Brain & Language 113 (2010) 39–44

Contents lists available at ScienceDirect

Brain & Language

journal homepage: www.elsevier.com/locate/b&l

Short Communication

# Representation of the speech effectors in the human motor cortex: Somatotopy or overlap?

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ARTICLE INFO

*Article history:*
Accepted 28 January 2010

*Keywords:*
Motor cortex
Somatotopy
Brain
Meta-analysis
Speech
Respiration
Lips
Tongue
Swallowing

ABSTRACT

Somatotopy within the orofacial region of the human motor cortex has been a central concept in interpreting the results of neuroimaging and transcranial magnetic stimulation studies of normal and disordered speech. Yet, somatotopy has been challenged by studies showing overlap among the effectors within the homunculus. In order to address this dichotomy, we performed four voxel-based meta-analyses of 54 functional neuroimaging studies of non-speech tasks involving respiration, lip movement, tongue movement, and swallowing, respectively. While the centers of mass of the clusters supported the classic homuncular view of the motor cortex, there was significant variability in the locations of the activation-coordinates among studies, resulting in an overlapping arrangement. This "somatotopy with overlap" might reflect the intrinsic functional interconnectedness of the oral effectors for speech production.



## 1. Introduction

Somatotopy – the orderly representation of the body along the extent of the sensorimotor cortex (and other neural structures) – is one of the foundational concepts of human neuroscience. The proposal of somatotopic organization has received support from functional neuroimaging studies, showing specific activations of particular locations in the motor cortex associated with movement of specific joints, as well as from electrical stimulation and transcranial magnetic stimulation (TMS) studies, showing that stimulation of discrete locations in the motor cortex or the scalp overlying it can lead to the movement of discrete parts of the body, rather than whole-limb or whole-body movements.

The major challenge to somatotopy is evidence for overlapping representations of effectors along the motor cortex. For example, there is good evidence that there are multiple, distributed representations of the fingers within the hand area, and that they are intermingled with one another (Dechent & Frahm, 2003; Schieber, 2001). However, such "mosaic" representations have been most reliably demonstrated *within* a functional domain (e.g., the fingers within the hand representation) rather than between domains (e.g., hand and face). This overlap might reflect the connectivity of effectors that are functionally co-activated, such as the fingers within the hand area for smooth control of manual movement.

Along the same lines, another important motor behavior requiring strong functional linkages among effectors is speech. The flow of activation of the effectors for speech production is generally conceptualized as respiration, phonation, and articulation, wherein expiratory air flow from the lungs leads to vibration of vocal folds in the larynx to produce the basic sound wave, which is then filtered and amplified by a series of oral articulators, including the pharynx, tongue, soft palate, lips, and jaw. Penfield's cortical stimulation studies from the 1930's and 40's provided support for the existence of somatotopy within the orofacial region (Penfield & Rasmussen, 1950; Penfield & Roberts, 1959), although these studies were not able to disentangle the larynx representation (shown as "vocalization" in the Penfield homunculus) from the other speech effectors: "…although vocalization may occur as an isolated response to stimulation, and consequently might be expected to have a constant sequential position in relation to the lips and tongue, we are forced to conclude that its representation really overlaps that of lips, jaw, and tongue movement" (Penfield & Rasmussen, 1950, p. 91). Recent fMRI work has clarified this arrangement (Brown, Ngan, & Liotti, 2008; Loucks, Poletto, Simonyan, Reynolds, & Ludlow, 2007; see Brown et al., 2009, for a meta-analysis of phonation studies). In addition, Loucks et al. (2007), using functional magnetic resonance imaging (fMRI), found an interesting example of overlap within the orofacial region, namely

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doi:10.1016/j.bandl.2010.01.008

between the representations of the expiratory muscles and the larynx. Respiration is shown in the homunculus as a "trunk" function (Penfield & Rasmussen, 1950; Penfield & Roberts, 1959), therefore quite distant from the orofacial region. Since human vocalization occurs overwhelmingly on expiration, this overlap might therefore reflect the important need to couple expiration and phonation during voluntary vocalization.

In order to examine the existence of somatotopy vs. overlap in the speech motor system, we ran a series of voxel-based meta-analyses using the "activation likelihood estimation" method. These analyses encompassed 54 functional neuroimaging studies of respiration, lip movement, tongue movement, and swallowing (pharyngeal activity). The results are described in terms of functional linkages within the motor system for speech production. Although these effector-specific imaging studies looked at non-speech movements, fMRI work from our lab has shown that non-speech movements of these effectors activate similar if not identical regions of the motor cortex as does their activation through speech tasks (Brown et al., 2009; see also Chang, Kenney, Loucks, Poletto, & Ludlow, 2009).

## 2. Results

While most of the studies used in the meta-analyses reported activations across the whole brain, we focused our analyses on the peaks within the primary motor cortex of the precentral gyrus in order to examine somatotopy there. The Talairach coordinates of the ALE clusters within the primary motor cortex for the four meta-analyses are shown in Table 1 and are plotted graphically on a 3-dimensional rendering of the left hemisphere in Fig. 1A. It is important to note that all four meta-analyses showed motor-cortex foci that were equally bilateral (see Table 1).

In the most fundamental sense, the locations of the centers of mass for the various effectors conformed to the scheme of the Penfield homunculus, with respiration being represented dorsally in the "trunk" area, and the lips, tongue, and pharynx having a systematic dorsal-to-ventral arrangement within the orofacial region of the motor cortex, extending ventrally into the Rolandic operculum at the bottom of the central sulcus. However, two major exceptions were noted. (1) Respiration gave a second peak, this time outside of the trunk area in the orofacial region (Ramsay et al., 1993). As mentioned in the introduction, Loucks et al. (2007) demonstrated an overlap between expiration and phonation in this region, and we confirmed that most of the studies contributing to this peak were of expiration rather than inspiration. Hence, this peak most likely represents the expiratory muscles rather than the diaphragm. (2) Lip movement gave a second peak, this one sitting extremely close to the pharynx peak. This included two foci in the right hemisphere (see Table 1). An analysis of the lip movement tasks across the papers did not permit us to assign different dimensions of lip movement to these two lip foci, such as puckering vs. lip retraction.

Beyond this consideration of centers of mass, there was significant overlap in the fields of the ALE clusters, reflecting between-paper variability in the locations of the ALE foci. Fig. 1B presents a 3-dimensional scatterplot of the contributing motor-cortex foci from all the papers for each effector, thereby showing the spatial spread of the reported maxima in the precentral gyrus for each effector. As can be seen, the fields overlap extensively. This variability in the locations of the activation foci across papers can be considered as an indicator of the degree of overlap of the effectors in the motor cortex.

## 3. Discussion

The combined results of these four meta-analyses support both somatotopy and overlap within the orofacial motor cortex, not unlike findings for the hand area. While the centers of mass of the ALE foci were distributed according to the scheme specified in the Penfield homunculus, there was great variability in the locations of the effectors between studies, thus reflecting overlap among the effectors. In addition, we observed a second lip peak that occurred very close to the pharynx, hence being a second manifestation of overlapping representations.

Penfield and colleagues used electrical brain stimulation during neurosurgery to demonstrate specific activation of the effectors of the body, and thereby establish the homuncular map of the human motor cortex (Penfield & Rasmussen, 1950; Penfield & Roberts, 1959). More recently, TMS of the motor cortex has been used to show similar effector-specific activations or inhibitions. For example, D'Ausillo et al. (2009) showed that TMS of the tongue area facilitated perceptual discrimination of tongue-articulated phonemes, whereas TMS of the lip area facilitated discrimination of lip-articulated phonemes.

Even Penfield himself reported overlap in the cortical maps of the effectors in this region. For example, he found evidence for overlap between lip and tongue, and between lip and larynx (via vocalization). Using fMRI, Loucks et al. (2007) reported overlap be-

**Table 1**
ALE clusters in the primary motor cortex. The Talairach coordinates of the major ALE clusters for the four meta-analyses are presented. Three subdivisions of the motor cortex (M1) are informally assigned, as in Fig. 1: dorsal, in the region of Talairach *z* coordinates 50–60; mid, in the region of Talairach *z* coordinates 30–45; and ventral, in the region of Talairach *z* coordinates 16–28, in the vicinity of the Rolandic operculum. The columns labelled as *x*, *y*, and *z* contain the Talairach coordinates for the weighted center of each cluster. The ALE score shown is the true value multiplied by $10^3$. The volume (vol.) column shows the size of each cluster in $mm^3$. The "%" column represents the percentage of studies reporting activations in M1 for that ALE focus divided by the total number of studies for that effector. Abbreviations: LH, left hemisphere; RH, right hemisphere.

| Task | M1 | Hemisphere | *x* | *y* | *z* | Vol. ($mm^3$) | ALE ($\times 10^3$) | (%) |
|---|---|---|---|---|---|---|---|---|
| Respiration | Dorsal | LH | −18 | −24 | 64 | 24,000 | 10.00 | 66.7 |
| | | RH | 18 | −20 | 60 | 24,000 | 13.45 | 57.1 |
| | Mid | LH | −46 | −6 | 44 | 2136 | 6.09 | 42.9 |
| | | RH | 46 | −4 | 40 | 2832 | 6.40 | 42.9 |
| Lip | Mid | LH | −52 | −14 | 38 | 16,928 | 17.31 | 80.0 |
| | | RH | 50 | −12 | 38 | 14,464 | 11.39 | 55.6 |
| | Ventral | LH | −56 | −8 | 20 | 16,928 | 13.98 | 30.0 |
| | | RH | 54 | −6 | 16 | 14,464 | 10.71 | 33.3 |
| | | RH | 46 | −6 | 24 | 14,464 | 7.63 | 33.3 |
| Tongue | Ventral | LH | −54 | −6 | 26 | 19,808 | 50.75 | 91.3 |
| | | RH | 56 | −6 | 28 | 20,872 | 52.60 | 78.3 |
| Swallowing | Ventral | LH | −54 | −8 | 18 | 20,720 | 43.45 | 81.8 |
| | | RH | 56 | −6 | 22 | 28,920 | 30.34 | 45.5 |