Links between perception and production: examining the roles of motor and premotor cortices in understanding speech.

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1. Introduction

Speech is a hugely important signal in human behaviour, allowing individuals to share thoughts and emotions with others as part of complex social interactions. As an action, or rather a set of actions (involving highly coordinated movements of the larynx, tongue, jaw, lips and soft palate), speech production is a highly complex sensorimotor behaviour, from the perspectives of both the speaker and the listener. Though historically seen as distinct, the neural mechanisms controlling speech perception and speech production mechanisms are now conceptualized as largely interacting and possibly overlapping. Indeed, from the very first months of life, speech perception and production are closely related. Speaking requires learning to map the relationships between oral movements and the resulting acoustical signal, which demands a close interaction between perceptual and motor systems.

In the mid 20th century, a Motor Theory of Speech Perception (MTSP) was proposed, which suggested a strong link between speech production and perception mechanisms; through a series of empirical tests, the theory was tested, strongly contested, and largely abandoned. However, following the late-century discovery of mirror neurons in macaques, and in the context of a developing field of human neuroscience research interested in the interactions between sensory and motor systems and the grounding of cognitive processes in the motor system (a field often referred to as "cognitive embodiment"), the theory enjoyed an unexpected revival. In this chapter, we outline the empirical basis for the original MTSP, describing its main tenets. We then discuss how, equipped with modern methods to probe neuromotor systems, researchers in cognitive neuroscience first described the involvement of the motor system in non-motor tasks such as auditory speech processing. Focussing on research published in the last decade, we highlight the ways in which authors have since elaborated theoretical accounts to clarify whether this motor involvement is at the foundation of language comprehension. In particular, we draw attention to the use of multivariate analyses of functional MRI responses to speech that allow more detailed descriptions of the content of motor responses to speech, and the refinement of experimental designs to address the specificity and possible predictive/causal roles for motor cortical involvement in speech perception.

2. Motor theories of speech perception in the 20th century

The Motor Theory of Speech Perception (MTSP) was developed at the Haskins Laboratories in the United States in the 1950's (Liberman, 1957) and revised in 1985 (Liberman & Mattingly, 1985), in the midst of infructuous attempts at developing a machine that would read aloud text for the blind (a scientific endeavour that would have tremendous impact on the way that we understand the nature of the speech signal; for a review, see (Shankweiler & Fowler, 2015). These machines operated by producing sequences of discrete sounds associated with alphabetic segments - however, this is not representative of natural speech, where sequences of vowels and consonants are produced as smooth integrated sequences instead of concatenations of individually produced sounds. Largely as a consequence of this phenomenon of "coarticulation", the same speech sound (e.g. /d/) becomes associated with different acoustic realizations depending on the phonetic and prosodic context - for example, the /d/ sounds in /di/, /da/ and /du/ are acoustically different because of the different neighbouring vowels (Liberman, 1957). This essentially eliminates the possibility of phoneme- or alphabet-like discrete acoustic segments in speech, and this complicated the development of reading machines because they could not generate speech that was intelligible to listeners when produced at a natural rate. This observation also posed a theoretical problem – how does human speech communication successfully establish parity between receivers and senders in the face of such acoustical variability? The MTSP was developed to account for this well-known "lack of invariance problem" in speech perception, which is still often considered one of the main goals of speech perception research (Galantucci, Fowler, & Turvey, 2006; A. M Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967).

One of the main tenets of the MTSP was that speech perception and production are intimately linked. Indeed, Liberman and colleagues wrote, in 1967, that "[...] *the perceiver is also the speaker and must be supposed, therefore, to possess all the mechanisms for putting language through the successive coding operations that result eventually in the acoustic signal*" (p. 452). The MTSP thus proposes that there must exist a link between perceptual and motor codes for speech. Though the idea of coupling between perceptual and motor systems was shared by numerous researchers across a range of fields beyond language (see (Prinz, 1997), in its revised form (Liberman & Mattingly 1985) the MTSP focussed only on speech-related mechanisms, with one of its main claims being that the conversion from the speech acoustic signal to a speech motor gesture occurred within a biologically specialized "speech" (phonetic) module in the brain. According to the MTSP, each speech sound (phoneme) is associated with a specific combination of motor commands, such as "tongue elevation" or "lip protrusion". Thus, another main tenet of the MTSP was that the ability to categorize the speech sounds in the incoming speech stream into phonemes and syllables is accomplished by tracking the intended articulatory patterns - that is, recovering the intended (invariant) motor gesture from the interlocutor's own motor repertoire (a process often referred to as analysis-by-synthesis). This suggestion was based upon the finding that whenever articulation and the resulting acoustic patterns diverge, perception tracks the intended articulation (in our example, a closure of the vocal tract between the tongue and the alveolar ridge to form /d/). In other words, the relation between phonemes and articulation is closer to a one-to-one relationship than the relationship between phonemes and the acoustic signal. Thus, according to the theory, the intended articulatory patterns represent the elemental objects of speech perception.

The theory was, and still is to some extent, highly controversial (Fowler, Shankweiler, & Studdert-Kennedy, 2015; Fowler, 1996; Galantucci et al., 2006; Lane, 1965; Rizzolatti & Arbib, 1998; Stasenko, Garcea, & Mahon, 2013). The main points of contention were (and still are), (1) the idea of a specialised speech module and the focus on speech-specific processes, (2) the notion of motor invariants. In particular, the notion of an innate vocal-tract synthesiser that would be used to derive motor invariants from the acoustic signal has been contested and various alternatives proposed. However, there has not been a clear replacement for the MTSP, and the idea of a close interaction between perceptual and motor systems remains. As will become clear in the following sections, the MTSP, despite its shortcomings, continues to have a major influence on the field of speech perception research.

3. Cognitive neuroscience of speech perception in the 21st century

The advent of Mirror Neurons and motoric accounts of perception

In the last decade of the 20th century, work from the laboratory of Giacomo Rizzolatti at the University of Parma made a huge impression on the field of neuroscience. In studies of awake macaques, Rizzolatti and colleagues described single cells in the premotor cortex (area F5 of the frontal lobe) that fire during performance of an action (e.g. grasping a piece of food) and when observing the same action performed by another individual (in this case, researchers in the laboratory; (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti & Craighero, 2004). This one-to-one mapping of perception and production led these authors (and many others) to posit a role for such "mirror neurons" in action understanding – that is, the suggestion that an individual learns how to make sense of the actions of others by simulating these actions in their own motor cortex. This finding was taken up with great enthusiasm, with many authors in the field of human cognitive neuroscience seeking evidence for equivalent mechanisms in the human brain. Respected neuroscientists such as Ramachandran even went so far as to declare that "mirror neurons will do for psychology what DNA did for biology" (Ramachandran, 2000). Notably, the lack of scope for single cell recordings in humans meant that such endeavours could only claim to identify mirror *systems* in the brain, typically those showing topographical overlap between perception and execution of actions (e.g. Decety et al., 1997; di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Grafton, Arbib, Fadiga, & Rizzolatti, 1996).

Alongside the work on visual observation and its correspondence with action (motor) programmes, the Rizzolatti group had also explored observation-execution in the auditory modality. Kohler et al. (2002) reported the discovery of neurons in F5 that fired when the monkey performed actions such as ripping paper and vocalizing, and when hearing the sounds produced by those actions. In their paper, they suggest that the location of these mirror neurons in the non-human homologue of "Broca's area"[1] - a region associated with speech production since seminal neuropsychological case reports from the mid 19th century – might support an account of language evolution based on the representations of actions and their auditory consequences in inferior frontal cortex.

The idea behind motor theories of speech perception is that the same neural tissue that is involved in producing speech is also involved in perceiving speech. However, because the production of speech is an intricate, multi-stage process involving control of dozens of muscles distributed in the abdomen, neck and face, and requiring both speed and precision, there is more than one candidate region for such sensorimotor interactions. The "core" cortical speech network involves large parts of the human brain, including the ventral part of the central sulcus (which contains the primary motor area or M1v), the precentral gyrus and sulcus (which contains the ventral lateral premotor cortex or PMv), the medial aspect of the superior frontal gyrus (which contains the medial premotor areas pre-SMA and SMA), the cingulate motor area (CMA) and the inferior frontal gyrus (IFG) (see Figure 1).

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[1] The term "Broca's area" refers to an anatomically ill-defined portion of the inferior frontal region that often includes pars triangularis and pars opercularis. For a discussion of this topic see Tremblay & Dick 2016.

Subcortical motor areas implicated in speech production include the cerebellum, basal ganglia and thalamus (e.g. (Bohland & Guenther, 2006; Tremblay, Deschamps, Baroni, & Hasson, 2016; Tremblay & Small, 2011b). Anatomically, M1v, PMv, SMA and CMA contribute to descending (motor) pathways, meaning that these regions have direct control over lower motor neurons located in the brainstem and, ultimately, over the muscles of phonation and articulation (Breshears, Molinaro, & Chang, 2015; Dum & Strick, 1991; Jenabi, Peck, Young, Brennan, & Holodny, 2015; Jurgens, 2002, 2009). The IFG, in contrast, does not, and it is also not involved in the cortico-striatal motor loop implicated in motor planning for speech (Alexander, Crutcher, & DeLong, 1990).

Depending on their architecture and connectivity, the different parts of the motor system contribute to different operations such as sequencing, motor initiation and execution, and may not be the most likely targets for perceptual-motor integration. Instead, regions believed to contain motor representations for speech may be the ideal sites. The *Directions Into Velocities of Articulators* (DIVA) model of speech production (Guenther, Ghosh, & Tourville, 2006), a dominant neurobiological model in the field, proposes that the ventral part of the lateral premotor cortex (PMv) contains speech motor programs. Interestingly, the PMv, along with surrounding tissue in M1v and the pars opercularis of the IFG (IFG_{op}), has been the target of most investigations into the motor theories of speech perception. However, there remain questions about the extent to which the different regions exhibit mirror-like properties, and whether these reflect functional differences between these cortical sites.

As human cognitive neuroscience began to produce reports of "mirror"-like perception-production links for hand and arm actions, so authors in the cognitive neuroscience of speech began to investigate the possibility of common involvement of the IFG_{op} and adjacent PMv in the perception and production of speech. Two key functional magnetic resonance imaging studies (fMRI) provided some of the earliest evidence for overlap of brain responses during perception and production of simple syllables such as "ba" and "da" (Wilson, Saygin, Sereno, & Iacoboni, 2004), as well as a suggestion that these responses were somatotopically organised[2] (Pulvermuller et al., 2006). Specifically, it was shown that

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[2] Somatotopy is the point-for-point correspondence of an area of the body to a specific area in the brain. Such organization is found, with different levels of precision, throughout the sensorimotor system.

the perception of distinct speech sounds (phonemes[3]) recruits motor areas varying spatially according to involvement of different speech articulators (e.g. phonemes involving lip movements, such as /p/, engaged relatively non-overlapping parts of the precentral gyrus as compared to phonemes requiring tongue movements, such as /t/). The latter finding was used to argue for a specific involvement of the motor/premotor[4] cortex in the perception of heard speech, rather than a general or non-specific sound-to-action response. Similarly, transcranial magnetic stimulation (TMS) of M1 to generate motor-evoked potentials (MEPs) in lip and hand muscles showed that lip MEPs were enhanced during perception of audio and visual speech, but this was not the case for hand MEPs, supporting the notion of a somatotopic involvement of the motor system in speech perception (Watkins, Strafella, & Paus, 2003). In a study further probing somatotopy using TMS, it was shown that hearing words requiring pronounced tongue movements (i.e., words including /r/) was associated with stronger tongue MEPs compared to words involving less pronounced movements of this articulator (Fadiga, Craighero, Buccino, & Rizzolatti, 2002). However, none of these studies addressed a key theoretical issue at the heart of any motoric account of speech perception, in that they did not show any causal or mechanistic role for motor/premotor cortex in speech perception accuracy or sensitivity. Further, the studies on MEP modulation targeted M1v, which controls the execution of movements, rather than PMv and IFG_{op} that are associated with the representation of speech motor plans (Guenther et al., 2006). As discussed above, PMv and IFG_{op} are more likely targets for perception/production interactions; it is possible, however, that stimulation of M1 cascades to premotor areas with which it is connected.

Later studies employed TMS to modulate activation in motor and premotor cortical sites and examine the effects on speech perception performance. Here, authors reported impaired syllable recognition performance after TMS to premotor cortex (Meister, Wilson, Deblieck, Wu, & Iacoboni, 2007). This finding was developed by a later TMS study (D'Ausilio et al., 2009) reporting a somatotopic double dissociation, where stimulation of lip M1 selectively *enhanced* syllable recognition performance for consonant-vowel plosives beginning with a bilabial closure (e.g. /pa/, /ba/), while stimulation of tongue cortex impaired recognition for other syllables (e.g. /ta/, /da/). A point to note in these studies was

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[3] the smallest unit of speech that can be used to make one word different from another word. For example, the difference in meaning between the English words cat and bat is a result of the exchange of the phoneme /k/ for the phoneme /b/.

[4] In this chapter, we use the expression "(pre)motor cortex" to refer to the ventral central sulcus (M1), ventral precentral gyrus and sulcus (PM), and posterior part of the IFG (pars opercularis).

that they almost invariably involved an active task, in which participants were, for example, required to make fine-grained phonemic judgements (e.g. discriminating /ba/ from /pa/), to segment the incoming speech stream into phonemic constituents (e.g. breaking down "cat" into /k/, /æ/ and /t/), or to identify syllables against noise. Active tasks such as these may not be representative of the manner in which speech is naturally processed in day to day situations, a point that was raised by a number of critics (e.g. Scott, McGettigan, & Eisner, 2009; see below) who claimed that there was therefore insufficient evidence that motor representations are engaged in an automatic or obligatory fashion in the service of everyday speech perception as posited by MTSP (otherwise such effects should be seen also for passive listening in quiet).

The overall viewpoint emerging from these studies (and many others) was one that leaned at times toward a strong interpretation of the Motor Theory – that the perception of speech gestures is fundamental to the understanding of speech. However, responses to these claims were mixed, and provoked a series of influential opinion and review papers (Hickok, 2009, 2010; Lotto, Hickok, & Holt, 2009; Scott, McGettigan, & Eisner, 2009). The next section offers an overview of some of the arguments on both sides, and summarises what we see as the three prominent theoretical standpoints on the role of motor cortex in speech perception, as they stood at the end of the first decade of the millennium.

The new Motor Theory of speech perception: support and criticisms

Initially, studies investigating motor contributions to speech perception tended to make positive assertions about the importance of motoric representations – indeed, some authors claimed an "essential" role for motor/premotor cortex in the recognition of speech (Meister et al., 2007; Pulvermüller & Fadiga, 2010).

Other authors presented a view that cautioned a limited interpretation of the motor involvement in speech perception and emphasised the paucity of evidence for this in the face of overwhelming data suggesting a primary role for a ventral processing stream in temporal cortex supporting speech perception (Scott, Blank, Rosen, & Wise, 2000; Scott & Johnsrude, 2003). In a critique of the posited "action understanding" interpretation of mirror neurons (and mirror systems) Hickok (2009) sets out eight problems for the field to consider, including concerns about the empirical evidence for an action understanding role in non-human primates, raising criticism of the neuroanatomical parallels between macaque F5 and human "Broca's area", and presenting evidence for dissociations between action production and perception deficits in human patients. Most relevant for our current discussion, Hickok invokes perception-production dissociation data from aphasic patients to argue that there is little evidence that mirror theories of action understanding generalize to speech perception. Like other critics of the Motor Theory, Hickok acknowledges that motor systems may well have some role in supporting speech perception, in particular when this places large demands on executive, attentional or working memory processes (e.g. through requiring phonemic segmentation) or when the process is challenged by noise: "However, this influence is modulatory, not primary" (Hickok, 2009, p. 1240).

Scott and colleagues (2009) offer a detailed critique of experimental methods, pointing out the lack of suitable acoustic control conditions in fMRI studies (or, the lack of statistical comparison with these control conditions; see Wilson et al., 2004), the presence of challenging listening conditions and/or demanding phoneme segmentation tasks in behavioural and TMS work, and the lack of evidence for an essential role of speech production for successful perception during development or in the patient literature. Responding to the strong claim of a specialized speech "module" in the brain, they point out that IFG (including the opercular part [IFG_{op}]), PMv and M1v respond to passive listening to a wide range of sounds, including tool sounds, music and non-verbal emotional vocalizations. Instead of being essential to speech perception, Scott et al. rather argue that there could be an alternative role for motor knowledge in the perception of auditory stimuli, which might reflect a more general sound-to-action response. Specifically, they call upon behavioural data showing that turn-taking behaviour in human conversation happens with very low latencies, using this evidence to propose that auditory-motor connections in the brain might be particularly crucial in supporting smooth transitions in communicative interactions.

Pulvermuller & Fadiga (2010) make a claim for the importance of perception-action networks in supporting language comprehension, from speech recognition to semantic and syntactic processing of words and sentences. In terms of speech perception at the phonemic and syllabic level (our focus for this chapter), their main arguments centre around evidence for specificity of perceptual responses in motor cortex through somatotopy. While they acknowledge criticisms for a context dependency on responses in terms of the importance of noisy or degraded listening conditions, they make the argument that such contexts are in fact much more representative of normal everyday speech perception, and as such, the evidence from these studies is still valid in the evaluation of the MTSP. Galantucci, Fowler & Tulvey (2006) were similarly encouraged by mirror neuron accounts, but concluded that the limitations of the original MTSP included having too strong a focus on speech: they argue that general cognition shows many indications of the importance of motor systems for comprehension. While rejecting the tenet of the MTSP that there should be a specialized module in the brain for speech, they remain strongly in favour of gestures as the primary objects of perception. In contrast, Massaro & Chen (2008) have claimed that their Fuzzy Logical model, which describes perception in terms of prototypical pattern recognition based on the integration of several sources of input information (e.g. voice, face) can account for some of the most important experimental evidence for the MTSP (e.g. the invariance of /d/ despite variation in formant transitions depending on the following vowel; (Liberman, Delattre, & Cooper, 1952)). Crucially, where the emergence of Mirror Neurons encouraged Galantucci et al. (2006) as supporting evidence for some form of MTSP, Massaro & Chen rather pose the question of how a mirror mechanism can actually explain perception: "…mirror neurons cannot account for perception, because they would overgeneralize. The macaque certainly experiences the difference between seeing a conspecific action and performing its own action, but the same mirror neurons are activated by these very different events and experiences." (Massaro & Chen, 2008, p.456).

Motor cortex and speech: Prominent viewpoints

Thus, by the end of the last decade, a number of dissenting voices had emerged on the topic of the "revived" version of the MTSP, yet some quite fervent and strong-form support remained. The concerns raised by critics presented clear challenges for the field – namely, to better describe the perceptual representations of speech sounds in motor cortex (i.e. Are these equivalent in perception and production of speech? At what level of abstraction are they encoded?), and to further characterize when and how these representations might contribute to speech perception (and crucially, to assess the *importance* of those contributions for language comprehension). While there remained some authors still arguing for an essential role (e.g. Pulvermuller & Fadiga, 2010), there were two main viewpoints contesting this. First, some argued that motor knowledge is not essential for speech perception, but may play a significant role in supporting this process under certain circumstances. The second main viewpoint extended this stance, suggesting that a focus on basic phonemic/syllabic perception mechanisms might actually have distracted from a more important role for motor responses in spoken communication as an interactive, social process (e.g., in turn-taking; Scott et al., 2009). In one form of this view, Pickering & Garrod (2013) advocate something superficially more aligned with MTSP, which proposes the use of forward models in spoken communication to allow a conversational agent to make predictions during both production and comprehension at a number of levels in the linguistic hierarchy. Here, however, they allow both for "prediction-by-simulation" and "prediction-by-association" mechanisms; while clearly characterizing speech comprehension as action perception, their main argument is for mechanisms that smooth the coordination and alignment of communicative processes in dialogue, and thus allow for relatively more flexibility in how this might be achieved.

In the next sections, we turn to the experimental evidence that emerged around the time of, and subsequent to, the publication of these influential review papers. We consider in particular the extent to which these studies addressed the two challenges described above: 1) to describe the nature of speech representations in motor cortex, and 2) to identify their precise role in speech perception and language comprehension, as well as more general social interactions.

4. Gathering evidence: recent developments in the cognitive neuroscience of motor theories of speech perception

Several highly cited papers in the initial resurgence of interest in MTSP and its potential neural bases contributed supporting evidence from fMRI (Pulvermuller et al., 2006; Wilson et al., 2004) and TMS (D'Ausilio et al., 2009; Fadiga et al., 2002; Meister et al., 2007; Watkins et al., 2003) in healthy young listeners. In this section, we consider how these methods, and related experimental designs, have been advanced in recent years to progress our understanding of motoric responses to speech. We also include newer evidence emerging from other methods – EEG and MEG have allowed for closer inspection of the dynamics of motor involvement in perception, while electrocorticography (ECoG) has provided greater spatial resolution and specificity than the former techniques by measuring directly from the cortical surface.

Perceptual representations of speech in the cortical motor system

The studies of Wilson and colleagues (2004) and Pulvermuller and colleagues (2006) offered thought-provoking indications of perception-production links in passive listening to speech.

As described above, the observations of somatotopic overlap in these responses argued for a specificity in representation, suggestive of underlying mirror-like activity: perception of speech sounds involves activation of the corresponding motor plans (or gestures; Galantucci et al., 2006) used to produce those sounds. However, spatial overlap of responses offers limited insights into whether the activations actually reflect matching underlying representations, and whether the responses code for physical (articulatory) or more abstract properties of speech.

Recent fMRI studies have provided more nuanced evidence, and perhaps because of their milder stance, they have received far less attention. A strong MTSP view would predict a preferential and selective response to speech over other sounds in motor cortex – if perception is dependent on the activation of corresponding motor programmes, this should be specific to sounds within the listeners' native speech repertoire. However, Wilson & Iacoboni (2006) had found contradictory evidence, showing greater responses of the motor system to non-native syllables compared with native, and showing correlations between response magnitude and sound producibility only in superior temporal regions. In a more refined approach, a passive perception paradigm in fMRI using native speakers of English showed that there was no difference in the magnitude of premotor responses to English plosive consonants compared with producible ingressive click sounds (used communicatively, but not linguistically, in English). These sounds were, however, differentiated by the posterior superior temporal sulcus (Agnew, McGettigan, & Scott, 2011), lending support to the view that the extraction of meaningful linguistic percepts in speech is predominately a process carried out in the ventral auditory processing stream (Scott & Johnsrude, 2003). Allowing for a softer version of the theory, where motor activations to sound are not necessarily speech selective in terms of the magnitude of the BOLD response, there should nonetheless be evidence for common representations of motor-related information in perception and production. However, this has not been the case. It has been shown in fMRI that while PMv is active in both speech perception and production, it is only sensitive to phonetic details (syllable structure) in speech production/rehearsal and not in passive speech perception (e.g. Tremblay & Small, 2011b). This stands in contrast to evidence from studies directly measuring the movements of the articulators, using techniques such as electropalatography (measuring tongue contact with the hard palate) and Doppler ultrasound imaging (measuring tongue kinematics), which have shown that hearing speech can evoke corresponding movements of the tongue in a "mirroring" fashion (D'Ausilio et al., 2014; Yuen, Davis, Brysbaert, & Rastle, 2010). This speaks to another important element of MTSP – that motor knowledge should be used in an obligatory fashion during speech perception.

It can be argued that fMRI bears insufficient resolution, in time or space, to fully address the question of whether motor knowledge is used in the perception of speech. In recent years, multivariate analyses of the BOLD response have allowed descriptions of speech representations during perception at a finer granularity. Moving beyond the relatively coarse subtraction analyses of earlier studies, researchers have employed machine learning techniques to classify the responses to stimuli and speakers based on the spatial patterning of activation (multivoxel pattern analysis; MVPA) in a brain region of interest or within a "searchlight" volume passing through the brain (e.g. Formisano, De Martino, Bonte, & Goebel, 2008). This has afforded greater sensitivity in the classification of perceptual responses to speech, often revealing areas of activation that were obscured by regional averaging for subtraction (e.g. (Abrams et al., 2013). With regard to the possibility of a motor involvement in speech perception, multivariate statistics also present a means of characterising the *content* of neural representations. Representational Similarity Analysis (RSA; (Kriegeskorte, Mur, & Bandettini, 2008) uses cross-correlation of the neural responses to different stimulus categories within a region of interest to generate a representational dissimilarity matrix (RDM) – this RDM can be compared with matrices constructed from responses in other brain regions, participant groups, or data types (e.g. perceptual ratings, correlations of stimulus properties) to identify the nature of the representations in the region of interest. RSA was recently employed to describe the content of representations in regions of cortex showing overlapping activation in the production and perception of both clean and degraded spoken syllables (Evans & Davis, 2015). Significant correlations were found between neural responses and searchlight RDMs describing the acoustic form of speech, as well as those describing the categorical identity of the syllables. This revealed abstract (i.e. categorical), and not form-related, representation of syllabic identity and phonemic content within left somatomotor cortex (extending over pre- and postcentral gyrus) during passive listening to speech, but no evidence for motor representation of phonetic features, such as place of articulation.

Other work has argued in favour of feature-level representations, although the findings have not been consistent across studies. MVPA of passive responses to spoken syllables was used to identify context-independent encoding of phonetic features, by testing for generalization across an orthogonal feature (e.g. testing representation of place of articulation by training a classifier on /p/ versus /t/ and testing for generalization to /f/ vs. /s/) (Correia et al., 2015). This revealed representation of phonetic features across perisylvian cortex, including M1v, Pmv, IFG_{op}, STG and somatosensory sites. However, there was variation in the topography of feature representation, where information on place and manner of articulation was identified in regions such as IFG, while voicing information was largely contained within superior temporal and somatosensory cortices. Another study used MVPA to examine the location of consonant articulatory features during a passive syllable processing task, and found that articulatory features were represented in superior temporal cortex but predominately not within motor or premotor areas (Arsenault & Buchsbaum, 2015).

The inconsistent involvement of motor/premotor regions in the description of articulatory features in perception argues against an obligatory engagement of motor representations or mechanisms, as might be expected if there were an essential motor response in speech perception. Previous investigations claiming strong somatotopic representation of speech in motor cortex have used plosive stimuli varying in place of articulation (see Wilson et al., 2004; Pulvermuller et al., 2006), which is a feature that in such contexts may strongly engage the motor system (consider the contrastive tongue positions for /t/ versus /k/, and compare with the relatively consistent tongue configurations in a fricated /s/ and a plosive /t/) but is not reflective of the perceptual separability of heard phonemes across a wider range of sounds and feature combinations (Arsenault & Buchsbaum, 2015). However, the evidence does suggest that premotor cortex can represent some specialisation for speech motor programmes, in a way that the brain does not represent other, non-speech, sounds (e.g. birdsong;(Tremblay, Baroni, & Hasson, 2013). To the extent that motor regions are involved in the perceptual representation of speech, the challenge remains to account for when, and how, such representations might be engaged in the service of speech comprehension.

Despite such advances, one of the main limitations of the fMRI method is its low temporal resolution and indirect measure of brain activity. In recent years, a number of compelling studies of speech perception and production have emerged from work using electrocorticography (ECoG), which involves direct recordings of electrical activity from the cortical surface typically obtained from patients awaiting resection of tissue for the treatment of epilepsy (Bouchard, Mesgarani, Johnson, & Chang, 2013; Cheung, Hamiton, Johnson, & Chang, 2016; Mesgarani, Cheung, Johnson, & Chang, 2014); see also Flinker, Piai & Knight, this volume). Unlike fMRI, ECoG, and electrophysiological approaches in general have a high temporal resolution (≥1000 Hz). And yet, similar to findings with fMRI, ECoG studies have also suggested a relatively inconsistent profile for motor representations of speech articulatory information. Brain responses sensitive to the acoustic features of speech were found in the superior temporal cortex during passive listening to connected speech – specifically, these were predominately organised with respect to manner of articulation rather than place (Mesgarani et al., 2014). In contrast, responses during speech production found in the pre- and post-central gyrus (i.e. including PMv and M1) were organized according to place of articulation (Bouchard et al., 2013). Greater similarity in the organisation of responses across temporal and somatomotor sites during perception, compared with that between perception and articulation within somatomotor cortex itself, suggested that the content of somatomotor responses during perception and production is not equivalent (Cheung et al., 2016), consistent with some of the earlier fMRI evidence (Tremblay & Small, 2011).

How can these findings be tied together? The current body of evidence, although mixed, certainly suggests some capacity for articulatory information to be represented in the brain's perceptual responses to speech. Thus, we cannot accept a strong "anti-MT" argument that motor/premotor cortex is only involved in basic sound-to-action behaviours, such as tracking the rhythm of a repeating sound or in conversational turn-taking. However, the variability in the extent to which certain features are accessed during speech perception, in the consistency of activation and informational content across perception and production responses, and in the distribution of this information across somatomotor and sensory regions of cortex, raises problems for the interpretation that articulatory information forms the basis for speech perception. Thus, we turn to the second challenge: if articulatory information *can* be present in motor/premotor cortex during perception, when does this occur, and how does it contribute to the success of speech comprehension?

Functional roles of motor responses to speech: task-dependency, environmental factors, taking turns?

A major criticism of the neurobiological studies arguing for an MT interpretation of motor responses to speech pointed out that these were often identified under particular stimulus and task contexts (e.g. Scott et al., 2009). A large number of empirical studies has since supported a context-dependent role for motor and premotor cortex in speech perception. These studies largely follow two main themes: investigating the role of task demands on phonological processes, and modelling perception of connected speech under challenging listening conditions.

A view gaining increasing support is that representations in motor cortex may be redundant in basic speech comprehension but useful for challenging listening conditions, for example in the presence of noise or distortion, or under specific task demands. A series of TMS experiments provide interesting evidence in support of a task- and environment- dependent role for the PMv in speech processing. Meister and colleagues reported that TMS applied to the PMv interferes with participants' ability to discriminate sublexical speech sounds in the presence of noise (Meister et al., 2007). Interestingly, however, it was later demonstrated that the effect of TMS to PMv during sublexical speech processing in the absence of ambient noise is dependent upon phonological processing demands, with only the most demanding phonological task being affected by TMS (Sato, Tremblay, & Gracco, 2009). Indeed, in that study, out of three phonological tasks - phoneme identification, syllable discrimination (same/different) and phoneme discrimination (same/different) - only phoneme discrimination (which requires segmentation and comparison of the first phoneme of two syllables) was affected by TMS. Thus, the evidence suggested that the contribution of the premotor cortex to speech perception varies as a function of both task demands and environmental conditions (e.g. quiet vs. presence of noise). A recent TMS study compared TMS applied to PMv and STG during the processing of partially degraded auditory words in the context of a semantic task (semantic judgments, e.g. "man-made or natural?") and a phonological task consisting in phoneme identification and requiring segmentation (Krieger-Redwood, Gaskell, Lindsay, & Jefferies, 2013). Consistent with previous studies, the results demonstrate that the phonological task is affected by TMS to PMv; however, they show no effect of TMS for the semantic task, which the authors interpret as suggesting that the PMv is not necessary for speech comprehension but only in explicit phonological processes. The authors thus suggest that PMv is not involved, or at least not crucially so, in mapping sounds to meaning (or more generally in semantic processing). In contrast to the PMv results, TMS to STG interfered with both the phonological task and the semantic task, thereby suggesting a role for mapping sound to meaning for the STG, but not the PMv.

In their seminal fMRI study of sentence comprehension employing a range of degraded speech forms, Davis and Johnsrude (M H Davis & Johnsrude, 2003) identified a particularly elevated response to noise-vocoded sentences in the left IFG_{op}, relative to undistorted speech and a noise baseline condition; this was replicated in a later study of noise-vocoded word perception (Hervais-Adelman, Carlyon, Johnsrude, & Davis, 2012). A more nuanced aspect to this finding is that premotor and IFG engagement is enhanced in particular for speech that is degraded but still partially intelligible (e.g. for moderate to high levels of noise masking; (Du, Buchsbaum, Grady, & Alain, 2014; Osnes, Hugdahl, & Specht, 2011). Thus, there has gradually emerged a view that a variety of regions including motor and premotor sites might form a compensatory mechanism in the support of degraded speech perception. It is posited that this involves top-down guidance or constraint of auditory processes during perception, dependent on task context (e.g. Davis & Johnsrude, 2007; Skipper, Goldin-Meadow, Nusbaum, & Small, 2007).

Investigating the nature, and consequences of, context-dependency allows comparison of competing theoretical standpoints – for example, where a direct realist account would claim that the contents of motor activations during speech processing should represent the articulatory information available in the signal, a constructivist account would instead posit the such correspondence is not necessary and that motor activations might instead assist perception in a predictive and task-dependent fashion (see Callan, Callan, Gamez, Sato, & Kawato, 2010)[5]. In line with the latter view, an effective connectivity analysis (using dynamic causal modelling) on fMRI data collected during a speech-in-noise task reported top-down connections from premotor cortex to auditory regions, but only for listening to (partially) intelligible speech (and not for non-speech control sounds; (Osnes et al., 2011). Similarly, premotor regions have been specifically implicated in the response to training-related feedback during a speech perceptual learning paradigm (Hervais-Adelman et al., 2012). A speech-in-noise study including MEG and MRI experiments indicated that such involvement was not only correlated with task outcome, but might be predictive of it - within left IFG and premotor cortex sites showing responses during perception and

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[5] For a more detailed explanation of these competing theoretical positions, see Samuel (2011)

production of speech, there were significant differences in BOLD and in pre-stimulus event-related synchronisations and desynchronisations (in the alpha, beta and gamma ranges), when comparing correct and incorrect trials of a speech categorisation task (Callan et al., 2010). Complementary findings from EEG identified mu suppressions localised to left and right pre- and post-central gyrus during syllable discrimination in noise, but only for active listening – furthermore, only suppression in the left hemisphere was predictive of performance (Bowers, Saltuklaroglu, Harkrider, & Cuellar, 2013). Studies of MEPs and tongue kinematics have further shown that expectation of a phoneme can increase excitability of the tongue during perception (D'Ausilio et al., 2009), and that the degree to which individuals exhibit specific "mirroring" articulatory engagement during passive listening to speech is predictive of their success in categorising syllables in noise (D'Ausilio et al., 2014). Notably, a multivariate analysis of BOLD responses to speech in noise showed that classification of phoneme identity in premotor cortex (including IFG) was successful from SNRs as low as -6 dB, whereas superior temporal cortex showed classification when the speech signal was much more audible (at +8 dB SNR; Du et al., 2014). Thus, it appears that the speech motor system acts to constrain perception through the top-down communication of predictions to auditory cortex during sensory stimulation. There may, however, also be domain-general aspects to the engagement of PM and IFG by speech perception. Wild and colleagues (2012) explicitly tested the hypothesis that modulations of the BOLD response in a range of brain regions expressly index effortful listening, and found that regions including IFG and PMv tended to be implicated more strongly under conditions where speech is both degraded *and* attended.

To date, there has been little evidence explicitly testing the prediction of Scott and colleagues (2009), that motor cortex may be predominately associated with other forms of sound-to-action responses such as conversational turn-taking, and not with mechanisms for comprehension. Studies of spoken and musical interaction have aimed to characterize the neural basis of turn-taking and have presented affirmative evidence for a motor involvement in supporting the fine timing of communicative interactions (Bögels, Magyari, & Levinson, 2015; Foti & Roberts, 2016; Hadley, Novembre, Keller, & Pickering, 2015). In a study of piano duet playing, TMS-induced disruption of dorsal PM (associated with motor simulation in a variety of tasks) caused delays in turn-taking, which were more marked for sequences in which the partner's turn (preceding the delay) was familiar because the participant had also previously rehearsed it – this effect was not found for SMA (associated with motor imagery), thus suggesting a role for online simulation in the execution of smooth interactions during joint behaviour (Hadley et al., 2015). During listening to spoken conversation, sustained EEG responses between turns, localized to PM (and inferior parietal cortex), were associated with hearing an unexpectedly long delay before a speaker's response to a request (usually associated with reluctance or hesitation), while activity associated with the speaker's response itself was localized to superior temporal cortex (Foti & Roberts, 2016). The authors argue that their findings align well with Scott et al.'s (2009) proposition that ventral and dorsal auditory processing streams perform differing functions during the perception of speech sounds.

Taken together, the findings from cognitive neuroscience studies in healthy young adults have allowed for developing a more detailed account of motor processing in speech perception, which suggests a role for motor/premotor areas in task- and environment-dependent phonological processing during speech perception, and more complex coordinated actions such as turn taking.

5. Widening the scope: Evidence from patients, development and healthy ageing

The study of special populations offers a unique opportunity to examine the effect of damage to motor/premotor regions, either normal or pathological, on speech perception. However, one difficulty with this approach is that there have been very few reports of focal damage to these regions. Another difficulty is related to the fact that, following stroke, the brain reorganises itself, which obscures the study of brain/behaviour relationships. Nevertheless, case studies have traditionally suggested that inferior frontal/premotor damage leads to a deficit in speech production in the absence of a deficit in speech perception, a clinical presentation usually referred to as non-fluent aphasia (or Broca's aphasia). Non-fluent aphasia has been viewed as opposite to fluent (Wernicke's) aphasia, defined as an auditory comprehension deficit in the absence of speech production deficits, which is associated with lesions to posterior superior temporal areas. It should be noted, however, that mild speech perception symptoms have repeatedly been documented in non-fluent aphasics, and that this has been a subject of contention since the 19th century in the field of aphasiology (see (Lecours, Chain, Poncet, Nespoulous, & Joanette, 1992), for example, for an account of a debate at the 1908 Neurology Society in Paris).

Several studies conducted on non-fluent patients with left hemisphere stroke have reported no deficit to speech perception (Hickok, Costanzo, Capasso, & Miceli, 2011; Rogalski, Peelle, & Reilly, 2011; Stasenko et al., 2015). For example, Hickok et al (2011) studied 24 patients with a left-hemisphere ischemic stroke affecting (at least) the IFG (pars triangularis [IFG_{tri}] and or opercularis [IFG_{op}]), using a set of same-different discrimination tasks involving non-word and word comprehension in quiet. In an auditory-visual discrimination task, patients showed impaired performance, but there was no relationship between the severity of their fluency disorder and their perceptual discrimination skills. One potential issue with these studies, however, is that in many of them performance is at (or near) ceiling, suggesting that perhaps the tasks used are unsuitable to detect subtle changes to speech processing skills. In the neurostimulation literature, these types of tasks do not tend to be affected by TMS to premotor cortex or IFG. One study used a more challenging auditory word-picture matching task with normal and degraded auditory stimuli to measure performance in aphasic patients and normal controls (Moineau, Dronkers, & Bates, 2005). The results demonstrate a deficit in the degraded auditory condition for both fluent and non-fluent aphasics, suggesting an impact of frontal lobe damage on speech processing (though the site of the lesion was not examined, warranting prudence in interpreting these results). Using a different approach focusing on lesion location instead of behavioural symptoms, Schwartz et al (Schwartz, Faseyitan, Kim, & Coslett, 2012) correlated brain lesions to auditory comprehension errors in a large sample of 106 post-stroke patients with different types of aphasia and found that errors were correlated with lesions located mainly in the superior temporal area, as was expected, but also, to a limited extent, in the left posterior IFG. Hence, there is some clinical evidence, though relatively limited, supporting the notion that posterior IFG may play a role in auditory speech comprehension.

The study of normal aging provides an alternative framework to test at least two non-mutually exclusive hypotheses about the motor theories of speech perception. The first hypothesis is that, if the motor/premotor cortex is key to speech perception, an age-related decline in the anatomy and functioning of these regions would be expected to lead to a difficulty processing speech. The second hypothesis is that presbyacusis - the decline in the peripheral hearing system associated with aging - should be associated with a compensatory action of the motor/premotor cortex to help maintain performance by relying more strongly on preserved motor knowledge, similar to the hypothesis that a degraded auditory signal is associated with stronger recruitment of the motor/premotor cortex (see above).

Several studies have examined brain activity using fMRI during sentence comprehension tasks at various levels of intelligibility in young and older adults (Eckert et al., 2008; Erb & Obleser, 2013; Harris, Dubno, Keren, Ahlstrom, & Eckert, 2009; Hwang, Li, Wu, Chen, & Liu, 2007). None of those studies reported an age-related increase in activation during the processing of sentences in low intelligibility in the motor/premotor cortex. However, it is possible that sentence comprehension does not require access to detailed motor representations; it is a simple task that may rely on top-down cognitive and linguistic processes to recover the missing information, rather than on motor knowledge, and this higher-order information may be more important when there is less available context. Consistent with this notion, Peelle et al. examined the relationship between hearing and brain activity during a sentence comprehension task at various intelligibility levels in older adults. The results show no evidence of a motor/premotor modulation as a function of hearing thresholds (Peelle, Troiani, Grossman, & Wingfield, 2011). One exception is a brain morphometry study, in which performance during a sentence comprehension task presented at different intelligibility levels was compared in young and older adults. Results demonstrated a positive correlation between performance and grey matter volume in the left IFG (pars triangularis) (Wong, Ettlinger, Sheppard, Gunasekera, & Dhar, 2010). However, it is unlikely that pars triangularis, which lies immediately anterior to the frontal operculum and is not classified as premotor cortex, contains motor knowledge of speech sounds. Speech tasks providing less linguistic context (e.g. using word-level instead of sentence-level stimuli) provide a slightly different picture. For instance, using a picture-word matching task performed under various intelligibility levels, Wong et al. (Wong et al., 2009) found an increase in the activation of the premotor cortex (in a broadly defined region encompassing MFG and M1) that was positively correlated with performance. Similarly, a recent MRI study combining structural and functional measures found that the structure of the left premotor cortex mediates the negative effect of age on BOLD signal during a speech perception task consisting of passive audio-visual word presentation (videos of a talking female producing words) (Tremblay, Dick, & Small, 2013). In contrast, in a study examining simple word repetition performed by adults ranging in age from 20 to 65 years showed no age-related modulation in activity in the PM or the IFG during the task (Manan, Franz, NazlimYusoff, & Mukari, 2015).

Sublexical speech perception tasks, which presumably represent the greatest level of difficulty from a speech perception perspective since they offer no lexical or contextual information to aid speech perception, are more scarce in the literature. In a recent study examining the relation between age and speech perception, it was found that, controlling for hearing, speech perception declines with age. This behavioural decline was examined using a mediation approach, to determine whether age-related speech decline is mediated by structural or functional brain changes. No direct or indirect relationship between speech perception and the function and structure of the premotor cortex or IFG was found (Bilodeau-Mercure, Lortie, Sato, Guitton, & Tremblay, 2015). An age-related decline in the cortical thickness of the PMv was found, but it did not have an effect on speech perception. However, the intelligibility of the speech stimuli was associated with a modulation of the activity in the left PMv, in an age-independent fashion (though the relationship between BOLD and speech intelligibility was positive, which is inconsistent with a compensatory function).

Taken together, the aging literature on speech perception, as well as the clinical literature reviewed at the beginning of this section, provides relatively inconclusive evidence in support of a role for the motor/premotor cortex in speech perception. There is a tendency for the results to suggest that more difficult tasks, such as sublexical perception and tasks involving degraded auditory stimuli, might engage the premotor cortex more strongly in elderly individuals and lead to a decline in performance in patients. However, the only study of sub-lexical processing with ageing did not report such an effect. Additional studies are needed to examine a wider range of tasks in line with the context-dependent motor theory of speech hypothesis.

6. Further Perspectives

From motor theories of speech perception to embodied theories of language

The discovery of the mirror neurons in the monkey, and subsequent discovery of a system in the humans exhibiting mirror-like properties not only served as a catalyst for the study of speech perception/production interactions but also triggered a parallel research bloom in other fields of cognitive neuroscience. The discovery that premotor areas were engaged in goal-oriented action observation (e.g. Decety et al., 1997; di Pellegrino et al., 1992; Grafton et al., 1996) and motor imagery (Roth et al., 1996) was soon followed by the discovery that action words (e.g. Hauk, Johnsrude, & Pulvermuller, 2004; Pulvermüller, Härle, & Hummel, 2001), and action sentences (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Tettamanti et al., 2005) also activated premotor areas. The finding of motor/premotor cortex activation during language comprehension has been interpreted to suggest that specific action representations are activated during action language understanding. This phenomenon is often referred to as *language embodiment*. This is contrast with the classical "disembodied" view that cognition is mediated, at least in part, by symbolic representations. Just as the MTSP has generated extensive discussion, so has the question as to whether motor/premotor representations are necessary or accessory to language comprehension more broadly (e.g. Fernandino & Iacoboni, 2010; Hickok, 2009; Mahon, 2015)). As is the case for speech perception, several studies have shown that motor/premotor cortex responses during action language processing are context-sensitive (e.g. (Alemanno et al., 2012; Schuil, Smits, & Zwaan, 2013; Tettamanti et al., 2008; Tomasino, Weiss, & Fink, 2010). Thus, the two fields of research shared some similar issues with interpretation of the evidence. Only limited clinical evidence favours the embodied language hypothesis - for example, it has been shown that processing of action verbs is impaired in patients with motor disorders such as Parkinson's disease (Boulenger et al., 2008) and motor neuron disease (Bak & Hodges, 2004), supporting the notion of a role for the motor system in action language comprehension. Moreover, Fazio et al. examined the ability of aphasic patients with lesions to the posterior IFG, and no apraxia, to perform an action comprehension task and showed that, compared to age-matched controls, action comprehension was reduced (Fazio et al., 2009), establishing a link between language and action comprehension deficits. A Voxel-based Lesion Symptom Mapping approach (VLSM), has further identified linguistic and non-linguistic action comprehension deficits in aphasia (Saygin, Wilson, Dronkers, & Bates, 2004). Behaviourally, the results demonstrated that both behaviours were impaired. However, the lesion mapping analysis revealed distinct lesion foci, with a focus in the IFG/PM for non-linguistic action understanding and more distributed and non-overlapping lesioned site for linguistic action processing. This is consistent with fMRI studies conducted in healthy subjects showing that distinct parts of the premotor cortex were active during action observation compared to processing of action sentences (Tremblay & Small, 2011a) or action word processing (Postle, McMahon, Ashton, Meredith, & de Zubicaray, 2008).

In sum, the motor theory of speech perception and the language embodiment hypothesis suggest that hearing language (e.g. "kick") activates motor representation for at least two distinct purposes: to retrieve the motor programs associated with the sounds being processed (here the phonemes /k/, /ɪ/, /k/), but only under specific conditions and depending on the task, and to retrieve those associated with the meaning of the words (here, the action of kicking with the foot). However, recent studies examining the implication motor/premotor cortex in language comprehension did not provide support for a causal role, as TMS had no effect on comprehension *per se* (Krieger-Redwood et al., 2013; Tremblay & Small, 2011b) – although, in the Krieger-Redwood et al. study the focus was not specifically on action language, but on word comprehension more generally. Alternative interpretations have been put forward, for example, a unifying role for PM in "motor syntax" (Fazio et al., 2009), but this suggestion awaits empirical support. It will be important, in the future, to study these two questions together in order to better understand the roles of the motor system in speech perception and language comprehension, and how these relate to each other.

Perception-production links beyond motor cortex: sensorimotor transformations in posterior cortical fields

In developing more integrated models of speech, we should consider a growing literature that has described consistent perception-production links *outside* motor/premotor cortex. An important requirement of successful spoken language use is the existence of parity, such that signallers and receivers can exchange roles (Fitch, 2010); this necessitates some capacity for conversion between input and output signals. Overlapping activations have been observed for speech perception and production, throughout superior temporal cortex and extending medially and posteriorly toward the parietal lobe (McGettigan et al., 2011; Tremblay & Small, 2011b). Some studies have reported equivalent activation in posterior fields on the planum temporale (PT) and around the temporoparietal junction or TPJ (including the supramarginal gyrus; SMG) during input and output (Tremblay & Small, 2011), or indeed stronger responses during imagined/covert speech than during listening to speech (Buchsbaum, Hickok, & Humphries, 2001; Hickok, Buchsbaum, Humphries, & Muftuler, 2003). These latter findings are suggestive of a role in sensorimotor transformations and representations rather than basic auditory perception or imagery, and some authors have presented PT and the temporoparietal junction as a candidate region for the phonological store in working memory (e.g. Buchsbaum & D'Esposito, 2008). Such regions are potentially more central to speech sensorimotor processes than motor/premotor cortex: in a study of pseudoword perception and production, it was found that the magnitude of the BOLD response in PM was not modulated by syllabic complexity in perception, but that right PT did show such a sensitivity (Tremblay & Small, 2011b). In this case, the authors suggested context-dependent involvement of motor cortex in their study, where performance of the tasks required only a coarse-grained representation of articulatory detail, whereas this engaged PT in a more obligatory fashion (see also (Deschamps & Tremblay, 2014), for passive sensitivity to syllabic structure in PT). Existing findings suggest a functional heterogeneity within sub-regions of the PT, where the caudal part in particular is insensitive to auditory feedback during speech yet is activated by tasks requiring auditory-to-motor conversion (whether for reading aloud or silently; Tremblay et al., 2013) – elaboration of the representations and processes subserved by these cortical fields, as well as their anatomical and functional connections with other fronto-temporal nodes of the language system, will be integral to the future development of neurobiological models of speech (Dick & Tremblay, 2012).

7. Conclusion

Which is the most likely role for motor cortex in speech perception?

We have described progress in the field of cognitive neuroscience in its quest to elaborate the role(s) of motor/premotor cortical fields in the perception of spoken language. Drawing together findings from neuroimaging, electrophysiology and brain stimulation in healthy participants, as well as considering the evidence from brain injury and healthy ageing, we acknowledge that motor processes and/or representations are involved in speech understanding, but that this is strongly dependent on context. As it stands, the empirical evidence suggests that while motor/premotor involvement in speech perception is neither fundamental nor essential, it cannot be dismissed as fully redundant. By now, many studies have demonstrated the online engagement of motor/premotor cortex by heard speech, with causal implications for perceptual performance. The degree to which these "motor responses" extract and represent the articulatory information in the signal is as yet unclear - in the same way that the detectability of motor cortical activations appears to be dependent on the task and the listening situation, it may also be the case that similar factors modulate the granularity of representations within these sites. While there are interesting data emerging that support a qualitatively different role for motor cortex in the timing of conversational interactions – surely the natural habitat of speech – these are still few in number, and it remains to be seen whether these really are more fundamental to the evolution of spoken communicative behaviours across humanity.

Accepting that the motor/premotor cortex performs a variety of roles in speech perception, it is appropriate that neurocognitive models of speech processing should more keenly reflect the overlap and integration of processes within the input and output systems that have previously received rather independent treatment. Going forward, it will become increasingly important to model and measure the engagement of neural systems during contextualised and dynamic communicative interactions, rather than continuing to focus almost exclusively on speech as the disembodied and unilateral transmission of signals from talkers to listeners (McGettigan, 2015; Pickering & Garrod, 2013; Schilbach et al., 2013). This brings methodological challenges, for example in designing fMRI paradigms and analyses that can mitigate factors such as speech-related head movements associated with free conversation. When studying both perception and production of speech and considering the extensive and overlapping regions of the brain involved, it also becomes increasingly important to consider neural responses at the level of networks as well as local cortical representations – techniques such as independent components analysis can reveal the independent modulation of overlapping cortical nodes by task and condition, and the separation of domain-specific from domain-general contributions to task performance (see e.g. Geranmayeh et al., 2012). The comparison of speech and non-speech sound processing could also provide useful information to understand underlying computations and distinguish domain general from (potentially) speech-specific ones. Thus, a combination of more naturalistic designs and analyses combining region and network approaches might be key to furthering current understanding of the neural interactions underpinning perception and production.

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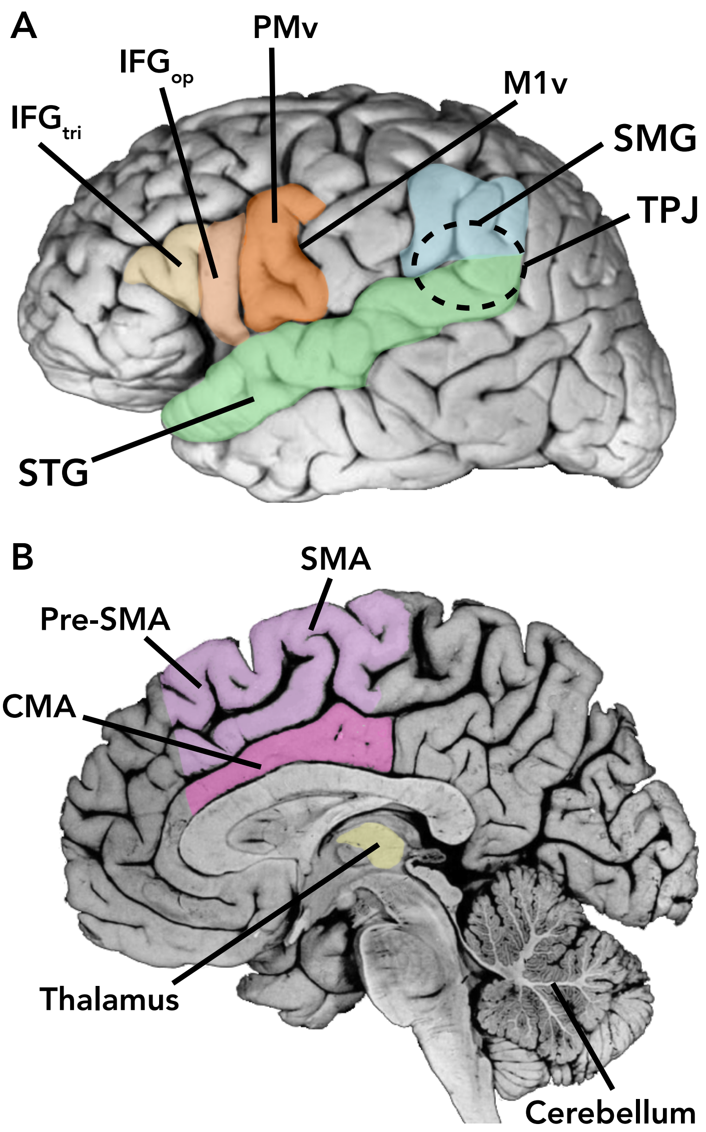

Figure 1. Illustration of the main regions involved in the perception and production of speech. A. Lateral view of a human brain. B. Sagittal view of a human brain. IFG_{tri} = Inferior Frontal Gyrus, pars triangularis; IFG_{op}; PMv = ventral premotor cortex; M1_{v} = ventral primary motor cortex; SMG = supramarginal gyrus; TPJ = temporoparietal junction; STG = superior temporal gyrus; CMA = cingulate motor area; Pre-SMA = pre supplementary motor area; SMA = supplementary motor area. Note that the primary auditory cortex and planum temporale are not visible from the surface as they are located medial to the STG. Other deep structures involved in speech processes are the basal ganglia and insula.