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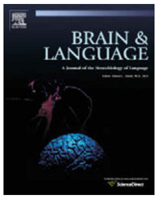

Short Communication

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

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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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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

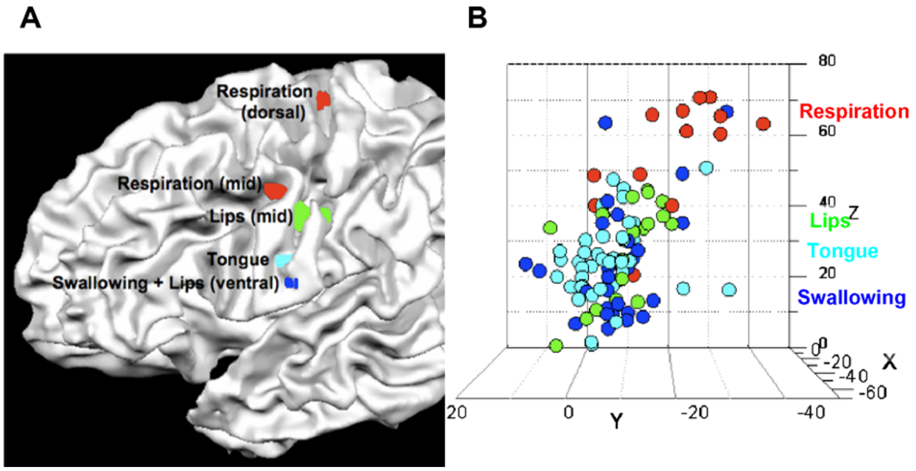

Fig. 1. Major ALE foci in the primary motor cortex for the four meta-analyses. (A) The centers of mass of the six principal ALE foci rendered onto a 3D brain in Talairach space, highlighting their locations along the precentral gyrus. See Table 1 for the Talairach coordinates of each focus. For convenience, the left hemisphere is shown, but very similar results are obtained with the right hemisphere, for which the Talairach coordinates are present in Table 1. Note that the locations of the ventral lip peak and the peak for swallowing are nearly identical. For clarity, three subdivisions of the motor cortex are informally assigned, as in Table 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. Note that the peak for "Lips (mid)" has the false appearance of being a doublet. It is actually a single peak, but the 3-dimensional rendering of this peak by Brain Voyager on the cortical mesh appears to place the peak on both sides of the postcentral gyrus. (B) Scatterplots of the Talairach coordinates contributing to each meta-analysis, as color-coded by motor mechanism as in panel A, where red = respiration, green = lip movement, cyan = tongue movement, and blue = swallowing. The *x*, *y* and *z* axes of the plot refer to the axes of Talairach space. Very similar results are obtained with the right hemisphere. Note that panels a and b are designed to have the same antero-posterior orientation.

tween the larynx and expiratory muscles. We confirmed this result in the meta-analysis by showing a respiratory peak in the orofacial region that was associated with studies of expiration rather than inspiration.

The strongest evidence for a "convergence zone" in the orofacial motor cortex was found in a region extending dorsoventrally between Talairach axial slices 30 and 20, where we observed proximate representations for the pharynx, lips, and tongue in the vicinity of the Rolandic operculum. It is noteworthy that jaw movement leads to activation near this zone (Onozuka et al., 2002, 2003), in keeping with its presumed location in the motor homunculus. Furthermore, there is a clinical condition known as anterior opercular syndrome (also called Foix-Chavany-Marie syndrome; see Weller, 1993), defined as a "central disturbance of volitional control of the facio-linguo-glosso-pharyngeo-masticatory muscles" (Weller, 1992, p. 295), which is due to bilateral infarctions of the Rolandic opercula. Dysarthria, dysphagia, and dysphonia are its principal symptoms. The prevalence of this disorder is low, resulting in relatively few published cases. Such studies do not often report exact spatial coordinates and/or quantitative measurements of lesion volume. Nevertheless, the mere existence of such a syndrome suggests that there may be a convergence zone bilaterally for the speech articulators in the region of the Rolandic operculum.

The second means of showing overlap among the effectors aside from the centers of mass was through the variability in the locations of the ALE peaks across studies. Ideally, the best way to show overlapping representations is by using a within-subject, rather than between-subject, approach. Single-subject fMRI analysis from our lab has supported this overlap among the oral effectors (Brown and Liotti, unpublished observations). For the meta-analyses, we relied instead on the variability of motor-cortex coordinates across studies, thereby highlighting the overlapping fields of the ALE clusters for each effector. However, it is important to keep in mind what other sources of variability might be present in performing a cross-study analysis. These include inter-subject variability, differences in task type across studies, limitations in spatial resolution of fMRI and PET, imprecision in relating MNI to Talairach coordinates, differences between using whole-brain activation foci vs. ROI's, among other limitations in performing meta-analyses. Likewise, in thinking about evidence for somatotopy more generally, it is important to consider methodological differences between techniques based on stimulation (electrical stimulation and TMS) and those based on recording hemodynamic changes in the brain (fMRI and PET), especially with regard to the focality of their effects.

The results of the present study provide an overall picture of "somatotopy with overlap". This is perhaps a reflection of a system that is highly integrated at both the anatomical and functional levels (Schieber, 2001). Speech requires a smooth flow of activity between expiration, phonation, and articulation, and so a system that shows discreteness with overlap might be the most efficient way to achieve this from the perspective of neural architecture, in a manner similar to the way that the fingers of the hand seem to be represented. A multi-effector pathological condition like anterior opercular syndrome might be a clinical manifestation of this convergence of effectors in the motor cortex, most especially in the region of the Rolandic operculum.

4. Conclusion

In our attempt to clarify somatotopy vs. overlap for the speech effectors in the motor cortex, we found evidence for both types of arrangement, namely discrete centers of mass concordant with the Penfield homunculus but with overlapping fields superimposed upon that arrangement.

5. Methods

5.1. Inclusion criteria for papers

Meta-analysis of 54 published neuroimaging studies was performed using "activation likelihood estimation" (ALE) analysis. The studies are summarized in Table 2. Our inclusion criteria were: (1) that the papers provided either Talairach or MNI coordinates for their activation foci (thereby excluding papers that reported

Table 2
Overview of studies included in the four meta-analyses. Four parallel ALE meta-analyses were performed. The references for each analysis are shown, as organized by motor mechanism: respiration, lip movement, swallowing (involving the pharyngeal muscles), and tongue movement. The column "n" refers to the number of subjects in the study. The "modality" column refers to whether the study used positron emission tomography (PET) or functional magnetic resonance imaging (fMRI). The "task" column refers to the task of interest for inclusion in the meta-analysis. The "foci" column refers to the number of activation foci for that task.

Reference	*n*	Modality	Task	Foci
Respiration				
1. Colebatch et al., 1991	6	PET	Inspiration	5
2a. Ramsay et al., 1993	5	PET	Inspiration	5
2b. Ramsay et al., 1993	5	PET	Expiration	9
3a. Fink et al., 1996	6	PET	Inspiration	14
3b. Fink et al., 1996	6	PET	[b]Inspiration	6
4. Evans, Shea, & Saykin, 1999	5	fMRI	Inspiration	14
5. Isaev, Murphy, Guz, & Adams, 2002	6	PET	Inspiration	13
6. McKay, Evans, Frackowiak, & Corfield, 2003	6	fMRI	Hypercapnea	26
[a]7. Nakayama, Fujii, Suzuki, Kanazawa, & Nakada, 2004	10	fMRI	Abdomen inflation	2
Lip movement				
1. [a]Lotze, Erb, et al., 2000	7	fMRI	Lip pursing	2
2. [a]Lotze, Seggewies, Erb, Grodd, & Birbaumer, 2000	30	fMRI	Lip pursing	2
3. [a]Rotte, Kanowski, & Heinze, 2002	9	fMRI	Lip pursing	17
4. Gerardin et al., 2003	7	fMRI	Lip pursing	18
5. Hesselmann et al., 2004	6	fMRI	[b]Lip pursing	2
6. Dresel et al., 2005	15	fMRI	Whistling	30
7. [a]Hanakawa, Parikh, Bruno, & Hallett, 2005	8	fMRI	Lip retraction	4
8. Dresel, Haslinger, Castrop, Wohlschlaeger, & Ceballos-Baumann, 2006	13	fMRI	Whistling	10
9. [a]Pulvermuller et al., 2006	12	fMRI	Lip depression	2
10. Brown et al., 2008	16	fMRI	Lip pursing	15
Swallowing				
1. Hamdy et al., 1999	10	PET	Water swallowing	9
2. Zald & Pardo, 1999	8	PET	Saliva swallowing	21
3a. Martin, Goodyear, Gati, & Menon, 2001	14	fMRI	Saliva swallowing	6
3b. Martin et al., 2001	14	fMRI	Water swallowing	6
4. Fraser et al., 2002	8	fMRI	Water swallowing	8
5. Dziewas et al., 2003	10	MEG	Water swallowing	9
6. Suzuki et al., 2003	11	fMRI	Saliva swallowing	5
7. Furlong et al., 2004	8	MEG	Water swallowing	5
8. Martin et al., 2004	14	fMRI	Saliva swallowing	15
9. Harris et al., 2005	8	PET	Water swallowing	17
10a. Martin et al., 2007	9	fMRI	Saliva swallowing	33
10b. Martin et al., 2007	9	fMRI	Water swallowing	24
11. Lowell et al., 2008	14	fMRI	Saliva swallowing	34
12a. Paine et al., 2008	7	fMRI	Water swallowing	21
12b. Paine et al., 2008	7	fMRI	Water swallowing	5
12c. Paine et al., 2008	7	fMRI	[b]Water swallowing	8
Tongue				
[a]1. Wildgruber, Ackermann, Klose, Kardatzki, & Grodd, 1996	10	fMRI	Vertical move	4
[a]2. Pardo, Wood, Costello, Pardo, & Lee, 1997	6	PET	Tongue protrusion	2
3. Corfield et al., 1999	8	fMRI	Tongue protrusion	17
[a]4. Zald et al., 1999	8	PET	Horizontal move	4
5. Riecker et al., 2000	10	fMRI	Horizontal move	4
[a]6. Lotze , Erb, et al., 2000; Lotze, Seggewies, et al., 2000	7	fMRI	Vertical move	2
[a]7. Alkadhi, Crelier, Boendermaker, Golay, et al., 2002	12	fMRI	Horizontal move	1
[a]8. Alkadhi, Crelier, Boendermaker, Hepp-Reymond, & Kollias, 2002	12	fMRI	Horizontal move	2
[a]9. Curt et al., 2002	12	fMRI	Horizontal move	2
10. Rotte et al., 2002	9	fMRI	Horizontal move	12
[a]11. Stippich, Ochmann, & Sartor, 2002	14	fMRI	Vertical move	2
12. Dziewas et al., 2003	10	MEG	Vertical move	4
13. Fesl et al., 2003	24	fMRI	Horizontal move	8
[a]14. He et al., 2003	18	PET	Horizontal move	1
[a]15a. Shinagawa et al., 2003	14	fMRI	Tongue Protrusion	6
[a]15b. Shinagawa et al., 2003	14	fMRI	Horizontal (to right)	6
[a]15c. Shinagawa et al., 2003	14	fMRI	Horizontal (to left)	6
16. Furlong et al., 2004	8	MEG	Tongue pressing	4
[a]17. Hauk, Johnsrude, & Pulvermuller, 2004	14	fMRI	Vertical movement	2
18. Hesselmann et al., 2004	6	fMRI	[b]Horizontal move	2
19. Martin et al., 2004	14	fMRI	Tongue elevation	23
[a]20a. Shinagawa et al., 2004	17	fMRI	Tongue protrusion	2
[a]20b. Shinagawa et al., 2004	17	fMRI	Horizontal (to right)	2
[a]20c. Shinagawa et al., 2004	17	fMRI	Horizontal (to left)	2
21a. Watanabe et al., 2004	24	fMRI	Tongue press to left	18
21b. Watanabe et al., 2004	24	fMRI	Tongue press to right	17
21c. Watanabe et al., 2004	24	fMRI	Tongue retraction	11
[a]22. Pulvermuller et al., 2006	12	fMRI	Vertical movement	2

Table 2 (*continued*)

Reference	n	Modality	Task	Foci
[a]23. Vincent, Bloomer, Hinson, & Bergmann, 2006	6	fMRI	Horizontal, vertical move	2
[a]24. Stippich, Blatow, Durst, Dreyhaupt, & Sartor, 2007	14	fMRI	Vertical move	2
25. Brown et al., 2008	16	fMRI	Vertical move	11

[a] Indicates ROI study.

[b] Indicates high-level contrast (i.e. an experimental condition was compared to another experimental condition).

activations using neuroanatomical labels alone); and (2) that the subjects were healthy individuals and not part of clinical populations. The majority of studies employed standard block designs, and most used rest as a control condition.

5.2. Activation likelihood estimation (ALE) Analysis

Four parallel ALE meta-analyses were performed for four motor mechanisms related to speech production: (1) respiration (7 papers, 94 activation foci across the whole brain); (2) lip movement (10 papers, 102 foci); (3) tongue movement (25 papers, 183 foci); and (4) swallowing (12 papers, 242 foci), an indicator of pharyngeal-muscle contraction. While we intended to include jaw movement as a fifth analysis, there was an insufficient number of papers to do so. Only three publications would have met our inclusion criteria (Onozuka et al., 2002, 2003; Takahashi, Miyamoto, Terao, & Yokoyama, 2007). We have previously performed an ALE meta-analysis of the location of the larynx area of the motor cortex via studies of speaking, singing, and syllable production (Brown et al., 2009).

Coordinates for activation foci from conditional contrasts were taken from the original publications. No deactivations were examined in these meta-analyses. We used the implementation of ALE (Laird, McMillan, et al., 2005) that is contained within the BrainMap database (http://brainmap.org; Fox & Lancaster, 2002; Laird, Fox, et al., 2005). MNI coordinates were automatically converted to Talairach coordinates using the method of Lancaster et al. (2007). All coordinates were then blurred with a full-width-at-half-maximum of 12 mm. The ALE statistic was computed for every voxel in the brain according to the algorithm developed by Turkeltaub, Eden, Jones, and Zeffiro (2002). A permutation test using 10,000 permutations was performed to determine the statistical significance of the ALE results, which were thresholded at $p < 0.01$ using the "false discovery rate" correction for multiple comparisons (Laird, McMillan, et al., 2005). The centers of mass of the ALE clusters from the primary motor cortex are plotted in Fig. 1A on a 3D rendering of a brain that was spatially transformed into Talairach space using Brain Voyager (Brain Innovation, Maastricht). This brain is partially inflated so as to permit visualization of activity in the depths of the central sulcus. Each center of mass was localized on axial slices of this Talairach-normalized anatomical MRI within Brain Voyager. Regions of interest were painted around each center of mass on their respective axial slices using a 3 mm cube, and the group of them was exported onto the surface view for visualization of somatotopy. Scatterplots of the original Talairach coordinates from all studies for each meta-analysis were created using Origin Pro 8, as shown in Fig. 1B.

Although ALE scores provide a reflection of the cross-study congruence of activation, a second factor to consider is how many of the papers contributing to a given meta-analysis actually reported activation in a brain region corresponding to an ALE focus of interest (see "Region-of-Interest Analysis" in Brown, Ingham, Ingham, Laird, & Fox, 2005). Hence, we determined the percentage of all studies in a given meta-analysis that showed activation corresponding to the M1 ALE foci for that analysis. In order to increase the reliability of our findings, we excluded ALE foci that were present in fewer than 20% of the contributing studies, since these foci came overwhelmingly from a small number of papers and were thus unreliable.

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