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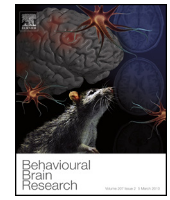

Research report

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 sternohyroid 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 aphonia [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

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