Communication with Emblematic Gestures: Shared and Distinct Neural Correlates of Expression and Reception

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Abstract: Emblematic (or symbolic) gestures allow individuals to convey a variety of thoughts and emotions ranging from approval to hostility. The use of such gestures involves the execution of a codified motor act by the addresser and its perception and decoding by the addressee. To examine underlying common and distinct neural correlates, we used fMRI tasks in which subjects viewed video clips of emblematic one-hand gestures. They were asked to (1) take the perspective of the addresser and imagine executing the gestures ("expression" condition), and to (2) take the perspective of the addressee and imagine being confronted with the gestures ("reception" condition). Common areas of activation were found in inferior frontal, medial frontal, and posterior temporal cortices with left-hemispheric predominance as well as in the cerebellum. The distinction between regions specifically involved in the expression or reception condition partly resembled the dorsal and ventral stream dichotomy of visual processing with junctions in inferior frontal and medial prefrontal cortices. Imagery of gesture expression involved the dorsal visual stream as well as higher-order motor areas. In contrast, gesture reception encompassed regions related to semantic processing, and medial prefrontal areas known to be involved in the process of understanding the intentions of others. In conclusion, our results provide evidence for a dissociation in representations of emblematic gesture processing between addresser and addressee in addition to shared components in language-related areas. *Hum Brain Mapp 33:812–823, 2012.*   © 2011 Wiley Periodicals, Inc.

Key words: dorsal stream; functional MRI; inferior frontal cortex; medial frontal cortex; ventral stream

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INTRODUCTION

Verbal and nonverbal communication is central to human life. It allows us to convey information such as thoughts, intentions, and feelings to other people. While language is the most important form of communication, gestures play a significant role in facilitating human interaction [McNeill, 1992]. Typically, gestures accompany speech, movements of the body or facial expressions underlining the actor's intentions or feelings [Kendon, 1997]. However, information can also be conveyed nonverbally just by dedicated symbolic hand and arm movements which have been termed "emblematic gestures" [Kendon, 1997; McNeill, 1992].

Emblematic gestures are symbols or signs expressed by intentional bodily movements of a person addressing somebody else. The form of emblematic gestures and, thus, their constituent movements are not arbitrary but learned, empirically determined and dependent on a certain cultural context [Kendon, 1997]. Emblematic gestures are highly conventionalized, unambiguous and easily recognizable within a specific cultural setting (e.g., "thumb up"). Unlike sign language, they do not build a continuous, coherent system of signs and therefore cannot be combined to complex linguistic structures [Goldin-Meadow, 1999]. Importantly, they convey emotional content since they are used to either complement or reprehend, offend and threaten the addressee [Kendon, 1981]. Accordingly, emblematic gestures portray a universal phenomenon in human nonverbal communication and may represent a behavioral model for the study of the cerebral structures participating in basic communication processes.

The use of gestures links the intention to express a meaning with a motor act. Hence, understanding a certain gesture's meaning implies the recognition of the action. The putative human mirror neuron system [di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti and Craighero, 2004] might provide a neuro-anatomical basis for this behavior since it suggests a shared circuit for the integration of one's own and other people's actions. Consequently, an ideomotor framework has been proposed which assumes a "common representational format" of action and perception in general [Iacoboni, 2009] and thereby provides insight into the interrelation of actions, observation of actions and, ultimately, social interaction. In addition, the interpretation of meaningful motor acts has been attributed to "simulating" [Blakemore and Decety, 2001] or "mentalizing" [Gallagher and Frith, 2003]. Thus, action recognition of emblematic gestures is complemented by "mentalizing about the states of others" [Keysers and Gazzola, 2007] to understand the information intended to be communicated by the addresser of the gesture [de Lange et al., 2008]. Most likely, this process involves medial frontal cortex structures [Amodio and Frith, 2006; Uddin et al., 2007]. In addition, previous functional imaging studies on gesture processing have implicated the role of the putative mirror neuron system, including inferior frontal and parietal cortices, in imitation [Muhlau et al., 2005] and generation of abstract and pantomimic gestures [Bohlhalter et al., 2009; Fridman et al., 2006; Schippers et al., 2009]. Furthermore, perception and interpretation of meaningful gestures were shown to bear similarities in activation patterns when compared to language [Xu et al., 2009] and sign language comprehension [Husain et al., 2009].

As a complement to these studies, we aimed at investigating both the reception and expression of gestures in a single functional MRI paradigm to disentangle shared and distinct components of this framework. We chose well-defined and conventionalized emblematic gestures as stimuli because they allow for an exploration of basic nonverbal communication

with a strong emotional content. Specifically, to mimic communication with emblematic gestures, we employed imagery of executing the gestures ("expression" condition) as a model for the addresser and imagery of being confronted with the same gestures ("reception" condition) as a model for the addressee. We hypothesized that both processes share common cerebral representations in language-related brain areas, frontal midline structures, and the mirror neuron system. Further, we hypothesized a dichotomy of nonoverlapping brain areas with parietal and inferior frontal areas involved in the mental generation and medial frontal and temporal areas involved in the evaluative decoding of the emotional content of emblematic gestures.

MATERIALS AND METHODS

Participants

Twenty healthy right-handed volunteers (10 women; mean age 23.8 ± standard deviation of 1.3 years; range: 21–27 years) with no history of neurological or psychiatric disorders participated in the study. All subjects had normal or corrected-to-normal vision. Handedness was assessed using the Edinburgh inventory (mean score 81.1 ± 9.4) [Oldfield, 1971]. The ability to identify and describe experienced emotions was tested with the 20-item version of the Toronto Alexithymia Scale (TAS-20) [Bagby et al., 1994]. To minimize variability in gestural perception, all participants had German as their first language and were raised in Germany. None of the participants was proficient in sign language.

All subjects gave informed written consent. The study was approved by the local ethics committee. One of the male participants was excluded from the analysis due to a summed TAS-20 score of 70 which is above the clinical threshold of 61 and considered to indicate an impairment of perception and processing of emotion [Bagby et al., 1994]. In addition, a female participant was excluded due to extensive artifacts during fMRI scanning, resulting in a total of 18 subjects (nine women).

Stimuli

Stimuli consisted of silent video clips with durations of 3 s showing the execution of 25 different emblematic gestures. The gestures were executed by one actor with the right arm (Fig. 1A–C). All gestures started from the same initial posture (Fig. 1D) and evolved as a natural motor act. Video clips of 3 s duration showing the static hand posture and a meaningless control gesture served as controls. To exclude the potentially confounding perception of facial expressions, only the trunk and the right hand and arm of the gesturer were displayed. Pretesting in a group of 56 age-matched control subjects (24 women; mean age 26.2 ± 2.9 years; range: 22–29 years) was conducted to guarantee that all gestures were clearly
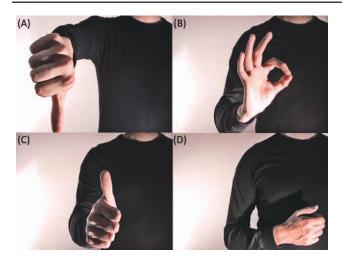
Figure 1.

Film stills to illustrate examples of the 25 emblematic gestures. The mean SAM scores for valence were 7.3 ± 1.1 for "thumb down" (**A**), 2.7 ± 1.1 for "A-ok" (circle of thumb and index finger; **B**), and 2.1 ± .8 for "thumb up" (**C**). The gesturing started from the same initial position which also served as the static posture (**D**). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

recognizable. Participants watched video clips of 27 emblematic gestures and were asked to describe their meaning and emotional content. Since two gestures appeared to be ambiguous and were therefore excluded, we used 25 well-defined emblems for the experiment.

Task Design

Subjects were presented with two separate runs of video clips ("expression" and "reception" conditions) arranged in a pseudo-randomized manner. The sequences of video clips were counter-balanced across subjects and across runs. Video clips of 25 emblematic gestures were shown once per run, whereas each of the control stimuli was shown 10 times per run. Individual video clips were interspersed with a black screen of variable duration (randomized from 10 to 13 s to prevent circular effects).

The instruction for the subjects was to view the videos attentively and to take a perspective toward the gestures shown. In one condition, the subjects were instructed to put themselves into the position of the addresser and to imagine executing the presented gesture as soon as its meaning was conceived ("expression" condition). In the second condition, the subjects were requested to put themselves into the position of the addressee and to imagine to be confronted with someone gesturing at them ("reception" condition). The order of the tasks was also balanced across subjects.

Following the fMRI experiment, participants were asked whether they had been consistently able to follow the instructions, or whether they had any difficulties with the tasks. The video clips were presented again, and the subjects were required to describe the meaning of each gesture. In addition, they completed the self assessment manikin (SAM) for all the gestures to measure valence, arousal, and dominance associated with their affective response to the video clips [Bradley and Lang, 1994]. In this picture-oriented assessment, scores ranged from 1 to 9 for either of the categories (positive to negative for valence; low to high for arousal; small to large for dominance).

Stimulus Presentation

The video clips were presented using Presentation Version 12.1 (Neurobehavioral Systems, Albany, CA). Synchronization with the MR scanner was achieved via TTL-pulse. The participants were presented with the visual stimuli via projection onto a semitransparent screen (inside the scanner room) with an LCD-projector (positioned outside the scanner room). They lay supine in the MRI scanner and viewed the projections through a mirror attached to the head coil.

Functional Magnetic Resonance Imaging

All subjects underwent MRI using a 3 T Siemens Magnetom Trio (Erlangen, Germany). We acquired an EPI sequence (TE 40 ms; TR 3,500 ms; flip 90°; matrix 192 × 192; 43 contiguous slices to cover the whole brain, resulting voxel size $1.5 \times 1.5 \times 3$ mm^3) and a high-resolution T1-weighted MPRAGE sequence (TE 4 ms; TR 1,850 ms; matrix 256 × 256; 320 contiguous slices; voxel size $0.75 \times 0.75 \times 0.75$ mm^3).

Data Preprocessing and Analysis

Functional imaging data were preprocessed and analyzed using SPM5 (Wellcome Department of Cognitive Science, London, UK) implemented in Matlab (MathWorks, Natick, MA). All volumes were spatially realigned to the first volume in the series and normalized to the MNI standard EPI-template resulting in a $2 \times 2 \times 2$ mm^3 resolution. To account for anatomical inter-individual variability and to match the statistical requirements of the general linear model [Friston et al., 2000], normalized images were smoothed with a Gaussian kernel of 8 mm.

We analyzed the data on a single-subject basis in an event related-model. As regressors in the general linear model, we used "expression" (E) and "reception" (R) and defined the contrasts "E," "R," "E versus R," and "R versus E" on the single subject level for the emblematic gestures and the two control stimuli separately. Since we were specifically interested in capturing the BOLD response in relation to the emblematic nature of the gestures, the onset of the regressors in the design matrix was

set for 2 s after beginning of the video and convolved with a canonical hemodynamic response function implemented in SPM. This onset was chosen because the meaning of the evolving emblematic gestures could be fully conceived at least 2 s after the beginning of the video clips. The individual contrasts were entered into a random effects group analysis with the factor "subject" as random factor.

To capture shared areas involved in both the expression and reception conditions, we performed a conjunction analysis for the emblematic gestures [Nichols et al., 2005] using a logical *AND* function ("E ∩ R"). For the differential second level analyses of "E versus R" and "R versus E," we entered the subjects' individual contrast images into a one-sample *t*-test. In addition, we used a full factorial design to test for potential interactions between conditions and tasks. This design allowed us to analyze the differences between meaningful and meaningless gestures across tasks ("E" and "R"). Finally, we modeled another full factorial analysis in which possible influences of order effects (nine participants started with the "E" task whereas the other nine started with the "R" task) were addressed as a between-subject factor. In all analyses, we applied a significance threshold of $P < 0.001$ at the voxel level (uncorrected), combined with a threshold of $P < 0.05$ at the cluster level, corrected for multiple comparisons across the whole brain (false discovery rate, FDR).

RESULTS

Behavioral Tests

All participants could accurately describe the meaning of each gesture as was expected from the pretesting. Also, all of them indicated that they had no difficulty following the instructions to perform the tasks. The SAM analysis revealed that ascribed valence, arousal, and dominance differed between individual gestures. For valence, the mean value was $5.3 \pm$ standard deviation of 1.4 (range: 2.1–7.3); for arousal, the mean value was 5.3 ± 1.1 (range: 3.3–7.3); for dominance, the mean value was $5.3 \pm .9$ (range: 3.3–6.7). Thus, the values in all three categories were balanced between high and low valence, arousal, and dominance across all emblematic gestures (a value of 5 would indicate the ideal mean in this nine-point scale). The values of the static posture (e.g., valence: 5.0 ± 0.7) and the meaningless gesture (e.g., valence: 4.9 ± 0.9) indicated that they were perceived as neutral stimuli. The participants did not ascribe a meaning to either the static posture or the control gesture.

Emblematic Gestures

Main effects of expression and reception conditions

No effect of task order was found between subjects, providing a valid basis for all further group analyses. The expression condition revealed extensive left-dominant bihemispheric activations including the occipital lobes, posterior medial and inferior temporal gyri, superior and inferior parietal lobules, supplementary motor area (SMA), dorsal and ventral premotor cortices (PMd and PMv), inferior frontal gyri extending to the insula and temporal poles, dorsolateral prefrontal cortex (dlPFC), and the cerebellum (Fig. 2A). In addition, activations were found in the basal ganglia (broad cluster encompassing putamen, pallidum, and striatum) and the thalamus.

Similarly, the gesture reception condition involved broad, confluent clusters of activation with left-hemispheric dominance (Fig. 2B). While the clusters in the occipital lobes, cerebellum, inferior frontal gyri, and anterior temporal lobes resembled those found in the expression condition, the posterior temporal cluster encompassed the left temporo-parieto-occipital junction (angular and supramarginal gyri) but did not extend to the superior parietal lobule. Likewise, the involvement of PMd and PMv appeared to be less pronounced. Additional extensive activation involved the left pre-SMA extending to anterior medial prefrontal cortex (mPFC). Subcortical clusters were found in the amygdala as well as in the basal ganglia and the thalamus bilaterally.

Conjunction analysis of expression and reception conditions

The conjunction analysis yielded a widespread bihemispheric system of activation (Table I; Fig. 3). This circuit included primary and higher-order visual areas like the cuneus, precuneus, lingual, and middle occipital gyri. In addition, clusters were found in left inferior frontal gyrus (partes orbitalis, triangularis, and opercularis) extending to PMv, PMd, and the insula as well as in left dlPFC. Further activations included the left inferior parietal lobule and the right inferior frontal gyrus as well as right parahippocampal gyrus and amygdala. Further subcortical activations were seen in right caudate nucleus, right putamen, and bilaterally in the cerebellar hemispheres.

Expression vs. reception

The comparison of expression versus reception yielded a left-dominant distribution of activation changes, primarily involving the parietal lobes (Table II; Fig. 4). The most prominent clusters were seen in the superior and inferior parietal lobules including the adjacent postcentral gyrus. In the frontal lobes, a lateral cluster was found in the left ventral precentral sulcus, extending rostrally to the inferior frontal gyrus (pars opercularis) and caudally to the precentral gyrus (PMv). Additionally, medial frontal clusters of activation comprised the left SMA, extending to the medial cingulate cortex (cingulate motor area, CMA). Furthermore, activations were seen in posterior temporal/occipital cortex bilaterally.

Reception vs. expression

When imagery of gesture reception was contrasted with imagery of gesture execution, positive activation changes
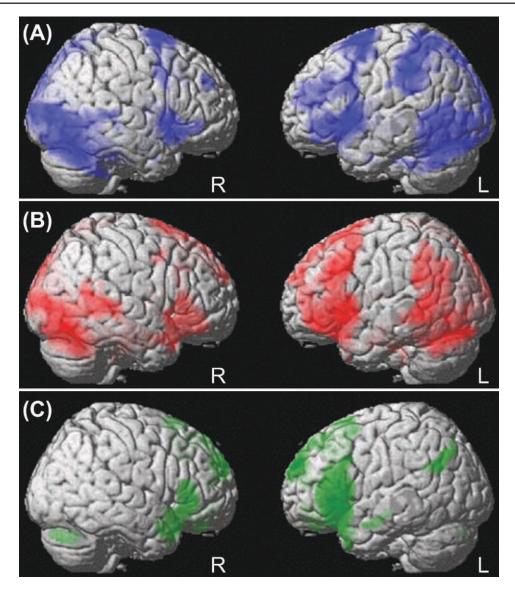
Figure 2.

Main effects of the expression and reception conditions. Second-level group analysis results: (**A**) Imagery of gesture expression, (**B**) imagery of gesture reception, and (**C**) contrast of meaningful emblematic gestures vs. meaningless control gesture (across expression and reception conditions). Overlay of clusters onto a rendered standard template ($P < 0.05$, FDR-corrected at the cluster-level). Abbreviations: L, left hemisphere; R, right hemisphere. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

comprised the frontal and anterior temporal lobes with a left-hemispheric predominance (Table III; Fig. 4). The most extensive cluster of activation was found in the anterior aspect of the left mPFC, extending further to the frontal pole. A separate cluster in its vicinity was detected in left anterior cingulate cortex. Further sites of activation were seen in the left ventrolateral prefrontal cortex (vlPFC) including partes orbitalis and triangularis of the inferior frontal gyrus. Also in the left hemisphere, a distinct cluster in dlPFC and adjacent PMd was found. In the temporal cortex, activation comprised bihemispheric middle and superior temporal gyri in the temporal poles.

Control Stimuli

Expression and reception of the static posture yielded widespread activations of the occipital lobe, in primary and higher-order visual areas, and the cerebellum (see Supporting Information). The expression condition showed

TABLE I. Conjunction analysis of the expression and reception of emblematic gestures

Region	BA	Extent (voxel)	Z value	Coordinates		
				x	y	z
L inferior frontal gyrus (P*or*/P*tr*/P*op:* vlPFC and PMv)	44/45	8,668	6.05	−48	9	8
L claustrum			5.85	−33	2	−1
L inferior parietal lobule	40	798	5.43	−53	−40	38
R inferior frontal gyrus (P*tr*/P*op*)	44/45	1,695	5.42	53	14	−6
R putamen				30	4	−1
R caudate				13	0	13
R middle frontal gyrus (dlPFC)	6	149	4.50	53	10	46
R parahippocampal gyrus		175	4.40	30	−12	−11
R amygdala				33	−2	−20
L/R cerebellum		21,116	7.54	42	−63	−19
R lingual gyrus	19		7.16	49	−70	−7

Coordinates are given in Talairach space after MNI to Talairach conversion using a non−linear algorithm [Lacadie et al., 2008] ($P < 0.05$, FDR-corrected at the cluster-level).
Abbreviations: BA, Brodmann Area; dlPFC, dorsolateral prefrontal cortex; L, left; PMv, ventral premotor cortex; P*op*, pars opercularis; P*or*, pars orbitalis; P*tr*, pars triangularis; R, right; vlPFC, ventrolateral prefrontal cortex.

additional activation of right PMd and dlPFC as well as in the right putamen, whereas the clusters in the reception condition were restricted to occipital regions. The differential contrasts ("E vs. R," "R vs. E") did not reveal any significant voxels.

The pattern of broad occipital and cerebellar clusters was similar in the expression and reception conditions of the *meaningless control gesture* (see Supporting Information). In addition, the activation extended to superior parietal cortex and the temporo-parieto-occipital junction bilaterally in the expression condition. Further clusters were found in SMA and PMd bilaterally, in right dlPFC, and in the inferior frontal gyri bilaterally. Subcortical clusters were located in putamen and pallidum bilaterally with a strong left-hemispheric dominance. In contrast, the reception condition yielded smaller clusters in the left inferior frontal gyrus, and in inferior parietal as well as posterior temporal cortices bilaterally. The contrast "R vs. E" showed distinct clusters in the SMA (Talairach coordinates: 0, −8, 52) and in the left putamen (−19, −2, 6), extending to the thalamus and the striatum, whereas no significant activation was observed in the inverse contrast ("E vs. R").

Factorial Analysis: Emblems and Control Gesture

The formal interaction analysis ("E"/"R" × "emblematic gesture"/"control gesture") yielded no significant clusters of activation. Still the contrast "emblematic gestures vs. control gesture" (across "E" and "R" conditions) revealed
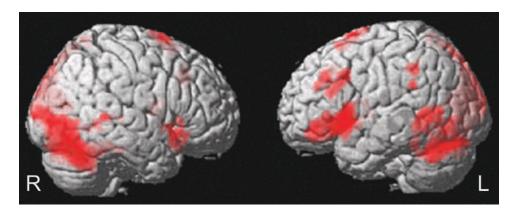

Figure 3.
Conjunction analysis of the expression and reception of emblematic gestures. Second-level group analysis results: Conjunction of gesture expression and reception conditions ("E ∩ R"). Overlay of clusters onto a rendered standard template ($P < 0.05$, FDR-corrected at the cluster-level). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

TABLE II. Differential contrast: expression vs. reception of emblematic gestures

Region	BA	Extent (voxel)	Z value	x	y	z
				Coordinates		
L midcingulate gyrus (CMA/SMA)	24/6	581	3.92	−1	3	30
L precentral sulcus (incl. P*op*: PMv)	6/44	107	4.09	−40	5	9
L postcentral gyrus/inferior parietal lobule	2/40	1,625	4.75	−59	−22	38
R postcentral gyrus/inferior parietal lobule	2/40	297	3.88	57	−16	38
R superior parietal lobule	7	131	3.87	35	−48	52
L precuneus	7	1,023	5.12	−3	−58	52

Abbreviations: CMA, cingulate motor area; L, left; PMv, ventral premotor cortex; P*op*, pars opercularis; R, right; SMA, supplementary motor area.

a predominantly frontal and left-hemispheric pattern with local maxima in left and right inferior frontal gyri, left anterior cingulate, left temporal pole and posterior superior temporal gyrus, as well as in the cerebellum (Table IV; Fig. 2C). The inverse contrast did not yield any significant activation.

The contrast "emblematic gestures vs. control gesture" ("E" condition only) revealed two distinct clusters in the left inferior frontal gyrus. For the "R" condition, the contrast "emblematic gestures vs. control gesture" resulted in a widespread left dominant circuit including clusters in mPFC, inferior frontal gyrus, posterior temporal lobe, inferior parietal lobule, and the cerebellum. The inverse contrast ("control gesture vs. emblematic gestures") did not yield any significant activation for the "E" or "R"

conditions, respectively (see Supporting Information for an overview of these additional main effects).

DISCUSSION

Emblematic gestures are widely used for conveying socially relevant information between individuals. This study investigated the neural correlates of the imagined execution of such codified gestures as well as the imagined reception of the same gestures. Using fMRI, we mimicked nonverbal communication by instructing our subjects to observe emblematic gestures either with the mindset of the addresser or from the perspective of the addressee. Our results show that in accordance with our
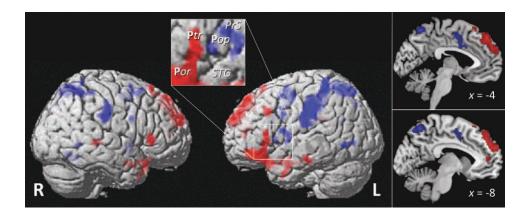

Figure 4.

Differential contrasts: expression vs. reception and reception vs. expression of emblematic gestures. Second-level group analysis results: Overlay of the contrasts of expression vs. reception (blue) and reception vs. expression (red) onto a normalized standard brain; 3D view to display surface clusters (columns on the left) and additional sagittal view to display mesial clusters (right column). Note the distinction of predominantly frontal to parietal regions involved in imagery of gesture expression and frontal to temporo-polar regions involved in imagery of gesture reception with a junction in left inferior frontal and precentral gyri. Also in left superior frontal cortex, more rostral clusters were found in the gesture reception condition which included the anterior cingulate when compared with more posterior regions in the gesture expression condition (SMA and adjacent cingulate cortex). (P < 0.05, FDR-corrected at the cluster-level; coordinates are given in Talairach space.) Abbreviations: L, left; P*or*, pars orbitalis; PrS, precentral sulcus; P*tr*, pars triangularis; P*op*, pars opercularis; R, right; STG, superior temporal gyrus.

TABLE III. Differential contrast: reception vs. expression of emblematic gestures

Region	BA	Extent (voxel)	Z value	Coordinates		
				x	y	z
L superior frontal gyrus (mPFC)	8/9/10	1,065	4.47	−4	47	43
R superior frontal gyrus (PMd)	6	115	3.91	8	31	56
L middle frontal gyrus (dlPFC)	9	128	3.62	−39	22	30
L anterior cingulate	32	104	3.85	−14	43	14
L inferior frontal gyrus (P*or*/P*tr*: vlPFC)	47/45	693	4.51	−43	36	−8
L middle temporal gyrus (temporal pole)	20	123	3.77	−50	−6	−19
R superior temporal gyrus (temporal pole)	38	126	4.18	42	16	−17

Abbreviations: dlPFC, dorsolateral premotor cortex; L, left; mPFC, medial prefrontal cortex; PMd, dorsal premotor cortex; P*or*, pars orbitalis; P*tr*, pars triangularis; R, right; vlPFC, ventrolateral prefrontal cortex.

hypothesis the subjects exhibited common cerebral representations of both conditions in broad, bihemispheric circuits as well as a dichotomy of nonoverlapping, task-specific brain regions with junctions in the frontal cortex.

Common Neural Representations of Gesture Expression and Reception

We found a widespread bilateral, left-dominant system as a common representation for the imagined expression and reception of emblematic gestures. It involved primary and higher-order visual areas and the inferior parietal lobule, language-related regions in the temporo-parietal junction and inferior frontal gyrus [Lau et al., 2008] as well as PFC and the anterior cerebellum. Roles of parietal, inferior frontal, and premotor cortices have previously been described in observation and imitation tasks of gestures and object-related actions [Decety et al., 1997; Iacoboni et al., 1999; Meltzoff and Decety, 2003; Muhlau et al., 2005; Sakreida et al., 2005]. Thus, our findings are consistent with the notion of a shared interface of both execution and perception of movement as is typical for the putative human mirror neuron system [Aziz-Zadeh

et al., 2006; Iacoboni, 2009] and coincide with results of an fMRI study in which actual gesturing was compared with gesture observation [Schippers et al., 2009]. Furthermore, both the expression and reception conditions in the present study required the subjects to recognize the presented gestures as an intentional motor act [de Lange et al., 2008].

Imagery of Gesture Expression: Distinct Circuits

The contrast "imagery of gesture expression versus reception" yielded a left-dominant dorsal circuit with extensive activation clusters in the parietal cortex for both emblems and the meaningless control gesture. Although our study employed a mere cognitive task, these activations resemble previous studies of gesture production [Bohlhalter et al., 2009; Carmo and Rumiati, 2009; Fridman et al., 2006; Muhlau et al., 2005] and agree with the notion of an integrative role of parietal cortex in visuospatial attention and selective motor planning [Culham and Valyear, 2006]. Furthermore, it is known from lesion studies that damage to parietal areas induces deficits in motor programming [Leiguarda and Marsden, 2000].

TABLE IV. Differential contrast: emblematic gestures vs. control gesture (across expression and reception conditions)

Region	BA	Extent (voxel)	Z value	Coordinates		
				x	y	z
L inferior frontal gyrus (P*or*/P*tr*/P*op*: vlPFC and PMv)	44/45/47	3,377	6.06	−41	21	−15
R inferior frontal gyrus (P*or*/P*tr*/P*op*: vlPFC)	44/45/47	996	5.75	56	30	3
L superior frontal gyrus (mPFC)	8/9/10	1,845	5.75	−8	57	22
L anterior cingulate	32	570	4.65	−6	28	33
L middle temporal gyrus (temporal pole)	21	157	4.55	−51	−11	−14
L middle frontal gyrus	11	434	4.28	−4	37	−16
L superior temporal gyrus	39	475	3.97	−53	−58	28
R cerebellum		605	4.64	9	−83	−23

Abbreviations: dlPFC, dorsolateral premotor cortex; L, left; mPFC, medial prefrontal cortex; PMd, dorsal premotor cortex; PMv, ventral premotor cortex; P*op*, pars opercularis; P*or*, pars orbitalis; P*tr*, pars triangularis; R, right; vlPFC, ventrolateral prefrontal cortex.

Along with inferior and superior parietal cortex, motor imagery of emblematic gestures elicited activations in supplementary and cingulate motor areas in this study. The SMA with its strong connections to primary and nonprimary motor regions is a central area for movement generation and motor control [Picard and Strick, 2001]. The adjacent CMA is thought to belong to "cognitive cingulate sections" (as complemented by "affective sections" in rostral anterior cingulate) also involved in complex motor control [Bush et al., 2000].

In summary, this differential activation pattern comprised cortical areas engaged in motor imagery and concurred with dorsal stream areas of visual processing [Goodale, 2008; Goodale and Milner, 1992; McIntosh and Schenk, 2009]. In contrast, no significant differences between the expression and reception conditions became apparent for the static hand posture. For the meaningless control gesture, the same contrast revealed clusters in the left basal ganglia and SMA, according with their role in motor imagery [Kasess et al., 2008]. Furthermore, the comparison of emblematic gesture expression with the meaningless control gesture showed the left inferior frontal gyrus to be specifically involved in processing the meaning of gestures.

When comparing the emblem expression condition's main effects with those of the conjunction analysis of expression and reception, it becomes apparent that the latter yielded clusters in the inferior parietal lobule whereas an involvement of the superior parietal lobule was merely found in the expression condition. This distinction can be explained by the model of two functional subdivisions of the dorsal system [Rizzolatti and Matelli, 2003]. According to this model, a dorso-dorsal component would be involved in on-line control of actions (necessary for the expression condition), and complemented by a ventro-dorsal component responsible for action understanding and space perception (required for both the expression and reception conditions in this study).

Imagery of Gesture Reception: Distinct Circuits

The emblematic gesture reception condition, when compared with imagery of gesture execution, yielded left-lateralized activation clusters in lateral inferior and medial frontal as well as anterior temporal regions. In contrast, there were no significant activations in the contrast of reception vs. expression for the two control stimuli. This indicates that the pattern observed in the reception of the emblematic gestures was specifically related to processing their meaning.

The temporal pole has been described as a multimodal hub in semantic processing [Patterson et al., 2007]. Thus, the analogy of regions involved in semantic processing to the activation pattern found in this study suggests common mechanisms for decoding the meaning of the gestures and language comprehension [McNeill, 1992]. This notion of a common system for speech and gestures has also been sub-

stantiated by a recent fMRI study [Xu et al., 2009]. Another study explicitly examined processing of gestures along the language—gesture continuum comparing American Sign Language (ASL) and emblems to meaningless gestures [Husain et al., 2009]. Although methodological differences in task design (instructions) and participant type (healthy versus prelingually deaf participants) impede a direct comparison with the present experiment, some similarities are apparent. As in this study, the authors found support for the importance of semantic decoding in the process of emblem perception. Furthermore, ASL and emblem perception were shown to share common circuits in inferior frontal and middle temporal gyri.

Consistent with our results, bilateral temporal pole activation was also found in an fMRI experiment where subjects were instructed to recognize gestures which expressed the empathic processing or mentalizing of the addresser [Gallagher and Frith, 2004]. As in this study, these activations went along with a cluster in pregenual anterior cingulate cortex. This area is thought to play a prominent role in monitoring of behavior and coincides with a cluster in a meta-analysis of functional imaging studies related to empathy [Seitz et al., 2006]. This rostral subdivision of the anterior cingulate cortex has been characterized as an "affective section" [Bush et al., 2000] and was tentatively described as an area related to the interpretation and valuation of thought [Rushworth et al., 2007; Seitz et al., 2009].

Another medial cluster was found in the superior medial frontal cortex, rostral to the SMA proper. This area, comprising the pre-SMA, has been characterized as a region involved in motor-related cognitive tasks as distinguished from the SMA proper as a "concrete" motor area [Picard and Strick, 2001]. The cluster extended to the anterior paracingulate cortex, an area previously suggested to play a crucial role in social interaction, especially in the context of passive observation and prospective intention [Walter et al., 2004]. This segregation of medial premotor and prefrontal areas fits well with the differential activation of pre-SMA and SMA proper in this study.

Junctions of Ventral and Dorsal Streams: Addresser versus Addressee

A junction of the expression and reception conditions was found in the left inferior frontal gyrus. While the conjunction analysis of the two conditions yielded a single cluster that comprised large portions of the inferior frontal gyrus, pars opercularis, and the adjacent precentral gyrus were more active in the expression condition whereas partes triangularis and orbitalis were more active in the reception condition. The segregation of the inferior frontal gyrus [Keller et al., 2009] corresponds to cytoarchitectonic differences of Brodmann Areas (BA) 44 and 45 [Amunts et al., 1999] and different patterns of connectivity with motor and sensorimotor regions for BA 44 and prefrontal

regions for BA 45, respectively [Petrides, 2006]. As a complement, neuroimaging studies suggested functional subdivisions of inferior frontal cortex parallel to the anatomical findings. More rostral representations were described for semantic processing [Bookheimer, 2002], whereas more caudal activations have been attributed to the motor act of both language and sign language production [Horwitz et al., 2003]. Notably, a specific involvement of rostral inferior frontal cortex was found in emotionally relevant semantic processing of sentences [Beaucousin et al., 2007]. In analogy to our results in this study, this activation was paralleled by a cluster in the pre-SMA.

The differential activation of inferior frontal cortex in this study might also be interpreted in the context of the mirror neuron theory with the notion that mirror neurons are more active during imitation than during observation [Iacoboni et al., 1999]. Although the mirror neuron theory has been extensively debated recently [Hickok, 2009], the human area BA 44 may be considered to be a homologue to the "classic" mirror neuron site in monkey area F5 which is strongly connected to premotor and parietal regions [Binkofski and Buccino, 2004]. Accordingly, inhibition of the pars opercularis with repetitive transcranial magnetic stimulation yielded an impairment of imitation in healthy subjects [Heiser et al., 2003]. Our present findings provide support for a distinction of regions primarily involved in motor imagery of gestures as opposed to more rostral areas in the inferior frontal cortex in the reception condition.

Functional neuroimaging studies of movement observation in general and gesture processing in particular complement these findings showing a functional diversity of the inferior frontal cortex. A recent fMRI study comparing preparation with execution of different gesture types revealed a rostral to caudal temporal gradient of activation in vlPFC and PMv for intransitive gestures [Fridman et al., 2006]. Due to our study design, we cannot distinguish temporal components of the different tasks. However, the results of our motor imagery task are consistent with those of the gesture execution in the study by Fridman et al. Also, a predominant involvement of left pars triangularis (and less of pars opercularis) was recently described for recognition of intransitive gestures [Villarreal et al., 2008]. Our findings accord with an fMRI study in which the rostral parts of the inferior frontal gyrus (i.e., pars orbitalis) were found to be important when the observation of expressive gestures accompanied by facial expressions were contrasted with noninformative movements [Lotze et al., 2006]. In parallel, an involvement of pars opercularis was found when the imitation of emotional facial expressions was contrasted with an observation of the same expressions [Carr et al., 2003]. These results point to a role of vlPFC/orbitofrontal cortex in emotional processing [Elliott et al., 2000]. Taken together, we have demonstrated a functional segregation of inferior frontal and caudal premotor cortex in cognitive gesture processing.

In conclusion, common and differential cerebral representations of emblematic gesture processing comprised large-scale circuits. In particular, imagining gesture execution involved the dorsal visual stream as well as higher-order motor areas. In contrast, imagining gesture reception encompassed regions related to semantic processing in inferior frontal and temporal cortices as well as medial and lateral prefrontal areas known to be involved in understanding the intentions of others. Junctions were found in inferior frontal and medial frontal cortex with a rostro-caudal dichotomy. Although our expression and reception conditions were cognitive tasks by nature, this dichotomy may be consistent with the notion of a functional distinction between motor-related and perceptual domains in the inferior and medial frontal cortex. One could speculate that such functional distinctions may have a counterpart in differential micro-anatomical characteristics [Geyer, 2004].

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