Broca's area is jointly activated during speech and gesture production

Steven Brown and Ye Yuan

Despite the frequent suggestion in the literature that Broca's area is a common link between vocal and gestural models of the origins of language, this has never been established within a single motor-production study. In the present functional MRI experiment, participants were asked to describe the spatial properties of objects (e.g. a motorcycle) using speech, pantomime, and drawing. Pairwise conjunction analyses revealed that the left inferior gyrus – in combination with the left basal ganglia and ventral anterior thalamus – was jointly activated for the production of speech and pantomime but not for the conjunctions with drawing. Drawing and pantomime instead showed strong overlap in the intraparietal sulcus and superior parietal region bilaterally. These results provide the first demonstration in a production study that Broca's area is jointly activated by speech and gesture when depicting the same semantic content. *NeuroReport* 00:000–000

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Department of Psychology, Neuroscience & Behaviour, McMaster University, Hamilton, Ontario, Canada

Correspondence to Steven Brown, PhD, Department of Psychology, Neuroscience & Behaviour, McMaster University, 1280 Main St. West, Hamilton, ON, Canada L8S 4K1
Tel: +1 905 525 9140 ×23892; fax: +1 905 529 6225;
e-mail: stebro@mcmaster.ca

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Introduction

Broca's area – located in the left inferior frontal gyrus (IFG) of the human brain [1] – is a region that has been associated with language ever since the mid-19th century [2], most especially in connection with motor aspects of phonological processing [3] and with syntax [4]. Although the role of Broca's area in language has been historically associated with speech production, more-recent gestural theories of language origin have implicated Broca's area in gestural communication as well [5–7], suggesting that this area may in fact be multimodal. Neuroimaging support for this idea comes from studies of perception. For example, Xu *et al.* [8] had participants view video clips of an actor performing gestures (pantomimes or emblematic gestures) or listen to an actor speaking words having the same meaning as the observed gestures. A major point of overlap was found in the left IFG. Similar results were reported by Straube *et al.* [9] and Andric *et al.* [10].

To the best of our knowledge, no comparison between speech and gesture has been performed in a motor-production study. Although perceptual studies are certainly relevant, a more direct test of the hypothesis that Broca's area is a multimodal communication area should come from the analysis of production. We carried out such a comparison by using functional MRI to examine three modalities of communicative production: speech, pantomime, and drawing. Participants performed a task in which they had to describe the structural properties of objects, for example a motorcycle. In different conditions, they did this using either speech, pantomime, or drawing, the latter being done with an MRI-compatible drawing tablet that permitted participants to see their drawings. We used a conjunction analysis to look for shared activations between pairs of modalities of production, with the major goal being to identify areas common to the production of speech and pantomime. Based on the perception literature, we predicted that Broca's area would be one such area.

Methods

Participants

Twenty-one right-handed individuals (17 females, mean age 20.4), most of them undergraduate majors in a studio arts program, participated in the functional MRI experiment after giving their informed consent (Hamilton Integrated Research Ethics Board, McMaster University). The mean fine arts training of the participants was 5.5 years. Participants had normal or corrected-to-normal vision (using corrective lenses) and no history of neurological disorders, psychiatric illness, alcohol or substance abuse, and were not taking psychotropic medications. They received monetary compensation for their participation.

Stimuli and task

Detailed methods of this experiment are given in Yuan, Major-Girardin and Brown [11]. The 'object description' task reported here was the subtraction control in the previous study. We report the results of the description task against a baseline condition of fixation for the three motor modalities of speech, pantomime, and drawing. The stimuli for the experiment were words representing inanimate objects, including binoculars, football helmet,

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and helicopter. Participants were explicitly instructed to focus on the structural properties of the objects and to avoid representing the objects' uses so as to maintain a descriptive emphasis on the objects themselves, rather than on people. It is important to note that no participant described a given object using more than one production-modality (i.e. there was no within-subject repetition), and the full set of object/modality pairings was achieved in a between-subject manner by creating three separate stimulus sets across the pool of 21 participants, as produced using a Latin squares approach. For the drawing condition, participants produced images on an MRI-compatible drawing tablet [12,13] using their right hand. They had full visual feedback of their drawings during the task.

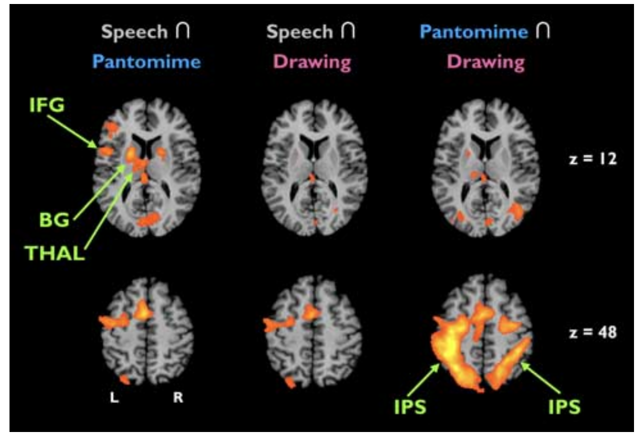
During a task epoch, a given object-related word and the associated production-modality were displayed for 8 s, during which time the participants were instructed to plan what they were going to do but to not respond physically. The screen was then replaced by a grey canvas, and participants were given an 18 s production phase to depict the stimulus item using the assigned modality. There was then a 4 s 'stop' signal, followed by a 'ready' screen for 2 s as a transition between stimuli. Each task epoch thus lasted 32 s. For the analysis, the stop and ready periods were eliminated, resulting in 26 s epochs made up of 8 s of planning and 18 s of production. During the baseline fixation trials, a crosshair was displayed for 16 s. Each of the four MRI scans had a duration of 7 min (420 s).

Detailed imaging parameters and imaging-analysis methods are reported in Yuan, Major-Girardin and Brown [11]. Functional image analyses were conducted using BrainVoyager QX (version 2.8.0; Brain Innovation, Maastricht, The Netherlands). Images were normalized to the Talairach template [14]. Each participant's task-versus-fixation contrast was processed using a fixed-effects analysis, corrected for multiple comparisons using a Bonferroni correction at a threshold P value of less than 0.05, followed by a random-effects group-level analysis thresholded at false discovery rate q value of less than 0.001. Pairwise conjunction analyses were performed at false discovery rate q value of less than 0.05 ($k=4$).

Results

Figure 1 shows the results of the three pairwise conjunction analyses across the three modalities. The speech/pantomime conjunction showed activations in the left IFG (Talairach coordinates −45, 5, 13 in Brodmann area 44), as well as in the putamen bilaterally (−18, 2, 10 and 21, 5, 13) and the left ventral anterior thalamus (−3, −10, 16) that is the thalamic target of the basal ganglia. Neither of the conjunctions with drawing showed IFG activations, although they both showed a weak activation in the left putamen. The lower panel of Fig. 1 shows that pantomime and drawing shared extensive bilateral, but left-dominant, activations in the intraparietal sulcus (IPS)

Fig. 1



Conjunction analysis. Axial views of the pairwise conjunction results from the description versus fixation contrast for each modality. Left panel: conjunction of speech and pantomime; middle panel: conjunction of speech and drawing; right panel: conjunction of pantomime and drawing. Results are displayed at false discovery rate q value less than 0.05. The Talairach z coordinate is shown to the right of each row of slices. The left side of the slice is the left side of the brain. BG, basal ganglia, highlighting the putamen; IFG, inferior frontal gyrus (Brodmann area 44); IPS, intraparietal sulcus; L, left; R, right; THAL, thalamus, highlighting the ventral anterior thalamus.

and the superior parietal lobule, which were absent in the two conjunctions with speech. The strongest IPS peaks were at −30, −58, 52 in Brodmann area 7 and at −36, −40, 49 in area 40. The pantomime/drawing conjunction also showed bilateral activations in the region of V5/MT+ associated with motion perception (not shown). The peak coordinate in the left hemisphere was at −48, −70, 4 in Brodmann area 37.

Discussion

Theories of language origin tend to be polarized between 'vocal' and 'gestural' models [6,7,15–17]. However, one thing that they have in common is the claim that Broca's area is a critical area for the emergence of language in humans, suggesting that this area is not just vocal but is multimodal. Although previous perceptual studies have confirmed the multimodal nature of Broca's area, no previous study has directly examined this issue using multimodal production. In the present fMRI study, participants created descriptions of objects based on word prompts, and did so using speech, pantomime, and drawing. Pairwise conjunction analysis revealed that the left IFG was jointly activated for speech and pantomime, but not for the conjunctions with drawing. This overlap in Broca's activation in a motor-production task supports previous findings using perceptual tasks [8–10].

Another neural system that was jointly activated in the speech/pantomime conjunction, but not in the conjunctions with drawing, was the basal ganglia, including the putamen bilaterally and the ventral anterior thalamus that is the thalamic target of the basal ganglia. The basal ganglia, like the IFG, have been implicated in the evolutionary origin of speech and language [18]. One feature that the basal ganglia shares with Broca's area is a role in sequencing [19]. This might distinguish drawing from speech and pantomime in the current experiment. Both speech and pantomime work in a relatively linear and sequential fashion to depict the objects or actions being represented, whereas drawing is often much less linear. For example, people often draw the outlines of multiple objects before filling in the fine-grained details. So, the activation results reported here might reflect the different strategies that people bring to drawing, as compared with speech and gesture.

In a previous study from our laboratory on the drawing of geometric figures [13], we demonstrated that drawing could indeed activate the IFG and basal ganglia. However, this effect was task-dependent. In particular, the IFG and basal ganglia were only activated during a copying task, but not when drawing the same types of geometric figures from memory, as in the current object-description task. Copying is the most imitative form of drawing, and the IFG and basal ganglia have been implicated in imitation, both vocal [20] and gestural [21] (although see [22]). Hence, the failure to activate the IFG and BG in the drawing condition in the current study might have been more related to the memory-driven manner in which the drawing task was performed compared with a more model-based copying task [13,23].

Drawing and pantomime jointly activated the IPS and area V5/MT+ bilaterally, which were not present in either conjunction with speech. We have argued elsewhere that the capacity for drawing is an evolutionary offshoot of the system for producing iconic gestures such as pantomimes [13]. Drawing is essentially a tool-use gesture that 'leaves a trail behind' in the form of the resulting image. Brain areas like the IPS and V5/MT+ support this underlying similarity between drawing and pantomime as visuomanual activities that produce iconic depictions [24].

Conclusion

In his classic 1861 essay, Broca [2] defined two general issues in the neuroscientific study of language: on the one hand, the multimodal nature of linguistic expression ('speech, mimicry, typing, picture writing, figurative writing … '), and on the other, the coupling between mechanisms of production (*émission*) and perception (*réception*). In the present study, we used production tasks to replicate what has been found using perception tasks that Broca's area is jointly activated by speech and gesture when controlling for the task and the semantic content of the stimuli. Beyond the IFG, areas that were jointly activated by speech and gesture included the basal ganglia and its target nucleus in the thalamus. This combination of cortical and subcortical areas comprises a network that seems to be critical not only for the overlap between perceptual and motor mechanisms of communication but also for the cross-modal overlap between the voice and hand as effectors of communication.

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Conflicts of interest

There are no conflicts of interest.

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