Neuroscience and Biobehavioral Reviews 139 (2022) 104730

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Beyond language: The *unspoken* sensory-motor representation of the tongue in non-primates, non-human and human primates

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ARTICLE INFO

Keywords:
Tongue
Sensorimotor control
Cortical representation
Neural plasticity
Comparative neuroscience

ABSTRACT

The English idiom "*on the tip of my tongue*" commonly acknowledges that something is known, but it cannot be immediately brought to mind. This phrase accurately describes sensorimotor functions of the tongue, which are fundamental for many tongue-related behaviors (e.g., speech), but often neglected by scientific research. Here, we review a wide range of studies conducted on non-primates, non-human and human primates with the aim of providing a comprehensive description of the cortical representation of the tongue's somatosensory inputs and motor outputs across different phylogenetic domains. First, we summarize how the properties of passive non-noxious mechanical stimuli are encoded in the putative somatosensory tongue area, which has a conserved location in the ventral portion of the somatosensory cortex across mammals. Second, we review how complex self-generated actions involving the tongue are represented in more anterior regions of the putative somatomotor tongue area. Finally, we describe multisensory response properties of the primate and non-primate tongue area by also defining how the cytoarchitecture of this area is affected by experience and deafferentation.

1. Introduction

As other senses, touch connects our sensory experience with external physical reality. Through touch, humans and other mammals develop awareness of the barrier between the external world and our body (Guéguen, 2002) and are informed when the mechanical, chemical, or thermal features of the external world represent a significant threat for our survival (Owens and Lumpkin, 2014). We can perceive touch on various skin surfaces (e.g., face: Won et al., 2017; forearm, thigh and shin: Ackerley et al., 2014) and non-skin regions (e.g., cornea: Beiderman et al., 2015, Zalevsky and Belkin, 2013; teeth: Bono and Haggard, 2019). The primate hand (and mammalian forepaw) has been of particular interest for somatosensation research as perhaps the best example of a glabrous (not hairy) body region with exquisite and highly localized tactile sensitivity (Ackerley et al., 2014; Weinstein, 1968). The hand (or the paw in other mammals) has also received peculiar attention in motor research due to the fine motor repertoire of fingers and ease of study (Ngeo et al., 2014). However, the hand is not unique: rather it shares many sensory attributes with another versatile and highly evolutionarily-adapted effector, namely the tongue.

First, primates' hands and tongues are both crucial for most everyday behaviors, and indispensable for survival. Human and non-human primates use primarily their hands (Lemelin and Diogo, 2016; Lemelin and Schmitt, 2016; Vereecke and Wunderlich, 2016) and tongue to explore the external environment (especially at the very early stages of infancy (Adolph and Franchak, 2017; Fessler and Abrams, 2004; Rochat, 1989); both are also used to perform complex object manipulations (Hayashi, 2015).

Second, the hand and tongue are the only motor effectors used as articulators by humans (Sandler, 2009; Woll, 2014). The brain areas involved in the motor control of the hand and tongue are not only cortical neighbors (Kuehn et al., 2017), but also strongly interconnected (Gentilucci et al., 2001), appearing to share some neural resources for motor planning such as the direction of motor actions executed with the hand and the tongue (Vainio et al., 2018). Third, both the palmar regions of the hand (especially the fingertips) and the mucosa of the tongue are characterized by a high density of peripheral receptors sensitive to touch when compared to other body regions (Abraira and Ginty, 2013).

Fourth, both the fingertips and lingual surfaces are innervated by

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https://doi.org/10.1016/j.neubiorev.2022.104730
Received 17 December 2021; Received in revised form 6 April 2022; Accepted 6 June 2022

similar mechanoreceptors which permit detection of multiple genres of tactile events (Roudaut et al., 2012). In the hand, different afferents respond to specific types of skin deformation, which in turn helps to shape tactile percepts (Saal and Bensmaia, 2014). For example, Meissner's and Pacinian corpuscles detect texture and different frequencies of vibrotactile stimulation (Johnson et al., 2000), whereas Merkel cell-neurite complexes support shape discrimination and sensing of sustained pressure (Johnson et al., 2000). Similar classes of mechanosensitive cells and neurons (e.g., Merkel complexes, various encapsulated corpuscles, and free nerve endings) have been observed in the oral mucosa, the tissue that encloses the muscular structure of the tongue (humans: Hashimoto, 1972; non-human primates: Halata and Baumann, 1999; non-primates: Watanabe, 2004, Tachibana et al., 1997).

Finally, as one would expect given their dense sensory innervation, the hand and tongue are both characterized by their tactile spatial resolution and high sensitivity to diverse types of touch. Due to the tongue's unique anatomy (see below), most somatosensory studies of the tongue have used methods specifically designed to test tactile sensitivity within the oral cavity and have not been optimized for other body parts (e.g., fungiform papillae count or nerve microstimulation: Bangcuyo and Simons, 2017; Linne and Simons, 2017; Lukasewycz and Mennella, 2012; Petrosino and Fucci, 1984; Trulsson and Essick, 2010). However, a few studies have measured tactile sensitivity on both tongue and finger with standardized stimulation methods to directly compare the two effectors, testing both normative (Miles et al., 2018) and clinical populations (Jacobs et al., 2002; Cordeiro et al., 1997). The results of these few studies suggest that the tongue has finer sensitivity to pressure and texture capacities compared to the fingertip (Miles et al., 2018).

Despite the many parallels between hand and tongue somatosensation and functional relevance in the motor system, there has been vastly more research and synthesis of findings regarding the hand's sensory properties (Abraira and Ginty, 2013; Greenspan and LaMotte, 1993; Vallbo and Johansson, 1976) and primate cortical somatosensory representation (for reviews see: Woolsey et al., 1942; Kaas, 1983; Blake et al., 2002; Lipton et al., 2010; Cartmill et al., 2012; Borich et al., 2015; Tamè et al., 2016; Omrani et al., 2017).

Here, we will fill this gap, focusing on the primate tongue sensorimotor capacities. We first review basic anatomical principles of the lingual muscles, their innervation, and the behavioral relevance of the tongue's sensorimotor capacities for primates. We then provide an overview of the neural targets of the tongue's peripheral sensorimotor neurons in the few species of non-primate mammals for which information is available, along with non-human and human primates. We focus particularly on the cortical organization of the sensorimotor tongue areas, and also discuss plastic experience-dependent modulations and response properties of the cortical sensorimotor tongue representation across mammals with particular emphasis on non-human and human primates.

1.1. Why is the tongue an outlier in the sensorimotor system? A brief anatomical survey

Compared with other mobile appendages (like the limbs), the tongue exists in a rather unusual sensory environment, in that it resides most of the time within the body, namely in the mouth and upper throat (intraoral cavity). As shown in Fig. 1, the intraoral cavity is traditionally divided into three smaller cavities: the *vestibule*, the *oropharynx*, and the *oral cavity proper* (Becker, 2000; Laine and Smoker, 1995; Roy and Varshney, 2013; Yousem and Chalian, 1998). The vestibule is the most external portion of the oral cavity and sits between the facial (out--facing) surface of the teeth, and the internal surface of the cheeks and lips. The most internal portion of the intraoral cavity, the oropharynx, lies between the soft palate and the vocal folds of the larynx, and adjoins the oral cavity proper with the larynx. The oral cavity proper is located within the boundaries of the lingual (tongue-facing) surface of the teeth, the hard palate, the inner gums, and the sublingual space.

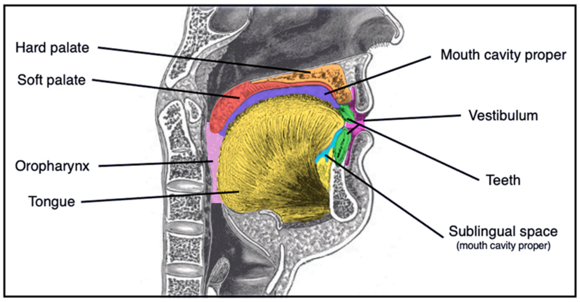

Fig. 1. Gross anatomy of the human intraoral cavity. Both intraoral organs and cavities are labelled for descriptive clarity. Drawing adapted from (Gray, 1878).

Compared to most bodily cavities, the mouth is unusual in the richness of its peripheral receptors and its mixed somatosensory properties, some comparable to the skin, and others typical of the visceral body (Haggard and de Boer, 2014). Within the oral cavity proper, multiple tissue types (skin, muscle, teeth) are in close proximity, and interact constantly. Although a lingual structure is present in all vertebrates (Iwasaki, 2002), primates - and humans in particular - have a unique tongue shape, size, and muscular architecture compared to other mammals (Abd-El-Malek, 1939; Miyawaki, 1974). The tongue is divided in three regions (tip, body, and base) based on its muscle structure (see section 1.3.) and pattern of sensorimotor innervation (section 1.4.). The tongue is particularly large relative to the intraoral cavity: when the mouth is closed, the tongue occupies almost 90% of its total volume (Ding et al., 2018).

The tongue as effector is also an outlier given its extreme reliance on somatosensation. Unlike most of the other densely innervated structures of the human body (e.g., fingertips), one's own tongue cannot be seen (except in a mirror). This makes the tongue a consciously-controlled, non-visceral body regions where touch and proprioception (Adatia and Gehring, 1971; Grover and Craske, 1991) provide almost all sensory information. In addition, whereas similarly manipulable appendages like hands, paws, or forelimbs are primarily engaged in exploration and manipulation of objects, the tongue can perform not only these tasks, but also is involved in highly diverse behaviors, ranging from gulping down a beer on a hot day to declaiming a Shakespearean monologue. The tongue is a particularly interesting case of a complex effector that holds down its evolutionarily ancient 'day job' in performing quasi-vegetative functions (for instance its involvement in reflexive swallowing) while simultaneously being able to perform movements requiring the highest degree of cognitive and motoric planning and skill.

1.2. The unique histological composition of the tongue

As part of the oral cavity, the tongue has some histological features typical of the internal milieu. It is enclosed by a thin and moist membrane – the oral mucosa (mostly lining mucosa, Ciano and Beatty, 2015; Collins and Dawes, 1987; Squier and Kremer, 2001). Although the oral mucosa has a similar histological composition as the skin (Presland and Dale, 2000) it is also specialized for its particular environment, in that it is fully glabrous (Yousef et al., 2019), composed by a thicker layer of squamous (scaly) epithelial cells than the skin (Barrett et al., 2005) and also heals more quickly than skin (Turabelidze et al., 2014; Whitby and Ferguson, 1991). The absence of hair and its robust and easily repairable epithelium make the oral mucosa especially pliable (Gartner, 1994), suitable for manipulation of different food types (Squier and Kremer, 2001) and protected against invading pathogens (Hovav, 2014).

Lining mucosa covers most of the lingual surface and is important functionally, as it allows the tongue to be flexible, elastic and easily deformable. The major exception to this rule is the top or dorsum of the tongue, which is covered by a layer of specialized mucosa, one specifically resistant to loading forces exerted during mastication (Squier et al., 1976). The stratified squamous epithelium of the dorsum of the tongue is normally organized in tiny raised protrusions (papillae, Squier, 2011), some bearing taste buds (Bragulla and Homberger, 2009) - another highly specialized sensory feature of the tongue.

1.3. *Lingual myoarchitecture*

Understanding the complex muscular structure of the tongue - its myoarchitecture - is essential for understanding how the tongue can perform such a wide range of movements (see section 1.6). In contrast with symmetrically paired and independently moveable body parts like the limbs and eyes, the tongue is a single organ symmetrically spanning the body midline, albeit one containing many constituent muscles (Sanders and Mu, 2013). Although other highly manipulable effectors like the hand or forepaw tend to be contralaterally represented cortically and subcortically, it is still unclear whether each side of the tongue has a bilateral or more strongly lateralized cortical representation. This is true even for non-speech related movements (Forrester and Rodriguez, 2015; Wildgruber et al., 1996) or gustatory functions (Stevenson et al., 2013) - a topic we return to below.

Returning to myoarchitecture, the tongue is predominantly a complex of striated muscle, one enclosed by a layer of oral mucosa and connective tissue. Tongue muscles are grossly divided into intrinsic and extrinsic muscle groups, each related to a set of movements or functions (Brand and Isselhard, 2014). The extrinsic lingual muscles (genioglossus, hyoglossus, styloglossus and palatoglossus, as shown in Fig. 2) extend to the tongue from neighboring attachments on the mandible, the hyoid bone, and the temporal bone.

These extrinsic lingual muscles serve to translate the tongue in space within the mouth. The styloglossus and the palatoglossus muscles are an antagonistic muscle pair that share a similar pattern of innervation (Ziermann et al., 2018) and embryonic origin (Cobourne et al., 2019), but move the tongue in opposing directions. While the genioglossus allows tongue protrusion, the styloglossus pulls the tongue backward (Clemente, 2007; Glass et al., 2020). Likewise the palatoglossus and the hyoglossus, each move the tongue elevate the posterior portion of the tongue (Campos et al., 2012)lower/retract the tongue, respectively(El Omda and Winters, 2021). Altogether, extrinsic muscles play a crucial role in both mastication (Naganuma et al., 2001; Napadow et al., 1999) and speech production (Kuehn and Azzam, 1978).

By contrast, intrinsic lingual muscles (superior longitudinal, vertical, transversal and inferior longitudinal) lack a bony attachment, comprise the main body of the tongue, and play a role in determining its shape and spatial orientation (Blount and Lachman, 1953; Sinclair,1972; Standring 2005). Intrinsic muscle fibers (Stål et al., 2003) are oriented either along the longitudinal 'back-to-front' lingual axis (the superior and inferior longitudinal muscles) or across the longitudinal axis (the vertical and transverse muscles). Contraction of longitudinal muscle fibers permits tongue shortening and retraction, whereas contraction of the transversal and vertical fibers permits tongue elongation, flattening and widening (Stone, 1990). Curiously, the orientation of fibers changes across tongue subregions, with most fibers being oriented along the longitudinal axis in posterior and inferior regions of the tongue, and more fibers across the longitudinal axis predominating in the anterior and superior regions (Gilbert et al., 1998).

Finally, multiple fibrous connective structures (lingual septa; Abd-El-Malek, 1939) provide attachment for multiple intrinsic lingual muscles. Among the lingual septa, the median septum divides the tongue in two symmetrical halves and provides attachment for both transversal and longitudinal superior muscles.

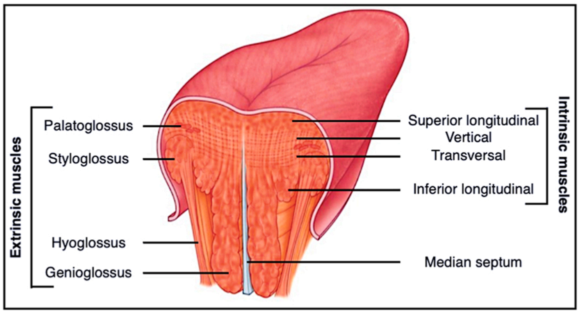

Fig. 2. Muscular composition of the human tongue. The four extrinsic lingual muscles are labelled on the left. The four intrinsic lingual muscles are labelled on the right. (Shafik Abd-El-Malek, 1955; Touré and Vacher, 2006).
Image adapted from Drake et al., 2005).

1.4. *Sensory-motor innervation of tongue muscles*

The richness of the tongue's peripheral receptors is one of its distinctive features. Afferents in different tongue regions (surface and tongue muscles) have very specific sensory properties (Trulsson and Essick, 1997). The tongue surface (like the dorsum or its lateral surface) is innervated by mechanoreceptive afferents that are typically rapidly adapting, have very small receptive fields,[1] and respond to extremely low mechanical forces ($\leq$2mN). In contrast, sensory receptors in tongue muscles are mostly slowly adapting, have broader receptive fields and respond to higher mechanical forces ($\geq$4mN, see Fig. 3, and Türker et al., 2006). Relevant to the question of tongue sensorimotor lateralization (discussed in depth in sections 2 & 3), some receptive fields have been shown to be extend up to 1–2 mm across the tongue midline (Trulsson and Essick, 1997).

Finally, peripheral mechanoreceptors are unevenly distributed along the body of the tongue, with higher density of peripheral receptors in anterior and mesial (middle) tongue regions than posterior and lateral regions (Trulsson and Essick, 1997). This peculiar distribution of receptors has been described as an oral analogue of the retinal fovea (Haggard and de Boer, 2014). As shown in Fig. 4, multiple cranial nerves carry somatosensory afferents to their cortical targets, and motor efferents to their lingual muscles.

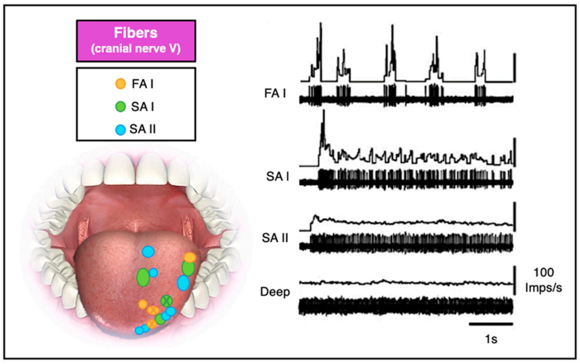

Fig. 3. Receptive field and response characteristics of mechanoreceptive afferent fibers of the cranial nerve V, innervating the anterior two thirds of the tongue and the deep tongue in humans. On the left of the panel, we show locations and relative sizes of the receptive field of the three different types of superficial afferents (Fast adapting type I (FA I), slowly adapting type I (SA I), and slowly adapting type II (SA II). Receptive fields marked with a cross indicate fields located on the ventral side of the tongue. All other fields were located on the dorsal side. On the right of the panel we show examples of recordings from four different types of afferents; FA I, SA I, SA II, and Deep tongue.
Figure adapted from (Türker et al., 2006).

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[1] A receptive field is the area - typically contiguous - of a sensory surface that will drive responses in a receptor or connected sensory neuron.

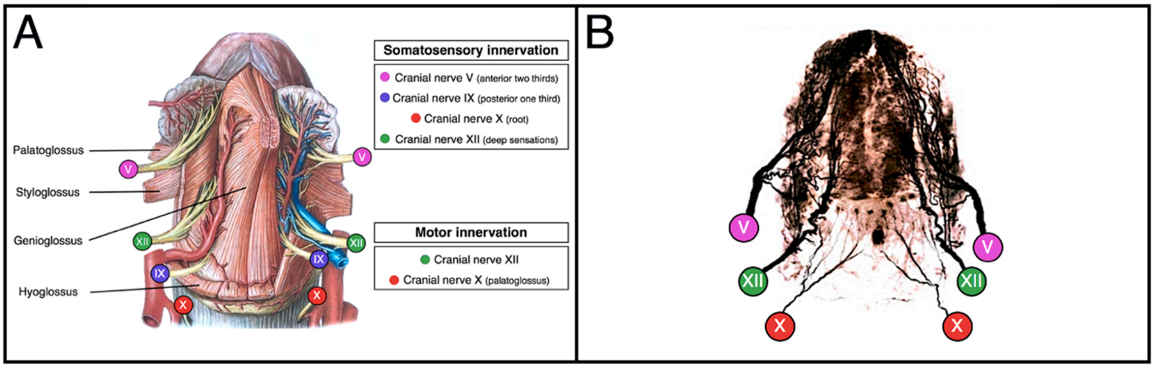

Fig. 4. (A) Blood supply and somatosensory and motor innervation of tongue muscles in humans. The four lingual extrinsic muscles (Palatoglossus, Styloglossus, Genioglossus and Hyoglossus) are labelled on the left of the panel. (B) Nerve map of the whole tongue in humans showing the innervation pattern of the mandibular branch of the trigeminal nerve (cranial nerve V), the vagus (cranial nerve X) and the hypoglossal nerve (cranial nerve XII). Readers interested in a more in-depth discussion should consult Mu & Sanders (2010), Sawczuk & Mosier (2001), and Zur et al., (2004).
(a) Figure adapted from Paulsen and Waschke (2018). (b) Figure adapted from Mu and Sanders (2010).

Somatosensory innervation of the anterior two-thirds of the tongue is supplied by the mandibular branch of the trigeminal nerve (cranial nerve (CN) V), while the posterior third is innervated by the glossopharyngeal nerve (CN IX). The posterior tongue root is innervated by the vagus nerve (CN X), while deep sensations in the tongue muscle are transmitted by the hypoglossal nerve (CN XII).

Motor innervation of the tongue is supplied by the hypoglossal nerve (CN XII), with the exception of one extrinsic muscle, the platoglossus, which is innervated by the vagus nerve (CN X). There are a number of sensorimotor reflexes involving tongue sensation and movement - like the pharyngeal or 'gag' reflex - that range from simple to quite complex (see Miller, 2002 for an overview). As with other reflexes, sensory inputs are processed in a local circuit arc, and are not centrally mediated (Miller, 2002; Walker, 1990).

Afferent neurons that transmit sensory information towards the central nervous system and efferent neurons that carry motor commands to the peripheral nervous system have cell bodies located in distinct cranial nerve nuclei within the brainstem. (Maezawa, 2017; see Fig. 5 below). These pathways project either contralaterally or bilaterally according to the cranial nerve nuclei that are involved. Based on the pattern innervation pattern, four regions of the tongue can be defined: the anterior two-thirds of the tongue (cranial nerve V), the posterior third (cranial nerve IX), the posterior tongue root (cranial nerve X) and the deep tongue (cranial nerve XII). As depicted in Fig. 5, these regions differ in their afferent pathways and cortical targets. Tactile events perceived on the anterior two-thirds of the tongue are transmitted to their cortical targets (bilateral areas 3a, 3b, 1 and 2 of the ventral primary somatosensory cortex, Geyer et al., 1999) through the trigeminal ganglion, the brainstem and the thalamus (for a review see Shibukawa, 2009). By contrast, stimuli perceived in posterior tongue regions, in the tongue root and deeply within the lingual structure are sent to their cortical targets only contralateral to the stimulation site, through the medulla (see Fig. 5 for further details on second order neurons of cranial nerves IX, X and XII) and the thalamus. Different patterns of innervation between different tongue regions are linked to differences in perception with the tongue, with recent evidence supporting poorer tactile sensitivity on the back of the tongue compared to the tip of the lingual structure (Pamir et al., 2020). (Although this review mainly focuses on the cortical representation of the tongue, please view box 1 for a short overview on tongue representations in subcortical and cerebellar structures).

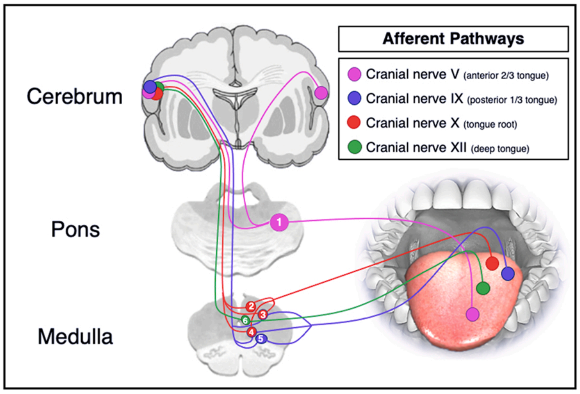

Fig. 5. Afferent pathways of different tongue afferents in the human tongue. Fibers of the mandibular branch of the trigeminal nerve reach their sensory nucleus in the brainstem (1) through the trigeminal ganglion. Electrical signals are then sent to their cortical targets (within the ventral portion of the primary somatosensory cortex) both ipsilaterally and contralaterally to the stimulation site. Electrical signals transmitted by cranial nerves IX, X and XII reach their cortical target contralateral to the stimulation site through the medulla. The second order neurons of fibers of cranial nerve IX are located within the nucleus of tractus solitarius (3), the nucleus ambiguous (4) and the inferior solitary nucleus (5). The second order neurons of fibers of cranial nerve X are located within the dorsal nucleus of vagus (2), the nucleus of tractus solitarius (3) and the nucleus ambiguous (4). The second order neurons of fibers of cranial nerve XII are located within the hypoglossal nucleus (6).

Our understanding of the peripheral sensory innervation of the tongue is quite extensive, and nerve maps of the whole tongue have recently been drawn for humans (see Fig. 4.B., Mu and Sanders, 2010b). Nonetheless, this knowledge is still incomplete - unsurprisingly given that the application of staining techniques to investigate the innervation of human tongue musculature has been only explored over the last decade (Mu and Sanders, 2010a). Despite the dominant role of the tongue in perhaps the defining human behavior - speech - and its unusually sophisticated repertoire of movements, relatively little is known about the architecture of cortical targets that receive input from peripheral sensorimotor afferents innervating the tongue (Mu and Sanders, 2010a).

1.5. BOX 1 Tongue representations in cerebello-thalamic-cortical circuits

Tongue muscles are widely represented outside cortex as indeed the somatotopic maps observed in motor and somatosensory cortices are replicated throughout many of the brain areas that compose sensorimotor networks (Belyk et al., 2021). At early stages of processing within the brainstem, sensory signals arising from the tongue have been shown to be processed within a specialized circuit, independently from other facial structures like the jaw, cheeks, and airways (Moore et al., 2014). Early evidence in humans (Corfield et al., 1999) have used functional magnetic resonance imaging (fMRI) to show that tongue contractions are linked with significantly enhanced activation within the thalamus, the supplementary motor cortex (SMA) and the cerebellum. Non-human primate data have confirmed that tongue muscles are represented across multiple cortical sites, spreading over various regions of the frontal lobe, including SMA, pre-SMA (Morecraft et al., 2001, 2007), rostral, medial and caudal regions of the cingulate cortex (Amiez and Petrides, 2014; Morecraft et al., 2001, 2007; Procyk et al., 2016).

Cerebellar nuclei of both non-human primates (Bowman and Aldes, 1980) and humans (Boillat et al., 2020) have also been associated with different tongue movement patterns. For example, studies conducted with rhesus macaques (Macaca mulatta; Bowman and Aldes, 1980) showed that electrical stimulation of the dentate nucleus evoked both lateralized contractions and tongue protrusions, whereas stimulation of the fastigial nucleus mostly elicited tongue protrusions. 7 T fMRI results in humans (Boillat et al., 2020) extended these results by showing that the tongue has multiple representations within the cerebellum, across multiple lobules. This is consistent with the existence of multiple somatotopic maps within the cerebellum (Boillat et al., 2020; Buckner et al., 2011; Grodd et al., 2001; Manni and Petrosini, 2004; Mottolese et al., 2013; Rijntjes et al., 1999; Rosina and Provini, 1983; Schlerf et al., 2010). Overall, multiple representations of tongue sensation and movement across various cortical and cerebellar sites have been implicated in primate learning, and monitoring and performing fine and complex motor actions with their tongue.

1.6. Tactile capacities of the human tongue

The tongue's sensitivity to tactile stimuli has often been studied either in relation to the digestion of liquids and food (Frank et al., 1992) or to other intraoral touches (e.g., the tongue touching other intraoral tissues like teeth or palate). In particular, tactile capacities of tongue and palate have often been investigated together for their joint impact in processing texture attributes of liquid and solid substances (Engelen et al., 2002; Kokini et al., 1977; Lauga et al., 2016; Thomazo et al., 2019; for a review also see Liu et al., 2017).

However, the tongue alone plays an essential role in tactile perception as touching pieces of food with the tongue may be essential for evaluating whether their size, texture and temperature are suitable for swallowing and digesting. Tongue mechanoreceptors detect the texture and viscosity - roughly the stickiness - of food (Araujo and Rolls, 2004), a property that changes with the tongue's temperature: with a slight increase of 1–3 °C compared to baseline tongue temperature, viscosity sensitivity is enhanced (Lv et al., 2020). The temperature of the tongue surface often varies, especially during eating (e.g., when drinking a glass of cold water or eating a bowl of hot soup). As viscosity normally *decreases* with increased temperatures, enhanced viscosity perception at higher temperatures is crucial to allow constant viscosity perception capacities at different tongue temperatures.

Tongue somatosensation combined with movement also allows the organism to estimate more global properties, such the size of an object in the mouth (Dellow et al., 1970; Engelen et al., 2002) along with features that allow for its identification and/or disambiguation from other objects (Anstis, 1964; Anstis and Loizos, 1967; La Pointe et al., 1973). For example, we could imagine having a raisin placed on the dorsum of our tongue. By exploring the raisin with our tongue we can not only tell its size, but also its overall shape, wrinkliness, hardness, texture, and taste (cf. raisin meditation task: Nelson, 2017; Warren et al., 2017).

In tandem with other intraoral surfaces (Bono and Haggard, 2019), tactile perception with the tongue can be influenced by contextual information and real-world knowledge. For instance, we can estimate the size of objects impacting the tongue via a combination of tactile sensations arising from the tongue muscles along with 'top-down' predictions about the current position and state of our tongue in our mouth. However, such predictive cognitive model can lead to perceptual bias (Wei and Stocker, 2017). It is currently not clear how perceptual biases affect tongue-mediated size estimation: different studies have shown that size estimation of objects inserted in the mouth can lead to both overestimation (Bittern and Orchardson, 2000; Dellow et al., 1970; Melvin and Orchardson, 2001) and underestimation biases (Crutchfield et al., 2016; Topolinski and Türk Pereira, 2012). More recent evidence suggests that size estimation perceptual biases with the tongue (both overestimation and underestimation) depend on a series of Bayesian predictions (Crutchfield et al., 2018). The time spent orally exploring an object (Tomita et al., 2017) or the subjective hunger level of participants (Crutchfield et al., 2018) change the priors in these predictions. Being hungry may lead us to underestimate the size of food inserted in the mouth. Conversely, the more time spent touching food with the tongue (e.g., chewy and fibrous foods such as meat or thick bread), the more likely we are to overestimate the food size.

The tongue's tactile capacity allows humans not only to perceive object size but also to identify more complex features like stereognosis - the ability to perceive 3D shapes in space - and roughness. Stereognosis is vital for survival, for instance to chew and swallow without choking (Boliek et al., 2007; Jacobs et al., 1998), and is an ability that often diminishes with increasing age, even in individuals without eating and swallowing disorders (Kawagishi et al., 2009). Roughness perception is crucial to identify and orient different materials that contact intraoral surfaces and, during mastication, may require different chewing patterns (Howes et al., 2014). Fine roughness variations can be perceived with the tongue, with particles as small as 0.50 μm being perceived as rough (Jones et al., 2004; Linne and Simons, 2017). Finally, the tongue's tactile capacities allow humans to discriminate not only the properties of external objects but also changes in their internal state (e.g., temperature variations). Temperature perception with the tongue is highly precise, with warm being perceived with little or no heat variations, and cold with at least 5 °C temperature variations (Green, 1986).

1.7. Tongue motor kinematics

The extrinsic and intrinsic lingual muscles (see section 1.3) can operate independently, or in combination to produce fine tongue movements at a wide range of speeds (Kuberski and Gafos, 2019). The aim of this section is to provide a broad review of some of the kinematics of the principle movements of the tongue. These kinematics have been mostly investigated in the literature as a means of studying cortical representations of tongue movements in human and non-human primate studies.[2] Tongue movements studied in primates range from non-lateralised protrusion (see Fig. 6. A) to more complex, lateralised kinematics (see Fig. 6. B and 6. C).

Lateralised tongue protrusions are common especially when eating. Indeed, every time we try to displace a piece of food out of our teeth on either side of the mouth, we perform a lateralised tongue protrusion. Both lateralised and non-lateralised tongue protrusions contact other intraoral structures (e.g., the dentition, gingivae, hard palate, velum, and pharynx) and facilitate moulding of the food particles into a bolus in preparation for swallowing (Matsuo and Palmer, 2009). Tongue protrusions also underlie haptic explorations of the mouth, as well as human-specific communicative acts such as speaking, singing, and whistling (Belyk et al., 2019; Belyk and Brown, 2017).

Well-executed and successful tongue movements are contingent upon proprioceptive and sensory surface feedback. This is true not only for highly concerved movements such as chewing and swallowing, but also for human-specific ones. Correctly pronouncing a word or

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[2] For more exhaustive reviews of specific subfields, the reader may wish to consult other reviews, such as Hiiemae and Palmer (2003) for tongue movements in feeding and speech, Maezawa (2017) for sensorimotor integration, or computational modelling papers investigating how muscle forces are coordinated to generate movement in musculoskeletal systems (Wilhelms-Tricarico, 1995; Gérard et al., 2006; Stavness et al., 2012).

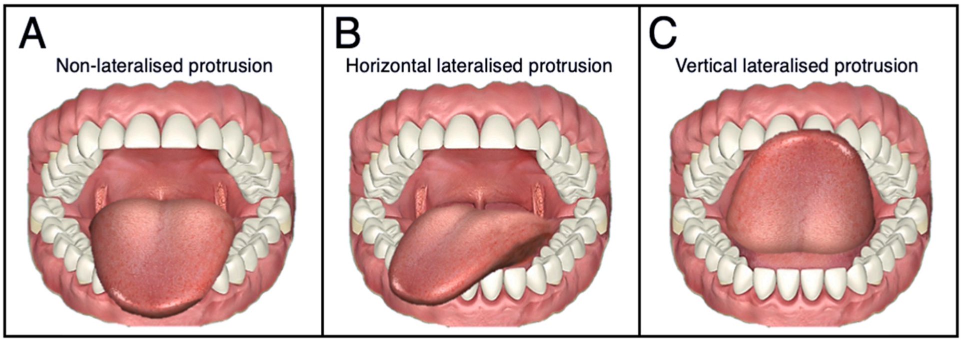

Fig. 6. Repertoire of fine complex tongue kinematics most frequently used in non-human and human studies primate studies: non-lateralised (A) and lateralised horizontal (B) and vertical (C) tongue protrusion.

accurately whistling a tune relies heavily on perceptual feedback from the tongue and surrounding oral tissue. For instance, the production of alveolar consonant sounds (e.g., the sounds /t/ and /d/) requires the tip of the tongue to stroke the alveolar ridge, which is a small protuberance of the gum, located just behind the central maxillary incisors. The perception of a contact force exerted on the alveolar ridge by the tongue triggers the tongue to exert a continuous tissue compression on the alveolar ridge. This generates a complete closure of the vocal tract, crucial for building up sufficient intraoral air pressure for accurate production of the consonant. Similar somato-motor interactions are required for other consonants (Löfqvist and Gracco (2002). As a final intuitive example, anyone who has had a local oral anaesthetic during a visit to the dentist will likely have experienced some difficulties in pronouncing words - for a more formal investigation of this effect, see Niemi et al. (2006), for a more domain-general approach see Grigoriadis et al. (2017) and for a description of body image distortions after oral anesthesia see Türker et al., (2005). To sum up, tongue movements are not only caracterised by fine kinematics and precisely controlled speed, but they are also highly relevant for most everyday behaviors essential for survival.

2. Cortical bases of the sensory-motor processing in non-human mammals

In this section we review a selection of studies investigating the neural bases of somatosensory and motor control of the tongue non-human primates and the broader mammalian clade where information is available. The review takes a particular focus on cortex where acomprehensive view of tongue somatosensory and motor cortical representations across different phylogentic domains is tractable.

2.1. *Neural substrates of tongue somato-motor processing in non-primate mammals*

The rat has been the subject of most electrophysiological studies investigating the cortical bases of tongue sensation and movement in non-primate mammals (Cullins et al., 2019; Guggenmos et al., 2009; Yamamoto et al., 1981, 1988); other early investigations were carried out in rabbits (Woosley and Wang, 1945; Gould, 1986), dogs (Bromiley et al., 1956) and raccoons (Welker and Seidenstein, 1959). Data across these species suggest that a tongue representation in the rostral portion of the ventral primary somatosensory cortex is broadly conserved across these species.

In the first intraoral stimulation electrophysiological experiment in rodent somatosensory cortex, Yamamoto et al. (1981) mechanically or thermally stimulated the tongue tip of Wistar rats (*Rattus norvegicus*) while recording the response of individual neurons of the rat somatosensory brain region (whose map was firstly reported by Welker, 1971). Yamamoto et al. (1981) found that the cortical targets of afferents responding to touch on the tongue have locations that do not overlap with regions previously shown to respond to taste (Yamamoto et al., 1980). Rather, tongue tactile and taste sensations was represented along a gradient within the ventral portion of the rodent somatosensory and gustatory areas (Yamamoto et al., 1980), with touch-responsive neurons located dorsally, thermal-responsive neurons centrally, and taste-responsive neurons more ventrally. Yamamoto et al. (1988) demonstrated that motor engagement might modulate this pattern; here, the authors recorded neurons in rats that were either induced to lick or exposed to passive repetitive touch. Some ventral mechanosensitive units were responsive only to passive tongue stimulation irrespective of motion direction, but more anterior neurons were responsive to both licking and food chewing.

Training of a new licking skill (e.g., licking with a constant and specific pressure) lowered the threshold for elicitation of motor responses but does not cause plastic changes in the architecture of the cortical tongue representation (Guggenmos et al., 2009). Similar findings were observed even when rats were trained to learn a new motor skill involving the tongue, like performing complex motor kinematics with the tongue to enable water release (Cullins et al., 2019). Clemens et al. (2018) described the response properties of the rat oral somatosensory cortex to passive mechanical stimuli (air puffs) of varying temperature, gustatory stimuli, and single-cell electrical stimulation. Their results suggest sensorimotor integration of stimuli within the oral somatosensory cortex, as the initiation of orofacial movements resembling feeding-related behavior (e.g., licking) was shown to be elicited by microstimulation of the oral somatosensory cortex. Although thermal stimuli were shown to be strongly represented (with larger responses to cold), taste-related information was encoded with no clear spatial tuning of responses to different gustatory stimuli (e.g., bitter, sweet and neutral).

In summary, the topography, the multisensory response properties, and the degree of plasticity of the non-primate sensorimotor tongue area in cortex have been at least preliminarily, if not conclusively, explored. Conversely, to our knowledge, none of the non-primate studies have directly investigated the degree of lateralization of tongue representation in somatosensory areas. The question of lateralization is one of both theoretical and clinical interest. The tongue is unusual in that it is a finely controlled appendage but is singular rather than duplicate and midline rather than lateralized, which is a notable contrast compared to the digits and limbs. This arrangements requires a high degree of coordination between muscles on both sides of the tongue. Clinically, dysphagia - often associated with tongue control (see below) - does not seem to be related to damage to one hemisphere or another (Daniels et al., 2017; Falsetti et al., 2009; Hamdy et al., 1999; Paciaroni et al., 2004). However, to our knowledge none of the behavioral paradigms used in non-primate mammal have addressed the separate or coordinated control and sensation of the two sides of the tongue.

2.2. Tongue representations in primate somatosensory cortex

Non-human primate research can provide a closer approximation to the neural architecture of the human primary somatosensory cortex due to the greater similarity in the tongue's form and function (Gillespie-Lynch et al., 2014) as well as the phylogenetical proximity (Bruce and Ayala, 1979; Siepel, 2009).

Gross brain anatomy is largely conserved across species (Brodmann, 1909; Passingham, 2009). The neurophenotypic similarity among primates is supported by gross genotypic similarity Genomic studies show that humans share between 92% (New World and Old World monkeys; Mattison and Vaughan, 2017, also see Fig. 7) and 96% (Chimpanzee, Pan troglodytes; Varki and Altheide, 2005) of genetic homology with non-human primates. Interestingly, one of the key genetic differences between human and non-primate mammals has been identified in genes that affect vocal learning and orofacial motor control (Condro and White, 2014).

The most informative studies have used invasive methods to study the brains of primates in greater detail than would otherwise be possible (for a review of the most relevant studies see: Kaas et al., 2006; Toda and Kudo, 2015). These studies are best interpreted in light of the phylogenetic relationships of their model species which have spanned New World monkeys, Old World monkeys and prosimian galagos (see Fig. 7).

In primate brains including humans, primary somatosensory area (S1) is organized in four cytoarchitectonic areas (Brodmann areas 3a, 3b, 1, and 2, see Fig. 8).[3] Areas 3b and 1 are primarily tuned to the perception of cutaneous inputs (Kaas, 1983), whereas areas 3a and 2 mainly receive thalamic inputs originating from receptors located on muscles (Krubitzer et al., 2004; Pons et al., 1985). Areas 3a and 3b are often called "S1 proper", and receive an abundance of inputs from the ventroposterior nucleus of the thalamus. Area 3b lies on the rostral bank of the post-central gyrus and chiefly represents the contralateral body surface in a mediolaterally elongated band of cortex. Along this mediolateral axis, all the bodily structures are represented in a roughly somatotopic manner with the face and the intraoral regions being represented in its most ventral portion (about one third of the S1, Iyengar et al., 2007).

Recording the activity of individual cortical neurons has been crucial for charting sensorimotor processing of the tongue (Martin and Sessle, 1993) as well as for delineating the receptive fields of single neurons (Toda and Taoka, 2002, 2004). However, an approach that is unique to non-human primate research is the application of electrophysiological mapping in combination with histological tracing (Jain et al., 1995). This technique consists of the subdermal injection of retrograde trans-synaptic tracers, which are transported from the receptor endings of sensory neurons in the periphery to cortical targets in the central nervous system. After electrical stimulation mapping of cortex, monkeys are sacrificed, and their brains are dissected and evaluated for tracer presence and spread. The pairing of electrical stimulation and histological tracing studies in the same animal provides a highly detailed, bidirectional, and robust mapping between the sensory periphery and cortex. Due to the strong phenotypic and genetic similarities between humans and non-human primates (as discussed above), electrophysiological mapping combined with histological tracing provides valuable insights into the cortical organization of both non-human and human primates.

2.3. Multiple tongue-responsive fields in primary somatosensory cortex of non-human primates

The conceptualization of primate somatosensory cortex as a medial-to-lateral, "tail to tongue" somatotopic map is not a new one (Woolsey et al., 1942). Tongue-responsive neurons were found in early recording studies in both Old World monkeys (Macaques, *Macaca mulatta*; Marshall et al., 1937) and New World monkeys (Spider monkeys, *Ateles Ater*; Pubols and Pubols, 1971), with single units located in the ventral portion of S1 responding to light mechanical stimulation of the contralateral side of the tongue.

However, the idea that a given body part like the tongue has a single representation in S1 was challenged quite early. In particular, different receptor types that respond to different touch submodalities (e.g., texture, strain or vibration) on a given body part (e.g., the tip of the tongue) have cortical targets which are unevenly distributed in separate architectonic fields across S1 (Powell and Mountcastle, 1959). Multiunit microelectrode recordings from the ventral portion of somato-motor cortices of Old World monkeys (macaques, *Macaca mulatta*, Dreyer et al., 1975 and *Macaca fascicularis,* Nelson et al., 1980) and New World monkeys (owl monkeys, *Aotus trivirgatus*, Merzenich et al., 1978; squirrel monkeys, *Saimiri sciureus*, Cusick et al., 1986; white-fronted capuchin monkey, *Cebus albifrons,* Felleman et al., 1983) suggested that the intraoral cavity and tongue (as well as other body parts; Kaas et al., 1979) are represented several times in a mosaic of spatially and cytoarchitectonically distinct areas. Furthermore, different cortical representations of the tongue appear to vary as a function of the tactile submodality that they represent, along with the size of their peripheral receptive fields (Dreyer et al., 1975).

For example, the ventral portion of area 3b and the anterior aspect of ventral area 1 receive inputs generated by the light mechanical stimulation of superficial skin and mucosal sites (e.g., the tongue dorsum or the lip, Merzenich et al., 1978). Although preliminary mapping studies with New World monkeys show inconsistencies in the representation of some face parts across areas 3b and 1, with light mechanical cutaneous stimulation being processed only in area 3b (Sur et al., 1982), later investigations conducted on New World monkeys support a double representation of light mechanical stimulation of the tongue surface across both areas 1 and 3b. Similar findings were also observed in Old World monkeys (Nelson et al., 1980). Although the two tongue representations in areas 3b and 1 have a very similar organization and are approximate mirror images of each other (Felleman et al., 1983), they differ in their relative size, with the representation of face and intraoral structures being 35–40% larger in area 3b than in Area 1 (Merzenich et al., 1978), thus suggesting that the level of cortical magnification for the tongue is quite high within area 3b, but less so in area 1.

The ventral portion of areas 2 and 3a and the posterior aspect of ventral area 1 respond to lateral tongue stretch and sustained tongue pressure (Dreyer et al., 1975). Since area 2 has been shown to contain systematic representations of deep body structures (like joints or muscles, Merzenich et al., 1978), anatomic fields within area 2 may contain a representation of stimuli generated in the deep lingual musculature, conveyed to the cortex by CN XII (see section 1.4).

2.4. Functional organization of tongue-responsive fields in primary somatosensory cortex of non-human primates

The functional organization of primary somatosensory (particularly area 3b, Krubitzer and Kaas, 1990) and visual cortices (areas 17 (V1) and 18 (V2), see Boynton and Hegdé, 2004; Casagrande and Kaas, 1994; Froudarakis et al., 2019 for reviews) is often examined in tandem with architectonic mapping of the post-central gyrus as the cytoarchitectonic borders and internal structure can be unambiguously identified using a combination of staining for myelin, cytochrome oxidase, and other cellular or molecular markers. An understanding of the cellular composition of these areas also supports our understanding of how they

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[3] M1 and S1 as functional and cytoarchitectonic definitions are often confounded with the anatomical landmarks of the pre- and post-central gyri. The primary motor or primary sensory cortex (Brodmann's area 4, or areas 3a/3b), are instead lie within the central sulcus, where they are inaccessible to traditional ECoG surface electrode grids.

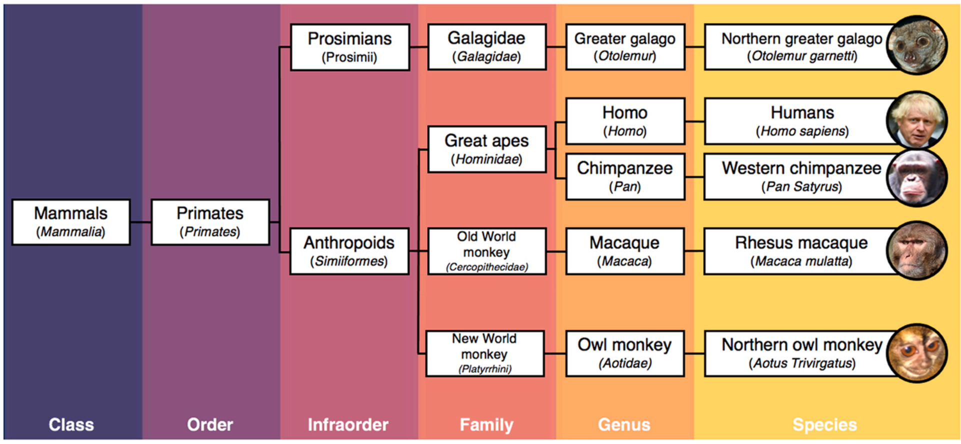

Fig. 7. Phylogenetic tree showing inter-species relations within the order of primates. The species shown in the right panel have been recruited as experimental sample in the studies reviewed in the current paper. Scientific names of class, order, infraorders, families, genera and species are shown between brackets.

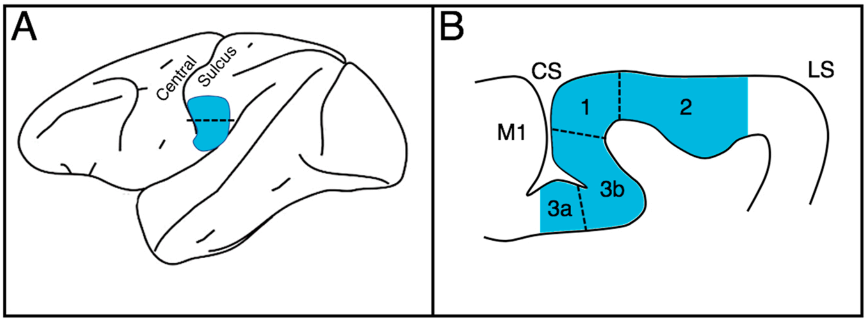

Fig. 8. (A) Lateral view of primate's brain (macaque). The coloured area roughly corresponds to the location of the ventral portion of the primary somatosensory cortex (S1), which responds to the stimulation of orofacial structures. The dashed line corresponds to the section shown in **B**. (B) Cytoarchitectonic divisions of the posterior bank of the central gyrus (Brodmann areas 3a,3b,1,2). Dotted lines indicate the boundaries of cytoarchitectonic areas. CS=central sulcus, LS=lateral sulcus.

function.

Barrels (Catania and Kaas, 1995) or *ovals,* (Jain et al., 2001) have been defined as anatomically distinct subunits within area 3b. Ovals are separated by distinct myelin septa, and have been shown to independently respond to light mechanical touches delivered to discrete peripheral sites (like the palm and different digits, Jain et al., 1998). Neurons within the same oval often have similar receptive fields properties, (e.g., they respond to touches delivered on the same peripheral bodily region, like the contralateral tongue).

Early comparative studies (Green and Walker, 1938; Walker and Green, 1938) examined the functional relevance of receptive fields using unilateral surgical ablation of the S1 and M1 tongue areas in Old World monkeys (Macaques, *Macaca mulatta*; Baboons, *Papio papio*; Mangabey, *Cercocebus aethiops*), Great Apes (Chimpanzees*, Pan Satyrus*) and New World Monkeys (Spider monkey, *Ateles Ater*). These studies showed residual ipsilateral neural responses for lateralized mechanical stimuli delivered on the tongue (Walker and Green, 1938). Similarly, feeble self-generated lateralized retractions of the tongue could still be performed after cortical ablation of the contralateral tongue area in the primary somato-motor cortex (Green and Walker, 1938). These findings suggest that somato-motor tongue representations receive direct somatosensory input or direct motor output, both contralaterally *and* ipsilaterally.

Tongue-responsive neurons with ipsilateral peripheral receptive fields have been reported in microelectrode recording studies with both New World (owl monkeys, *Aotus trivirgatus*, Cusick et al., 1989; squirrel monkeys, *Saimiri sciureus*, Manger et al., 1995) and Old World Monkeys (crab-eating macaque, *Macaca fascicularis*, Jones et al., 1986). A later study of owl (*Aotus Trivirgatus*) and squirrel monkeys (*Saimiri sciureus*, Jain et al., 2001) used a composite of electrophysiological mapping and histological tracing methods to record area 3b neural responses to gentle tapping that was applied on several facial and intraoral regions (see Fig. 9A). Several discrete myelin-dense ovals corresponded to ipsilateral and contralateral representations of the teeth and tongue, with a complex and interdigitated topography. In particular, the inferior part of area 3b contained an ipsilateral sensory representation ventrally, and a contralateral sensory representation more dorsally. Both the contralateral and ipsilateral zones contained separate representations for the teeth and tongue. This configuration has been observed by more recent studies conducted with New World monkeys (owl monkeys, *Aotus trivirgatus*; squirrel monkeys, *Saimiri sciureus*; marmoset, *Callithrix Jachus*, Iyengar et al., 2007), prosimian primates (e.g., northern greater galago, *Otolemur Garnetti,* Sur et al., 1980; Kaas et al., 2006, see Fig. 9B) and Old World monkeys (see Fig. 9C), including various macaque species (*Macaca radiata* and *Macaca mulatta,* Cerkevich et al., 2013, 2014; *Macaca nemestrina*, Manger et al., 1996; *Macaca fuscata* and *Macaca fascicularis*, Ogawa et al., 1989; *Macaca fuscata*, Toda and Taoka, 2002).

As shown in Fig. 9, there are slight differences in the neural architecture of the portion of S1 that responds to mechanical stimuli within the intraoral cavity in Old World and New World monkeys (Cerkevich et al., 2014; Qi and Kaas, 2004). In Old World macaques, the arrangement of the myelin-dense ovals representing contralateral and ipsilateral intraoral structures (dentition and tongue) is oriented mediolaterally.

Contralateral representations of the teeth and tongue lay in the posterior bank of the central sulcus within area 3b, while ipsilateral representations are found more anterolaterally, lateral to the tip of the central sulcus on the exposed surface of the cerebral cortex within the anterior portion of area 3b. This interdigitated topography is observed in

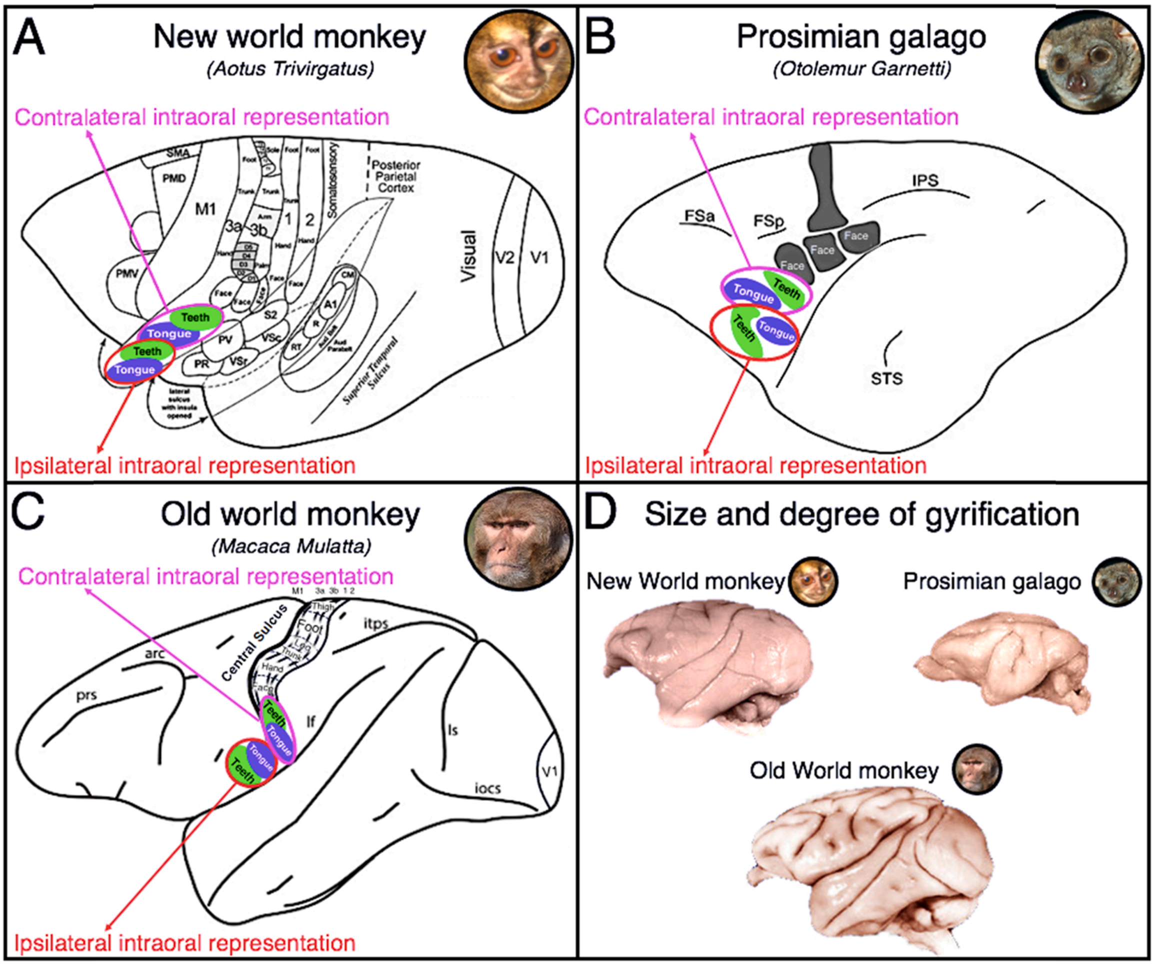

Fig. 9. Contralateral and ipsilateral neural representation of oral structures (teeth and tongue) in New World monkeys (Owl monkeys, Aotus trivirgatus, A), Prosimian galago (Otolemur Garnetti, B) and Old World monkeys (Macaque, Macaca mulatta, C). (D) Degree of gyrification of cerebral structures across human and non-human primates (brain images were provided by the Comparative Mammalian Brain Collection at the University of Wisconsin-Madison and Michigan State University).

Images were adapted from Kaas A and B) et al. (2006) and a composite of maps was adapted in **C** from Rushmore et al. (2019) and Manger et al. (1996).

both New World monkeys and galagos; by contrast, in macaques a mirror image arrangement across the central sulcus has been observed (Manger et al., 1996;see Fig. 9C).

Combined multiunit microelectrode recording and histological tracer injections have also been used to characterize cortico-cortical projections between area 3b and other cortical sites within and beyond S1 in New World (owl, squirrel, and marmoset, Iyengar et al., 2007) and Old World (macaque, Cerkevich et al., 2014) monkeys. The tongue area within area 3b projects to areas 3a, 1, and 2, as well as to the secondary somatosensory area (S2), the gustatory cortex (which lies on the anterior insula, at the base of the central sulcus; Ogawa, 1994), primary motor, and premotor areas (Cerkevich et al., 2014; Iyengar et al., 2007). These cortico-cortical projections linking various tongue representations across different primary sensory areas might exert a crucial role in allowing populations of neurons with multisensory response properties to communicate across different cortical sites. In other words, in parallel with non-primate findings (see section 2.1), cortico-cortical connections may promote the interaction of M1 (primary motor cortex) and S1 neurons responding to motor actions executed with the tongue (e.g., tongue protrusion, see section 2.5).

In sum, although the structural organization (Nieuwenhuys, 1994) and the relative size and degree of gyrification of the cerebral structure varies across families of primates (Hofman, 2014 see Fig. 9D), mapping studies with different primate species suggest that multiple submodality-specific tongue representations across different cytoarchitectonic areas have consistent properties across non-human primate families (Krubitzer, 1995; also see Table 2).

2.5. Somato-motor response properties of tongue-responsive somatosensory neurons in non-human primates

Integrating information across sensory modalities supports a richer perception of the sensory environment within the internal milieu of the mouth. Multisensory integration is crucial for perception (Briscoe, 2016; Stein and Meredith, 1993). The accuracy of perception in a given sensory modality and the control of perceptually guided actions are often enhanced when multisensory signals are available (for reviews, see Stein, 2012 and Stokes et al., 2015). Multisensory information - for instance simultaneous input from vision and proprioception - permits more accurate guidance and coordination of motor actions (Goodale, 2014). However, the intraoral cavity is an unusual case, in that actions performed with the tongue, such as moving food within the mouth during mastication, receive little sensory support from vision as the tongue itself is not typically visible. Rather, gustatory (Todrank and Bartoshuk, 1991), olfactory (Duffy, 2007), auditory (Schneider and Mooney, 2018) and tactile/proprioceptive inputs (Danilov et al., 2007; Jansson, 1983; Lamm et al., 2005; Lozano et al., 2009; Pamir et al., 2020; Vuillerme et al., 2008) guide the execution of most intraoral daily activities. Tactile perception is particularly important: for instance, the perception of tactile features of food particles on the tip of the tongue is essential for eliciting the complex series of movements involved in swallowing.

Somatosensory cortical organization seems to reflect such a need for multimodal integration. The ventral portion of primate S1 is tuned not only to somatosensory inputs arising from different regions of the tongue musculature and surface, but it also receives connections from the ventral portion of the primary motor cortex (Toda and Kudo, 2015). The integration of touch with the proprioceptive cues generated by movement is demonstrated by several studies that have investigated how neural responses in S1 are modulated when animals produce self-generated movements of the tongue (Lin et al., 1994a, 1994b; Lin and Sessle, 1994). Lin et al. (1994a) found that the firing rate of the majority of neurons within the orofacial portion of the non-human primate S1 to contralateral passive mechanical touch can be modulated by execution of self-generated actions like tongue protrusion and biting. However, the rate at which somatosensory neuron firing rates adapted (either slowly or rapidly adapting) to tongue motor actions did not predict how their firing rate was modulated (e.g., phasic, tonic or decreased) during the execution of motor tasks. These findings suggest that although somato-motor tongue neurons in S1 play a role in motor control guidance, the way in which neurons respond to tactile stimulations received on the tongue in resting conditions cannot predict their activity pattern during tongue movements. In other words, although S1 has been shown to encode both motor and sensory actions, it responds differently to tactile stimuli and motor actions.

Lin et al. (1994b) further observed that neurons within ventral S1 have directional sensitivity, such that their firing rate varies as a function of the direction of tongue protrusion. Although S1 and M1 both encode the direction of tongue movements, the directional-dependence of firing rates in S1 is stronger (Arce et al., 2013). In line with previous data (Lin et al., 1994a) and with findings on other motor effectors (e.g., the arm; (Arce et al., 2013; Georgopoulos et al., 1986; Hatsopoulos et al., 2004; Quian Quiroga et al., 2006; Shenoy et al., 2003), the laterality of the receptive fields of somato-motor tongue-responding neurons within S1 after passive mechanical stimulation did not predict their directional sensitivity during the execution of motor actions. In other words, a neuron preferentially responding to mechanical touches delivered on the left side of the tongue did not necessarily alter its firing rate during lateralized tongue protrusions to the left of the mouth despite producing similar tactile stimulation on the surface of the tongue.

Altogether, these data show substantial interplay between tongue motor actions and the activity of S1 tongue-responsive neurons. Intriguingly, the pattern of somato-motor neural responses during passive tactile stimulation does not correlate with their response before or during the execution of lingual tasks. We suggest that tongue-responsive neurons within S1 may have two general processing modes. One mode might encode the sensory properties of tactile events, whereas the other processing mode might provide subsidiary guidance to tongue fine motor control.

Given the presumptive involvement of somato-motor S1 tongue-responsive neurons during tongue motor tasks, another crucial question resides in understanding how perceptual inputs originating in S1 are then transferred to motor cortices to guide and integrate motor execution. A network of bilateral cortico-cortical connections between and within somatosensory and motor cortical areas (Hatanaka et al., 2005; Huang et al., 1989a; Huang et al., 1989b) may transmit hybrid somato-motor inputs generated in somatosensory areas to motor and premotor areas, which similar to the control of other effectors (Chen, 2004; Tamè et al., 2015). This somato-motor connectivity in S1 may play a crucial role in guiding and refining the execution of intraoral movements. Similarly, tongue movements generate tactile and proprioceptive information that may then be transmitted between cerebral hemispheres through bilateral cortico-cortical connections via the corpus callosum. Given that the electrical stimulation of the tongue somatosensory area alone can elicit tongue movement (Huang et al., 1989a; Hatanaka et al., 2005; Arce et al., 2013), we suggest that tactile capacities of the tongue and its neural representation in S1 would then represent a potential lingual sensory-motor *jumpstarter* (or a facilitator) which can be then used to guide and enrich the experience of self-generated tongue motor functions.

2.6. Plasticity of the somato-motor tongue representation in non-human primates

Non-human primates heavily rely on their mouth to carry out a wide range of daily functions, ranging from foraging (Manrique and Call, 2011) to tool use (Hayashi, 2015; Sirianni et al., 2018; Simpson et al., 2019; Manrique and Call, 2011) and vocalizations (Koda et al., 2018). Given this range of behaviors, learning a new motor skill involving the tongue is not uncommon in the non-human primate experience. For instance, an orangutan manipulating a newly acquired stick with his mouth and tongue must learn how much force to exert with each tongue muscle in order to hold the stick steady (Fox et al., 1999; O'Malley and McGrew, 2000). Such motor learning involving novel objects has been used as a test for plasticity in the motor system, albeit typically using digital or manual manipulation.

For instance, several studies on New World Monkeys (Owl monkeys, *Aotus trivirgatus*, Jenkins et al., 1990; Recanzone et al., 1992; Wang et al., 1995; Squirrel monkeys, *Saimiri boliviensis Peruviensis*, Nudo et al., 1996) show that learning a new skill involving digits (e.g., vibration discrimination or pattern detection) elicits plastic functional reorganization of the hand representation in both M1 (Nudo et al., 1996) and S1 (Jenkins et al., 1990). With such learning, S1 neurons have shown modified temporal response properties (Recanzone et al., 1992) and altered neuronal response specificity after training (Wang et al., 1995).

A number of studies have shown that the somatosensory tongue representation is dynamic, and adapts to short- and long-term changes in either movement or in the internal milieu. In line with a number of studies on rats (see Section 2.1), several studies on Old World monkeys (Macaques, *Macaca mulatta*) have shown that learning a new orolingual motor task like tongue protrusion affects somato-motor neuronal response as well as neuronal temporal dynamics (Arce-McShane et al., 2014, 2016; Sessle et al., 2005, 2007).

Preliminary studies (Sessle et al., 2007, 2005) showed that over a short time scale, a newly-trained tongue protrusion task led to an increased proportion of responsive neurons within ventral S1 and M1. The increased proportion of S1 and M1 task-modulated neurons was maintained over time, and was still present two weeks after the cessation of training. These changes at the cortical level are associated with greater success in learning the novel behavior (Arce-McShane et al., 2014). Orolingual training also reduced the across-trial firing rate variability, and both S1 and M1 neurons conveyed more information about tongue protrusive force after training (Arce-McShane et al., 2014). Finally, learning new motor skills involving the tongue also modified the temporal dynamics of both S1 and M1 neurons, with patterns of synchronized spiking and local field potentials - which have shown to be implicated in neural communication and neuroplasticity (Singer and Gray, 1995; Thorn and Graybiel, 2014) - emerging across somato-motor areas a few days after lingual motor training (Arce-McShane et al., 2016). The available data show that the somato-motor representation of the tongue is experience-dependent and plastically reorganized to support the behavioral flexibility of primates.

2.7. Neural representation of self-generated tongue actions in non-primates and non-human primate motor cortex

Although the motor and premotor cortex have been the primary focus of interest of many primate and non-primate studies conducted during the last 150 years, the *kind* of information potentially encoded by these cortical areas has only started to be clarified during the last two decades (Graziano, 2016). In particular, the motor cortex of both non-human primates (Graziano et al., 2002) and non-primates (e.g. mice and rats, Ebbesen et al., 2018) is characterized by a very rough, mosaic somatotopical arrangement with different cortical sites tuned to specific *behavioral categories* (e.g., grasping). Complex self-generated actions that involve several effectors including the tongue - such as grasping food with an hand and bringing that to the mouth for mastication - are represented in ventral portions of the motor cortex in non-primates (Yamamoto et al., 1988), Old world monkeys (Macaques, *Macaca nemestrina*, Ferrari et al., 2003; Gallese et al., 1996; Gentilucci et al., 1988; Maranesi et al., 2012; Rizzolatti et al., 1988; for a review also see Ferrari et al., 2017), New World monkeys (squirrel monkeys, *Saimiri sciureus* and owl monkeys, *Aotus trivirgatus*, Gharbawie et al., 2011) and prosimians (Northern greater galago, *Otolemur Garnetti,* Stepniewska et al., 2009).

Although these studies demonstrate how feeding-related actions or hand-to-mouth movements are represented in motor cortices of both primates and non-primates, they do not directly investigate how the tongue itself is represented. The actions used in previous paradigms (e.g., hand to mouth movement or licking) often involve other body parts, such as the hand or other intraoral surfaces. As a consequence, knowledge about the representation of motor actions involving only the tongue in non-human primates is still coarse and would benefit from new paradigms in which animals are trained to perform self-generated actions involving only the lingual musculature.

3. Neural bases of tongue sensory-motor processing in human normative and clinical populations

The human tongue is a complex muscular structure that is jointly controlled by voluntary motor processes (i.e., speech production) and automatic or unconscious motor processes (i.e., reflexive swallowing, vegetative respiration). However, otherwise automatic movements can also be subject to voluntary control (i.e., volitional swallowing, speech breathing, breath holding: Martin-Harris, 2006; Matsuo and Palmer, 2009). Accordingly, the following sections review neuroscientific research on the neural pathways serving the tongue as an organ of sensation, as well as voluntary and automatic movement (also see Table 2).

3.1. *Cortical representation of human tongue somatosensation*

The cortical representation of the tongue has been studied using various neuroimaging tool like MRI. However, the anatomical position of the tongue within the oral cavity, and the space constraints around the head that are inherent in MRI (through both the bore diameter and RF coil dimensions) impose practical obstacles to delivering mechanical stimulation to the tongue. All intraoral tissues (tongue included) are covered with an extra layer of biofilm which is composed of saliva (Watanabe and Dawes, 1990), bacteria (Gizani et al., 2009) and various additional proteins (Pramanik et al., 2010). The thickness of this layer is not constant over time but varies as a function of the salivation secretion rate (Naumova et al., 2013), at a rate modulated by external factors, as any dental patient can attest. The average thickness of the salivary film varies from 0.07 mm before swallowing to 0.10 mm during the peak of the swallowing process (Collins and Dawes, 1987). The intrinsic viscosity of the oral biofilm makes the point of application of stimuli less precise - particularly if electrical stimulation were used - thus increasing the apparent variation between individuals if stimulated at difference phases of salivary secretion. More prosaically, the experience of having one's tongue stimulated while lying down and staying as still as possible during scanning can be quite a challenge even to the experienced MRI participant. It is perhaps not surprising that many more studies have investigated somatosensation in the much more accessible hands, feet, and limbs. Although studies using various non-invasive (e.g., fMRI, PET and MEG) and invasive (e.g., ECoG) methods have attempted to overcome the technical and practical difficulties of stimulating the human tongue in neuroimaging contexts, only relatively coarse and preliminary evidence is available regarding the organization of cortical sites responding to mechanical, non-noxious stimuli applied on the tongue in humans.

Using functional magnetic resonance imaging (fMRI), specific subregions within S1 have been shown to respond selectively to mechanical stimulation delivered manually (at the frequency of ~1 Hz) on three different intraoral surfaces: the right lower lip, the right maxillary incisor, and the right anterior portion of the tongue (Miyamoto et al., 2006). Activation in response to contact with all three surfaces was observed only contralaterally to the side of stimulation and appeared to follow the somatotopic arrangement expected from other primates. Within ventral S1, an orderly somatotopic map was maintained following a dorsal to ventral axis representing the lips, teeth, and tongue, respectively (3 Hz, Sakai et al., 1995).

Roughly similar findings were observed also in different positron emission tomography (PET) studies delivering either manual strokes (Pardo et al., 1997) or vibrotactile stimulations (Boling et al., 2002) to both sides of the tongue. In addition to cortical responses contralateral to the stimulation (ventral portion of areas 3/4, at approximately 28 mm above the intercommissural plane, Pardo et al., 1997), ipsilateral foci at the central sulcus were also evident only in the left but not in the right hemisphere. Although the authors speculated that the atypical pattern of regional cerebral blood flow responses to tactile stimulation of the tongue may arise from the role of human tongue in speech production, bilateral responses have been reported in a later PET study (Boling et al., 2002) and we note that the absence of activation in one hemisphere is weak grounds on which to conclude a functional difference between hemispheres. Similar findings were also observed in a fMRI study applying a soft cotton pad soaked in saline to either side of the tongue (Mascioli et al., 2015).

The cortical representation of the tongue may be lateralized, and this lateralization may vary across subdivisions of the tongue surface and be modulated by experience. For example, unconscious preferences in the sidedness of masticatory movements – called chewing-side preference (Diernberger et al., 2008; Pond et al., 1986) and equivalent to sidedness effects observed for the hand (Jung et al., 2003, 2008)- have been shown to have an influence on the pattern of cortical activation. Passive stimulation to the tongue on the preferred chewing side of the mouth activates S1 more strongly than the non-preferred chewing side (Minato et al., 2009). However, the right hemisphere may be overall more dominant for processing passive touch to the tongue, as right hemisphere fMRI activation is observed more robustly during stimulation to either side of the tongue (Sakamoto et al., 2010). This right-hemisphere activation bias may be particularly present for the postero-lateral tongue surface (although see Sakamoto et al., 2008; Minato et al., 2009; Pardo et al., 1997 for evidence not supporting this activation bias). More generally, differences in cortical activation for subsections of the tongue might be related to the pattern of cranial nerve afferents innervating the anterior and posterior portions of the tongue (Kandel et al., 1991; also see section 1.4 for further details). Somewhat surprisingly, and in contrast with other body parts (e.g., leg; Dietrich et al., 2017) the pattern of organization of S1 responding to the tongue preserves the basic dermatomal structure of the spinal cord (Kirshblum et al., 2011).

Finer timing information regarding tongue-related somatosensory responses has been shown with magnetoencephalography (MEG) using Somatosensory Evoked Fields (SEFs) in response to tongue stimulation. In these studies, stimulation was always non-noxious and ranged from mild electrical stimulation (Karhu et al., 1991; Maezawa et al., 2008; Nakahara et al., 2004; Sakamoto et al., 2008) to the application of passive mechanical stimuli, typically in the form of strokes delivered manually with a stick (Disbrow et al., 2003; Nakamura et al., 1998; Tamura et al., 2008; Yamashita et al., 1999). Early components of lingual SEFs were observed bilaterally either at 14 ms (Tamura et al., 2008) or at 19 ms after stimulation (Sakamoto et al., 2008).

Middle-latency components were also identified bilaterally, with a peak latency ranging from 25 ms to 80 ms across different studies (Disbrow et al., 2003; Karhu et al., 1991; Maezawa et al., 2008; Nakahara et al., 2004; Nakamura et al., 1998; Yamashita et al., 1999). Although all studies reported initial and middle-latency components as originating from bilateral S1 though some caution is merited given the challenge of MEG source localization, some evidence supports contralateral dominance (Tamura et al., 2008).

Electrocorticography (ECoG) and stereotactic EEG (sEEG) are invasive electrophysiological methods that measure the electrical activity of exposed brain regions by placing electrodes directly on the cerebral cortex, or implanting contacts within cortex. Used exclusively in clinical populations (especially epileptic patients) to localize and then surgically remove the precise origin of seizures (Engel, 1996), these techniques also bridge human results with invasive intracranial non-human studies. Much of our knowledge about human primary sensorimotor cortex is due to exceptional early studies led by Krause (1911), Foerster (1936) and Penfield and collaborators (Penfield and Boldrey, 1937; Penfield and Rasmussen, 1950; Penfield et al., 1954; Penfield, 1958) which extensively used invasive cortical electrical stimulation for surgical treatment of epilepsy. Using this technique, they located the cortical representation of intraoral cutaneous stimuli in a ventral portion of S1 in humans, which if stimulated elicited sensations of intraoral touch.

ECoG and sEEG have been used to investigate and further refine the neural representation of the tongue in humans - clinically vital given the cortical tongue area must be spared during cortical resection to avoid postoperative dysphasia (Rasmussen, 1975). Breshears et al. (2015) summarize results from several ECoG studies, suggesting that the human tongue area occupies a fairly wide portion of ventral somatosensory cortex, extending superiorly up to 5 cm above the Sylvian fissure, and posteriorly along the suprasylvian bank of the central and parietal operculum (defined as the cortex laterally adjacent to the insula and often referred to as S2, Mălîia et al., 2018). The tongue representation extends over most of the postcentral sulcus (3 cm posterior to the central sulcus; Urasaki et al., 1994), with area 1 having the largest relative cortical area devoted to the tongue (~2.5 cm, Roux et al., 2018).

ECoG studies have also shown that different tongue regions are finely somatotopically represented, with the tip of the tongue being represented dorsally relative to the back of the tongue (see Fig. 10, Picard and Olivier, 1983; Boling et al., 2002; Roux et al., 2018).

Most ECoG studies report that the number of cortical sites representing different tongue regions is unevenly distributed, with the majority of 'tongue sites' showing preferential activity for the tip of the tongue (Buren, 1983; Picard and Olivier, 1983; Tanriverdi et al., 2009). However this view is challenged by more recent studies (e.g., Roux et al., 2018) that aimed at mapping the human somatosensory cortex in a large number of subjects. They reported that within the S1 tongue area most electrode contacts responded preferentially to the tongue body (or middle tongue, see section 1.1, Roux et al., 2018). Although the tongue representation within the ventral portion of the postcentral gyrus shows a clear superior-to-inferior pattern, ECoG studies do not report any tongue somatotopy along the rostral-to-caudal axis of S1 tongue representations (Roux et al., 2018).

In addition to a tongue-responding area, the somatotopical arrangement of human S1 includes a representation of different intraoral regions interacting with the tongue during speech (e.g., soft palate: Carey et al., 2017). These multiple representations mostly overlap with those of other lower face regions (e.g., lips and cheeks: Sereno and Huang, 2006) and have high potential relevance to speech production. Alveolar (e.g., /t/), retroflex (e.g., /ʈ/), palatal (e.g., /c/) and velar (e.g., /k/) consonants are differentiated by the interplay of different tongue regions (tip: alveolar and retroflex; body: palatal; base: velar) and other intraoral structures, such as the alveolar ridge (Bouchard et al., 2013; Carey et al., 2017). Tongue sensations processed in different cortical sites specifically responding to a portion of the tongue (e.g., the tip of the tongue) could be independently transferred – via putative cortico-cortical connections (Battaglia-Mayer and Caminiti, 2019) – to M1 areas representing specific effectors involved in the production of complex vocalized sounds. This putative cortical arrangement could then enhance the fine intraoral sensorimotor control necessary for human speech production (Behroozmand et al., 2015).

Studies using ECoG electrodes for *direct electrical stimulation* (Picard and Olivier, 1983; Tanriverdi et al., 2009), suggest that the tongue has a predominantly contralateral S1 representation. Picard and Olivier (1983) stimulated multiple tongue sites, with patients reporting 87% contralateral somatosensory responses, with only few units showing either a ipsilateral (6%) or bilateral responses (7%, Picard and Olivier, 1983). However, neurons responding to the ipsi- or bilateral tongue are not reported in subsequent studies (Tanriverdi et al., 2009). More recent studies addressed this point by showing that electrical stimulations of the tongue area within S1 elicits responses (e.g., tingling sensations) predominantly on the contralateral side of the tongue (Roux et al., 2018).

Despite these advances in our understanding permitted by non-invasive neuroimaging and ECoG/sEEG, our knowledge of human tongue somatosensory representation is still quite coarse. Although all

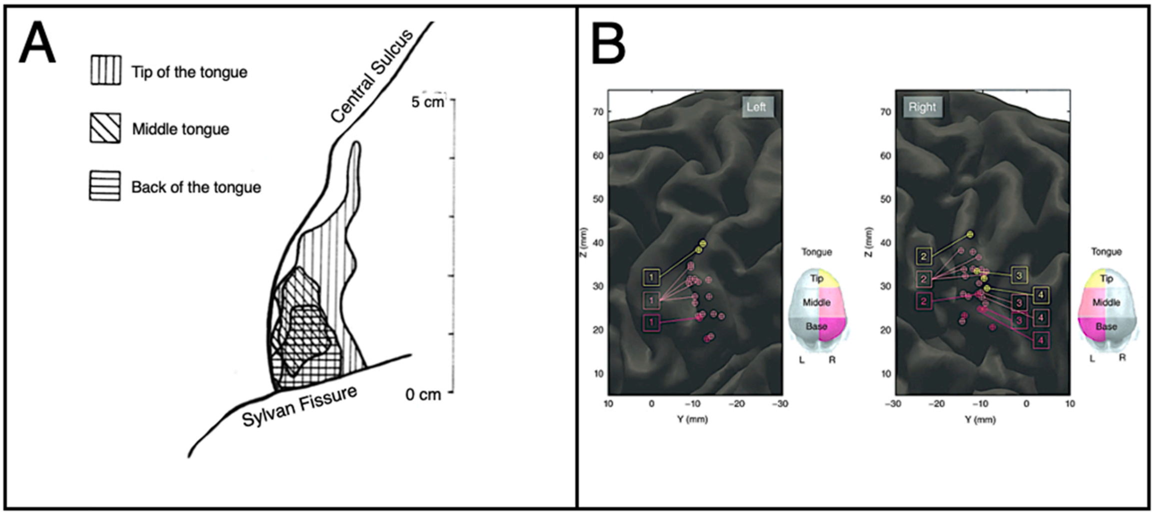

Fig. 10. Somatotopic arrangement of tongue sensory responses in the ventral portion of the postcentral gyrus.
Adapted from Picard and Olivier, 1983 and Roux et al., 2018).

studies reported here support a contralateral representation of somatosensory inputs, ipsilateral processing of somatosensory stimuli is only observed inconsistently. This configuration is also observed in studies with either higher spatial resolution (e.g., fMRI studies) or temporal resolution (e.g., MEG studies), thus suggesting that this result is not the result of methodological limitations. Finally, preliminary evidence from intracranial recording studies (Picard and Olivier, 1983; Tanriverdi et al., 2009; Roux, 2018) suggest that the sensory-motor representation of tongue in humans may be quite finely somatotopically organized. Rather, in parallel with the fingers (Mattos et al., 2015), the observed results could depend on the fact that contralateral and ipsilateral responses are motor-task-specific. These studies pave the way for asking more detailed questions about cortical tongue somatosensory representation - for instance the segregation/integration of more complex tongue somatosensory features or whether different tongue regions (or afferent input transduced by different cranial nerves) are somatotopically organized in the ventral portion of the tongue cortical area in humans.

3.2. *Cortical representation of voluntary tongue movements*

An advantage that human studies have over non-human studies (both primates and non-primates, see section 2.7) is that human participants can easily be instructed to perform actions solely involving the tongue, whereas non-human animals require extensive behavioral training; it is also difficult to train isolated movements. In line with non-human findings in primates, complex actions that require the coordination of hand and mouth (such as self-feeding or perioral exploration) have integrated representations in the ventral portion of the precentral gyrus (Desmurget et al., 2014). However, the specificity in the actions performed by humans allows us to draw more accurate conclusions on how solely tongue-related actions might be represented in precentral cortical areas.

Functional Magnetic Resonance Imaging (fMRI) studies investigating the neural representation of the oral cavity have given particular attention to the motor representation of the tongue (Corfield et al., 1999; Lotze et al., 2000; Riecker et al., 2000; Stippich et al., 2002; Fesl et al., 2003; Shinagawa et al., 2003; Xiao et al., 2017) often in relation to the adjacent representation of the lips (Gerardin et al., 2003; Hanakawa et al., 2005, 2017). The response properties of the ventral portion of M1 have been investigated by using a heterogeneous set of methods and experimental paradigms (see Table 1 for a visual summary of the results). The question of laterality has been of particular interest in human studies: experiments show consistent bilateral activation in response to non-lateralized tongue protrusions (Corfield and colleagues (1999); Hesselmann et al., 2004; Meier et al., 2008), with few exceptions(Vincent et al., 2006; Grabski et al., 2012).[4]

Although lateralized tongue movements are commonly used in clinical practice as a training technique to improve oral and pharingeal swallowing in dysphagic patients (Milazzo et al., 2019), they have also been used to investigate the topography of the tongue representation M1. In neurologically healthy humans, these movements evoke bilateral activation along the ventral precentral gyri (Ogura et al., 2012; Riecker et. al, 2000, Fesl et al., 2003).

Using focal transcranial magnetic stimulation (TMS) on the tongue motor area (mainly sending signals through the hypoglossal nerve (see section 1.4)), motor evoked potentials (MEP) of lingual muscles have also been bilaterally elicited (Rödel et al., 2003). Despite the overall bilateral pattern of cortical activation, higher mean amplitudes were observed contralateral to the stimulation side. MEG-based Movement Related Cortical Fields (MRCFs) - typically used to examine sensorimotor processing in the upper and lower limbs (Hari et al., 1983)- have also been used to probe the organization of the neural motor representation of the oral cavity (Cheyne et al., 1991). Cheyne et al. (1991) observed that MRCFs were observed over the left hemisphere after execution of repetitive horizontal self-paced, non-lateralized tongue protrusions, with the source of the magnetic field being estimated to be originating from the ventral portion of the left motor area.

Again using MRCFs, Nakasato et al., (2001) showed a similar pattern of results when limiting the degree of motion of participants' tongue and controlling the execution timing of the motor task. Later experiments (Maezawa et al., 2017) identified bilateral MRCFs originating from the ventral portion of the motor area, both before and after voluntary self-paced tongue movement using a trigger signal based on tongue electromyogram (EMG) data.

A further line of research directly targeted the question of neural lateralization of intraoral surface representation. Preliminary insights were first provided by a single case study (Chen et al., 1999), who showed that TMS to either hemisphere elicited motor responses on a given side of the tongue, thus suggesting a bilateral representation of either side of the lingual muscle. The study was later replicated in a larger sample (Svensson et al., 2003). While a later study (Maezawa et al., 2014) still supports a bilateral representation of the tongue within the ventral portion of M1, it also suggests a contralateral hemispheric dominance in tongue motor control, with the oscillatory activity within M1 as measured by EEG showing greater coherence with the muscle asctivity in the contralateral tongue as measured by electromyography (EMG).

Although the lion's share of evidence currently available seem to support a bilateral tongue action representation in humans, further research is needed to consolidate the current knowledge regarding the neural representation of non-verbal voluntary tongue movements in humans. Bilateral representation of actions in the motor cortex is not an isolated case for the the tongue, but it has also been observed for several other body parts (i.e, limb: Heming et al., (2019); hand (Horenstein et al., 2008). However, it is unlikely that human M1 supports independent ipsilateral and contralateral control of tongue movements as it does for the hand (Downey et al., 2020).

Finally, as with the tongue representation within S1, ECoG has also shed more light on the spatial representation of the tongue in S1 (Uematsu et al., 1992; Urasaki et al., 1994; Roux et al., 2020). Tongue-responsive M1 is dorsal to the representation of the larynx and inferior to that of the lips (Breshears et al., 2015); it occupies a cortical area as large as that of the hand (Roux et al., 2020). It extends widely in the ventro-rostral portion of M1, up to 5 cm superior to the Sylvian Fissure and 4.5 anterior to the central sulcus (Urasaki et al., 1994).

ECoG studies have shown that the bilateral motor responses (like tongue contraction; Roux et al., 2020) can be observed on the tongue not only when stimulating the gyrus immediately anterior to the central sulcus (areas 4 and 6), but also when stimulating either the *tongue--responsive S1* (see section 3.1, Tanriverdi et al., 2009) or more rostral sites (Uematsu et al., 1992), thus suggesting preliminary grounds for a parallel with non-human primate studies, with the tongue S1 being conceived as a facilitator that guides and enriches the experience of self-generated tongue motor functions (see section 2.4).

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[4] Tongue movement is a particular challenge for neuroimaging, for various reasons. First, the kinds of isolated and repetitive movement that are most felicitous for well-powered fMRI experiments are physically demanding for participants when lying still; they are also essentially impossible to monitor simultaneously, although real-time MRI of the vocal tract (Carey et al., 2017) can be used to estimate participants' movements in a different imaging run. Second, tongue and mouth movement change the electromagnetic field around the head, both from electrical muscle activity (relevant for EEG/MEG) as well as from stimulus-time-locked changes in the local magnetic field that can extend into brain regions, and can affect MRI image reconstruction algorithms, particularly when acceleration methods are used. Head motion and distortions resulting from increased swallowing may have an additional impact. These problems can be at least partially mitigated by careful experimental timing, experienced participants, and well-trained movements, as well as interleaving tongue movements between imaging volumes (e.g., sparse scanning, (Gaab et al., 2003; Hall et al., 1999; Amaro et al., 2002)).

Table 1

Topography of the human tongue motor area across different studies. Relevant details of the experimental paradigm, method and results are reported in different columns of the table. (**IM**=Imaging method, **SP**=stimulation pattern, **TPA**=tongue protrusion approach, **M1**=Activation site in the ventral portion of M1, **HNL**= horizontal non-lateralized tongue protrusion, **HL**= horizontal lateralized tongue protrusion, **VNL**=vertical non-lateralized tongue protrusion, **VL**=vertical lateralized tongue protrusion, **B**=bilateral activation of motor areas, **L**=predominant activation of the left hemisphere, **R**= predominant activation of the right hemisphere).

Authors	Year	N	IM	SP	TPA	M1	Additional observations
Corfield et al.	1999	8	fMRI	Self-paced (~1-Hz)	HNL	B	Participants rested their tongue against the hard palate and upper front incisors during control condition.
Riecker et al.	2000	30	fMRI	Self-paced	HL	B	3 test conditions (HL, production of lexical and non-lexical syllables). Lexical syllables elicited only left responses.
Stippich et al.	2002	14	fMRI	Acoustically triggered (3 Hz)	VNL	B	Participants performed real movements and imagined movements. Bilateral activations were observed for both.
Shinagawa et al.	2003	15	fMRI	Visually cued	HL	B	Stronger activations on M1 contralateral to the preferred chewing side, in line with S1 studies (see section 3.1, Minato et al., 2009)
Fesl et al.	2003	24	fMRI	Self-paced (~1-Hz)	HL	B	Inter-subject variability prevented an accurate definition of the anatomic configuration of primary motor tongue area.
Hesselman et al.	2004	6	fMRI	Self-paced	HNL	B	The execution of lip pursing lay superior to the response elicited by the tongue motor task.
Vincent et al.	2006	6	fMRI	Self-paced	VL	R	Idiosyncratic variations in the activation location within the right M1 were observed across participants
Meier et al.	2008	5	fMRI	Visually cued	HNL	B	The motor tasks that participants performed in this experiment involved the whole body.
Grabski et al.	2012	11	fMRI	Visually cued	HNL	B/L	No significant difference in the cortical activation was observed between jaw lowering and lips pursing.
Xiao et al.	2017	20	fMRI	Visually cued (1 Hz)	VNL	B	Orofacial movements topographically represented in M1 (from superior to inferior: lip pursing, VNL and grinning)

3.3. *Cortical representation of tongue automatic motor processing*

The human tongue contributes to complex movements such as swallowing that can be controlled either by reflexive or voluntary processes (Hamdy et al., 1999; Martin and Sessle, 1993; Martin-Harris, 2006; Matsuo and Palmer, 2009; Shafik Abd-El-Malek, 1955).[5] Swallowing involve highly complex motor sequences which not only require the fine coordination of multiple effectors such as the lingual, pharyngeal, laryngeal and esophageal muscles (Jean, 1984; Le Révérend et al., 2014), but also dynamic and immediate adjustment of these effectors to avoid choking, or biting the tongue or cheeks. Accordingly, from the neural control of swallowing (Hamdy et al., 1999; also see Martin and Sessle, 1993 for a review on the topic) necessarily involve contributions not only from tongue movement but also the broader orofacial musculature. This interplay is made clear through one of the most clinically relevant sequelae of cerebral stroke, namely dysphagia, or difficulties in swallowing. Dysphagia has been reported to relate to patients' abilities to exert tongue pressure (Konaka et al., 2010; Lee et al., 2016); tongue pressure training is potentially a promising therapy for dysphagia (Moon et al., 2018).

3.4. *Plasticity of tongue-related action representation in humans*

The neural representation of the tongue has typically been described as being ventral to the classically defined hand area (Penfield and Boldrey, 1937). As such, the tongue representation is a good candidate for exploring the potential organizational differences arising in individuals affected by the congenital absence of a hand (Funk et al., 2008). Using fMRI, Funk and colleagues observed that patients had larger tongue related activations in S1/M1 contralateral to the congenitally absent hand relative to the other hemisphere, and relative to healthy controls. In line with other findings showing that the mere spatial layout of the cortical representation of different body parts may not exclusively dictate remapping in the sensorimotor systems (Hahamy and Makin, 2019), these findings demonstrate some degree of plasticity in cortical motor representations, and potentially suggest that neurons that would normally be fated to become cortico-spinal efferents for the hand may instead develop into cortico-bulbar efferents for the tongue in the absence of their usual peripheral targets.

In parallel with animal studies conducted on rats (see section 2.1, Guggenmos et al., 2009), the plasticity of the cortical representation of motor actions carried out with the tongue has also been investigated in humans (Svensson et al., 2003). Training tongue movements increases the excitability and size of the portion of ventral somato-motor cortices that can elicit tongue movements if probed with transcranial magnetic stimulation (McMillan et al., 1998a; McMillan et al., 1998b; Wilson et al., 1993). Although training-dependent modulation can persist over time in non-human primates (see section 2.6), these changes are not preserved after 2-weeks of extinction in humans (Svensson et al., 2003).

Finally, brain-computer interface (BCI) systems capable of decoding the neural activity directly from the cortical surface (Rao, 2013) have recently been adopted as a method to study tongue movements and its cortical representation. For example, BCI has been used to detect and classify tongue movements from single trial EEG (Kaeseler et al., 2020; Kaeseler et al., 2022). BCI systems have also been used to show that tongue-protrusion-dependent activity in the putative tongue motor area changes as a function of training for both performed and imagined tongue motor actions (Blakely et al., 2014). However, although accuracy in motor imagery performance improved with time, the increase in accuracy was not correlated with modulation of M1 high-gamma activity, thus suggesting that the effects of motor imagery training with the tongue are not necessarily translated into changes in the M1 cortical activity. Notably, a similar approach has been later used to decode inner speech (Martin et al., 2018; Moses et al., 2019).

In sum, as is the case with non-primates (see section 2.1) and non-human primates (see section 2.6), systematic changes in the neuronal activity of the tongue motor representation within somato-motor areas can directly reflect how the brain learns and adapts itself to feedback received from the external environment.

3.5. *Encoding properties and multisensory properties of sensory-motor tongue-responding neurons in humans*

Recording brain activity using intracranial electrodes has been crucial for understanding the types of stimuli to which the tongue

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[5] A potential source of uncertainty in these studies comes from the use of water injections to induce volitional swallowing behavior (Dziewas et al., 2003; Hamdy et al., 1999; Satow et al., 2004), which blur the distinction between volitional and automatic swallowing. Experimental paradigms examining natural, uncued swallowing events (Martin et al., 2001) may represent a more promising alternative. The acquisition of dynamic images from the oropharyngeal muscles could then be used as an alternative to traditional cued fMRI paradigms to determine the onset of natural swallowing events.

representation is tuned. In line with non-human primates (see section 2.5, Lin et al., 1994a, 1994b), ventral somato-motor cortices respond not only to motor actions but their high-gamma activity is also modulated as a function of the kinematics (position, speed, velocity and acceleration) of fine tongue motor control (Conant et al., 2018).

Studies using ECoG have also refined the current knowledge on the type of information encoded by the motor tongue area in humans, thus showing that not only does the ventral portion of M1 responds to specific verbal (e.g., the production of alveolar consonts, Bouchard et al., 2013) and non-verbal actions (e.g., licking the lips with the tongue tip, Kern et al., 2019), but it also represents imagined self-generated actions (e.g. non-lateralized tongue protrusion, Miller et al., 2010).

Classic non-invasive neuroimaging studies first highlighted that the human tongue area is bilaterally activated (Cogan et al., 2014) not only during the articulation of speech sounds but also during passive listening (Edwards et al., 2010; Pulvermüller et al., 2006; Wilson et al., 2004). Similar results have been observed with single pulses of TMS being applied to the left tongue region within M1 (D'Ausilio et al., 2014; Fadiga et al., 2002; Sato et al., 2010). Exposure to bitonal sounds that require mild-to-strong tongue movements is linked with early (100–200 ms after the onset of the presented sound; Sato et al., 2010) enhanced excitability of the tongue area in M1 (Fadiga et al., 2002), while evoking a pattern of tongue motor synergies similar to those occurring during active speech production (D'Ausilio et al., 2014).

An ECoG study (Cheung et al., 2016) expanded these results showing that the ventral portion of the motor cortex (which includes the presumptive tongue motor area) responds to acoustic sensory properties of speech, with individual cortical sites tuned for specific spectro-temporal acoustic properties. These results show that the tongue motor area in humans is not only active during performed or imagined actions involving the tongue, but it exerts a role in encoding primary sensory information related to the acoustic features of the sounds that humans can produce. Finally, more recent TMS evidence (Vicario et al., 2022) show that pictures of disgusting foods, facial expressions of distaste and even vignettes of highly disapproved-of moral violations may reduce the excitability of the tongue region within M1, by suppressing the amplitude of MEPs generated from the tongue.

In conclusion, available data show that the sensory-motor representation of the tongue encodes perceptual and motor features of intraoral actions for both verbal and non-verbal gestures, and its organization is plastically shaped by experience and deafferentation.

3.6. *Does cortical organization of the tongue area differ between human and non-human primates?*

While non-human primate S1 maintains separate representations of the contralateral and ipsilateral tongue, evidence thus far suggests that humans appear to have a single field that is either bilateral or contralaterally dominant. This seemingly *reduced* level of specialization in humans is surprising in light of findings that larger absolute brain size is correlated with greater neural specialization across species (Striedter, 2005). As the number of neurons in the brain increases, the metabolic cost of maintaining the same proportion of interareal connectedness increases exponentially, leading to strong selective pressures for further local specialization (Deacon, 1990; Ringo, 1991). We speculate that this difference between human and non-human primates could be due to the change of the functional role of the tongue in humans. Monkeys rely more heavily than adult humans on orofacial somatosensory experiences, since they use the mouth for a wide variety of species-specific behaviors, such as examining the external environment (Parks and Novak, 1993) and tool use (Hayashi, 2015; Sirianni et al., 2018). The use of the mouth to examine and explore external objects is common during both human (Rochat, 1989; Ruff et al., 1992; Belsky and Most, 1981; Fenson et al., 1976) and non-human primate infancy (Simpson et al., 2019). Although non-human primates conserve the use of mouth - and tongue - for environment exploration and tool use in non-feeding-related actions throughout development (O'Malley and McGrew, 2000), this behavior loses most of its functional relevance in human adults. The reduced reliance on such oral behaviors in human adults might underlie the rather coarse-grained intraoral cortical representation we observed in humans. Future mapping studies investigating how the sensory-motor tongue cortical representation changes through human development could pave the way to a new and promising line of research. In particular, results could shed renewed light on how the neural architecture of the human sensory-motor tongue representation is affected by the changing functional role of the tongue that characterizes human development.

Furthermore, the fine motor control of orofacial structures is one of several traits that makes humans capable of producing speech (Hauser et al., 2002; Jarvis, 2019; Belyk and Brown, 2017). Much of the encoding of human speech sounds is determined by precise, rapid, and bilateral movements of the tongue. Humans are likely to use tactile cues to guide tongue placement (see section 1.5). We hypothesize that since these movements are strictly bilateral, speech motor control may benefit from the integration of feedback from the two sides of the tongue. Combined with the loss of the functional relevance of tool manipulation with the tongue in adult humans, the emergence and use of speech (which entails the use of complex and yet quite limited, repetitive and poorly lateralized repertoire of tongue movements) may help to drive bilateral integration of tactile tongue cues. Separate somatosensory representations of the left and right tongue within S1 might then either be masked through learning-induced representational plasticity, or potentially elided over evolution.

We hasten to note that all of these speculations rely on very incomplete data. As an example, we know almost nothing about the tongue or larger intraoral representation in other great ape species, or in more vocal non-human primates; it is also entirely possible that the few species of non-human primate that have been extensively studied using electrophysiology are not representative of the larger primate family. Moreover, we cannot exclude that the lack of evidence in support of distinct functional and cyto/myeloarchitectonic ovals within human S1 - each independently representing the ipsi- and contralateral tongue - is not due to lack of resolution or sensitivity in in-vivo neuroimaging methods, or even to the influence of cortical folding patterns and gyrification on cyto/myeloarchitecture and connections (Chavoshnejad et al., 2021; Van Essen, 1997).

4. Summary

Most of the main properties of the tongue cortical representation (e.g., anatomical localization and lateralization) are broadly conserved across different orders (primates and non-primates) and between different families of primates (human and non-human primates, see Table 2). However, crucial differences are observed across phylogenetic domains in the cortical representation of both non-noxious mechanical stimuli and motor actions, in the degree of neuroplasticity and in the encoding properties of somatosensory neurons.

First, non-human primates have discrete fields separately representing ipsi- and contralateral passive stimuli whereas the cortical arrangement in humans is cranial-nerve-dependent (see section 3.1, cranial nerve V, anterior tongue and nerve IX, posterior tongue). Notwithstanding the caveats outlined above, separate ipsi- and contralateral representations of the tongue may have merged during phylogenesis in tandem with the reduced role of the human tongue in lateralized exploration of the external environment and enhanced recruitment of the tongue in fine bilateral motor actions (e.g., speech production), which selectively recruit either the tip or the base of the lingual muscle.

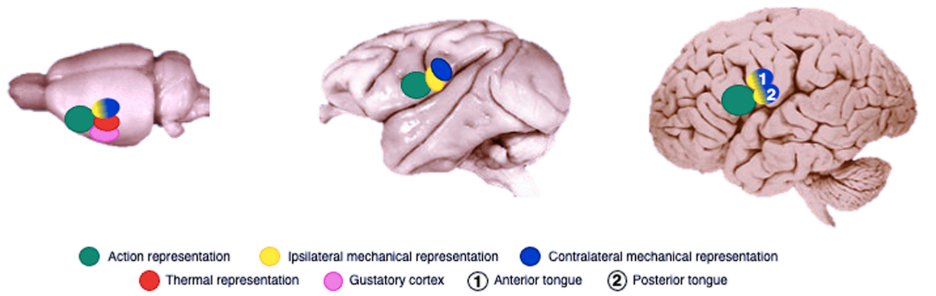
Second, although primary motor cortices have been shown to exert a role in encoding complex kinematics of motor actions involving the tongue, further research using paradigms that isolate tongue motion distinct from related orofacial muscles are needed to better understand

Table 2
Summary of the defining cytoarchitectonic and encoding properties of the somato-motor tongue representation across different phylogenetic domains (non-primates, non-human primates and human primates). Brain images (non-primates: brown rat (Rattus norvegicus); non-human primates: Rhesus Monkey (Macaca mulatta); human primates: Human (Homo sapiens)) were provided by the Comparative Mammalian Brain Collection at the University of Wisconsin-Madison and Michigan State University.

Tongue somato-motor representation

	Non-primates	Non-human primates	Human primates
Anatomical localisation	Ventral portion of somato-motor cortices	Ventral portion of somato-motor cortices	Ventral portion of somato-motor cortices
Degree of lateralisation	N/A (see section 2.1)	Bilateral, separate fields (ipsi- and contra-)	Bilateral (?), unique field
Representation of passive stimuli	Representation has a stimulus-specific arrangement (touch, thermal and taste)	Representation has a mouth-part-specific arrangement (teeth and tongue)	▪ Representation has a mouth-part-specific arrangement (lips, teeth and tongue) ▪ Tongue representation is tongue region dependent (tip, body and base)
Representation of actions	Anterior regions represent feeding-related actions	Anterior regions represent feeding-related, hand-to-mouth movements and ingestive actions	Anterior regions represent tongue specific actions and kinematics of motion
Degree of plasticity	▪ Training lowers threshold for the elicitation of motor responses ▪ Cytoarchitecture *NOT* affected	▪ Training triggers enhanced corticomotoneuronal excitability ▪ Cytoarchitecture is plastically affected	▪ Cytoarchitecture and corticomotoneuronal excitability are plastically affected by both experience and deafferentation ▪ Plastic changes NOT preserved over time
Somato-motor response properties	▪ Somatosensory neurons encode motor but NOT taste related information	Somatosensory neurons encode fine properties of motor actions (e.g., directional sensitivity)	▪ Somatosensory neurons encode tongue-specific motor actions, kinematics and acoustic features of tongue motor control ▪ Motor neurons responsive to performed and imagined tongue motor actions

Up-to-date topography



the cortical representation of tongue motor actions in non-human primates and non-primates.

Third, the tongue somato-motor representation is highly plastic in both primates and non-primates. Although accumulated experience in a motor task involving the tongue enhances cortico-motoneuronal excitability in both primates and non-primates (see section 2.1, 2.6 and 3.4), training of known and new motor skills involving the tongue may play a role in reorganizing the topography of the tongue somato-motor area in both human and non-human primates. These plastic topographic reorganizations are also observed after sensory deafferentation in humans.

Last, somatosensory neurons responding to the peripheral stimulation of the tongue encode basic information about lingual motor control in both primates and non-primates. Tongue-somatosensory responsive regions appear to encode more complex information, like the direction of tongue motion (human and non-human primates) and the acoustic consequences of tongue related actions (humans).

Data Availability

No data was used for the research described in the article.

Acknowledgements

This work was supported by a grant from NIH (R01DC017734) awarded to Fred Dick and a grant from EPSRC (EP/M026965/1) awarded to Jeremy Skipper. The authors would like to thank Gillian Forrester, Jeremy Skipper, Luigi Tamè and Raffaele Tucciarelli for their useful comments on previous versions of this manuscript.

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