Neuropsychologia 81 (2016) 230–237

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Neural basis of understanding communicative actions: Changes associated with knowing the actor's intention and the meanings of the actions

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ARTICLE INFO

Article history:
Received 8 April 2015
Received in revised form
14 December 2015
Accepted 1 January 2016
Available online 2 January 2016

Keywords:
Action observation
Mirror neuron system
Mirror neurons
Sign language
Communication
Inferior frontal cortex
Inferior parietal lobule

ABSTRACT

People can communicate by using hand actions, e.g., signs. Understanding communicative actions requires that the observer knows that the actor has an intention to communicate and the meanings of the actions. Here, we investigated how this prior knowledge affects processing of observed actions. We used functional MRI to determine changes in action processing when non-signers were told that the observed actions are communicative (i.e., signs) and learned the meanings of half of the actions. Processing of hand actions activated the left and right inferior frontal gyrus (IFG, BA 44 and 45) when the communicative intention of the actor was known, even when the meanings of the actions remained unknown. These regions were not active when the observers did not know about the communicative nature of the hand actions. These findings suggest that the left and right IFG play a role in understanding the intention of the actor, but do not process visuospatial features of the communicative actions. Knowing the meanings of the hand actions further enhanced activity in the anterior part of the IFG (BA 45), the inferior parietal lobule and posterior inferior and middle temporal gyri in the left hemisphere. These left-hemisphere language regions could provide a link between meanings and observed actions. In sum, the findings provide evidence for the segregation of the networks involved in the neural processing of visuospatial features of communicative hand actions and those involved in understanding the actor's intention and the meanings of the actions.

1. Introduction

People communicate with each other using speech and manual movements. Co-speech gestures can be integrated with speech and influence how spoken messages are interpreted (Goldin-Meadow, 1999). Some actions, such as pantomimes and emblems (e.g., "thumbs up", "thumbs down"), can convey meanings independently of speech (Ekman and Friesen, 1969; McNeil, 2005). Also, manual signs can encode meanings in a similar way to spoken words and be used in effective communication among users of signed languages.

The neural basis of manual communication, i.e., how communicative and meaningful hand actions are processed in the human brain, is still poorly understood (for a review, see Andric and Small, 2012). A vast number of studies has investigated processing of another person's goal-directed, but non-communicative, hand actions in the mirror neuron system (MNS, also often called the action observation network). This fronto-parietal system has been suggested to support understanding of the intentions of an actor through motor mirroring (Rizzolatti et al., 2001; Rizzolatti and Sinigaglia, 2010; Iacoboni et al., 2005). The key areas of the human MNS are the ventral premotor cortex, inferior frontal gyrus (IFG) and inferior parietal lobule (IPL). The human MNS is bilaterally organized (Aziz-Zadeh et al., 2006, Molensberghs et al., 2012). The left-lateralized language network partly overlaps the MNS. The key language areas, such as the left IFG and the posterior temporal cortex (posterior middle and inferior temporal gyri, MTG/ITG), are activated by spoken language but also by communicative hand actions that convey meanings (Lui et al., 2008, Xu et al., 2009; Andric et al., 2013). Although it is clear that both the MNS and language areas participate in processing of communicative and meaningful hand actions, the factors that drive their recruitment remain unclear.

Successful communication via hand actions requires (1) that the observer is aware of the communicative intent of the actor (i.e., why the actor performed the actions) and (2) that she/he knows the meanings of the actor's hand movements. Little is known

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http://dx.doi.org/10.1016/j.neuropsychologia.2016.01.002
0028-3932/

about how these two factors that are important for action understanding modulate the neural processing of observed hand actions. Some previous studies have found differences in the neural processing of meaningful and non-meaningful hand actions (Andric et al., 2013; Husain et al., 2012; Decety et al., 1997). It is, however, unclear whether these differences were due to differences in the visuospatial features, familiarity, communicativeness or meaningfulness of the actions. No previous neuroimaging studies have investigated how processing of hand actions changes when their communicative nature or meaningfulness is learned, i.e., when observers "learn to understand actions".

Here, we used fMRI to investigate how neural processing of observed hand actions changes in the MNS and language regions when people (1) learn that the actions are communicative and (2) learn to associate meanings with the actions. In the first scanning session, non-signers viewed videos of bimanual hand actions, but did not know that they were communicative ("pre-training session"). This session was followed by training during which participants were told that these hand actions are signs in British Sign Language (BSL) and were taught to associate meanings with half of them. Then, participants were scanned again while viewing actions, some of which had known meanings and for the remainder the meanings were unknown ("post-training session"). First, this experimental design allowed us to determine the brain regions that are involved in the processing of dynamic visuospatial features of the hand actions. These brain areas should be activated in both pre- and post-training sessions. Second, the experimental design allowed us to determine the brain regions that are recruited for the processing of hand actions when they are known to be signs, i.e., when the actor's intention to communicate is known. These brain regions should be non-active in the pre-training session and actions with both known and unknown meanings should activate these regions in the post-training session. Third, the experimental design allowed us to determine the brain regions that are involved in linking meanings with the actions, i.e., regions that are activated more strongly during observation of known compared to unknown actions in the post-training session.

2. Material and methods

2.1. Participants

17 right-handed non-signers participated in the study. Data from one subject who did not follow task instructions was excluded. The data of 16 participants (6 males, 25–39 years) were included in the analyses. Participants were naïve to the purpose of the study and had no experience with sign language.

2.2. Stimuli

55 videos were used in this experiment, 40 of bimanual hand actions that resembled one-word signs used in BSL, 5 videos of the actor standing still and 10 videos of the actor moving her head or shoulders. All hand actions were bimanual and symmetric, i.e., the left and right hands performed identical mirror movements (see Möttönen et al., 2010). The recorded videos did not include any mouth movements. Aside from this, the recorded hand actions resembled real signs in BSL, although the actor who performed them had no training in sign language. Thus, these hand actions were simplified versions of BSL signs. It was important to use such stimuli in the current study, because we wanted to minimize the likelihood that the participants would guess that the hand actions were communicative (i.e., signs) before training. The meanings of the signs used in the study were nouns (e.g., string, magic, rain, cat, and book) and iconic (i.e., the form of the hand movements was related to their meaning) (see Möttönen et al., 2010). Some videos included a repeated movement. For example, in the sign for "rain" the hands with the fingers splayed move downwards twice. The still videos and those with head or shoulder movements were used in a baseline condition. The 40 videos of hand actions were divided into four sets of 10 actions (A, B, C and D) that were matched for duration. The mean duration of videos was 3.4 s (2.6–4.8 s). An additional 7 videos were used during the practice sessions (outside the scanner).

During functional scans, participants were presented with blocks of videos, each containing 5 hand actions from the same set (A, B, C or D) or 5 baseline videos. Each block of hand actions included 0–2 actions with a double movement, i.e., the same hand/arm movement was repeated in the same location of the space. Each baseline block included 4 still videos and 1 video with a head/shoulder movement, which was either a single movement or a double movement. The participants were asked to detect double movements during all blocks, including action and baseline blocks. The average length of each block was 17.4 s (16.3–18.5 s). Presentation of each block was followed by a fixation cross and the mean length of the fixation cross appearance was 6.6 s (5.6–7.7 s). During each functional scan, 30 blocks were presented (e.g., 10 blocks including videos from set A, 10 blocks including videos from set B and 10 blocks including baseline videos). The order of the blocks was pseudo-randomised.

2.3. Procedure

2.3.1. Task

During all functional scans, participants indicated after each block of 5 videos whether they had seen any double movements or not by pressing the response button with their left or right thumb (counter-balanced across participants). This task was practiced outside the scanner using an additional set of stimuli to confirm that each participant understood the task. The purpose of this task was to direct participants' attention to the features of the hand movements and to reduce the likelihood that the participants would realise that the hand actions are communicative. This task was successfully used in our previous study (Möttönen et al., 2010).

2.3.2. Pre-training session

Before the first scan, participants were told that they would see videos of hand movements and were instructed to focus on detecting repeated i.e. double movements in the videos (see Task). Thus, during the first functional scan, the participants did not know that the hand movements were meaningful signs in BSL. During the pre-training scan, half of the participants were presented with sets A and B and the other half were presented with sets C and D.

2.3.3. Pre-training questionnaire

After the pre-training scan, the participants were taken out of the scanner and told that the presented hand movements were signs in BSL and asked to answer following questions: (1) Did you realise that the hand movements were signs? (2) Did you associate any meanings with the signs?

2.3.4. Training

The participants were trained outside the scanner to associate meanings with half of hand actions they saw in the first session ("Old actions") and half of a new (previously unseen) set of signs ("New actions"). The trained actions were varied across participants so that half of the participants were trained to associate the meanings of sets A and C, and the other half were trained to associate meanings with sets B and D. The experimenter first