

## COGNITIVE NEUROSCIENCE

# The eye contact effect in request and emblematic hand gestures

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## Abstract

Request and emblematic gestures, despite being both communicative gestures, do differ in terms of social valence. Indeed, only the former are used to initiate/maintain/terminate an actual interaction. If such a difference is at stake, a relevant social cue, i.e. eye contact, should have different impacts on the neuronal underpinnings of the two types of gesture. We measured blood oxygen level-dependent signals, using functional magnetic resonance imaging, while participants watched videos of an actor, either blindfolded or not, performing emblems, request gestures, or meaningless control movements. A left-lateralized network was more activated by both types of communicative gestures than by meaningless movements, regardless of the accessibility of the actor's eyes. Strikingly, when eye contact was taken into account as a factor, a right-lateralized network was more strongly activated by emblematic gestures performed by the non-blindfolded actor than by those performed by the blindfolded actor. Such modulation possibly reflects the integration of information conveyed by the eyes with the representation of emblems. Conversely, a wider right-lateralized network was more strongly activated by request gestures performed by the blindfolded than by those performed by the non-blindfolded actor. This probably reflects the effect of the conflict between the observed action and its associated contextual information, in which relevant social cues are missing.

## Introduction

A substantial proportion of our communication during social interactions is non-verbal. A powerful form of non-verbal communication is gesture (Hari & Kujala, 2009). By reading different types of gesture, either emblematic or request, one can determine what others want to communicate or ask, respectively. Other types of non-verbal communication may occur in order to ensure successful communication during social interactions. Eye contact, for example, is used as a signal to convey willingness to interact (George & Conty, 2008; Senju & Johnson, 2009). If there is no eye contact, or mutual gaze, especially in Western culture, there is an indication of a lack of interest in entering or maintaining a communication. Thus, understanding the meaning of others' gestures and eye signals, and the consistency between the two, is probably mandatory for our everyday skillful communication with conspecifics.

The neural correlates of communicative and non-communicative gesture (e.g. transitive and meaningless) representation have been

well characterized by earlier functional imaging studies (Grèzes *et al.*, 1998; Villarreal *et al.*, 2008; Chaminade *et al.*, 2010; Schippers *et al.*, 2010; Lindenberg *et al.*, 2012). However, very little is known about the representation of different subcategories of communicative gestures, e.g. emblematic and request gestures, both of which are known to convey social intents. 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', 'victory', and 'OK'). Unlike gesticulation, which obligatorily requires speech, emblems, although possessing some linguistic properties, may co-occur with speech (McNeill, 1992, 2000; Kendon, 2004). Importantly, they convey meanings without an expectation of an overt and specific action from the addressee as a response (e.g. 'victory'). Request gestures, like emblems, are signs expressed by intentional bodily movements, and that convey communicative intents and may co-occur with speech. However, emblems are more interactional than request gestures, and, unlike the latter, convey commands and are used to

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initiate, maintain, regulate or terminate various types of interaction. They are also called instrumental gestures (Barten, 1979), i.e. designed to influence the immediate behavior of another (e.g. 'come here', 'give me', and 'hitchhiking'). To date, although they are different in terms of social intentions, emblematic and request gestures have not been investigated separately. Evidence in favor of the existence of specific or common neural substrates is still lacking.

Instead, these two different categories of gesture have been sometimes confused. For example, Montgomery *et al.* (2007) put both real emblematic hand gestures (e.g. 'OK' and 'thumb up') and gestures communicating commands (e.g. 'come here' and 'look there') in the same set of stimuli. But, as said before, the social intentions behind the two types of gesture are different from each other, as only request gestures are aimed at explicitly changing the behavior of others by communicating commands (Barten, 1979). To the best of our knowledge, there is only one neuroimaging study (Gallagher & Frith, 2004) in which the authors have sought to characterize the neural correlates of request gestures (called there instrumental gestures) in comparison with expressive gestures (expressing inner feeling states). They found that different neural networks were activated by the observation of request or expressive gestures. The perception of request gestures elicited activity in a left-lateralized system comprising the inferior frontal cortex and the middle frontal cortex. Such left-lateralized activities were discussed with reference to their role in language and imitation. In contrast, expressive gestures elicited activity in the anterior paracingulate cortex, the amygdala and the temporal poles bilaterally, and the right superior temporal sulcus. The authors highlighted the fact that these regions had previously been implicated in a neural network constituting the so-called 'social brain' (Brothers *et al.*, 1990; Johnson *et al.*, 2005; Adolphs, 2009). However, this study has an important limitation, i.e. the use of stimuli on which faces were blurred. On the one hand, this ruled out facial expression as a potential confound while gestures were being recognized. On the other hand, the absence of facial cues probably distorted the participants' perception of request gestures. In particular, gaze is one of the most important cues for the attribution of intentionality (Allison *et al.*, 2000; Castiello, 2003; Pelphrey & Morris, 2006). Accordingly, behavioral evidence suggests that eye contact (Sartori *et al.*, 2009; Ferri *et al.*, 2011; Innocenti *et al.*, 2012), in addition to facial expression (Ferri *et al.*, 2010), is essential for communication, especially for understanding another's request. Sartori *et al.* (2009) investigated the influence of a sudden presentation of a request gesture, i.e. the hand opening expressing 'give-me-the-object', on the kinematics of a reach-to-grasp and place sequence. The results showed that the social request interfered with the actual sequence by inducing a partial deviation of the hand trajectory towards the conspecific, provided that the eyes of the partner were available. In another study (Ferri *et al.*, 2010), participants either had to reach-grasp and feed the experimenter with a sugar lump (social situation), or had to reach-grasp and place the sugar lump into the mouth-like aperture of a body-shape (non-social situation). The social request was thus conveyed by a mouth request gesture (i.e. mouth aperture). It was demonstrated that participants' control of motor sequences changed in the social situation, as compared with the non-social situation, and as a function of eye contact occurrence between interacting people. Finally, Innocenti *et al.* (2012) observed that the sequence of reaching-grasping and lifting a bottle was interfered with by the pour request of a conspecific holding in his hand an empty glass only when he also directed his gaze towards the agent.

All in all, the behavioral evidence described above confirms previous descriptions of an 'eye contact effect' [for a review, see Senju & Johnson (2009)], as the phenomenon whereby perceived eye contact with another human face modulates certain aspects of the concurrent and/or immediately following cognitive processing.

In the present study, we investigated the impact of eye contact on the neuronal correlates of two different subcategories of communicative gesture, i.e. emblematic and request gestures. The majority of neuroimaging studies carried out so far have investigated the neural correlates of the 'eye contact effect' by comparing direct gaze processing with averted gaze processing [see, for example, Wicker *et al.* (1998)]. In our study, we decided to manipulate eye contact in a different way, with an actor blindfolded in the no-eye contact condition. Indeed, it has been shown (Adams & Kleck, 2005) that gaze direction enhances the attribution of emotional trait and behavioral intent (approach-avoidance) to neutral faces in an opposite way. Direct gaze led to more anger and joy (approach) dispositional attributions, whereas averted gaze led to more fear and sad (avoidance) dispositional attributions. In the present study, we deliberately selected gestures conveying behavioral positive intents. Such selection was performed in order to reduce, as much as possible, variability across stimuli. That said, the use of averted gaze, to be compared with the eye contact condition, would have introduced an important confound. In particular, averted gaze might have led to the attribution of avoidance intents to the agent (Adams & Kleck, 2005), thus conflicting with the social request conveyed by the observed gesture. For this reason, to obtain the condition with no eye contact, we used a blindfolded actor, meaning that it was simply not specified whether he was looking or not at the addressee. In this condition, the agent's gaze was completely prevented, as in real-life situations with an addresser wearing sunglasses and an addressee who cannot infer where the former is looking. Moreover, the averted gaze of an actor performing a gesture is a condition that potentially generates a conflict in the observer, owing to the incongruity between the direction of the gesture and the orientation of the agent's gaze. In our study, we wanted to avoid such conflict. Indeed, if we manipulated the direction of the actor's gaze, we would not be able to segregate cortical activations attributable to the conflict itself from those attributable to the lack of contribution of the social cue.

In the present study, we expected to find that eye contact occurrence, as a signal conveying willingness to interact, has a different impact on the neuronal activity recruited during the observation of request gestures from emblematic (and meaningless) gestures. Indeed, only request gestures, such as eye contact, are aimed at initiating, maintaining and regulating an interaction with the addressee.

## Materials and methods

### Participants

Twenty healthy young adults (mean age, 26.2 years; range, 22–34 years; five males) were included in the present study. All participants were right-handed as assessed by Edinburgh Handedness Inventory (Oldfield, 1971). They had normal or corrected-to-normal vision, and were naive regarding the purpose of the experiment. Participants gave their written informed consent to participate in the study, and were paid (€25) for their participation. The study was approved by the ethics committee of the University of Chieti, and was conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki.

### Functional magnetic resonance imaging (fMRI) data acquisition

All images were collected with a 3-T Philips Achieva scanner operating at the Institute of Advanced Biomedical Technologies (ITAB Fondazione G. d'Annunzio, Chieti, Italy). T1-weighted anatomical images were collected with a multiplanar rapid acquisition gradient-echo sequence (230 sagittal slices; voxel size,  $0.5 \times 0.5 \times 0.8$  mm; repetition time, 8.08 ms; echo time, 3.7 ms). Functional images were collected with a gradient echo-planar imaging sequence. Each subject underwent four acquisition runs, each including 220 consecutive volumes comprising 32 consecutive 3-mm-thick slices (0.5-mm gap) oriented parallel to the anterior commissure and covering the whole brain (repetition time, 2500 ms; echo time, 35 ms;  $64 \times 64$  image matrix;  $3 \times 3$  in-plane resolution).

### Stimuli and conditions

Stimuli consisted of 36 silent video clips of duration 2200 ms (Fig. 1), which was matched across conditions. Each video depicted an actor producing a gesture. Six depicted emblematic gestures. These

gestures convey meanings without an expectation of an overt and specific action from the addressee (e.g. 'OK' and 'well done'). Six depicted request gestures. These are gestures that are intended to regulate or change the behavior of others by communicating commands (e.g. 'come' and 'give me'). Finally, six depicted meaningless hand/arm movements (hereafter: meaningless gestures). Uni-manual and bi-manual gestures were equally distributed across the three categories. Given the complexity of the stimuli, and to avoid further sources of variability, such as that resulting from observing different actors, we decided to present gestures that were always performed by the same actor. The actor's face did not convey any emotion.

The actor could be either blindfolded or non-blindfolded. The average durations of the execution of gestures performed by the blindfolded and the non-blindfolded actor were 1526 ms and 1606 ms, respectively, for emblematic gestures, 1573 ms and 1680 ms, respectively, for request gestures, and 1906 ms and 2046 ms, respectively, for meaningless gestures. *t*-Tests excluded the possibility that they significantly differed from each other (emblematic,  $t_5 = 0.65$ ,  $P = 0.55$ ; request,  $t_5 = 0.74$ ,  $P = 0.87$ ; meaningless,  $t_5 = 1.82$ ,  $P = 0.09$ ). Repetitions of the



FIG. 1. Emblematic, request and meaningless gestures performed by the non-blindfolded actor and the blindfolded actor used as stimuli. Dashed lines represent the trajectory of hand movements in the video stimuli.



actor's starting position frame were put at the beginning of each video, and repetitions of the actor's end position frame (Fig. 1) were put at the end of each video, in order to match the durations of all of the stimuli. Moreover, the stimuli were not equated for amount of motion; however, the number of gestures with oscillating movements of the hand was balanced across conditions.

### Validation of the stimuli

A new sample of 20 right-handed (Oldfield, 1971), naive volunteers (15 females; age, 20–40 years) were recruited to validate the stimuli. All participants were Italian native speakers. The participant sat in front of a table on which his or her right hand was placed with the index and middle fingers on a keyboard. Each trial began with the presentation of a white fixation cross ( $0.6^\circ$ ) for 1000 ms on a PC monitor (19 inches), 57 cm distant from the participant's chest. Then, videos appeared on the center of the PC black monitor. After 2160 ms or when the participants gave a response, the video was replaced with a blank panel for 2000 ms. Then, a new trial was run. Participants performed a go/no-go task. Whenever the presented stimulus was a gesture, subjects had to respond as quickly as possible by pressing a key with the right hand (go condition). When the stimulus was a meaningless movement, they had to remain still (no-go condition). Half of the participants discriminated between emblematic and request gestures by pressing a left key with the index finger and a right key with the middle finger, whereas the other half did the opposite.

### Functional magnetic resonance imaging

Subjects lay supine in the scanner with the arms outstretched beside the abdomen. Visual stimuli were projected onto a back projection screen situated behind the subject's head, and were visible in a mirror put on the birdcage head coil. Sound-attenuating headphones were used to muffle scanner noise. The presentation of the stimuli and the recording of participants' responses were controlled with custom software (developed by G. Galati at the Department of Psychology, Sapienza Università di Roma, Italy) (Galati *et al.*, 2008, 2011), implemented in MATLAB (The MathWorks, Natick, MA, USA), with COGENT 2000 (developed at Functional Imaging Laboratory and Institute of Cognitive Neuroscience, University College of London, London, UK) and Cogent Graphics (developed by J. Romaya at the Laboratory of Neurobiology, Wellcome Department of Imaging Neuroscience, UCL, London, UK).

### Design and procedure

The event-related paradigm consisted of four acquisition runs of the gesture observation task. There was a pause of 5 min between each run. The experimental design was a  $3 \times 2$  factorial with type of gesture (emblematic vs. request vs. meaningless) and eye contact (non-blindfolded actor vs. blindfolded actor) as within-subject factors. The 36 stimuli (six for each experimental condition) were repeated three times in each run, giving a total of 108 trials. In each run, nine catch trials were also included. In these trials, participants had to categorize, by pressing previously assigned buttons, the gesture that they had just seen. These trials were signaled by replacing the post-stimulus fixation with a circle that worked as a go signal. Consequently, the participants knew to respond only after stimulus presentation. In total, the experiment consisted of 468 trials. The trial order was determined with the program OPTSEQ2 (Dale, 1999). Participants were instructed to pay attention to the visual stimuli and categorize them as soon as the go signal appeared. Before scanning, participants

were trained in the experimental task with all of the stimuli that would be presented during fMRI data collection. Each video stimulus was presented only once during the pre-scanning phase.

### Data analysis

#### Validation of the stimuli

In order to obtain a measure of overall performance that simultaneously takes into account speed and accuracy, we used the method first recommended by Townsend & Ashby (1983), which has subsequently been referred to as 'inverse efficiency' (IE) (Christie & Klein, 1995). For each participant, IE scores were calculated for each category of communicative gesture (emblematic and request) and actor (non-blindfolded actor and blindfolded actor). To this end, the median values for correct reaction times (RTs) were divided by their corresponding proportion correct scores, so that differences in RT performance decreased if differences in accuracy were large, but remained the same if accuracies were identical. Thus, IE scores provided a measure of overall performance. Lower IE corresponded to better performance. These IE scores were then subjected to ANOVA. Gesture (emblematic vs. request) and eye contact (non-blindfolded actor vs. blindfolded actor) were treated as within-subject variables. Whenever appropriate, *post hoc* analyses were performed with the Newman-Keuls method. An alpha level of 0.05 was used.

#### Functional magnetic resonance imaging

Functional magnetic resonance imaging data were analysed with SPM8 (Wellcome Trust Centre for Neuroimaging, University College of London, London). Functional images were first corrected for head movement, by use of a least-squares approach and six-parameter rigid body spatial transformation (Friston *et al.*, 1995), and for difference in acquisition timing between slices. The high-resolution anatomical image and the functional images were coregistered and stereotactically normalized to the Montreal Neurological Institute anatomical (T1) brain template used in SPM8 (Mazziotta *et al.*, 1995). Functional images were re-sampled with a voxel size of  $4 \times 4 \times 4$  mm, and spatially smoothed with a three-dimensional Gaussian filter of 6-mm full-width-at-half-maximum (Friston *et al.*, 1995).

The time series of functional magnetic resonance images obtained from each participant were then analyzed on a voxel-by-voxel basis according to the principles of the general linear model extended to allow the analysis of fMRI data as a time series (Worsley & Friston, 1995). The onset of each trial constituted a neural event, which was modeled through a canonical hemodynamic response function, chosen to represent the relationship between neuronal activation and blood oxygen level-dependent signal changes (Friston *et al.*, 1998). Trials in which a response was required were modeled as a separate condition and then excluded from further analyses, which concentrated on observation trials.

These subject-specific models were used to compute a set of contrast images per subject, representing the estimated amplitude of the hemodynamic response in each experimental condition as compared with the fixation baseline. Contrast images from all subjects were entered at the second stage into a  $3 \times 2$  repeated-measures ANOVA with non-sphericity correction (as implemented in SPM8), with gesture (emblematic vs. request vs. meaningless) and eye contact (non-blindfolded actor vs. blindfolded actor) as experimental factors. This procedure allowed us to test hypotheses about differences in hemodynamic response amplitude across conditions in the whole population from which our participants were extracted. Moreover, we

chose to perform ANOVA and *post hoc* tests, rather than simple *t*-tests, because of the complexity of our factorial design. Briefly, we first identified cortical regions responding either to the main effects or interaction by ANOVA. Then, we performed follow-up analyses of the same regions with *post hoc* tests on regionally averaged estimated  $\beta$ -values, to test the contribution of each experimental condition to significant effects. Note that there is no circularity (i.e. double dipping) (Kriegeskorte, *et al.* 2009), because *post hoc* tests were used to explore the real meaning of main effects and interaction, and not to further select voxels.

Using this analytical method, we first looked at regions showing a main effect of gesture, i.e. regions responding differentially to emblematic vs. request vs. meaningless gestures, without considering the eye contact factor. The resulting statistical parametric maps of the *F*-statistic were thresholded ( $P < 0.001$ , corrected) at the voxel level and by cluster size ( $k > 10$ ). Correction for multiple comparisons was performed with the false discovery rate (FDR). Then, we conducted follow-up tests of regions identified in the preceding step. Regional activations (mean  $\beta$ -values) were extracted with the MARSBAR toolbox (<http://marsbar.sourceforge.net/>) and exported to STAT software, where *post hoc* tests were used to evaluate the contribution of each class of gesture to the main effect, with Bonferroni correction for multiple comparisons.

Second, we looked at regions showing a main effect of eye contact, i.e. regions responding differentially for the non-blindfolded actor vs. blindfolded actor, without considering the nature of the gesture. The resulting statistical parametric maps of the *F*-statistic were thresholded ( $P < 0.001$ , corrected) at the voxel level and by cluster size ( $k > 10$ ). Correction for multiple comparisons was performed with the FDR.

Finally, we looked at regions responding to the interaction term. The resulting statistical parametric maps of the *F*-statistic were thresholded ( $P < 0.001$ , corrected) at the voxel level and by cluster size ( $k > 10$ ). Correction for multiple comparisons was performed with the FDR. Then, we conducted follow-up tests of regions identified in the preceding step. Regional activations (mean  $\beta$ -values) were extracted with the MARSBAR toolbox (<http://marsbar.sourceforge.net/>) and exported to STAT software, where *post hoc* tests were used to evaluate the contribution of each experimental condition to the interaction term, with Bonferroni correction for multiple comparisons. According to the aim of the present study, i.e. to investigate whether eye contact differentially impacted on emblematic and request gestures, the *post hoc* analyses reported here refer to the differences produced by the two levels of the factor eye contact on each kind of gesture, and to the differences between the emblematic and request gestures, when eye contact was either allowed or prevented.

## Results

### Validation of the stimuli

Inverse efficiency scores were calculated from the accuracy and RT values reported in Table 1. ANOVA revealed no significant effect of the factors gesture ( $F_{1,19} = 1.06$ ,  $P = 0.31$ ) and eye contact ( $F_{1,19} = 1.34$ ,  $P = 0.08$ ), or of their interaction ( $F_{1,19} = 0.91$ ,  $P = 0.35$ ). These results suggest that request gestures were as easy to recognize as emblematic gestures.

### Functional magnetic resonance imaging

Analysis on catch trials revealed that participants were capable of distinguishing request from emblematic gestures. Indeed, the mean

TABLE 1. Validation of the stimuli

	RT (ms)		Accuracy	
	Mean	SD	Mean	SD
E_NB	806.94	169.56	0.91	0.12
E_B	832.56	216.43	0.92	0.10
R_NB	769.74	165.33	0.84	0.12
R_B	824.70	220.22	0.84	0.15

E\_NB, Emblematic\_Not-Blindfolded; E\_B, Emblematic\_Blindfolded; R\_NB, Request\_Not-Blindfolded; R\_B, Request\_Blindfolded; SD, standard deviation.

accuracy was 80% (request gestures, 78%; emblematic gestures, 82%;  $t_{19} = 1.35$ ,  $P = 0.19$ ).

### Neuronal mapping of the main effect of gesture observation

Cortical regions sensitive to the main effect of gesture observation are detailed in Table 2 and Fig. 2. These regions were mostly located

TABLE 2. Montreal Neurological Institute (MNI) coordinates of peaks of relative activation of cortical areas responding to the main effect of gesture, the main effect of eye contact, and the interaction term

Anatomical description	Label	Side	MNI coordinates			Z-score
			x	y	z	
Main effect of gesture						
Inferior frontal gyrus (pars triangularis)	IFGtri	L	-45	30	21	4.56
Inferior frontal gyrus (pars orbitalis)/insula	IFGorb/aIC	L	-30	24	-9	5.39
		R	33	24	-6	5.13
Inferior frontal gyrus (pars opercularis)	IFGope	L	-60	6	18	4.54
Pre-supplementary motor area	Pre-SMA	L	-6	9	51	5.84
Ventral premotor cortex	PMv	L	-45	3	36	5.22
Inferior parietal lobe	IPL	L	-48	-30	48	6.28
Superior temporal sulcus (posterior)	pSTS	R	48	-39	0	4.93
Middle temporal gyrus (posterior)	MTG	L	-51	-69	15	4.45
Occipital cortex	OC	L	-33	-96	-9	6.57
		R	6	-96	-6	6.21
Cerebellum	C	R	33	-54	-30	4.36
Main effect of eye contact						
Precentral gyrus (inferior)	PcG	R	48	0	42	4.09
Middle temporal gyrus (posterior)	MTG	L	-51	-72	9	4.54
		R	48	-66	3	4.17
Gesture $\times$ eye contact interaction						
Dorsolateral prefrontal cortex	DLPFc	R	33	48	30	4.92
Inferior frontal gyrus (pars orbitalis)/insula	IFGorb/aIC	R	36	24	-12	4.83
Pre-supplementary motor area	Pre-SMA	R	6	12	51	4.90
Ventral premotor cortex	PMv	L	-42	-3	45	5.04
Ventral premotor cortex/inferior frontal gyrus (pars opercularis)/pars triangularis	PMv/IFGope-tri	R	48	3	30	5.23
Inferior parietal lobule	IPL	R	33	-48	45	5.04
Superior temporal gyrus	STG	R	63	-33	18	4.79
Fusiform gyrus	FFG	R	45	-48	-24	6.33
Middle/inferior temporal gyrus	MTG/ITG	R	45	-69	-12	5.24
Occipitotemporal cortex	OT	L	-30	-69	-15	5.83

L, left; R, right.

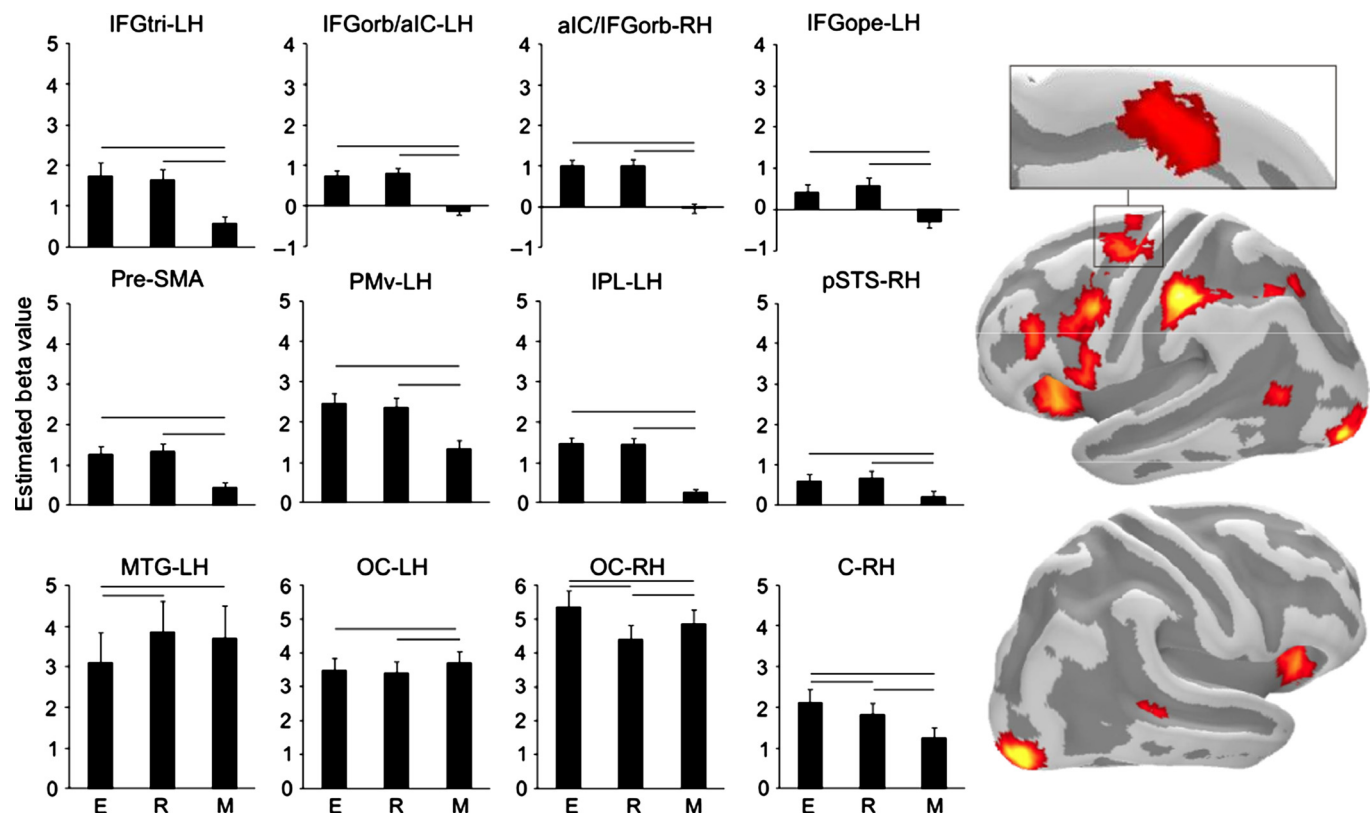


FIG. 2. Cortical regions (and estimated  $\beta$ -values) sensitive to the main effect of gesture (E, emblematic; R, request; M, meaningless). Group activation data are rendered on the cortical surface of a 'canonical' brain (Mazziotta *et al.*, 1995). Error bars indicate standard errors. Horizontal lines indicate  $P < 0.05$ .

in the left hemisphere, and encompassed the pars opercularis of the inferior frontal gyrus (IFGope-LH), the pars triangularis of the inferior frontal gyrus (IFGtri-LH), the pars orbitalis of the inferior frontal gyrus encompassing part of the anterior insular cortex (IFGorb/aIC-LH), the ventral premotor cortex (PMv-LH, area 6), the pre-supplementary motor area (pre-SMA) extending to the left superior precentral gyrus, the inferior parietal lobe (IPL-LH) extending to the superior postcentral gyrus, the posterior part of the middle temporal gyrus (MTG-LH), and the occipital cortex (OC-LH). In the right hemisphere, they were located in the anterior insular cortex encompassing the pars orbitalis of the inferior frontal gyrus (aIC/IFGorb-RH), the posterior part of the superior temporal sulcus (pSTS-RH), the occipital cortex (OC-RH), and the cerebellum (C-RH). *Post hoc* analysis on parameter estimates aimed at investigating the contribution of each kind of gesture to the main effect revealed that, except for the MTG-LH, the OC-LH, and the OC-RH, all of the above regions responded less to meaningless gestures than to emblematic gestures ( $P < 0.001$  in all cases) and to request gestures ( $P < 0.005$  in all cases), without differing from each other ( $P > 0.63$  in all cases). The MTG-LH responded less to emblematic gestures than to request gestures ( $P < 0.001$ ) and to meaningless gestures ( $P < 0.001$ ); request gestures and meaningless gestures did not differ from each other ( $P = 0.96$ ). The OC-LH responded less to emblematic gestures and request gestures than to meaningless gestures ( $P < 0.005$ ); emblematic gestures and request gestures did not differ from each other ( $P = 0.83$ ). The OC-RH responded less to request gestures and to meaningless gestures than to emblematic gestures ( $P < 0.001$  in both cases); request gestures and meaningless gestures differed from each other ( $P < 0.001$ ), with weaker responses to request gestures than to meaningless gestures. The C-RH responded less to meaningless gestures than to emblematic gestures ( $P < 0.001$ )

and request gestures ( $P < 0.005$ ); emblematic gestures and request gestures differed from each other ( $P < 0.05$ ), with weaker responses to request gestures than to emblematic gestures ( $P < 0.05$ ).

#### Neuronal mapping of the main effect of eye contact

No voxels survived the statistical correction; thus, we report on regions surviving the statistical threshold of  $P < 0.001$  uncorrected. Cortical regions sensitive to the main effect of eye contact, regardless of the kind of gesture, are detailed in Table 2. These regions were located in the right hemisphere inferior precentral gyrus and the middle temporal gyrus bilaterally (MTG-LH; right hemisphere middle temporal gyrus). *Post hoc* tests on parameter estimates showed that all of these regions were more strongly activated by the observation of gestures performed with eye contact than by those performed with the actor blindfolded ( $P < 0.001$  in all cases).

#### Neuronal mapping of the interaction term

The gesture  $\times$  eye contact interaction ( $P < 0.001$ , FDR-corrected) identified by ANOVA resulted in the set of clusters of activation detailed in Table S1 and Fig. 3. Clusters were defined as all contiguous activated voxels within 6 mm from the local maxima. These regions were mostly located in the right hemisphere, and encompassed the dorsolateral prefrontal cortex (DLPFC-RH), the pars orbitalis of the inferior frontal gyrus extending to the anterior insular cortex (IFGorb/aIC-RH), the ventral premotor cortex encompassing the inferior frontal gyrus (pars opercularis and pars triangularis) (PMv/IFGope-tri-RH), the pre-SMA, the inferior parietal lobule (IPL-RH), the superior temporal gyrus (STG-RH), the middle/inferior temporal gyrus (MTG/ITG-RH), and the fusiform gyrus (FFG-RH).

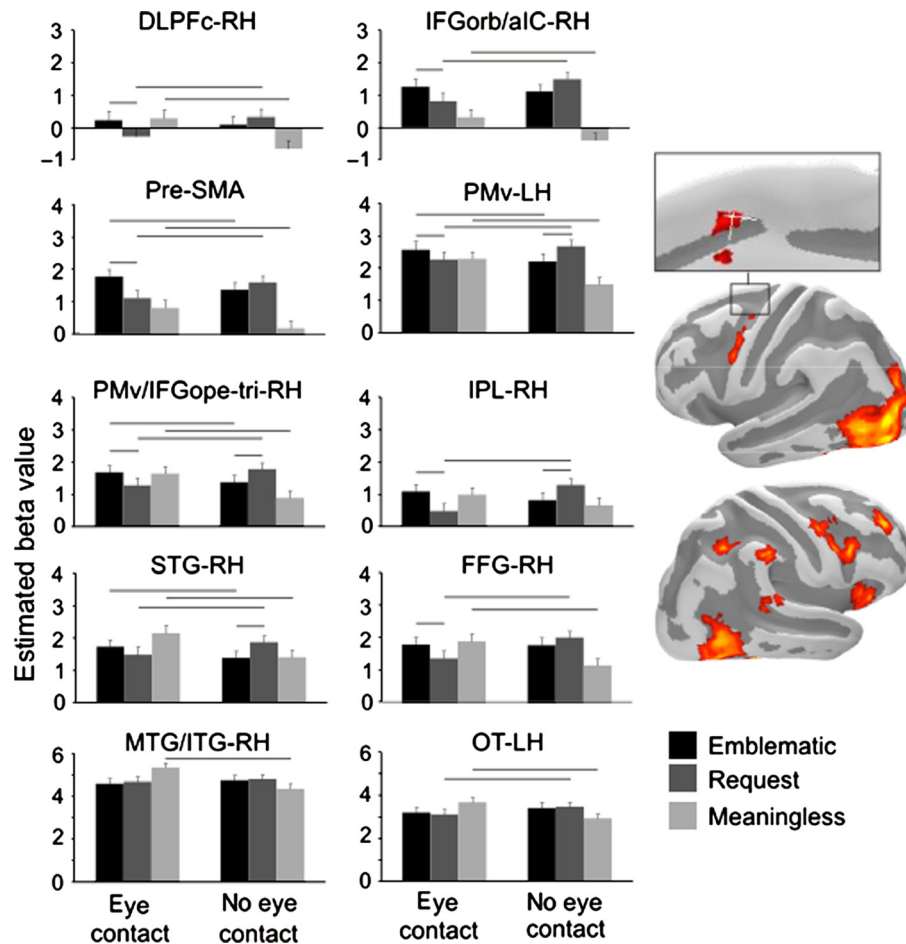


FIG. 3. Cortical regions (and estimated  $\beta$ -values) sensitive to the interaction term. Group activation data are rendered on the cortical surface of a 'canonical' brain (Mazziotta *et al.*, 1995). Error bars indicate standard errors. Horizontal lines indicate  $P < 0.05$ .

In the left hemisphere, cortical regions sensitive to the interaction term included the PMv-LH (area 6) and the occipitotemporal cortex encompassing the fusiform gyrus (OT-LH).

Regarding emblematic gestures, *post hoc* tests on parameter estimates revealed higher neural activation in the ventral premotor cortex bilaterally (PMv/IFGope-tri-RH and PMv-LH), the pre-SMA and the STG-RH during observation of the non-blindfolded actor than during observation of the blindfolded actor (PMv/IFGope-tri-RH,  $P < 0.05$ ; PMv-LH,  $P < 0.001$ ; pre-SMA,  $P < 0.01$ ; STG-RH,  $P < 0.05$ ). No areas showed higher neural activation during observation of the blindfolded actor than during observation of the non-blindfolded actor (Fig. 3).

Regarding request gestures, an opposite pattern of neural activation emerged. Indeed, we found higher neural activation during observation of the blindfolded actor than during observation of the non-blindfolded actor in the ventral premotor cortex bilaterally ( $P < 0.001$  in both cases), the pre-SMA ( $P < 0.001$ ), and the STG-RH ( $P < 0.05$ ). Moreover, the same modulation was found in the DLPFc-RH ( $P < 0.01$ ), the IFGorb/aIC-RH ( $P < 0.001$ ), the IPL-RH ( $P < 0.001$ ), the OT-LH ( $P < 0.01$ ), and the FFG-RH ( $P < 0.001$ ). No areas showed higher neural activation during observation of the non-blindfolded actor than during observation of the blindfolded actor (Fig. 3).

Finally, regarding meaningless gestures, higher activation was observed in all areas ( $P < 0.001$  in all cases) except the IPL-RH ( $P = 0.22$ ) when eye contact was allowed than when it was prevented.

Also, we compared neural activation across communicative (i.e. emblematic and request) gestures during observation of the non-blindfolded and blindfolded actor. Regarding the observation of gestures performed by the non-blindfolded actor, we found higher signals for emblematic gestures than for request gestures in the DLPFc-RH ( $P < 0.05$ ), the IFGorb/aIC-RH ( $P < 0.05$ ), the pre-SMA ( $P < 0.001$ ), the PMv-LH ( $P < 0.01$ ), the PMv/IFGope-tri-RH ( $P < 0.001$ ), the IPL-RH ( $P < 0.001$ ), and the FFG-RH ( $P < 0.001$ ). No areas showed higher activation for request gestures than for emblematic gestures performed by the non-blindfolded actor (Fig. 3). Regarding the observation of gestures performed by the blindfolded actor, an opposite pattern of neuronal activation emerged. Indeed, we found higher signals for request gestures than for emblematic gestures in the PMv-LH ( $P < 0.001$ ), the PMv/IFGope-tri-RH ( $P < 0.001$ ), the IPL-RH ( $P < 0.01$ ), and the STG-RH ( $P < 0.001$ ). No areas showed higher activation for emblematic gestures than for request gestures performed by the blindfolded actor (Fig. 3).

## Discussion

In the present study, we explored the impact of eye contact on the neuronal correlates of two subcategories of communicative gesture, i.e. request and emblematic. The main effect of gesture observation identified a left-lateralized network of brain regions responding more to the observation of both subcategories of communicative gesture,



i.e. emblematic and request gestures, than to meaningless gestures. However, when eye contact was considered as a factor, a right-lateralized network of brain regions showed a different modulation during the observation of emblematic and request gestures.

#### *A left-lateralized pattern of brain activation for communicative gestures*

Previous studies on gesture observation have investigated differences between communicative and other gesture categories, such as transitive (e.g. Montgomery *et al.*, 2007; Villarreal *et al.*, 2008) and expressive (Gallagher & Frith, 2004) gestures. To our knowledge, there have been no previous attempts to investigate differences between subcategories of communicative gestures, as in our case.

We found a network of brain regions responding more to emblematic and request gestures than to meaningless gestures, comprising the IFGop-LH, the IFGtri-LH, the IFGorb/aIC-LH, the PMv-LH (area 6), and the IPL-LH, but also the pre-SMA, the aIC/IFGorb-RH, the pSTS-RH, and the C-RH. The lack of difference that we found between emblematic and request gestures can be explained in terms of features that make them similar. Indeed, both kinds of gesture are communicative, convey social meaning, optionally co-occur with speech, and have some linguistic properties. Accordingly, a comparable pattern of left-lateralized brain activity has been previously described in different fMRI studies that have sought to characterize, although separately, the neural correlates of observing different types of communicative gesture, such as emblematic (e.g. Lindenberg *et al.*, 2012) and request (Gallagher & Frith, 2004) gestures. Villarreal *et al.* (2008) assessed cortical activity during the recognition of communicative gestures containing symbolic connotations (e.g. victory and salute), transitive gestures (i.e. pantomimes of actions involving tool use), and meaningless control movements. Stronger activation for communicative than for transitive gestures was found in the pars opercularis and pars orbitalis of the left inferior frontal gyrus (IFG-LH) and in the dorsolateral prefrontal cortex, bilaterally. The authors argued that the greater engagement of the IFG-LH reflected the symbolic/linguistic nature of intransitive gestures. Similarly, Lindenberg *et al.* (2012) have recently described a widespread bilateral, left-dominant system as a common representation for the imagined expression and reception of emblematic gestures. It included the IPL-LH and clusters in the IFG-LH (pars opercularis, pars triangularis, and pars orbitalis) extending to the ventral premotor and the dorsal premotor cortices. The fact that the left hemisphere is dominant during perception of hand communicative gestures, when either emblems or request gesture are investigated, is generally discussed in light of the left-hemisphere specialization for language. However, an alternative hypothesis has been proposed. Indeed, in order to understand to what degree systems that process symbolic gesture and language overlap, Xu *et al.* (2009) compared the brain responses to emblems and pantomimes with responses elicited by spoken English glosses that conveyed the same information. They found that both classes of stimuli activated a common, left-lateralized network of regions in the dorsal and ventral inferior frontal gyrus and the posterior parts of both the middle temporal gyrus and the superior temporal sulcus. The authors proposed that these areas, far from being committed to language processing, as has long been considered to be the case, play a broader role in human communication by functioning as a modality-independent system that links meaning with symbols. This alternative hypothesis is further corroborated by studies on the integration between gesture and speech perception (e.g., Willems *et al.*, 2007; Dick *et al.*, 2009; Skipper *et al.*, 2009), and is also in line

with the idea that a common control system is implemented in the IFG-LH for gesture and spoken language (Gentilucci & Dalla Volta, 2008; Gentilucci *et al.*, 2008).

All in all, this evidence suggests that emblems and request gestures, as linguistic signs (McNeill, 1992, 2000; Kendon, 2004), share the same representation. However, our results refine this previous knowledge by revealing that this is the case provided that one does not take into account social cues allowing emphasis to be placed on those differences between the representation of emblematic and request gestures that are related to their potential role in orienting and modulating interactions between individuals.

Besides the inferior frontal gyrus (and other language-related regions), additional regions discriminating between communicative (emblematic and request) and meaningless gestures were the pre-SMA and pSTS-RH. These activations are consistent with previous studies (Decety & Grèzes, 1999), so we will not speculate further on their function. What, instead, in our view deserves discussion is the greater activation we found in the MTG-LH during the observation of request and meaningless gestures than during the observation of emblematic gestures. This could be attributable to the dissimilar amounts of effort in retrieving the semantic components of different categories or subcategories of gesture. Middle temporal gyrus activity has been associated with language semantic memory processing (Bartha *et al.*, 2003). Specifically, lower activation of the MTG-LH when emblems are being observed can be explained by the tight binding between speech and gesture (see McNeill, 2005 for details). Evidence of such binding is provided by the observation that information received in a gesture may be recalled later as speech (Cassell *et al.*, 1999). Such information exchange should be stronger for emblems, which are unambiguously associated with well-defined words (e.g. 'ciao' and 'no'), than for requests, for which the association with a sentence is not univocally established to the same extent (e.g. 'give me in the hand' and 'come on'). From this point of view, it is not surprising that more effort is required to grab the verbal meanings of request gestures. This explanation is even more likely to pertain to meaningless gestures. Finally, it has been shown that the midtemporal cortex, as a multimodal node in the anterior ventral stream (Mesulam, 1998), is particularly involved during semantic processing of praxis movements (e.g., Peigneux *et al.*, 2004).

#### *A right-lateralized pattern of brain activations modulated by the different impacts of eye contact on emblematic and request gestures*

A right-lateralized network of brain regions showed different modulations during the observation of emblematic and request gestures, when eye contact was considered as a factor. At first glance, eye contact generally produced stronger activation in response to emblematic gestures, whereas its preclusion resulted in stronger activation in response to request gestures. Moreover, eye contact impacted on more nodes in this network during the observation of requests, than emblematic gestures.

The literature on social cognitive neuroscience assigns to the right hemisphere a possible role in processing information within social contexts (e.g. Sabbagh, 1999; Newman-Norlund *et al.*, 2008; Brancucci *et al.*, 2009; Noordzij *et al.*, 2009). It has been proposed that the right hemisphere, especially the inferior parietal cortex and the prefrontal cortex, plays a dominant role in interpersonal awareness, i.e. the way in which the self is connected to the other (Decety & Sommerville, 2003). Recent advances in the fields of developmental, social and cognitive neuroscience have also indicated the existence of the so-called 'social brain' (Johnson *et al.*, 2005; Adolphs, 2009),



a network of mostly right-lateralized structures specialized in processing social information such as faces (Haxby *et al.*, 2000), gaze (Nummenmaa *et al.*, 2010), and human actions (Pelphrey & Morris, 2006). It is commonly agreed that eye contact modulates the development and activation of this social brain network (Senju & Johnson, 2009).

We will now look in more detail at the different impacts of eye contact on the neuronal underpinnings of emblematic and request gestures.

As far as emblematic gestures are concerned, eye contact produced stronger activation in the pre-SMA, the PMv-LH, the PMv/IFGop-tri-RH and the STG-RH than the condition in which it was prevented. Conversely, regarding request gestures, greater engagement of the same brain regions was observed when contact with the actor's eyes was prevented. On the one hand, these results suggest that, in order to be integrated into the representation of emblematic gestures, information conveyed by the actor's eyes elicits greater recruitment of neural resources. On the other hand, the absence of a clear-cut social context, such as that shaped by eye contact, makes the representation of request gestures more demanding. Indeed, observing request gestures performed by the blindfolded actor elicited stronger activation in the IPL-RH and parts of the right hemisphere inferior frontal gyrus (IFG-RH) than observing request gestures combined with the eye contact. Keeping in mind that request gestures, but not emblematic gestures, are aimed at initiating actual interactions, these data are consistent with previous studies suggesting that the right mirror neuron system (MNS), encompassing the IFG-RH and IPL-RH, is part of a functional network that is more engaged during joint action (Newman-Norlund *et al.*, 2007a) than during imitative actions (Newman-Norlund *et al.*, 2007b) and actions carried out alone (Newman-Norlund *et al.*, 2008). Given the evidence that neural activity in the MNS is related to the extent to which participants are required to produce joint actions (Newman-Norlund *et al.*, 2008), it is not surprising that we found sites in the same system that are more sensitive to the impact of eye contact on request gestures than to the impact of eye contact on emblematic gestures. It is also important to note that only a small part of the left MNS, i.e. the PMv-LH, recruited during the observation of communicative gesture (see the previous paragraph) was found to be also responsive to the specific social cue manipulated in this work.

Besides the engagement of these regions in charge of coding for the motor representation of gestures, the activation of the right IFGorb/aIC-RH probably differences between emblematic and request gestures in the semantic integration of hand-related and eye-related information. Indeed, stronger activation was found while emblematic gestures were being performed by the non-blindfolded actor than while request gestures were being performed. A similar increase occurred during the observation of request gestures performed by the actor with whom eye contact was prevented than during the observation of the same types of gestures performed by the non-blindfolded actor. The modulation of the neural activity in the IFGorb/aIC-RH encompassed area 47, which has previously been assigned a role in semantic processing (Bookheimer, 2002; Hagoort, 2005; Willems *et al.*, 2007). Moreover, among other regions (Ethofer *et al.*, 2011), the anterior insula has been ascribed a role in processing social aspects of human gaze (Kurth *et al.*, 2010). It is already known that human gaze is a critical social cue that can reveal the dispositions, intentions and goals of others (George & Conty, 2008; Itier & Batty, 2009). Thus, the higher activation of the pars orbitalis of the inferior frontal gyrus extending to the anterior insular cortex during the observation of request gestures performed by a blindfolded actor than during the observation of request

gestures performed by the non-blindfolded actor might reflect the ambiguity between the high social value of the observed gesture and the lack of eye contact. Such a hypothesis is supported by the similar modulation of the neural activity found in the DLPFC-RH. It is plausible that the actor's social intention processing in the present study was generally more intense when conveyed by request gestures than when conveyed by emblematic gestures. Indeed, for the fully appreciation of the actor's social intention, only in the former case both information conveyed by the eyes (about his interest for entering an interaction) and information conveyed by hand movement (about the type of interaction itself) were required. Thus, the specificity for request gestures of the eye contact-driven response in the DLPFC-RH would be in agreement with the previous finding that activation in this area is greater when goal processing is more intense (for example, more subgoals are required in order to achieve the final goal; Fincham *et al.*, 2002). Moreover, the greater engagement of the dorsolateral prefrontal cortex for request gestures performed in the absence of eye contact than for those performed in the presence of eye contact may also reflect more difficulty in forming a gestalt representation of meaning (semantic integration). In line with this idea, Kuperberg *et al.* (2008) showed that particularly demanding semantic integrative processes, such as those required to build meaning from linguistic material associated with semantically incongruous contexts, recruit the DLPFC-RH. Considering communicative gestures as linguistic signs (McNeill, 1992, 2000; Kendon, 2004) and eye contact as a necessary condition to delineate a clear-cut social context (Senju & Johnson, 2009), the results of Kuperberg *et al.* (2008) may support the interpretation of our data. The preclusion of eye contact would produce a semantically incongruous and ambiguous context for request gestures, eliciting activity in the DLPFC-RH.

In summary, we propose that gesture observation is modulated by the possibility of accessing the actor's eyes, and that eye contact differentially modulates the neural activity involved in the perception of emblematic and request gestural content. This is because it increases the semantic information load in the former case, whereas it clarifies gestural information in the latter case. For emblematic gestures, eye contact enhances the semantic integration load by conveying information about the actor's mental state or intention. As revealed by our results, this implies higher activity in the premotor cortices and inferior frontal gyrus. In contrast, eye contact facilitates the semantic integration of request gestures into a social context, because it is necessary for building a clear-cut request. In other words, fully appreciating a request gesture first requires the identification of the gesture addressee, and eye contact conveys such information. Thus, as shown by our data, eye contact with the actor performing request gestures reduces the activity in the premotor cortices and inferior frontal gyrus, whereas its preclusion elicits activity in the DLPFC-RH, highlighting the fact that, in this case, the integrative process was particularly demanding (Kuperberg *et al.*, 2008). A different, not necessarily alternative, explanation is that the stronger activation with request gestures performed by the blindfolded actor is attributable to surprise, caused by the presence of conflicting information. This hypothesis is supported by evidence of increased activation in similar frontal regions as an effect of the conflict between the observed action and its associated contextual information (Wurm & Schubotz, 2012).

Consistent with the hypothesis that attention must be paid to information conveyed by the eyes in order to recognize the intention behind request but not emblematic gestures, we observed involvement of the fusiform gyrus and the occipitotemporal cortex only for the former. Brain regions in these cortices have been reported to

selectively respond during the perception of eye gaze, face, and face parts (Kanwisher *et al.*, 1997; Wicker *et al.*, 1998; Harris & Aguirre, 2010; Liu *et al.*, 2010; Pitcher *et al.*, 2011a,b).

An alternative explanation is that the two types of communicative gestures have very different relationships with speech. Request gestures are more ambiguous in their form, are much less conventionalized, and are open to interpretation in the absence of further context (social and/or linguistic). Let us consider, for example, the make-yourself-comfortable gesture. In this case, the palm-up open-hand gestures could be accompanying many different types of statement, such as 'look at that!' or 'there you are!' In the light of this, one could argue that participants had greater difficulty in semantically and pragmatically interpreting the request gestures, and, in order to glean as much from these gestures as possible in the impoverished environment in which they were presented, they clung on to any contextual cues available, i.e. the eye gaze. When this remaining contextual cue was also removed, interpreting the request gestures became particularly difficult and processing effort increased, thus leading to stronger activation in the presence of the blindfold.

In conclusion, eye contact allowed us to unveil differences in the neural correlates of two types of communicative gesture, namely emblematic and request gestures, which had not been previously investigated within a proper social context.

## Supporting Information

Additional supporting information can be found in the online version of this article:

Table S1. Schematic representation of the *post hoc* analysis (Bonferroni test) performed to explain the significant interaction between gesture and eye contact.

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## Abbreviations

aIC/IFGorb-RH, right hemisphere anterior insular cortex encompassing the pars orbitalis of the inferior frontal gyrus; C-RH, right hemisphere cerebellum; DLPFC-RH, right hemisphere dorsolateral prefrontal cortex; FDR, false discovery rate; FFG-RH, right hemisphere fusiform gyrus; FGtri-LH, left hemisphere pars triangularis of the inferior frontal gyrus; fMRI, functional magnetic resonance imaging; IE, inverse efficiency; IFG-LH, left hemisphere inferior frontal gyrus; IFGope-LH, left hemisphere pars opercularis of the inferior frontal gyrus; IFGorb/aIC-LH, left hemisphere pars orbitalis of the inferior frontal gyrus encompassing part of the anterior insular cortex; IFGorb/aIC-RH, right hemisphere pars orbitalis of the inferior frontal gyrus extending to the anterior insular cortex; IFG-RH, right hemisphere inferior frontal gyrus; IPL-LH, left hemisphere inferior parietal lobe; IPL-RH, right hemisphere inferior parietal lobule; MNS, mirror neuron system; MTG/ITG-RH, right hemisphere middle/inferior temporal gyrus; MTG-LH, left hemisphere middle temporal gyrus; OC-LH, left hemisphere occipital cortex; OC-RH, right hemisphere occipital cortex; OT-LH, left hemisphere occipitotemporal cortex encompassing the fusiform gyrus; PMv/IFGope-tri-RH, right hemisphere ventral premotor cortex encompassing the inferior frontal gyrus (pars opercularis and pars triangularis); PMv-LH, left hemisphere ventral premotor cortex; pre-SMA, pre-supplementary motor area; pSTS-RH, right hemisphere posterior part of the superior temporal sulcus; RT, reaction time; STG-RH, right hemisphere superior temporal gyrus.

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