Neuropsychologia 94 (2017) 13–22

Contents lists available at ScienceDirect

Neuropsychologia

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

The role of hearing ability and speech distortion in the facilitation of articulatory motor cortex

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ARTICLE INFO

Keywords:
Speech perception
Motor cortex
Transcranial magnetic stimulation
Motor evoked potentials

ABSTRACT

Excitability of articulatory motor cortex is facilitated when listening to speech in challenging conditions. Beyond this, however, we have little knowledge of what listener-specific and speech-specific factors engage articulatory facilitation during speech perception. For example, it is unknown whether speech motor activity is independent or dependent on the form of distortion in the speech signal. It is also unknown if speech motor facilitation is moderated by hearing ability. We investigated these questions in two experiments. We applied transcranial magnetic stimulation (TMS) to the lip area of primary motor cortex (M1) in young, normally hearing participants to test if lip M1 is sensitive to the quality (Experiment 1) or quantity (Experiment 2) of distortion in the speech signal, and if lip M1 facilitation relates to the hearing ability of the listener. Experiment 1 found that lip motor evoked potentials (MEPs) were larger during perception of motor-distorted speech that had been produced using a tongue depressor, and during perception of speech presented in background noise, relative to natural speech in quiet. Experiment 2 did not find evidence of motor system facilitation when speech was presented in noise at signal-to-noise ratios where speech intelligibility was at 50% or 75%, which were significantly less severe noise levels than used in Experiment 1. However, there was a significant interaction between noise condition and hearing ability, which indicated that when speech stimuli were correctly classified at 50%, speech motor facilitation was observed in individuals with better hearing, whereas individuals with relatively worse but still normal hearing showed more activation during perception of clear speech. These findings indicate that the motor system may be sensitive to the quantity, but not quality, of degradation in the speech signal. Data support the notion that motor cortex complements auditory cortex during speech perception, and point to a role for the motor cortex in compensating for differences in hearing ability.

1. Introduction

Successful speech perception is central to everyday communication and quality of life. It is therefore surprising that understanding of the neural bases underpinning speech perception remains limited. Although auditory-related areas are thought to be at the heart of the neural architecture for understanding speech, there is accumulating evidence that areas extending beyond primary and association auditory cortices are important for successful speech perception. Cortical regions including, but not limited to, ventral premotor cortex, inferior frontal gyrus, and supplementary and primary motor areas have also been suggested to be involved in speech perception (Adank et al., 2012; Callan et al., 2010; D'Ausilio et al., 2009; Londei et al., 2010; Skipper et al., 2005; Tremblay et al., 2012). Indeed, it is now largely accepted that articulatory motor areas are active when we perceive speech (Bartoli et al., 2015; Fadiga et al., 2002; Möttönen and Watkins, 2009; Wilson et al., 2004). Furthermore, the motor system does not seem to activate in a binary fashion when listening to either speech or non-speech; instead, excitability of articulatory motor regions during speech perception appears to be graded depending on the clarity of speech (Murakami et al., 2011). Murakami et al. (2011) demonstrated that lip motor evoked potentials (MEPs), elicited by transcranial magnetic stimulation (TMS) to the lip area of primary motor cortex (M1), are enhanced when perceiving speech-in-noise relative to perceiving speech without noise. This finding has been interpreted to reflect increased excitability in the cortical motor representation of the lips when listening to degraded speech.

These MEP findings are in line with behavioural changes that have been observed after receiving online TMS to primary lip and tongue areas. Paired-pulse TMS to M1 lip was found to lead to faster

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http://dx.doi.org/10.1016/j.neuropsychologia.2016.11.016
Received 11 May 2016; Received in revised form 18 November 2016; Accepted 20 November 2016
Available online 21 November 2016
0028-3932/

(facilitated) reaction times to lip-articulated stimuli in noise, and similarly for tongue-articulated stimuli following tongue stimulation, but with no change to reaction time when listening to speech in quiet (D'Ausilio et al., 2012). Similar findings have been shown for premotor cortex by Meister et al. (2007), who used 1 Hz repetitive TMS, which has been shown to result in inhibitory effects, to demonstrate that ventral premotor cortex (PMv) contributes to the perception of speech-in-noise. Crucially, Sato et al. (2009) also used inhibitory 1 Hz repetitive TMS and found that a contribution from PMv was absent when speech was presented without background noise, indicating that speech perception must be challenged before PMv contributes to listening to speech. These TMS findings resonate with fMRI observations of increased motor cortex recruitment during comprehension of degraded speech (Hervais-Adelman et al., 2012; Osnes et al., 2011). Taken together, data indicate that the motor cortex is preferentially engaged when listening to speech that is difficult to perceive, and that motor activation may be necessary for successful speech perception under challenging listening conditions.

The precise function of observed motor activity during speech perception, however, remains under active debate (Hickok et al., 2011; Lotto et al., 2009; Scott et al., 2009). Recent theories suggest that motor activation may form the basis for the mental simulation of perceived action, which may aid listeners when predicting upcoming speech signals (Gambi and Pickering, 2013; Pickering and Garrod, 2013; Wilson and Knoblich, 2005). Simulation theories of action perception argue that observing actions results in the automatic generation of motor plans required to perform the actions. Simulated motor plans are then used to inform forward models about the co-ordination of one's own muscles to generate a simulated course of movement in parallel with, or even in anticipation of, the movement being perceived (Grush, 2004). This type of forward model serves to anticipate others' actions as if they were produced by the observer (Locatelli et al., 2012), and may be used to disambiguate noisy, obscured, or ambiguous actions (Wilson and Knoblich, 2005). With regards to speech perception, these types of conditions may involve listening to speech in the presence of background noise, or listening to someone speaking in an unfamiliar accent (Adank et al., 2012; Adank and Janse, 2009) or manner of speaking (Borrie et al., 2013; Borrie and Schäfer, 2015).

Although it is well-established that perceiving speech draws upon hierarchically organized temporo-frontal processing pathways (Davis and Johnsrude, 2007, 2003), it is not clear what role premotor and primary motor regions play within this speech processing hierarchy. Knowledge of the nature of articulatory motor representations and their sensitivity to speech is incomplete. For example, it is unknown if, and how, increased motor excitability during perception of challenging speech is modulated by the nature and extent of the speech distortion. Accordingly, two possibilities currently exist for how the motor system responds to distortion in the speech signal. The first is that articulatory motor regions may activate whenever distortion is present in the speech signal, independent of the form or type of speech distortion. The second possibility is that articulatory motor regions may respond differently depending on the type of distortion in the speech signal. If the former is true, it would suggest that the motor system acts as a self-adjusting resource to provide additional information whenever auditory information is found to be insufficient. Support for this prediction comes from demonstrations of heightened motor excitability for both speech-internal distortion (Nuttall et al., 2016) and speech-external distortion (Murakami et al., 2011), yet these two sources of distortion have never been directly compared.

Conversely, if the second possibility is true, and activity in motor regions is differentially modulated depending on the type of speech distortion, this indicates that the motor system operates in a form dependent manner during speech perception. Indeed, this is in line with the hypothesis that prediction signals generated by forward models during perception are ideally suited to disambiguate biological sources of variation (Sebanz et al., 2006); for example, when perceiving speech signals that are difficult to understand due to an unfamiliar manner of speech production. This possibility resonates with common-coding accounts of action perception, whereby the motor system is most responsive to observed actions that the observer has experience producing themselves (Calvo-Merino et al., 2005). In this case, the motor system's prediction signal would be less well-suited to assist action understanding when the difficulty arises from a non-motor source, such as speech-shaped background noise, for example, which does not constitute an imitable action. To date, whether, and how, motor facilitation is affected by speech distortion type, or extent of speech distortion, is unknown.

Moreover, the quality of the speech signal received by auditory cortex is at the heart of motor simulation. However, previous considerations of speech signal quality have been limited to the properties of the speech stimulus. This is not the only means by which speech signal quality can be degraded. The first point in the speech processing chain begins with the ear, where differences in mechanical and electrical function at the level of the cochlea and auditory nerve can contribute to discrepancies in how the speech signal is processed, even when individuals have clinically normal hearing (Bharadwaj et al., 2015; Harris et al., 2009; Ruggles et al., 2012). Accordingly, it is possible that differences in auditory processing at the ear modulate motor activity in a manner that is qualitatively similar to the effect of a degraded speech stimulus. Indeed, our previous study demonstrated a significant correlation between peripheral hearing acuity and the extent of lip MEP facilitation during distorted relative to clear speech perception, which was not present for hand MEPs (Nuttall et al., 2016). Precisely how hearing abilities relate to the extent of motor activation in optimal and suboptimal listening conditions has not been studied. Relatedly, Peelle et al. (2011) found that moderate declines in peripheral auditory processing led to a systematic down-regulation of neural activity in auditory regions during speech processing, and may also contribute to loss of grey matter volume in primary auditory cortex. If motor system activation is interlinked with speech signal quality, as motor simulation accounts would propose, it may be that hearing ability plays a role in engagement of the motor cortex during speech perception. A second aim of this study, therefore, was to explicitly test the relationship between hearing ability and speech motor excitability under different challenging listening conditions.

In the present study, we first aimed to disambiguate between form dependent and form independent accounts of how speech distortion modulates motor activation during speech perception, and second, we investigated whether normal variation in hearing ability impacts speech motor facilitation. To this end, in a first experiment, MEPs were elicited during perception of three different types of auditory stimuli: 1) clear speech stimuli presented without background noise, 2) speech stimuli distorted via a motor perturbation introduced during prior stimulus creation (motor distortion), and 3) speech-in-noise (noise distortion), where intelligibility was matched to the motor-distorted speech based on equating percent correct identification between the two degraded stimuli types. For speech-in-noise stimuli, clear speech stimuli were presented in a steady background of speech-shaped noise. In a second experiment, we recorded MEPs during perception of 1) clear speech, 2) speech-in-noise that was 75% intelligible, and 3) speech-in-noise that was 50% intelligible. The same clear speech and noise type from Experiment 1 were used in Experiment 2, but signal-to-noise ratio was varied. All speech stimuli were disyllabic vowel-consonant-vowel sounds containing a mixture of consonants that were either lip- (/aba/, /apa/) or tongue-articulated (/ada/, /ata/). Chance performance was therefore always 25%. Stimulation was thus used to determine whether motor facilitation in lip M1 is sensitive to the nature and extent of speech signal degradation. In both experiments, we also measured hearing sensitivity to examine whether hearing ability is related to motor facilitation when perceiving different types of speech distortion.