



Seeing and hearing speech excites the motor system involved in speech production

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Abstract

The perception of action is associated with increased activity in motor regions, implicating such regions in the recognition, understanding and imitation of actions. We examined the possibility that perception of speech, both auditory and visual, would also result in changes in the excitability of the motor system underlying speech production. Transcranial magnetic stimulation was applied to the face area of primary motor cortex to elicit motor-evoked potentials in the lip muscles. The size of the motor-evoked potentials was compared under the following conditions: listening to speech, listening to non-verbal sounds, viewing speech-related lip movements, and viewing eye and brow movements. Compared to control conditions, listening to and viewing speech enhanced the size of the motor-evoked potential. This effect was only seen in response to stimulation of the left hemisphere; stimulation of the right hemisphere produced no changes in motor-evoked potentials in any of the conditions. In a control experiment, the size of the motor-evoked potentials elicited in the muscles of the right hand did not differ among conditions, suggesting that speech-related changes in excitability are specific to the lip muscles. These results provide evidence that both auditory and visual speech perception facilitate the excitability of the motor system involved in speech production.

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1. Introduction

Perception and production of actions likely involves bi-directional flow of information between sensory and motor regions of the brain. Motor-to-sensory feedback is thought to be necessary to update the sensory system and prepare for changes in sensory input. Sensory-to-motor transfer of information is likely to aid in the recognition, understanding and imitation of actions. Both mechanisms have been well researched with respect to visuo-motor integration but there is a relative paucity of information concerning audio-motor integration, particularly where this applies to speech.

Evidence for motor-to-sensory feedback during speech production, in the absence of speech perception, was revealed using positron emission tomography [28]. Changes in cerebral blood flow were seen in the left primary motor and secondary auditory cortex when subjects increased the rate at which they produced whispered speech. On the other hand, sensory-to-motor flow of information is implied by imag-

ing studies of visual perception of speech (speech-reading), which appears to lead to brain activation in motor and premotor regions, as well as in auditory cortex, particularly in the left hemisphere [6,24,25].

The activations of motor regions seen during visual perception of speech-related facial movements are consistent with findings from other imaging studies in humans [3,18] and with single unit recording in monkeys, which examined visual perception of hand movements [8,12]. It has been proposed that such changes are due to the activity of “mirror” neurons, which establish a “motor resonance” in the observer during action perception allowing a mapping of that perception onto a neural pattern underlying production of the same action [29,30]. The regions most commonly associated with this mirror-neuron activity are the left ventral premotor cortex, the inferior parietal lobe and the superior temporal sulcus.

In humans, studies using transcranial magnetic stimulation (TMS) and magnetoencephalography have demonstrated changes in primary motor cortex during visual perception of hand movements [1,9,13,16,33] and auditory perception [10,17]. In the TMS studies, the increased excitability of the motor system during action perception has

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been demonstrated to be muscle-specific and, most likely, cortical in origin [33]. The findings from magnetoencephalography support the cortical nature of this phenomenon [16,17]. Spinal cord excitability is modulated also by action observation but in a reversed pattern to that seen during action production; this may act to prevent actual production of the observed action [2].

In this study, we used TMS to examine whether auditory perception of speech modulated the excitability of the motor system underlying speech production. Such an effect would also be consistent with predictions from the motor theory of speech perception [23]. Although many of the articulatory gestures used in speech production are not visible to the listener even when observing the speaker, observation of the speaker during speech can affect its perception. For example, dubbing of foreign language films produces a disconcerting effect and, in the laboratory, McGurk and MacDonald [26] demonstrated that the perception of an auditory syllable could be altered dramatically by the observation of a different visual one. This effect may involve an imitation mechanism, and, therefore, motor activity, which in turn feeds back to sensory regions. In view of this, we examined whether visual perception of speech might also modulate motor excitability in the speech production system.

Using similar methods to those used in previous action observation studies, we measured the excitability of the motor system under different auditory and visual perception conditions. The size of the motor-evoked potential (MEP) in the lip muscles produced by TMS of the primary motor face area was our dependent measure of motor excitability. In a control experiment, we measured MEP size in the hand muscles in response to TMS of the primary motor hand area under the same conditions. Our expectations were that the size of the MEP in the lip muscles elicited by TMS of the primary motor face area would be increased by auditory perception of speech and by visual perception of speech-related lip movements, but not by auditory perception of non-verbal sounds nor by visual perception of other movements. We also anticipated that there might be a hemispheric asymmetry in the auditory speech perception condition related to the left hemisphere's specialisation for speech. Because these effects have been shown previously to be muscle-specific, at least for hand movements, we did not anticipate any changes in MEP size obtained in the control experiment from the hand muscles.

2. Methods

2.1. Subjects

Eight subjects participated in an experiment involving the lip muscles (three males, five females; average age: 27.25 ± 5.92 years; age range: 19–35 years). Another seven subjects participated in a control experiment involving the hand muscles (five males, two females; average age: 32.43 ± 4.50

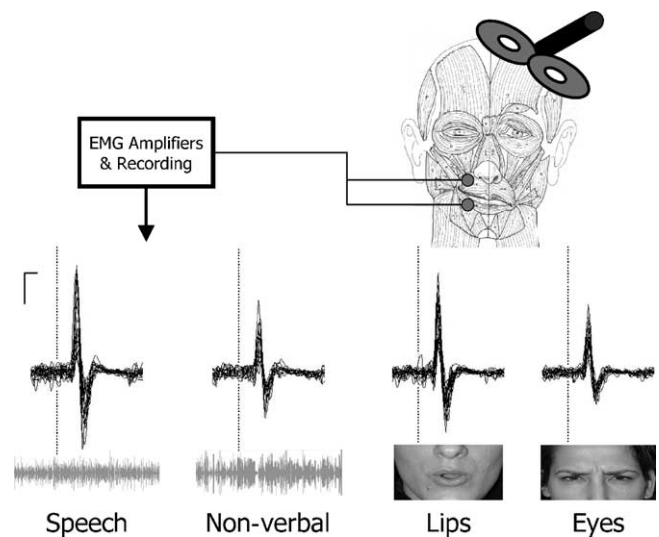


Fig. 1. Experimental set-up and typical MEP data. The upper half of the figure is a schematic showing the position and orientation of the stimulating coil and the placements of recording electrodes on the contralateral orbicularis oris muscle. The drawing of the head with face muscles is adapted from [19]. The lower half of the figure shows data from stimulation of the left primary motor face area in a single subject in each of the four experimental conditions. EMG recordings from individual trials are superimposed. The dotted line represents the time of stimulation. The horizontal bar represents 10ms and the vertical bar 0.5mV.

years; age range: 28–40 years). All gave their informed consent for the procedures, which were approved by the Research Ethics Board of the Montreal Neurological Hospital and Institute.

2.2. Electromyography

For the lips experiment, surface electrodes (Ag/AgCl; 10-mm diameter) were attached to the orbicularis oris muscle to record electromyographic (EMG) activity (see Fig. 1). This muscle is rarely at rest, so in order to stabilise baseline EMG activity during the study, subjects were trained for approximately 10 min to produce a constant level of contraction of the lip muscles by pursing them while receiving visual feedback indicating the amount of EMG activity. They were trained until a satisfactory constant level of contraction of between 20 and 30% of their maximum voluntary contraction was obtained. During the study, subjects were asked to produce this level of contraction whilst being stimulated. Contraction of the lip muscles also allowed us to find the lower active motor threshold and use, therefore, lower levels of stimulation than those necessary to elicit an MEP in the resting muscle.

For the hand experiment, the same procedures were followed as for the lips experiment, but the electrodes were attached to the first dorsal interosseous muscle of the right hand. As above, subjects were trained to maintain a constant level of contraction of this muscle during the experimental conditions.

2.3. Transcranial magnetic stimulation

Magnetic stimuli were generated by Magstim 200 and delivered by a figure-eight coil (each wing 3.5 in. diameter; Magstim, Dyfed, UK) connected through a BiStim module. The coil was placed tangential to the skull, such that the induced current flowed from posterior to anterior under the junction of the two wings of the figure-eight coil. The face area of primary motor cortex was located by first locating the hand area (where application of TMS elicited a muscle twitch in the contralateral hand) and then moving the coil ventrally and slightly anterior until an MEP was observed in the contralateral orbicularis oris muscle. The coil was held in a fixed position by a mechanical arm over the area where the lowest motor threshold was obtained for the muscle (either the orbicularis oris or the first dorsal interosseous) under contraction. The active motor threshold was determined as the intensity at which TMS elicited at least 5 out of 10 MEPs with an amplitude of at least 50 μ V. The intensity of the stimulator was then set to 120% of this active motor threshold for the stimulations applied during the experiment.

2.4. Experimental conditions

There were four experimental conditions.

- (1) Speech condition: listening to speech (continuous prose) while viewing visual noise.
- (2) Non-verbal condition: listening to non-verbal sounds (e.g. glass breaking, bells ringing, guns firing) while viewing visual noise.
- (3) Lips condition: viewing speech-related lip movements while listening to white noise.
- (4) Eyes condition: viewing eye and brow movements while listening to white noise.

The average size of MEPs in each of the four conditions was expressed as a percentage of the average MEP size obtained in a control condition, where subjects viewed visual noise and listened to white noise. The order of these five conditions was randomised across subjects. Each condition lasted approximately 3 min, during which 20 magnetic stimuli were applied at intervals of 5 s. There were intervals of approximately 5 min between conditions.

2.5. Data analysis

Continuous electromyography recordings were acquired during each condition with a 10-channel TMS-compatible system [35], which uses a sample-and-hold circuit that pins the amplifier output to a constant level for 2.5 ms, starting 100 μ s before the pulse, with about 3-ms recovery time. The amplifier's bandwidth was 0.1–500 Hz and the signal was sampled at 1.45 kHz. Rectified EMG sweeps starting 100 ms before the TMS pulse and ending 200 ms after were analysed individually for each condition in each subject

using Matlab 5.2 (The Mathworks Inc., Natick, MA). The size (area under the curve of the rectified EMG signal, mV·ms) of single MEPs and the average height of the baseline EMG activity preceding these MEPs (100 ms before the TMS pulse) were measured off-line for each of the 20 pulses per condition, per subject. The amount of baseline EMG activity is linearly related to MEP size. Even though our subjects were trained to maintain a contraction of the muscles during stimulation, we adjusted the average size of the MEPs in each condition and in each subject for the baseline EMG activity using analysis of covariance. The mean size of the adjusted and the raw MEPs for each experimental condition were expressed as a percentage of the mean size of the adjusted and the raw MEPs for the control condition, respectively. A within-subjects analysis of variance was used to assess the significance of the effect of experimental condition on these MEP ratios.

3. Results

In the lips experiment, data were obtained for stimulation of the left and right primary motor face area in eight subjects. The average active motor thresholds (percentage of maximum stimulator output) for stimulation over the face area of primary motor cortex were not significantly different between the two hemispheres (left: $47.88 \pm 6.98\%$; right: $50.13 \pm 8.01\%$; average difference: $2.25 \pm 8.31\%$).

Within-subjects ANOVA compared the main effects of hemisphere (left versus right) and condition (four conditions). There were significant main effects of hemisphere ($F(1, 7) = 14.89$, $P = 0.006$; left > right) and condition ($F(3, 21) = 5.32$, $P = 0.007$; Speech and Lips > Eyes conditions) but the interaction between hemisphere and condition was not significant ($F(3, 21) = 1.33$, $P = 0.30$). Even though this interaction was not significant, the main effect of hemisphere was highly significant and favoured the left. Furthermore, inspection of the means revealed MEP ratios greater than 100% for three of the four conditions following left hemisphere stimulation, whereas MEP ratios were less than 100% for all four conditions following right hemisphere stimulation (see Fig. 2a and b). This suggests that increased motor excitability relative to the control condition only occurred in the left hemisphere. For these reasons, we further explored the within-subject effect of condition in the two hemispheres separately and made paired comparisons between the hemispheres for each condition separately. Paired comparisons between hemispheres revealed significant differences in favour of the left hemisphere for the following conditions: Speech ($t(7) = 2.44$, $P = 0.045$); Non-verbal ($t(7) = 2.98$, $P = 0.020$); and Lips ($t(7) = 3.17$, $P = 0.016$).

For the left hemisphere alone, a one-way repeated measures analysis of variance revealed a significant main effect of experimental condition ($F(3, 21) = 4.45$, $P = 0.014$). Simple planned contrasts demonstrated that this was due to

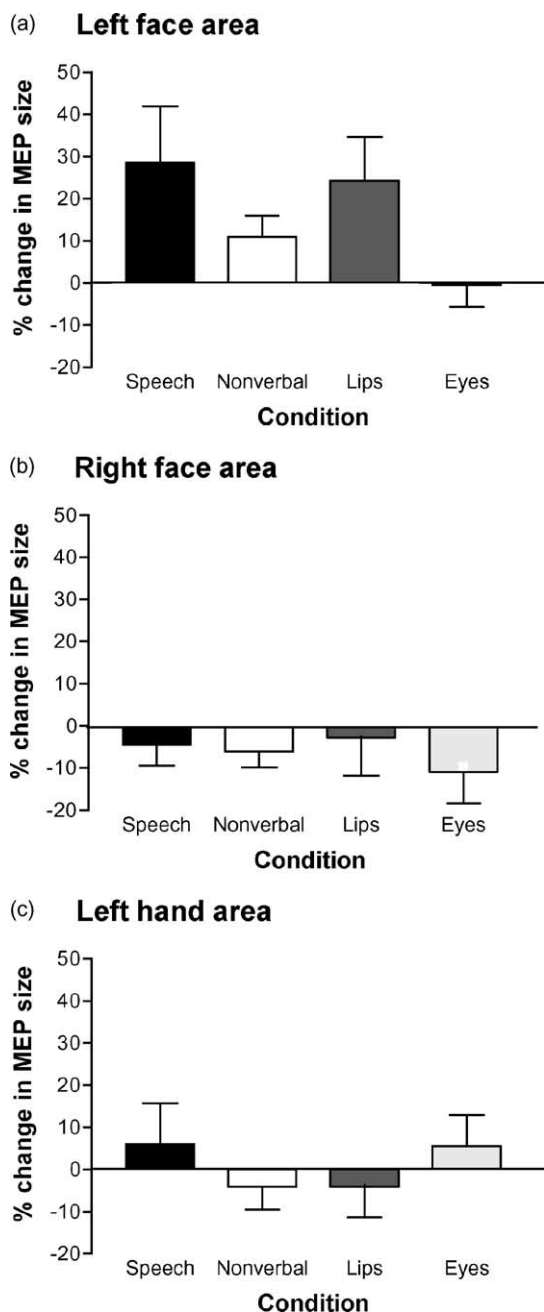


Fig. 2. Average group MEP sizes for the lips and the hand experiments. The group mean adjusted MEP sizes per condition expressed as a percentage change from the average for the control condition are shown for (a) stimulation of the left primary motor face area ($n = 8$); (b) stimulation of the right primary motor face area ($n = 8$); and (c) stimulation of the left primary motor hand area ($n = 7$). Error bars represent standard errors of the mean. The x -axis through the 0% level represents the mean MEP size in the control condition.

significantly higher adjusted MEP ratios, compared with the Eyes condition, for the Speech condition ($t(7) = 2.57$, $P = 0.037$) and the Lips condition ($t(7) = 3.00$, $P = 0.020$). In contrast, following stimulation of the right hemisphere, the average adjusted MEP ratios for all conditions were close to or below 100%, indicating that none of the conditions

increased motor excitability relative to the control condition. The main effect of experimental condition was not significant ($F < 1$) for the right hemisphere. There was no significant difference in baseline EMG activity between the left and right hemisphere or among experimental conditions for either hemisphere.

The analysis of the raw MEP data produced the same pattern of results. For the left hemisphere stimulation, there was a significant main effect of experimental condition ($F(3, 21) = 4.43$, $P = 0.015$). The raw MEP ratios were significantly higher compared to the Eyes condition, for the Speech condition ($t(7) = 3.18$, $P = 0.015$) and the Lips condition ($t(7) = 2.80$, $P = 0.027$). For the right hemisphere stimulation, there was no significant difference in the raw MEP ratios among conditions ($F < 1$).

In the hand experiment, data were obtained for stimulation of the left primary motor hand area in seven subjects. The average active motor threshold (percentage of maximum stimulator output) for stimulation over the hand area of left primary motor cortex was $38.57 \pm 5.71\%$. The average adjusted MEP ratios for each condition are shown in Fig. 2c. A one-way repeated measures analysis of variance revealed no significant differences among the experimental conditions ($F < 1$). The analysis of the raw MEP data and the baseline EMG activity also failed to reveal any significant main effect of condition ($F < 1$).

4. Discussion

These results demonstrate that speech perception, either by listening to speech or by visual observation of speech-related lip movements, enhanced excitability of the motor units underlying speech production, particularly those in the left hemisphere. The results are consistent with our predictions, namely that increases in MEP size would be seen during auditory and visual perception of speech. The size of the MEPs elicited under the auditory and visual speech perception conditions was significantly greater than those elicited under the condition in which subjects viewed movements of the eyes and brow. The MEP sizes obtained in the condition in which subjects listened to non-verbal sounds did not differ significantly from those obtained under the other conditions. This may have been due to a slight but not significant increase in excitability during the listening to non-verbal sounds condition, which in turn may be related to the ability of some subjects to produce these non-verbal sounds (e.g. make the sound of a car engine). This interpretation is also consistent with the finding for the listening to non-verbal sounds condition that left hemisphere stimulations elicited significantly greater MEP sizes compared with right hemisphere stimulations.

The finding that *listening* to speech enhanced motor excitability is consistent with a recent magnetoencephalography study reporting involuntary motor activity above the primary motor hand area in pianists *listening* to music

[17] and with the notion that auditory perceptions also feed-forward to motor regions as possible influences on the recognition, understanding and imitation of the actions used to produce such sounds. It is also consistent with the prediction of the motor theory of speech perception [23] that the auditory perception of speech involves mapping onto the speech production system. Further corroboration of these findings comes from a recent study [10], which demonstrated significant increases in MEPs recorded from the tongue in response to TMS of left primary motor cortex when listening to words and non-words containing consonants that required tongue movements in their production.

In contrast to the results of our study (and those of [10]), however, another TMS study [34] did not find facilitation of MEPs obtained in orbicularis oris at rest during auditory perception. MEP size was facilitated only during visual perception of spoken syllables that involved the orbicularis oris muscle in their production (i.e. 'ba' versus 'ta'). The negative finding for auditory perception previously reported [34] may have been due to methodological differences in that study compared with ours; sub- versus supra-threshold stimulation in resting versus contracted muscle, respectively, and listening to single syllables presented every 2 s compared with continuous speech stimuli.

The increase in excitability of the motor system underlying production of lip but not hand movements during visual observation of lip movements is in accord with the results of two previous TMS studies of visual observation of hand movements [9,33]. In those studies, the increased motor excitability was specific to the muscles used to execute the observed movement. It was somewhat surprising that the increased excitability during visual observation of lip movements only occurred for left hemisphere stimulation. But evidence suggests that the dominance of the left hemisphere for perception during lip-reading [4,5] as well as for production of mouth movements during spontaneous speech [15,36]. It should be noted that although the subjects were unable to lip-read and, therefore, could not understand clearly what was being said during the Lips condition, the movements observed were quite obviously speech movements. Further experiments are required to determine if non-speech-related lip movements (e.g. chewing) also increase the excitability of this motor system and whether the effect is asymmetric as seen for the speech-related movements.

The findings of increased motor excitability during visual and auditory perception of speech support the notion of a change in motor resonance during perception. Rizzolatti and colleagues [29,30] propose that such changes are mediated by the mirror-neuron system, which is located in the monkey in ventral premotor cortex. The changes in excitability of the motor system measured in our study were elicited in response to TMS of the primary motor cortex. This cortex does not receive direct inputs from visual cortex, nor does this cortex in the monkey contain neurons with mirror properties [12]. The changes in excitability are likely due, therefore, to inputs from premotor areas. It could also be argued

that these changes are due to brainstem or spinal mechanisms rather than cortical ones. But the results of several previous studies of action–observation of hand movements favour a cortical mechanism [2,9,13,16,33]; our findings are also consistent with this notion.

Our finding of a functional hemispheric asymmetry for perception of speech, namely increased excitability for left hemisphere stimulation but not for right, is also consistent with a cortical mechanism. The asymmetry was not due to differences in the stimulation thresholds between the two hemispheres or to differences in the amount of baseline EMG activity during muscle contraction. It is worth bearing in mind, however, that the interaction between condition and hemispheric side of stimulation was not significant, even though increases in excitability were significant in the left but not the right hemisphere. The most obvious explanation for this asymmetry is that due to the known left hemisphere specialisation for language, the perception of speech stimuli selectively modulated the motor cortex of the left hemisphere. It has been proposed that the left hemisphere specialisation for language is related to this hemisphere's specialisation for movement selection [20,21,32]. Apraxia of both left and right hands, as well as oral apraxia are typically seen following lesions of the left rather than right hemisphere [14,20]. In relation to these findings it has also been suggested that the left hemisphere is specialised for imitation [7]. This view is supported by the results of functional imaging studies [18]. Unfortunately, both previous TMS studies of speech perception [10,34] reported stimulation of the left hemisphere only, so no comparison with the right hemisphere has been made. The initial action observation studies in the hand/arm domain examined the left hemisphere only [9,33]. A recent report, however, found increased motor excitability during observation of movements of the contralateral hand for both left and right hemisphere stimulations and during observation of movements of the ipsilateral hand for left hemisphere stimulation only [1].

The changes in motor resonance associated with speech perception reported here are thought to mediate the imitation, recognition and understanding of such perceptions [29,30]. Imitation of speech sounds or vocalisations is not seen in non-human primates, but imitation of speech sounds and facial gestures have been demonstrated in human infants [22,27]. It has been suggested that the development of vocal imitation was a necessary prerequisite for the evolution of human speech [11]. This ability may have evolved from a mirror-neuron system, originally mediating imitation and understanding of seen actions, such as hand movements, and later involved in the imitation and understanding of speech [31].

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