulcus (area 8B)	+	+	+	+/−	++	+
Lower bank of principal sulcus (area 46V)	+/−	+/−	+++	+++	++	−
Ventrolateral prefrontal cortex (area 47L)	+	+/−	+++	++	+++	+++
Lateral orbital cortex (area 47O)	+	−	+++	++	+++	+++
Upper periarcuate cortex (area 8A)	+++	+	+++	+++	+++	+++
Lower postarcuate cortex (area 44)	+++	++	+++	+++	+++	+++
Lower prearcuate cortex (area 45A)	+	−	+	−	++	+
Promotor area (ProM)	+++	++	+++	+++	+++	+++
Rostral ventrolateral premotor cortex (area 6VR)	+++	+	+++	+++	+++	+++
Caudal ventrolateral premotor cortex (area 6VC)	++	+	+++	++	+++	+++
Rostral dorsolateral premotor cortex (area 6DR)	+	+	+++	+	++	++
Caudal dorsolateral premotor cortex (6DC)	++	+	+++	+++	+++	++
Supplementary motor area (area 6M)	++	+	+++	++	+++	++
Anterior cingulate cortex (area 24a)	+/−	−	+/−	−	++	+
Anterior cingulate cortex (area 24b)	+	−	+	+	++	+
Anterior cingulate cortex (area 24c)	++	+	+++	+++	+++	++
Anterior cingulate cortex (area 24d)	+	−	+	+	++	+
Posterior cingulate cortex (area 23c)	+	+	+	−	++	−
Primary motor cortex (area 4)	++	+	+++	+++	+++	++
Primary somatosensory cortex (area 3a)	+	+	+++	+++	+++	+++
Primary somatosensory cortex (area 3b)	+	+	+++	+++	+++	++
Primary somatosensory cortex (area 1)	+	−	++	+	++	+
Primary somatosensory cortex (area 2)	+	+	++	+	+++	++
Anterior secondary somatosensory cortex (PV)	+++	+	+++	+++	+++	+++
Posterior secondary somatosensory cortex (S II)	++	+	+++	++	+++	++
Frontoopercular cortex (gustatory cortex; G)	+	+	+++	+++	+++	+++
Insular proisocortex (IPro)	+	+/−	+++	++	++	++
Agranular insula (AI)	+	+/−	+++	+++	+++	++
Dysgranular insula (DI)	+	+	+++	+++	+++	++
Granular insula (GI)	+++	+	+++	++	+++	++
Cortex within intraparietal sulcus (area 5; PEa)	+	−	++	−	+	−
Anterior inferoparietal cortex (area 7; PFG)	+	−	++	−	+	−
Posterior inferoparietal cortex (area7; PG)	++	−	++	+	++	−
Anterior parietoopercular cortex (PFOp)	+	−	+	−	+++	−
Posterior parietoopercular cortex (PGOp)	+	−	++	−	++	−
Cortex within superior temporal sulcus (STS)	+	−	+	+/−	+/−	−

+++, heavy projection; ++, medium projection; +, weak projection; +/−, questionable projection; −, no projection. The distinction was made on the basis of simple visual inspection and therefore gives only a relative, not an absolute, measure of terminal distribution.

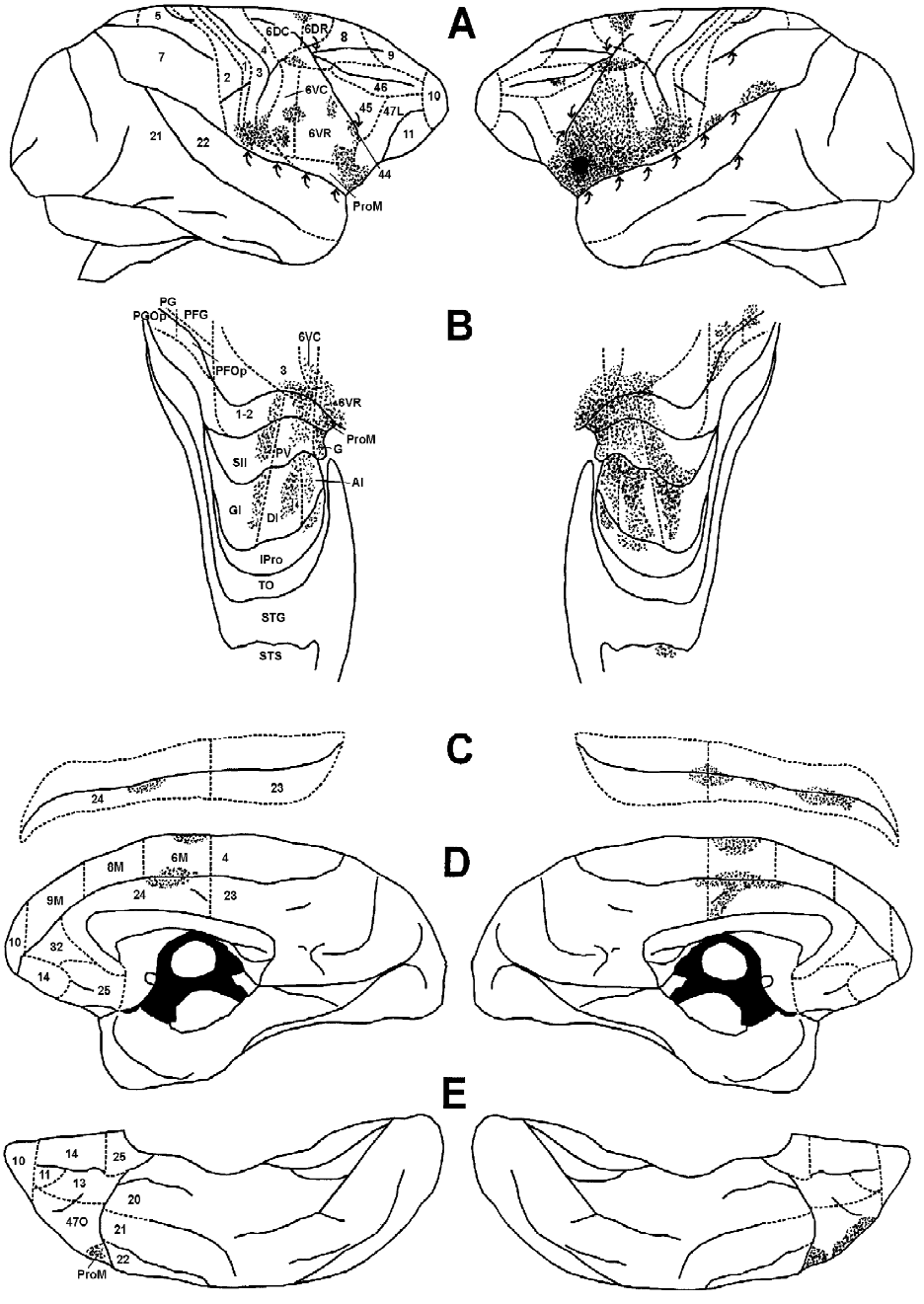

Fig. 2. Lateral (A), medial (D) and ventral view (E) of the rhesus monkey brain with projection areas common to all three experimental subjects. Drawings (B) and (C) represent unfolded views of the cortex buried within the Sylvian fissure and cingulate sulcus. The injection site is indicated by the solid black area in the lateral view. RI, retroinsular cortex; STG, superior temporal gyrus (lateral convexity); TO, temporo-opercular cortex; TP, temporopolar cortex. Further abbreviations, see Table 1.

(TPO), was found. The vast majority of the structures received a bilateral projection, with the ipsilateral projection always dominating the contralateral one. Only a few regions in the posterior parietal cortex received an exclusively ipsilateral projection in all three animals. Crossing took place in the corpus callosum, with the most rostral fibers crossing at about the level of the injection site and the most caudal fibers crossing at mid-diencephalic level.

4. Discussion

The present study shows that the cortical larynx area, as determined by electrical stimulation, maintains a very extensive projection system, with between 52 and 74 distinguishable cortical terminal fields in single animals. As the spread of the tracer at the injection site (radius ca. 1 mm) was somewhat larger than the activated area during

electrical stimulation (radius ca. 0.7 mm), and the center of the stimulation/injection site might have been not always identical with the center of the cortical 'larynx representation', the projection systems found in single animals, most probably, do not represent 'pure' larynx area projections, but include fibers from neighboring areas. In order to minimize this error, we have accepted only those projections common to all three animals. Nevertheless, still 36 projection areas remain.

A comparison of the present study with the only other study in which the projections of a functionally identified cortical larynx area were investigated [21], reveals slight differences. While the study of Jürgens [21] in the squirrel monkey with ^{3}H-leucine as anterograde tracer only reports projections that were also found in the present study, the latter describes a number of projections not reported in the squirrel monkey study. This discrepancy could be due to species or methodological differences. If the results of the present study are compared with those of Künzle [27], however, who investigated the projections of the 'cortical face area' in *Macaca fascicularis*, using a cocktail of tritiated leucine, proline and arginine, there is a similar discrepancy in the number of projections as between the present study and the squirrel monkey study. This suggests that the higher number of projections found in the present study is due to the higher sensitivity of the biotin dextranamine tracer in relation to ^{3}H-leucine. This suggestion is supported by the fact that only terminal fields that were heavily labeled in the present study, were also found in the squirrel monkey study, while none of the weakly labeled fields appeared in that study.

The projections of the cortical larynx area differ in several respects from the 'classical' motor cortex projections. There is general agreement that the primate motor cortex projects into the rostrally adjacent premotor cortex and caudally adjacent primary somatosensory cortex, into the supplementary motor area, secondary somatosensory cortex and inferoparietal cortex [27,29,41,58]. Projections, as described in the present study, to the lateral prefrontal cortex, orbital cortex, insula, anterior cingulate gyrus and to the temporal cortex have not been considered as typical motor cortex projections. The reason for these special connections lies in the special position of the larynx area within the motor cortex. While all the other motorcortical body representations are lined up along the central sulcus, the larynx representation lies far more rostrally. According to Hast et al. [16], the laryngeal muscle representation in the rhesus monkey occupies the whole area between the subcentral dimple caudally and the inferior branch of the arcuate sulcus rostrally, a region normally considered to be premotor rather than motor. Laterally as well, the larynx area takes an extreme position. Together with the caudally adjacent tongue representation, the larynx area occupies the lateral-most position of the motor cortex. Anatomical studies on the projections of the ventral premotor cortex make clear that the 'atypical' motorcortical larynx area projections are in fact typical ventral premotor cortex projections [28,37,42]. More specifically, the lateral prefrontal and anterior cingulate projections mainly derive from frontal areas rostral to area 4; the insular projections derive from areas near the Sylvian fissure; projections to the orbital and superior temporal cortex originate from areas combining a pre-motor with a peri-Sylvian position.

In the squirrel monkey, a retrograde tracing study has been carried out in which the input into the electrophysiologically identified larynx area was analyzed [22]. In this study, all structures having shown to receive anterograde projections from the larynx area in the present study, also showed retrograde labeling in the squirrel monkey. This means that virtually all the cortico-cortical projections of the larynx area are reciprocal. In the present study, a few cells retrogradely labeled by BDA were found. BDA is known as a very unreliable retrograde tracer [5]. Accordingly, the cells found in the present study do not give a representative picture of the afferent input of the cortical larynx area.

A number of structures receiving direct input from the cortical larynx area have been shown in recent PET (positron emission tomography) and fMRI (functional magnetic resonance imaging) studies to be activated during phonation. The main activation focus in these studies is the inferior precentral, premotor and postcentral cortex [4,17,19,32,50,52]. The activation in the inferior precentral and premotor cortex is in harmony with electrical stimulation studies [18,31,39,46,51]. According to these studies, the inferior precentral and premotor cortical areas contain the facial and intraoral muscle representation, respectively, of the primary motor cortex. The inferior postcentral cortex contains the somatosensory face representation [8,26,46]. Similar to the motor cortex, in the somatosensory cortex as well, intraoral structures are represented in the upper bank of the Sylvian fissure, while the external face is represented some distance away from the Sylvian fissure. Single-unit recordings in the rhesus monkey have shown that areas 3a and 2 receive mainly proprioceptive information from deep tissue, area 3b from superficial receptors and area 1 from both deep and superficial receptors [8]. In the present study, no difference was seen in the projections to areas 3a and 3b. Area 1, however, received a clearly smaller projection than area 3. Area 2 took an intermediate position. Lesions in the inferior postcentral gyrus in humans have been reported to cause speech disturbances ('afferent motor aphasia' according to Luria [34]). Electrical stimulation produces dysarthria and dysphonia [40]. Obviously, the interconnections between motor and sensory face area serve to integrate proprioceptive and tactile feedback from the oro-pharyngo-laryngeal region with vocal pattern generation.

The inferior postcentral areas 3a, 3b, 1 and 2 are not the only cortical areas with a somatosensory face representation. According to Krubitzer et al. [26], there are another two in the parieto-opercular cortex. One corresponds to the

classical secondary somatosensory cortex, SII, the other lies just rostral to SII and is called PV. PV and SII border the primary somatosensory areas 3, 1 and 2 on the upper lip of the Sylvian fissure. In the present study, projections were found from the cortical larynx into two regions of the parieto-opercular cortex, corresponding in their position to areas PV and SII of Krubitzer et al. [26].

Immediately posterior to the primary somatosensory face area, there is another sensory face representation, called 'associative face area' by Leinonen and Nyman [30], which receives a direct input from the motorcortical larynx area. Cytoarchitectonically, this region corresponds to area 7 of Brodmann [6]. Single-unit recordings in macaques have revealed that the neurons in this area are not only activated by tactile stimuli in the mouth region, but also by visual stimuli approaching the mouth, hand movements towards the mouth, reaching for an object with the lips and chewing movements [30,55]. PET studies demonstrated an increased activity in this region during speaking, singing and whispering [43,49,50]. Electrical stimulation of the region during speaking causes speech arrest [47], and lesions result in paraphasias in the form of phonemic substitutions and neologisms [7]. These findings make clear that the inferoparietal cortex represents a higher order sensorimotor coordination center which, among others, is involved in speech processing.

The inferofrontal areas 44 and 45 represent another higher order speech control region receiving direct input from the cortical larynx area. Its destruction is known since Broca (1861) to affect speech production. Electrical stimulation of this region during speaking produces speech disturbances [45]. PET and fMRI studies have demonstrated that areas 44/45 (Broca area) are activated during naming objects, reading aloud and repetition of acoustically presented words, but they are not active during repetitive pronunciation of single syllables [19,32,50]. This makes clear that Broca area is not involved in the basic motor control of phonatory and articulatory muscles, but serves speech control at a higher level. Monkeys do not have speech; but there is evidence that their homolog of Broca area also is involved in the control of higher level oral behavior. Single-unit recording studies in macaques have shown that there are neurons in area 44 which are activated during grasping an object with the lips as well as during observing another animal grasping an object with the lips [53]. Obviously, these neurons do not code muscle activities, but purposeful actions.

Massive projections have also been found from the cortical larynx area to the supplementary motor area and the cortex within the anterior cingulate sulcus. Despite the fact that electrical brain stimulation experiments suggest a somatotopic organization of these areas [33], the projections were not limited to a small part of these areas, but extended over a large anteroposterior distance. The supplementary motor area has been shown in PET studies to be regularly activated during speaking, singing and whispering [4,43,49]. Its electrical stimulation produces vocalization in humans [48]. In the monkey, in contrast, vocalization can be elicited only from the anterior cingulate gyrus, including the cortex within the anterior cingulate sulcus, but not from the supplementary motor area [25,54]. This difference has been interpreted as due to the fact that monkey calls are almost completely genetically determined in their acoustic structure and serve to signal specific emotional states of the animals, while the majority of vocal utterances in humans represent learned motor patterns, the production of which is largely independent of specific emotional states [23]. Lesions in the anterior cingulate cortex affect the voluntary control of emotional intonation in humans [24] as well as the voluntary control of vocalization initiation in monkeys [1,60].

Another prominent projection target of the cortical larynx area is the insula. Again terminal fields extend over a large anteroposterior distance, reaching from the agranular via the dysgranular to the granular insula. The insula, similar to the supplementary motor area and sensorimotor cortex, is regularly activated in PET studies during speaking, singing and whispering [4,43,49]. In the monkey, neurons have been found that are specifically activated by tactile stimuli in the mouth region [57]. In humans, insular lesions result in speech apraxia [9]. According to Habib et al. [13], the insula plays a mediating role between auditory input, speech output and communicative motivation. This suggestion is supported by the anatomical finding that the insula is directly connected with the facial sensorimotor cortex, Broca area, primary and secondary auditory cortex as well as several limbic structures, such as the anterior cingulate gyrus, orbital cortex and amygdala.

A weak labeling was also found in the upper lip of the superior temporal sulcus. This region represents auditory association cortex ('parabelt' region, according to Hackett et al. [14]). Activation in auditory association cortex has also been observed by Paus et al. [43] in a PET study in human subjects whispering words under noise-masking conditions. The authors interpreted the finding that there was an activation in the auditory association cortex despite the fact that the subjects could not hear themselves, by assuming that the activation represents corollary discharges of the facial motor cortex to the auditory association cortex, informing the latter about ongoing motor activities leading to phonation, that is, auditory feedback.

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