Research report

Somatotopy of the extrinsic laryngeal muscles in the human sensorimotor cortex

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HIGHLIGHTS

- We report the first somatotopic study of the extrinsic laryngeal muscles in humans.
- Vertical movement of the larynx activates ventral peri-central sensorimotor cortex.
- Upward and downward movement of the larynx activates overlapping cortical areas.
- The somatotopy of the extrinsic and intrinsic laryngeal muscles partially overlaps.

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ABSTRACT

The larynx is the major organ of vocalization. The intrinsic laryngeal muscles modify the internal shape of the larynx while the extrinsic laryngeal muscles move the entire larynx vertically in the airway. Previous neuroimaging research has established the somatotopic location of the intrinsic musculature of the larynx in the human motor cortex and showed it to be in an evolutionarily novel location compared to the homologous region in monkey cortex. In the current study, we attempted for the first time to determine the somatotopic localization of the extrinsic laryngeal musculature in humans. In a functional magnetic resonance imaging experiment, we had participants voluntarily move their larynx upward and/or downward in the airway in the absence of vocalization to engage the extrinsic laryngeal muscles or vocalize in the absence of vertical laryngeal movement to engage the intrinsic laryngeal muscles. Vertical movement of the larynx activated ventral pericentral sensorimotor cortex extending dorsally to overlap with the representation of the intrinsic laryngeal muscles. This pattern is a reversal from the somatotopy of the monkey, where the extrinsic laryngeal muscles are represented dorsally to the intrinsic laryngeal muscles.

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1. Introduction

The larynx is the organ of phonation. It houses the vocal folds, whose vibration is the principal sound-source for vocalization. Two different sets of muscles control laryngeal functioning: the intrinsic and extrinsic laryngeal muscles. The intrinsic muscles modify the positioning and tension of the vocal folds internal to the larynx, whereas the extrinsic muscles modify the vertical position of the entire larynx within the neck and connect the larynx to structures above or below it in the airway [1].

The intrinsic muscles of the larynx control two dimensions of vocal-fold movement within the larynx. First, the vocal folds can be adducted (brought together) or abducted (brought apart). In the adducted position, air passing between the vocal folds causes them to vibrate, producing the sound-source for vocal pitch. The second function of the intrinsic laryngeal muscles is to modulate vocal pitch. The tension of the vocal folds is modulated by the cricothyroid muscle [2], which influences the frequency of vibration of the fold folds. Contraction of this muscle lengthens and tenses the vocal folds, which increases vocal pitch [3]. The thyroarytenoid muscle lies within the vocal folds themselves and has a role in modulating vocal fold tension, although its relation to pitch is complex. This muscle can either lower or raise vocal pitch depending on interactions with the cricothyroid [4,5].

In contrast to the intrinsic muscles, the extrinsic laryngeal muscles control the vertical position of the larynx within the airway. Two sets of muscles pull the larynx in opposing directions along the vertical axis. Laryngeal elevators raise the larynx during swallowing and vomiting so as to protect the airway [6]. These muscles extend from the larynx to more-superior structures [1],

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including the mandible (mylohyoid, geniohyoid and anterior digastricus muscles), pharynx (thyropharyngeus muscle), tongue (hyoglossus and genioglossus muscles), and temporal bone (stylohyoid and posterior digastricus muscles). Laryngeal depressors, also known as the strap muscles, lower the larynx during yawning [7]. These muscles extend from the larynx to more-inferior structures [1], including the sternum (sternohyoid and sternothyroid muscles) and scapula (omohyoid muscle). Both sets of muscles have an influence on vocal pitch by altering the relative positions of the various laryngeal cartilages, which indirectly influences the tension of the vocal folds [8]. Indeed, vertical movement of the larynx is readily observed during pitch modulation. Untrained singers generally lower the larynx when they vocalize a low pitch [9] and raise the larynx while vocalizing a high pitch [10]. However, trained singers can maintain a relatively constant vertical position of the larynx across their vocal range [11].

The neural control of the larynx – and hence vocalization – was poorly understood until recently. We and others characterized a cortical larynx area in the precentral gyrus of the frontal lobe for the control of the intrinsic musculature of the larynx [12]. We had participants perform a series of vocal and non-vocal oral tasks, including singing, lip movement, tongue movement, and vocal fold adduction in the absence of vocalization (i.e., glottal stops). We showed that a region of the motor strip adjacent to the lip area controlled the intrinsic laryngeal muscles during both vocalization and vocal fold adduction. Other labs have confirmed that this region is distinct from adjacent somatotopic locations of the articulatory muscles [13]. The larynx area is more active during dynamic than monotonous vocalizations [14] and is activated by forced expiration [15]. While this region does contain the motor representation of the intrinsic laryngeal muscles it appears also to integrate several motor components of phonation including respiration, vocal fold abduction and pitch modulation. Hence, we refer to this region as the “larynx–phonation area” [12]. Indeed, the premotor portion of the larynx–phonation area participates in pitch perception [16] analogous to the motor representations of the articulators [17].

The larynx–phonation area includes two areas of activation in the precentral gyrus: a ventrolateral peak in primary motor cortex proper (Brodmann area 4) and a dorsolateral peak in premotor cortex (Brodmann area 6). The location of the larynx area within the precentral gyrus appears to be evolutionarily novel, since the cortical larynx-controlling region in monkeys is located in the ventral premotor cortex in a position considerably ventral to the larynx–phonation area in humans [18]. Electrical stimulation of this region in monkeys stimulates contraction of laryngeal muscles [18] but does not elicit vocalization [19]. In contrast, early somatotopic studies in humans revealed that vocalizations are readily elicited by electrical stimulation of motor cortex [20]. Furthermore, while bilateral lesions to this region have little effect on spontaneous [21] or conditioned [22] vocalizations in monkeys, even unilateral lesions in humans can cause severe aphony [23]. We previously proposed that the evolutionary reorganization of larynx motor cortex from a non-vocal area in monkeys to the vocal area that it is in humans may have been accompanied by a migration of the larynx-controlling region from its ventral location in monkeys to its more dorsal position in humans [12].

Much less is known about the cortical control of the extrinsic laryngeal muscles. To our knowledge, only one study has examined the cortical control of the extrinsic laryngeal muscles in any species. Hast et al. [18] observed that in monkeys the thyrohyoid muscle, which is a laryngeal elevator, and the sternohyoid muscle, which is a laryngeal depressor, are represented together in a cortical region dorsal to the intrinsic laryngeal representation. In humans, several brain imaging studies have examined the neural correlates of swallowing which includes a laryngeal component [24,25]. However, swallowing requires a complex sequence of oral and pharyngeal movements in addition to engaging the extrinsic laryngeal musculature. No study has examined the cortical control of these muscles in humans separately from the oral and pharyngeal muscles.

The major objective of the present study was to localize the cortical motor system controlling the extrinsic musculature of the larynx, especially vis-à-vis the recently characterized localization of the intrinsic laryngeal musculature in the primary motor and premotor cortex. We used functional magnetic resonance imaging (fMRI) to scan the brains of choir-trained singers as they voluntarily moved their larynx up and/or down in their neck in the absence of vocalizing. We compared these results to a vocalization task in which participants had to vocalize individual pitches at different points in their register in the absence of vertical movement. This is the first neuroimaging study to examine the somatotopic localization of the extrinsic laryngeal muscles. We predicted, based on the experiments of Hast et al. [18] in monkeys, that the region controlling the extrinsic musculature would be distinct from that controlling the intrinsic musculature of the larynx that we characterized in our previous study. In particular, we predicted in our earlier publication [12] that the extrinsic muscles would be localized in the Rolandic operculum, close to where the cortical larynx area is located in the monkey.

2. Experimental procedure

2.1. Participants

Twelve participants (seven males, five females), with a mean age of 27.0 years (ranging from 16 to 48 years), participated in the study after giving their informed consent (Medical Research Ethics Board, St. Josephs Hospital). Each individual was without neurological or psychiatric illness. Participants were all fluent English speakers but were unselected with regard to either native language or handedness. One participant was left-handed. All participants were chorally trained singers with 4–18 years of choral experience (mean = 9.5, SD = 4.7) and were able to minimize laryngeal movement during vocalization.

2.2. Tasks

Participants performed two oral tasks, each one according to a simple blocked design that alternated between a resting condition and an oral task. All tasks were performed with the eyes open. Participants performed all tasks with the mouth closed such that respiration was nasal. Participants underwent a 30-min training session on a day prior to the scanning session in order to learn how to perform these tasks in a highly controlled manner with a minimum of effort and head movement. They were trained to move their larynx up and/or down in their neck on command with no visible movement of the tongue or jaw. Successful training was confirmed by visual assessment of vertical movement of the thyroid notch. All participants succeeded in producing controlled movements in at least one direction (i.e., up or down).

During a single scan, participants performed extrinsic laryngeal movements. They were instructed to move their larynx down and/or up at a relaxed rate, typically 0.5 Hz. After each epoch of movement, participants allowed their larynx to passively return to its habitual position. Participants who could move their larynx in both directions (five of the 12 participants) performed downward movements during the first half of the scan and upward movements during the second half. The seven participants who could only move the larynx in one direction (five upward, two downward) performed movements in that one direction throughout the scan. During debriefing, all subjects reported that they were able to perform the task in the scanner, with no movement of the
jaw or tongue. No participant reported subvocalizing during this task.

As part of a separate study conducted in the same session, participants performed four scans of simple phonation (vocalization). They were instructed to softly hum individual pitches during the first half of a roughly 6 s natural breath phrase. They did this repeatedly during a 20-s task period. Hence, the mouth was to be kept closed, and respiration was done through the nose, similar to the laryngeal movement task. In each phonation block, an auditory cue indicated which of four possible pitches the participant should hum. The four pitches increased at an interval of a perfect fifth (seven semitones) from one another, spanning roughly two octaves. All pitches were within the participant’s vocal range and were calibrated to the lowest pitch comfortably produced by the subject, as determined by descending vocal sweeps. For the purposes of the present study, the brain activity for phonation was collapsed across the four pitch levels and the four scans.

2.3. Magnetic resonance imaging

Magnetic resonance images were acquired with a General Electric Achieva 3-Tesla MRI at the Imaging Research Centre at St. Joseph’s Hospital in Hamilton, Ontario. The participant’s head was firmly secured using foam pillows. Earplugs were used to help block out scanner noise. Participants alternated between task and rest according to a simple block design. During each task epoch, the name of the task positioned above a cross hair was projected from an LCD projector onto a screen mounted at the head of the MRI table, with an angled mirror on the head coil reflecting text from the screen into the participant’s field of view. During the rest periods, the word “Rest”, positioned above a cross hair, was projected onto the screen. Participants were instructed to keep their eyes on the cross hair at all times. All stimuli were presented using Presentation® software (version 14.4, www.neurobs.com).

Functional images sensitive to the “blood oxygen level dependent” (BOLD) signal were collected with a gradient echo sequence. Extrinsic larynx and phonation experiments used separate imaging parameters. For the extrinsic larynx task, the imaging parameters were 2000 ms TR, 35 ms TE, 9° flip angle, 31 slices, 4 mm slice thickness, 0 mm gap, 3.75 mm × 3.75 mm in plane resolution, 64 × 64 matrix, 240 mm field of view effectively covering the whole brain (124 mm of axial extent). A total of 196 brain volumes were acquired. Four volumes were discarded leaving 192 volumes over 6′24″ of scan time, corresponding with 12 alternations between 16 s epochs of rest and 16 s epochs of task.

Functional images for the phonation task were collected on the same participants as part of a separate study. Smaller voxels and longer scanning times were used in order to achieve a higher spatial resolution in the specific area involved in phonation. For that study, the imaging parameters were 2500 ms TR, 35 ms TE, 9° flip angle, 30 slices, 3 mm slice thickness, 0 mm gap, 2.25 mm × 2.25 mm in plane resolution, 64 × 64 matrix, and 192 mm field of view. A total of 260 volumes were acquired. Four volumes were discarded leaving 256 volumes over 10′40″ of scan time, corresponding with 16 alternations between 20 s epochs of rest and 20 s epochs of task.

2.4. Image analysis

Functional images were reconstructed offline, and the scan series was realigned and motion-corrected using BrainVoyager QX 2.4. Motion-correction analysis revealed that participants displayed very little head movement. Translational and rotational corrections did not exceed an acceptable level of 1.5 mm and 1.5°, respectively, for any participant. During the preprocessing stage, a temporal high-pass filter was applied at a cut off frequency of 0.0078 Hz, or 1/128 cycles. Three-dimensional spatial smoothing was performed using a Gaussian filter with a FWHM kernel size of 4 mm. Following realignment, each functional scan was normalized to the Talairach template [26]. The BOLD response for each task-block was modeled as the convolution of a 16 s (extrinsic larynx) or 20 s (vocalization) boxcar with a synthetic hemodynamic response function composed of two gamma functions. In a first-level fixed-effects analysis, beta weights associated with the modeled hemodynamic responses were computed to fit the observed BOLD-signal time course in each voxel for each participant using the General Linear Model, as implemented in BrainVoyager QX 2.4. Six head-motion parameters describing translation and rotation of the head were included as nuisance regressors. In a second-level analysis, contrast images for each task versus rest were brought forward into a random effects analysis. The resulting statistical parametric maps were interpolated to 1 mm isotropic voxels to facilitate comparison between conditions. A Monte Carlo simulation (AlphaSim) determined that an uncorrected p-threshold of p < 0.01 combined with a cluster threshold of k > 38 maintained a familywise error rate of p < 0.05. All figures and tables apply this threshold. Talairach coordinates were extracted using NeuroElf (neuroelf.net).

3. Results

Vertical movement of the larynx activated motor and somatosensory regions in ventral pericentral cortex, including right primary motor cortex (BA 4) extending dorsally into the larynx–phonation area, left premotor cortex (BA 6), and bilateral postcentral gyrus (BA 40) directly posterior to the orofacial motor cortex (Fig. 1 and Table 1). Further activations were observed throughout the motor system, including bilateral putamen and cerebellum as well as the right supplementary motor area (SMA; BA 6). Activation was also observed in the left insula (BA 13) and bilateral inferior parietal lobule (BA 40).

Surprisingly, only the dorsolateral larynx–phonation peak in premotor cortex was observed during phonation and only in the right hemisphere. While activation of both the ventromedial and dorsolateral larynx–phonation area were observed in both hemispheres for individual participants (not shown), these activations were weak and spatially variable. The limited activation observed during vocalization may have resulted from participants’ instructions to vocalize softly so as to minimize vocal effort and from the conservative thresholds required by the relatively strong signal observed during vertical movement of the larynx. Notably, the activation pattern for vertical movement of the larynx extended into the right dorsolateral larynx–phonation area as well as in the expected location of the homologous region in the left hemisphere.

Separate analyses for downward and upward larynx movement revealed remarkably overlapping patterns of activation in pericentral motor and somatosensory regions (Fig. 2 and Table 2). Both downward and upward movements activated the dorsolateral larynx–phonation area in the right hemisphere, bilateral ventral somatosensory cortex (BA’s 40/31/2), right SMA (BA 6), left putamen, and left cerebellum. Although activations for movement in the two directions overlapped substantially, the activations for downward movement spanned a considerably greater spatial extent. Further activations for downward movement included the right putamen, caudate nucleus and cerebellum, anterior superior temporal gyrus, parahippocampal gyrus, superior parietal lobule, inferior parietal lobule, and inferior frontal gyrus as well as left insula, thalamus, and anterior cingulate gyrus. However, a direct contrast between downward and upward movement yielded no significant differences in any region that was reported in the lower-level contrasts.
4. Discussion

The purpose of this study was to provide the first description of the somatotopy of the extrinsic laryngeal muscles in the human motor cortex. We had participants voluntarily move their larynx upward and/or downward in the airway in the absence of vocalization to engage the extrinsic laryngeal muscles, or vocalize in the absence of vertical laryngeal movement to engage the intrinsic laryngeal muscles. This experiment yielded three primary findings. First, vertical movement via the extrinsic laryngeal muscles engaged a large patch of the orofacial part of the sensorimotor cortex, which was not activated during vocalization. Second, upward and downward movement of the larynx engaged highly overlapping regions of sensorimotor cortex, despite engaging a non-overlapping set of effectors. Third, vertical movement of the larynx also engaged the dorsolateral larynx-phonation area in
Fig. 2. Brain activations for upward and downward larynx movement. Brain activations for vertical larynx movement are presented on an inflated brain. Both the right hemisphere (RH) and left hemisphere (LH) are shown. Gyri are lightly colored whereas sulci are darkly colored. The three horizontal panels show, respectively, upward movement, downward movement, and their overlap using color coding. Upward and downward movement of the larynx activate overlapping regions of primary motor and somatosensory cortex. Movement in either direction also activates the larynx-phonation area. Abbreviations: see legend to Fig. 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
premotor cortex but not the ventromedial larynx–phonation area in primary motor cortex (expected coordinates approximately ±40, −10, 32; [12]).

4.1. Oropharyngeal sensorimotor cortex

The major finding was that vertical movement of the larynx activated the ventral portion of pericentral sensorimotor cortex that controls the tongue and pharyngeal muscles [20]. Contrary to our predictions [12], this area of activation did not include the Rolandic operculum but instead regions posterior to it in the ventral pericentral gyrus. In contrast, vocal activation in the absence of vertical laryngeal movements did not occur beyond the usual extent of the larynx–phonation area. Participants were instructed to vocalize while maintaining a neutral vertical position of the larynx; this can be achieved either by failing to engage the extrinsic laryngeal muscles or by simultaneously engaging both the laryngeal elevators and depressors to create equal force in both directions. The unusually weak activation of the larynx–phonation area that was limited to its usual extent suggests that participants used the former strategy.

Notably, while our tasks were purely motoric, extensive activation was observed in the somatosensory cortex. We also observed activation in a region of the cerebellum that has been hypothesized to coordinate motor and somatosensory processes for the muscles of speech and vocalization [27]. Somatosensory feedback features strongly in computational models of speech production (e.g., [28]). Previous research has shown that vocal experience correlates with increased activation of somatosensory cortex posterior to the larynx–phonation area [29]. Electrophysiological studies similarly demonstrate that with training neural firing increases in both orofacial primary motor and somatosensory cortex [30].

Anesthetizing the vocal folds both perturbs pitch production and reduces sensorimotor activation [31], although trained singers may be able to reduce their reliance on somatosensory feedback when it becomes unreliable [32]. However, a similar pattern of sensorimotor activation is seen in studies of swallowing, a task which also raises the larynx [24,25]. These studies also observe strong somatosensory activations among participants unsolicited for musicality, suggesting that extensive somatosensory activity during vertical larynx movement may not be dependent on vocal experience.

The common activation between vertical larynx movement and swallowing may stem from two sources. First, the larynx is raised during swallowing [6] so that our larynx-movement task may engage a subset of the muscles engaged during swallowing. Second, many of the muscles involved in raising the larynx serve dual functions in that they can move the larynx if the tongue, pharynx and jaw are fixed in place or move the tongue, pharynx or jaw if the vertical position of the larynx is fixed. Ventral oropharyngeal sensorimotor cortex may contain the upper motor neurons for muscles that can either move the larynx or the articulators depending on the physiological context.

4.2. Laryngeal elevators and depressors

The laryngeal elevators and depressors activated highly overlapping portions of sensorimotor cortex, and direct contrasts between these two tasks revealed no significant differences. The current study presents the first report of the somatotopic location of the laryngeal depressors. Unlike the laryngeal elevators, the depressors are anchored to fixed structures below the larynx (e.g., the sternum) and the effect of contracting these muscles is therefore unlikely to

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vary with physiological context. The results of the present study suggest that these uniquely laryngeal muscles share a somatotopic location with the oropharyngeal muscles and with the laryngeal elevators.

Surprisingly, activations for downward movement occupied a greater spatial extent than upward movement (see Fig. 2) despite the smaller sample size for downward movement. This is even more surprising if one considers the fact that there are fewer laryngeal depressor muscles than elevators [1]. However, those participants who performed laryngeal movements in both directions always performed downward movement during the first half of the scan and upward movement during the second half. Despite the lack of significant differences between the two tasks, order effects may have influenced the difference in spatial extent that we observed between upward and downward laryngeal movement. The signal from T2* weighted images, such as those employed in fMRI, drifts downward throughout the course of a scan [33]. This may have resulted in less BOLD signal in the latter half of the scan, during which subjects performed upward movements. Alternatively, participants may have made larger movements of the larynx in the downward relative to the upward direction if the extent of upward laryngeal movement was limited by the epiglottis.

In the precentral gyrus of monkeys, the extrinsic laryngeal muscles are represented in the dorsal portion of the ventral precentral gyrus near the representation of the oropharyngeal muscles, the thyroarytenoid (an intrinsic laryngeal muscle that can either tense or relax the vocal folds) is represented slightly more ventrally, and the cricothyroid muscle (an intrinsic laryngeal muscles that tenses of the vocal folds) is represented still more ventrally [18]. Brown et al. [12] observed that the larynx–phonation area occupies a much more dorsal position in the human brain than would be predicted by homology with monkeys. Furthermore, in monkeys, the laryngeal muscles are represented in premotor cortex only, whereas the human larynx–phonation area occupies a region in the primary motor cortex as well. This led Brown et al. [12] to suggest that, over the course of human evolution, the ancestral representation of the intrinsic laryngeal muscles in the premotor cortex may have migrated dorsally and come to occupy a position in the primary motor cortex to form the larynx–phonation area.

A study using transcranial magnetic stimulation (TMS) in humans found that stimulation of two distinct cortical sites elicited motor-evoked potentials in the cricothyroid and thyroarytenoid muscles, respectively [34]. Notably, the cortical site for the cricothyroid was dorsal to that of the thyroarytenoid, which is a reversal from the observations of Hast et al. [18] in monkeys. Combined with the results of Rödel et al. [34], our data suggest a reversal of laryngeal somatotopy in humans compared to monkeys, with the cricothyroid muscle being represented most dorsally followed by the thyroarytenoid muscle, and finally by the extrinsic laryngeal muscles, which are represented most ventrally. However, this observation remains speculative since it is based on a paucity of information spanning diverse methodologies. Indeed, it is surprising that Rödel et al. [34] were able to distinguish the cortical representations of the cricothyroid and thyroarytenoid muscles in humans with the low spatial resolution of TMS, not least in light of the apparent proximity and partial overlap of these representations in monkeys [18].

4.3. Overlap between extrinsic and intrinsic somatotopy

Contrary to our predictions, vertical movement of the larynx produced activations that extended dorsally into the larynx–phonation area [12]. This finding was unexpected since no phonation occurred in this task. We explore three hypotheses that may explain the observed overlap. First, the force of tracheal pull during vertical movement may engage the intrinsic laryngeal muscles. Second, the intrinsic and extrinsic laryngeal muscles may co-contract during normal physiological functions, such as swallowing. Third, the larynx–phonation area may also contain a representation of the extrinsic laryngeal muscles.

First, vertical movement of the larynx may indirectly cause contraction of some of the intrinsic laryngeal muscles, even in the absence of phonation, since these muscles help to resist the force of tracheal pull. The mass of the trachea pulls the cricoid cartilage downward, and this force increases when the larynx is higher in the airway [35] as cited in [8]. The cricothyroid muscle—an intrinsic laryngeal muscle that primarily controls vocal-fold tension—helps to resist this downward force by pulling upward on the cricoid cartilage [36]. Raising the larynx may therefore automatically engage the cricothyroid muscle, resulting in activation of the larynx–phonation area. However, we observed that downward movement of the larynx also activated the larynx–phonation area but we are unaware of any research linking downward movement with increased tracheal pull.

Second, raising the larynx may trigger adduction of the vocal folds, since these actions co-occur during common actions such as swallowing and vomiting [6,37]. Our participants may therefore have adducted the vocal folds when they volitionally raised their larynx because these actions co-occur in everyday physiological functions. Indeed, adduction of the vocal folds alone is sufficient to activate the larynx–phonation area even in the absence of phonation [12]. However, it is unclear whether the same rationale applies to movement in the opposite direction. Lowering the larynx is associated with yawning rather than swallowing or vomiting. During a yawn, the larynx descends and the vocal folds remain abducted to allow the passage of air [7].

Finally, the larynx–phonation area may be engaged during vertical movement of the larynx because the extrinsic and intrinsic laryngeal muscles are tightly coupled during vocalization. The vertical position of the larynx has a modest influence on vocal pitch [8]. Speakers automatically use vertical movements of the larynx to modulate vocal pitch [9,10], and substantial vocal training is required to suppress this tendency [11]. The larynx–phonation area may therefore participate in coordinating the intrinsic and extrinsic laryngeal muscles.

One anatomical means of attaining such a linkage between motor control of the extrinsic and intrinsic laryngeal muscles is if the larynx–phonation area projected to all motor nuclei that contain lower motor neurons for the laryngeal muscles. This would require diverse projections to many lower motor nuclei and cranial nerves (CN). The laryngeal elevators are innervated by the trigeminal motor nucleus (CN V; anterior digastricus and mylohyoid muscles), facial motor nucleus (CN VII; posterior digastricus and stylohyoid muscles), and hypoglossal nucleus (CN XII; genioglossus, hypoglossus and geniohyoid muscles). The laryngeal depressors are innervated by the cervical spinal cord. Finally, the intrinsic laryngeal muscles are innervated by the nucleus ambiguus [38] through the recurrent and superior laryngeal nerves, which are branches of CN X [1,39].

A simpler alternative is that the larynx–phonation area may directly project to the nucleus ambiguus alone to control the intrinsic laryngeal muscles [40] but may reach other motor nuclei indirectly through intra-cortical connections with more ventral pericentral sensorimotor cortex. Indeed, the larynx–phonation area is both functionally and structurally connected with the ventral pericentral regions that the present study associates with vertical movement of the larynx [41], providing support for the simpler anatomical model. This model seems reasonable given the need to rapidly integrate effectors for respiration, phonation and articulation during speech production.
5. Limitations

This study was a first attempt at determining the somatotopic representation of the extrinsic laryngeal muscles in the human brain. While participants were trained to perform vertical laryngeal movements without engaging the oropharyngeal muscles – and reported doing so successfully during the experiment – task performance was not independently verified. Future research should combine brain-imaging techniques with electromyography to assess task performance and attempt to map individual muscles onto sensorimotor cortex.

6. Conclusion

We attempted for the first time to determine the somatotopic localization of the extrinsic laryngeal musculature in sensorimotor cortex. Vertical movement of the larynx in either direction engaged the ventral portion of the precentral and postcentral gyrus as well as the more dorsally situated larynx–phonation area. This overlap may be due to complex interactions between the intrinsic laryngeal muscles and forces generated by vertical movement of the larynx or by co-activation of the intrinsic and extrinsic laryngeal muscles during either everyday physiological functions or vocalizations. Nonetheless, our results suggest that the somatotopy of the laryngeal muscles follows a reversed pattern in humans compared to the homologous somatotopic locations in the monkey. Our data support the hypothesis that the larynx–phonation area is an evolutionary novelty in humans [12] that may have migrated near the representation of the lips and tongue to facilitate coordination between phonation and articulation during speech production.

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References