Neuropsychologia 75 (2015) 525–532

Contents lists available at ScienceDirect

Neuropsychologia

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

Excitability of the motor system: A transcranial magnetic stimulation study on singing and speaking

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ARTICLE INFO

Article history:
Received 13 October 2014
Received in revised form
1 June 2015
Accepted 22 June 2015
Available online 25 June 2015

Keywords:
Transcranial magnetic stimulation (TMS)
Primary motor cortex (M1)
Singing perception
Speech perception
Motor evoked potentials (MEPs)
Orbicularis oris

ABSTRACT

The perception of movements is associated with increased activity in the human motor cortex, which in turn may underlie our ability to understand actions, as it may be implicated in the recognition, understanding and imitation of actions. Here, we investigated the involvement and lateralization of the primary motor cortex (M1) in the perception of singing and speech. Transcranial magnetic stimulation (TMS) was applied independently for both hemispheres over the mouth representation of the motor cortex in healthy participants while they watched 4-s audiovisual excerpts of singers producing a 2-note ascending interval (singing condition) or 4-s audiovisual excerpts of a person explaining a proverb (speech condition). Subjects were instructed to determine whether a sung interval/written proverb, matched a written interval/proverb. During both tasks, motor evoked potentials (MEPs) were recorded from the contralateral mouth muscle (orbicularis oris) of the stimulated motor cortex compared to a control task. Moreover, to investigate the time course of motor activation, TMS pulses were randomly delivered at 7 different time points (ranging from 500 to 3500 ms after stimulus onset). Results show that stimulation of the right hemisphere had a similar effect on the MEPs for both the singing and speech perception tasks, whereas stimulation of the left hemisphere significantly differed in the speech perception task compared to the singing perception task. Furthermore, analysis of the MEPs in the singing task revealed that they decreased for small musical intervals, but increased for large musical intervals, regardless of which hemisphere was stimulated. Overall, these results suggest a dissociation between the lateralization of M1 activity for speech perception and for singing perception, and that in the latter case its activity can be modulated by musical parameters such as the size of a musical interval.

1. Introduction

Several studies have suggested that the perception of movement is associated with increased activity in sensory as well as in motor regions of the human brain (Buccino et al., 2001; Fadiga et al., 1995; Hari et al., 1998; Watkins et al., 2003). For instance, the perception of articulatory gestures involved in speaking has been shown to generate activation in the mouth representation of the primary motor cortex (M1) (e.g. Murakami et al., 2011; Sundara et al., 2001; Watkins et al., 2003). One of the mediators enabling this coupling between production and perception is thought to be the mirror neuron system (MNS) (Gallese et al., 1996; Rizzolatti and Craighero, 2004; Rizzolatti et al., 2001). Although its existence and exact role are still debated (see Hickok (2009) for a review), it has been suggested that the purpose of this mirror-like activity, also referred to as a phenomenon called "motor resonance", would be to allow humans to recognize, organize and understand other's action by mapping sensory information into a motor representation (Gallese et al., 1996; Rizzolatti and Craighero, 2004; Rizzolatti et al., 2001).

Transcranial magnetic stimulation (TMS) has been commonly used in humans as a non-invasive and focal tool to investigate motor activation patterns during the perception of movement, through the examination of the excitability of the primary motor cortex (M1) (e.g. Fadiga et al., 2002, 1995; Strafella and Paus, 2000; Watkins et al., 2003). One approach consists in comparing changes in the amplitude of magnetically induced motor evoked potentials (MEPs) under different circumstances (e.g. Fadiga et al., 1995; Sparing et al., 2007; Watkins et al., 2003), providing an indirect

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http://dx.doi.org/10.1016/j.neuropsychologia.2015.06.030
0028-3932/

measure of M1 activity. This technique has been used to characterize the excitability of the motor system underlying speech perception (see Devlin and Watkins (2007) for a review). For instance, Watkins et al. (2003) showed that viewing speech movements increased MEP amplitude after stimulation of the left hemisphere compared to the right, and that this increase in excitability was specific to the lip muscle as no change in excitability was found in hand muscles. Also, D'Ausilio et al. (2009) showed a double dissociation of the motor cortex structures implicated in the discrimination of language at the lip and tongue level, after stimulation of the left hemisphere. The activity measured on the lips was higher than on the tongue for the perception of speech movements involving mainly the lips (e.g. the articulation of the letters “b” or “p”), and it was higher when measured on the tongue as compared to the lips during the perception of speech movements involving mostly the tongue (e.g. the articulation of the letters “t” or “d”). Further converging evidence from neuroimaging studies as well as TMS studies support the idea that auditory and motor regions can be modulated by the presentation of different speech stimuli (e.g. Binder et al., 2004; Sato et al., 2009; Wilson and Iacoboni, 2006). For instance a recent TMS study has found that decreasing the auditory or visual intelligibility of speech articulation by adding noise or increasing the speed of articulatory movements increased the motor cortex excitability (lip muscle) compared to the conditions without noise or with slow articulatory movements (Murakami et al., 2011). These results support the notion that the motor system could also be specifically recruited in contexts where perception is difficult (e.g. D'Ausilio et al., 2012; Wilson, 2009). Altogether, these TMS and neuroimaging speech studies have suggested that left motor structures offer a specific functional contribution to the perception of speech, and have provided further insight in the somatotopic organization of facial representations in M1.

While there is now ample evidence linking the motor cortex with speech perception, very few studies have assessed its implication during the perception of singing. One such study has suggested a role for the right motor area in the perception of singing, by showing that TMS stimulation of the right larynx premotor representation modulated the reaction times of subjects having to categorize short tones that were either sung by a human voice or played by a machine (Lévêque et al., 2013). These results suggest that the premotor representation of the right larynx may play a functional role in the perception of a singing voice, which contrasts with the aforementioned involvement of left hemisphere motor representations for speech perception. Furthermore, Lévêque and Schön (2015) compared the involvement of motor cortex in perceptual tasks using different stimuli (i.e. vocal (sung), semi-vocal and non-vocal melodies) to investigate how cortical activity would be modulated by the type of stimulus. Using functional magnetic resonance imaging (fMRI), the authors found that the perception of vocal melodies involved greater activity in the right motor cortex as compared to the other conditions. While this result does not show that the right hemisphere is uniquely activated by the task (other neuroimaging studies have reported bilateral motor activations during the perception of singing (e.g. Callan et al., 2006; Özdemir et al., 2006)), it nonetheless suggests that right motor areas play a predominant role in singing perception.

The present study was designed to dissociate the motor regions involved in singing perception and speech perception with the use of TMS, as both types of tasks have been shown to involve and activate the motor cortex. In a singing perception task, participants were required to watch 4-s videos of a woman singing a 2-note ascending interval and then decide whether it matched a written interval, whereas in a speech perception task participants were required to watch 4-s videos of a woman briefly explaining a proverb and then decide if it matched a written proverb. Singing stimuli had previously been validated by Thompson and Russo (2007), who have found that interval size judgments of visual-only recordings of sung intervals were highly correlated with their veridical size. Observation of facial movements may have triggered an internal simulation of singing, which in turn led to the veridical judgments. The speech stimuli were designed in an attempt to relate our findings to the literature, as they were an adaptation from Sparing et al. (2007). During stimulus presentation, single TMS pulses were applied over the mouth (obicularis oris) representation of M1, as this muscle is specifically involved in the production of oral movements such as singing (although to a lesser extent than speaking). Because of the existing neuroimaging literature pointing to a right hemisphere contribution to singing as compared to speaking (e.g. Griffiths et al., 1999; Hugdahl et al., 1999; Sparing et al., 2007) and because melodic processing typically recruit the right hemisphere more than the left (e.g. Peretz and Zatorre, 2005), here we hypothesized that the observation of singing would increase the excitability of the right motor cortex more so than the left (as indexed by MEP amplitude). Conversely and in agreement with previous studies, we hypothesized that the observation of speech stimuli would increase the excitability of the left motor cortex more so than the right. Moreover, as the results of Thompson and Russo's (2007) study suggest that M1 activity can be modulated by the size of music intervals, this experiment also aimed to verify whether this effect could be replicated. More precisely, we expected to record larger MEPs for larger intervals because of the wider range of motion involved in the generation of these intervals. Finally, to assess the chronometry of motor cortex excitability, TMS pulses were delivered randomly in successive time windows ranging from 500 to 3500 ms (milliseconds).

2. Method

2.1. Participants

Twelve right-handed francophone students participated in the experiment (6 females, 6 males; 25.4 ± 3.01 years). One participant (female) did not complete the study as she was unavailable for the second part of the experiment, thus resulting in a final sample of 11 participants. None had a history of neurological disorders, including seizures, and all fulfilled the inclusion criteria for the safe use of TMS (Rossi et al., 2011, 2009). Subjects had minimal or no musical training (average duration of private lessons: 2.45 ± 2.50 years), and gave their written informed consent. The research protocol was approved by Université de Montréal's *Comité d'éthique de la recherche de la Faculté des arts et des sciences* (*CERFAS*).

2.2. Stimuli

Stimuli for the singing perception task consisted of audio–visual recordings from a female vocalist producing 12 ascending intervals (see Table 1 in the Supplementary materials for a list of intervals), ranging from 1 to 12 semitones, on the syllable *la* (Thompson and Russo, 2007). The intervals were produced by 2 different vocalists; they independently produced 12 intervals, each of them starting on a different note matching their own vocal range. The head, face and shoulders of the vocalist were displayed on the videos. In total, 24 4-s videos were created, 12 from each vocalist. The singing perception task consisted of a random selection of 70 recordings.

Stimuli for the speech perception task consisted of recordings from one of two women filmed separately and explaining one of 35 French proverbs, in a similar visual setting as for the singing stimuli (see Table 2 in the Supplementary materials for a sample