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ORIGINAL ARTICLE

Imitation and speech: commonalities within Broca's area

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Abstract The so-called embodiment of communication has attracted considerable interest. Recently a growing number of studies have proposed a link between Broca's area's involvement in action processing and its involvement in speech. The present quantitative meta-analysis set out to test whether neuroimaging studies on imitation and overt speech show overlap within inferior frontal gyrus. By means of activation likelihood estimation (ALE), we investigated concurrence of brain regions activated by object-free hand imitation studies as well as overt speech studies including simple syllable and more complex word production. We found direct overlap between imitation and speech in bilateral pars opercularis (BA 44) within Broca's area. Subtraction analyses revealed no unique localization neither for speech nor for imitation. To verify the potential of ALE subtraction analysis to detect unique involvement within Broca's area, we contrasted the results of a meta-analysis on motor inhibition and imitation and found separable regions involved for imitation. This is the first meta-analysis to compare the neural correlates of imitation and overt speech. The results are in line with the proposed evolutionary roots of speech in imitation.

Keywords Imitation · Speech · Broca's area · Inferior frontal gyrus · Activation likelihood estimation · Meta-analysis · Gesture

Introduction

The embodiment of communication is attracting an increased interest. This interest was sparked by hypotheses and findings surrounding the so-called "mirror neurons" (Arbib 2005), neurons that are active during the production as well as the perception of actions. Neurons with these properties have been observed in area F5 of the macaque monkey (Gallese et al. 1996; Kohler et al. 2002; Rizzolatti et al. 1996). Similar properties have been detected within inferior frontal gyrus (IFG), also referred to as Broca's area in humans (Buccino et al. 2001; Iacoboni et al. 1999; Rizzolatti and Arbib 1998; Rizzolatti and Craighero 2004). Broca's area in turn has been associated with speech generation. In his now classic report, Pierre Paul Broca (1861) described a man with a cavity in his left frontal lobe who was unable to speak fluently, leading to the notion that Broca's area is involved in speech production. Furthermore, Broca's area has been implicated in spoken language comprehension (Gough et al. 2005; Moss et al. 2005).

Recently a growing number of studies have proposed a link between IFG involvement in imitation and its involvement in speech (Arbib 2005; Hamzei et al. 2003; Kühn and Brass 2008; Nishitani et al. 2005; Watkins and

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Table 1 List of included studies on object-free hand imitation

Study	Stimuli	Modality	*N*	Foci	Contrast
Chaminade et al. (2002)	Hand manipulating Lego blocks	PET	10	6	Imitation > execution
Chaminade et al. (2005)	Hand moving	fMRI	12	20	Imitation > execution
Dinstein et al. (2007)	Finger gestures	fMRI	13	6	Task > rest
Grézes et al. (2003)	Hand movements	fMRI	12	8	Task > rest
Iacoboni et al. (1999)	Finger movements	fMRI	12	3	Imitation > execution
Iacoboni et al. (2001)	Finger movements	fMRI	12	1	Imitation > execution
Jonas et al. (2007)	Finger mvoements	fMRI	19	5	Task > rest
Koski et al. (2002)	Finger movements with goals	fMRI	14	15	Imitation with goal > without goal
Koski et al. (2003)	Mirrored finger movement	fMRI	8	26	Imitation > execution
Makuuchi (2005)	Finger gestures	fMRI	9	2	Imitation > execution
Makuuchi et al. (2005)	Finger gestures	fMRI	22	23	Imitation > execution
Molnar-Szakacs et al. (2005)	Finger movements	fMRI	58	4	Task > rest
Montgomery et al. (2007)	Finger gestures	fMRI	14	18	Task > rest
Montgomery et al. (2008)	Finger gestures	fMRI	12	16	Task > rest
Mühlau et al. (2005)	Hand/finger gestures	fMRI	12	23	Variable imitation > stereotype imitation
Rumiati et al. (2005)	Meaningful/meaningless hand movements	PET	10	9	Imitation > observation
Tanaka et al. (2001)	Finger gestures	fMRI	9	16	Task > rest
Tanaka and Inui (2002)	Finger gestures	fMRI	12	6	Imitation > observation
Williams et al. (2006)	Finger movements	fMRI	16	6	Task > rest
Williams et al. (2007)	Finger movements	fMRI	12	34	Imitation > execution

Paus 2004). These studies implicitly assume that the anatomical association between regions involved in imitation and language processing ought to occur for non-arbitrary reasons. This link could be explained by the strong relationship between hand gestures and speech. Oftentimes gestures are displayed even though the gesturer is aware of the fact that the person he is talking to cannot see his gestures, e. g., when using a telephone. Congenitally blind individuals have been shown to gesture even when speaking to other blind people who likewise cannot perceive the hand movements (Iverson and Goldin-Meadow 1998). Furthermore, the link between manual gestures and speech is supported by stutterers whose speech-related gestures freeze when their speech stops, whereas unrelated hand movements usually continue (Mayberry and Jacques 2000). In a neuroimaging study on sign language, the associated observed brain activation was similar to activation during overt speech (Levänen et al. 2001). These findings suggest a co-representation of speech and gesture in Broca's region and may reflect shared evolutionary roots of both functions.

A model on the stages of language's phylogeny by Arbib (2005) attempts to bridge the explanatory gap between mirror neurons, imitation, gestures and speech. He claims that language and gesture developed in an expanding spiral in which one component prepared the ground for further development of the other component, so language scaffolded gesture just as gesture did for language. Assuming that these evolutionary connections exist, one might expect to find rudiments of them in those functions at present, e. g., in terms of overlapping brain activation in neuroimaging studies on imitation and speech.

In order to explore the overlap of neural correlates of imitation and speech, the present study employed quantitative meta-analyses methods to assess the correspondence of neural activations across multiple neuroimaging studies on imitation and speech using the activation likelihood estimation (ALE) approach (Eickhoff et al. 2009; Laird et al. 2005; Turkeltaub et al. 2002). This approach reveals statistically significant concordance of activated voxels across multiple studies controlling for chance clustering. By seeking concordance at the voxel level, ALE tests for statistically reliable clustering of activations in standardized locations, avoiding spatial distinction errors and problematic incongruence of labeling across studies that can befall narrative-based reviews. With a subsequent contrast analysis, we then tested for unique locations of activity in imitation compared to speech within Broca's area.

Materials and methods

Selection of studies

For the imitation meta-analysis, we selected studies involving hand imitation without the involvement of

Table 2 List of included studies on speech generation

Study	Task	Modality	*N*	Foci	Contrast	Simple vs. complex speech
Andreasen et al. (1995)	Subjects generated words starting with the letter "C"	PET ($H_2^{15}O$)	13	6	Word generation > rest	Complex
Basho et al. (2007)	Subjects generated words to certain categories (e. g., body parts)	fMRI	12	6	Word generation > rest	Complex
Bohland et al. (2006)	Visual presentation of syllables	fMRI	13	184	Simple syllables > fixation	Simple/complex
Braun et al. (1997)	Subjects spoke words of a known song	PET ($H_2^{15}O$)	38	7	Fluent language > control	Complex
Bookheimer et al. (1995)	Visual presentation of words	PET ($H_2^{15}O$)	16	52	Read words aloud > control	Complex
Bookheimer et al. (2000)	Previously learned phoneme sequence, reciting month of the year	PET ($H_2^{15}O$)	8	34	Phoneme > rest Word generation > rest	Simple/complex
Brown et al. (2006)	Auditory presentation of typical adverbial phrases eliciting the generation of phrases to finish the sentence	PET ($H_2^{15}O$)	10	55	Sentence generation > rest	Complex
Brown et al. (2008)	Subjects were previously trained in glottal stops	fMRI	16	42	Glottal stops > fixation	Simple
Cardebat et al. (2003)	Auditory presentation of words	PET ($H_2^{15}O$)	6	10	Word production > rest	Complex
Chee et al. (1999)	Visual presentation of words	fMRI	24	48	Word reading > fixation	Complex
De Nil et al. (2000)	Visual presentation of words	PET ($H_2^{15}O$)	20	4	Overt word reading > silent reading	Complex
De Nil et al. (2003)	Visual presentation of words	PET ($H_2^{15}O$)	23	16	Overt word reading > rest	Complex
Etard et al. (2000)	Visually presented animals and objects or semantically related verb	PET ($H_2^{15}O$)	9	21	Naming > rest, verb > rest	Complex
Fiez et al. (1999)	Visual presentation of words	PET ($H_2^{15}O$)	11	15	Word reading > fixation	Complex
Fox et al. (1996)	Visual presentation of words	PET ($H_2^{15}O$)	20	13	Word reading > rest	Complex
Fox et al. (2000)	Visual presentation of a paragraph	PET ($H_2^{15}O$)	10	12	Correlation with syllable rate	Complex
Fox et al. (2001)	Visual presentation of paragraph or words	PET ($H_2^{15}O$)	29	5	Grand mean	Complex
Ghosh et al. (2008)	Visual presentation of monosyllables	fMRI	10	61	Production of monosyllables > passive viewing	Simple
Hagoort et al. (1999)	Visual presentation of words	PET (^{15}O butanol)	11	30	Overt word reading > silent reading	Complex
Heim et al. (2002)	Visual presentation of pictures	fMRI	12	5	Picture naming > rest	Complex
Ingham et al. (2000)	Visual presentation of words	PET ($H_2^{15}O$)	8	8	Word reading > rest	Complex
Ino et al. (2008)	Visual presentation of words	fMRI	14	12	Reading > word recognition	Complex
Jernigan et al. (1998)	Visual presentation of words	PET ($H_2^{15}O$)	8	6	Word reading > fixation	Complex
Kemeny et al. (2005)	Subjects generated syllables	fMRI	6	40	Syllable generation > rest	Simple/complex
Kerr et al. (2004)	Visual presentation of words	fMRI	14	22	Word reading > rest	Complex
Kircher et al. (2000)	Visual presentation of Rorschach inkblobs about which subjects spoke	fMRI	6	2	Correlation with amount of words	Complex

Table 2 continued

Study	Task	Modality	*N*	Foci	Contrast	Simple vs. complex speech
Kircher et al. (2004)	Visual presentation of Rorschach inkblobs about which subjects spoke	fMRI	6	31	Fluent speech > speech pause	Complex
Kleber et al. (2007)	Professional singers singing an Italian aria	fMRI	16	15	Overt singing > imagined singing	Simple/ complex
Lotze et al. (2000)	Previously learned syllables	fMRI	7	8	/pa/or/ta/or/ka/ > rest	Simple
Martin et al. (1996)	Visually presented animals and objects	PET ($H_2^{15}O$)	16	7	Naming > viewing objects	Complex
Mechelli et al. (2006)	Visually presented pictures	fMRI	12	22	Naming > fixation	Complex
Murtha et al. (1999)	Visually presented pictures	PET ($H_2^{15}O$)	10	47	Naming > rest	Complex
Nakamura et al. (2000)	Visual presentation of words	fMRI	10	5	Word reading > rest	Complex
Paulesu et al. (2000)	Visual presentation of words	PET ($H_2^{15}O$)	12	20	Word reading > rest	Complex
Paus et al. (1993)	Auditory presentation of words	PET ($H_2^{15}O$)	8	9	Reversed speech > overpracticed speech	Complex
Price et al. (1996)	Auditory presentation of words	PET ($H_2^{15}O$)	14	94	Repeating words > rest	Complex
Rektorova et al. (2007)	Visual presentation of words	fMRI	17	35	Reading > passive viewing	Complex
Riecker et al. (2000)	Reciting month of the year	fMRI	18	6	Overt speech > rest	Complex
Riecker et al. (2000)	Previously learned syllables	fMRI	10	8	/ta/repetition > rest	Simple/ complex
Riecker et al. (2002)	Previously learned syllables	fMRI	12	13	Isochronous sequence > perceptual baseline	Simple
Riecker et al. (2005)	Syllable repetitions synchronized to auditory clicks	fMRI	8	13	Syllable repetition > passive listening	Simple
Riecker et al. (2006)	Self-paced syllable repetitions	fMRI	8	13	Syllable repetition > passive listening	Simple
Rosen et al. (2000)	Subjects generated words to certain categories (e. g., drama)	PET	12	5	Word stem completion > rest	Complex
Rumsey et al. (1997)	Visual presentation of words	PET ($H_2^{15}O$)	14	24	Irregular pronounciation > fixation	Complex
Sakurai et al. (2000)	Visual presentation of words	PET ($H_2^{15}O$)	15	32	Word reading > rest	Complex
Schulz et al. (2005)	Subject recounted a story	PET ($H_2^{15}O$)	39	13	Voiced speech > unvoiced speech	Complex
Sörös et al. (2006)	Subjects repeated acoustically presented speech sounds	fMRI	9	36	Repetition > rest	Simple/ complex
Tan et al. (2001)	Visual presentation of words	fMRI	10	88	Reading regular characters > fixation	Simple
Tatsumi et al. (1999)	Auditory presentation of nouns, subjects generate associative verbs	PET ($H_2^{15}O$)	24	5	Verb generation > rest	Complex
Tourville et al. (2008)	Visual presentation of words	fMRI	11	27	No formant shift > passive viewing	Complex
Tremblay et al. (2006)	Visual presentation of words	fMRI	12	18	Word reading > fixation	Complex
Turkeltaub et al. (2002)	Visual presentation of words	fMRI	32	28	Word reading > fixation	Complex
Wildgruber et al. (1996)	Melody of a well-known Christmas song	fMRI	10	2	Syllable singing > rest	Complex
Wilson et al. (2004)	Auditory presentation of syllables	fMRI	10	6	Producing syllables > rest	Simple
Wilson et al. (2009)	Visual presentation of words	fMRI	9	48	Reading words > rest	Complex

Table 2 continued

Study	Task	Modality	*N*	Foci	Contrast	Simple vs. complex speech
Wise et al. (2001)	Previously learned phrase	PET ($H_2^{15}O$)	26	1	Phrase repetition > silent rehearsal	Complex
Xiong et al. (2000)	Subjects generated verbs associated with visually presented nouns	PET ($H_2^{15}O$)	20	6	Word generation > rest	Complex

objects. The coordinates were taken from a recent ALE meta-analysis on action observation and imitation (Caspers et al. 2010).

For the speech meta-analysis we used the database Brainmap Sleuth (http://brainmap.org/sleuth/index.html). We used the search terms [Diagnosis = Normals] AND [Behavioral Domain = Cognition.Language.Speech]. From the resulting papers, we selected those that presented contrasts reflecting brain activity during speech generation in comparison to a control condition. In order to test whether ALE subtraction analysis can potentially reveal unique activation within Broca's area, we searched for studies utilizing another task that reliably activates IFG but is not hypothesized to share a similar neural basis with imitation; we selected fMRI studies on inhibition which have reliably been associated with activity in right IFG (Aron and Poldrack 2005; Aron et al. 2004), including studies using the stop signal task and Go/NoGo task. We included coordinates resulting from analyses computed across the whole brain and not restricted using partial coverage, regions of interest or small volume correction.

We included data from fMRI and PET studies despite the fact that they have a different physiological basis because both methods have been used to identify the neural correlates of imitation and speech. Our rationale was to provide an all-embracing overview over the attempts to identify the neural correlates of imitation and speech. In total, a number of 20 object-free hand imitation studies with 247 foci of altogether 298 participants (Table 1), 58 overt speech studies with 1,401 foci of altogether 804 participants (Table 2) and 19 external inhibition studies with 123 foci of altogether 329 participants were included (Table 3).

Creation of ALE maps

The ALE method provides a voxel-based meta-analytic technique for neuroimaging data (Eickhoff et al. 2009; Turkeltaub et al. 2002). By means of the software Brainmap GingerALE (http://brainmap.org/ale/), statistically significant concordance in the pattern of brain activity among several independent experiments was computed. ALE maps display regions in the brain that comprise statistically significant peak activation locations from multiple studies. Coordinates reported in Talairach were converted to MNI using Lancaster's et al. (2007) transformation (icbm2tal). In the approach taken by ALE, localization probability distributions for the foci are modeled at the center of 3-D Gaussian functions, where the Gaussian distributions are summed across the experiments to generate a map of inter-study consistencies that estimate the likelihood of activation for each voxel, the ALE statistic, as determined by the entire set of studies. The false discovery rate (FDR) method was employed to correct for multiple comparisons at a significance threshold of $p < 0.01$ and a cluster threshold of 100.

Contrast analyses were calculated by means of ALE subtraction analysis, accounting for potential differences in sample size. To increase the specificity of the results, the analysis of differences was restricted to those voxels that showed an effect in main speech or imitation meta-analyses. The reported contrast analyses were thresholded at a corrected p value of <0.05.

Results

The results of the quantitative ALE analyses within IFG on imitation and speech as well as motor inhibition are presented in Fig. 1a–c.

In order to explore the similarity of brain activation in imitation and speech within Broca's area, the first analysis aimed at comparing the ALE maps resulting from neuroimaging studies on object-free hand imitation and overt speech (Fig. 1a). Direct overlap was observed in the left hemisphere at coordinate −54, 12, 7. Since the included speech studies spanned a broad range of stimuli from simple syllables to free word generation that had to be uttered, we split them up into simple speech containing syllables and repeated sequences and complex speech containing words and sentences (Fig. 1b). Direct overlap was observed between imitation and complex speech at coordinate −54, 12, 5 in the left hemisphere and between imitation and simple speech at 59, 11, 11 in the right hemisphere. By means of contrast analyses, we investigated whether the

Table 3 List of included studies on inhibition

Study	Stimuli	Modality	*N*	Foci	Contrast
Aron et al. (2006)	Go: visual, Stop: auditory	fMRI	13	13	Stop > Go
Aron et al. (2007)	Go: visual, Stop: auditory	fMRI	15	6	Stop > Go
Bunge et al. (2002)	Go: visual, NoGo: visual	fMRI	16	8	NoGo > Go
Chikazoe et al. (2009)	Go: visual, Stop: visual	fMRI	22	23	Stop > Go
Duann et al. (2009)	Go: visual, Stop: visual	fMRI	60	1	Successful Stop > Nonsuccessful Stop
Durston et al. (2002)	Go: visual, NoGo: visual	fMRI	10	6	NoGo > Go
Garavan et al. (1999)	Go: visual, NoGo: visual	fMRI	14	6	NoGo > Go
Garavan et al. (2002)	Go: visual, Stop: visual	fMRI	14	9	Successful NoGo > Nonsuccessful NoGo
Konishi et al. (1998)	Go: visual, NoGo: visual	fMRI	5	1	NoGo > Go
Konishi et al. (1999)	Go: visual, NoGo: visual	fMRI	6	1	NoGo > Go
Leung et al. (2007)	Go: visual, Stop: visual	fMRI	15	6	Stop > Go
Li et al. (2006)	Go: visual, Stop: visual	fMRI	24	8	Successful Stop > Nonsuccessful Stop
Liddle et al. (2001)	Go: visual, NoGo: visual	fMRI	16	9	NoGo > Go
Menon et al. (2001)	Go: visual, NoGo: visual	fMRI	14	7	NoGo > Go
Ramautar et al. (2006)	Go: visual, Stop: visual	fMRI	16	2	Stop > Go
Rubia et al. (2001)	Go: visual, Stop: visual	fMRI	15	5	Stop > Go
Rubia et al. (2001)	Go: visual, NoGo: visual	fMRI	15	7	NoGo > Go
Rubia et al. (2003)	Go: visual, Stop: visual	fMRI	20	2	Successful Stop > Nonsuccessful Stop
Tamm et al. (2002)	Go: visual, NoGo: visual	fMRI	19	3	NoGo > Go

concurrence observed within studies on object-free hand imitation was different to the concurrence within studies on simple as well as complex speech. In both subtraction analyses, no significant unique localization for imitation (nor speech) was found.

To provide evidence that unique location of activation within the region of IFG can technically be detected by means of ALE contrast analyses, we computed an ALE meta-analysis in a different behavioral domain, namely motor inhibition. Motor inhibition has typically been localized in IFG, in particular the right IFG (Aron and Poldrack 2005) (Fig. 1c). When performing a contrast analysis between imitation and inhibition, we found a selective cluster for imitation in right IFG: 60, 15, 12. Hence, we conclude that the observed overlap and, in particular, the absence of unique clusters for imitation and speech are meaningful and argue that the similarity of activation is not due to spatial constraints within Broca's area.

Discussion

The present study aimed at exploring the proposed link between imitation and speech by means of comparing the neural correlates of both functions within Broca's area employing quantitative meta-analyses tools. Assuming that an evolutionary connection between imitation and speech exists, we hypothesized to find rudiments of this link in terms of overlap in brain activation of both processes. In line with our predictions, we found overlap between the brain regions implicated by ALE meta-analysis on imitation and a separate meta-analysis on overt speech in left IFG.

The localization of concurrence for studies on object-free hand imitation in bilateral pars opercularis of IFG (BA 44) is in line with the results for imitation in the study of Caspers et al. (2010) that includes studies with imitation of other effectors such as foot or hand as well as object-related actions. We decided to only include manual object-free imitation since we considered this to be closest to typical speech-accompanying gestures. Our meta-analysis results (including 20 imitation studies) as well as the results of the previous study (including 32 imitation studies, Caspers et al. 2010) is at odds with a study by Molenberghs et al. (2009) that reported ALE concurrence only in dorsal premotor cortex (BA 6) not in the IFG (BA 44). Since the meta-analysis by Molenberghs and colleagues includes less studies that used a region of interest (ROI)-based approach and used a by now out-dated version of the ALE algorithm (Eickhoff et al. 2009), we feel confident to locate concurrence of object-free hand imitation in pars opercularis of the IFG. Likewise, the results of our overall speech analysis are in line with a previous meta-analysis on overt speech in non-stuttering subjects on eight studies (Brown et al. 2005) reporting a peak coordinate close to the one we found in left IFG. Contrary, another meta-analysis by Turkeltaub et al. (2002) on 11 studies reported a peak coordinate within the left precentral gyrus (BA4/6) not in

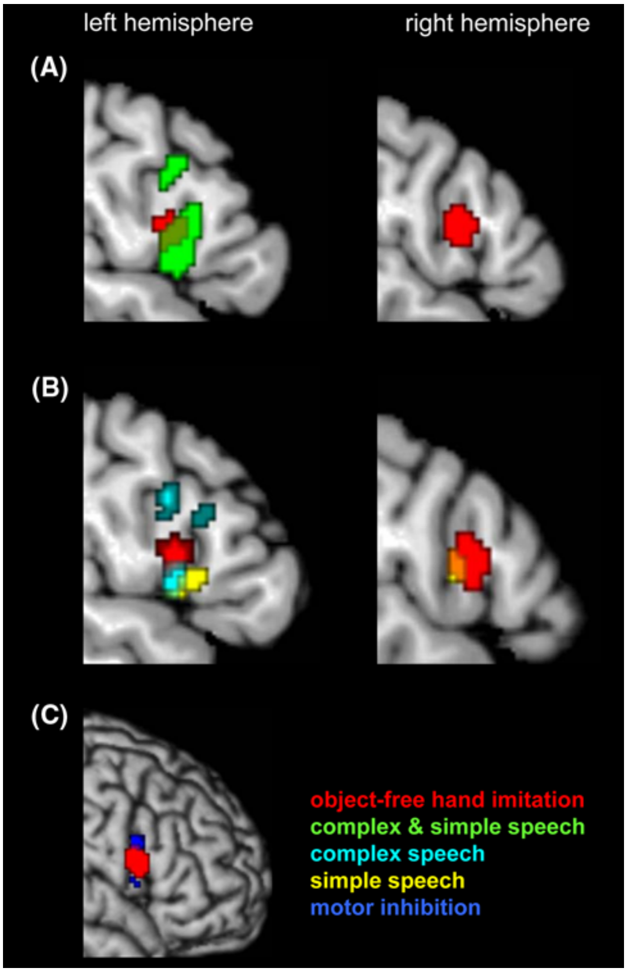

Fig. 1 ALE meta-analysis maps of bilateral IFG for neural correlates of object-free hand imitation (*red*) and **a** speech (*green*), **b** complex speech (*cyan*) or simple speech (*yellow*) and **c** motor inhibition (*blue*); $p < 0.01$, FDR corrected; the clusters shown are restricted to bilateral IFG defined by means of the Harvard Oxford Atlas

left IFG. But the authors themselves have suggested that peaks within left IFG were likely smoothed over by the high ALE values in the adjacent motor strip.

In order to differentiate between speech studies with simple syllable utterances that are most likely rather melodic and those in which complex words or entire sentences had to be pronounced, we computed two separate meta-analyses. We found stronger activity in the right hemisphere during simple syllable production and a stronger left lateralization during more complex word and sentence production. This is in agreement with a previous studies showing that singing (Ozdemir et al. 2006) as well as prosodic modulation in speech perception (Meyer et al. 2002) is more strongly associated with right hemispheric activation, since the repetition of syllables likely results in utterances that bear resemblance with singing. Similarly, it has been reported that patients with Broca's aphasia are able to sing the lyrics of a song better than they can speak the same words (Gerstman 1964; Yamadori et al. 1977) a finding that is also in line with a stronger left lateralization for speech as compared to melodic syllable utterances.

When comparing the localization of simple and complex speech with imitation-related concurrence, we found that complex speech-related activity overlapped with imitation within left IFG, whereas simple speech-related activity showed overlap within the right IFG. Subtraction analyses between simple and complex speech and imitation maps revealed no regions with unique localization, neither for speech, nor for imitation. This absence of distinct neural correlates within Broca's area argues in favor of an association between imitation and speech functions.

To preclude that it is technically impossible to detect unique areas of activation within Broca's area when computing a contrast of ALE analyses between coordinates of imitation and speech studies, we computed a meta-analysis on stop signal and Go/NoGo tasks that have commonly been associated with right IFG activity (Aron and Poldrack 2005; Aron et al. 2004) and compared it by means of an ALE contrast analysis with the imitation ALE. Interestingly, the inhibitory functions of right IFG have likewise been associated with the inhibition of imitative and overlearned responses (Brass et al. 2005). Therefore, the function of motor inhibition is not entirely unrelated to imitation. When subtracting the resulting regions of concurrence in motor inhibition processes from the imitation associated neural correlates, we found regions that are more strongly involved in imitation compared with motoric inhibition. The fact that motoric inhibition and imitation seem to have separable neural correlates underlines the importance of the observed absence of unique localization when comparing imitation and speech.

The observed overlap between neuroimaging correlates of object-free hand imitation and overt simple as well as complex speech is in line with the assumption that speech developed from gestures and manual actions (Arbib 2005). Furthermore, it fits to the motor theory of speech perception formulated by Liberman et al. (1952). According to this theory, the listener does not solve the invariance problem in speech perception in the auditory domain, but in the motor domain instead. Assuming that the acoustic patterns of speech can be different, the articulatory gestures that are needed to produce them are the same. Therefore, the idea is that the perceptual problem is solved by recruiting the production system of the listener. The listener mirrors the neuromotor commands of the articulators (e. g., tongue or lips) to understand the message (Liberman and Mattingly 1985). Further support for the intimate link of imitation and speech also comes from aphasic patients who are often apraxic, and apraxia often involves deficits in imitation (Heilman and Valenstein 2002). However, it is not yet clear whether this joint occurrence of syndromes results solely from a co-localization of praxis and speech or whether it can be regarded as a proof of its common mechanisms.

Defining the functional involvement of Broca's region on a higher level, namely as representing sequential information could explain its importance for speech as well as imitation (Nishitani et al. 2005). Lesion data suggest that the two hemispheres might have different roles in sequencing. Left hemispheric lesions affect predominantly verbal sequencing, whereas right hemispheric lesions affect nonverbal sequencing (Bookheimer 2002).

Conclusions

Taken together, the current meta-analysis has shown considerable overlap and no unique localization for overt speech and object-free manual imitation-associated neural correlates within Broca's area. This is necessary though not sufficient evidence for the notion that imitation and speech have a common neural basis and is in line with patient data and previous theoretical accounts on the evolutionary roots of speech in imitation. Therewith, the current meta-analysis provides first evidence for neuroanatomical overlap between speech and imitation that has previously only been inferred.

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Conflict of interest The authors report no conflict of interest.

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