

Research report

Premotor cortex in observing erroneous action: an fMRI study

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Abstract

The lateral premotor cortex (PMC) is involved during action observation in monkeys and humans, reflecting a matching process between observed actions and their corresponding motor schemata. In the present study, functional magnetic resonance imaging (fMRI) was used to investigate if paying attention to the two observable action components, objects and movements, modulates premotor activation during the observation of actions. Participants were asked to classify presented movies as showing correct actions, erroneous actions, or senseless movements. Erroneous actions were incorrect either with regard to employed objects, or to performed movements. The experiment yielded two major results: (1) The ventrolateral premotor cortex (vPMC) and the anterior part of the intraparietal sulcus (aIPS) are strongly activated during the observation of actions in humans. Premotor activation was dominantly located within Brodmann Area (BA) 6, and sometimes extended into BA 44. (2) The presentation of object errors and movements errors allowed to disentangle brain activations corresponding to the analysis of movements and objects in observed actions. Left premotor areas were more involved in the analysis of objects, whereas right premotor areas were dominant in the analysis of movements. It is suggested that the analysis of categorical information, like objects, and that of coordinate information, like movements, are pronounced in different hemispheres.

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1. Introduction

How do we recognize others subjects' actions? It is suggested that when we observe actions, their corresponding action schemata are triggered, including a 'goodness-to-fit' evaluation between the observed action and the triggered action schema [44,46]. An action schema can be described on two levels, the goal of an action and its implementation [3], the latter of which can be defined by the actors' movements and involved objects. Since the goal itself is not observable, the triggering of an action schema within the observing subject is necessarily based on at least one of the two observable components of implementation, i.e., objects and movements [7,13,14,25].

Regarding cortical areas that are involved in action

observation, research in humans [9,26] and monkeys [21,38,45] indicates an outstanding role of the PMC. According to Rizzolatti and coworkers [44], in monkeys this cortex is a store of motor schemata. It responds whenever an observed action triggers a stored motor schema, and possibly also when both are subsequently subjected to a matching process. However, it remains unclear if observed objects and observed movements are processed differently within the PMC. The aim of our study was to clarify this question in the human PMC, using whole-brain fMRI.

We set out to dissociate both components of observed actions by manipulating objects and movements respectively. Subjects were scanned while observing actions and action slips, i.e., actions in which the implementation impedes the goal achievement [52]. Two types of action slips were employed. By violating the choice of an object, we realized actions with action-inappropriate objects (*object errors*). By violating a movement, we realized actions

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with action-inappropriate movements (*movement errors*). In clinical research, these two error types are also classified as ‘substitutional action slips’ and ‘qualitative action slips’, respectively [51]. In case that object-related observations and movement-related observations were processed differently within PMC, we expected these two types of errors to yield significantly different premotor activations.

2. Materials and methods

2.1. Participants

Twelve healthy right-handed students (five female and seven male, aged 20–29 years, mean age 23.3) participated in the study. All had normal or corrected-to-normal vision. Participants gave written consent prior to testing. The experimental standards were approved by the local ethics committee of the University of Leipzig.

2.2. Stimuli and procedure

Movies were presented that showed either correct actions, actions characterized by object errors, actions characterized by movement errors, or aimless object manipulations (baseline condition). The stationary camera, filming the actor, was positioned over the actor’s shoulder facing downwards onto the hands. Thus, the participants observed the scenery from the actor’s perspective. The number of presented hands (one or two) and objects (one to three) was balanced between conditions. Each movie lasted 6 s, with 2 s showing a frozen image composed of the movie’s first picture and 4 s showing the movie itself. Frozen pictures were presented in order to allow a first perceptual orientation over the scenery before the proper action observation started. Each trial was preceded by a short visual cue of 1 s that announced the next movie. The inter-stimulus-interval was 7 s. Overall, 36 trials were presented per condition. Trials were presented randomly throughout the session such that successive trials always belonged to different conditions.

2.3. Tasks

In the *correct action* condition, movies showed an action that was performed correctly, such that the intended goal was achieved (Fig. 1 and Table 1). In the *object error* condition, the actors’ hands and several objects were presented, like, e.g., a black shoe, black shoe cream, and brown shoe cream. Instead of using the black shoe cream, the hands chose the context-inappropriate object, i.e., the brown shoe cream, and put some of the brown shoe cream onto the black shoe. In the *movement error* condition, an action was performed, but a movement not appropriate to manipulate the concerned object was made, such as, e.g., holding a coin transversal to the opening of a piggybank.

Accordingly, in both conditions *object error* and *movement error*, the obviously intended goal was not achieved. In the *baseline* condition, an object was chosen and ‘thoughtlessly’ moved. Participants had to classify the observed scenes as ‘correct actions’ (leftmost button), ‘erroneous actions’ (middle button), and ‘movements’ (rightmost button) using a response box. Participants were asked to respond as soon as possible while watching the movie. In case they had not responded until the movies’ end, a question mark appeared, indicating that 2 s were still left to answer. A feedback indicated whether the answer was correct (‘+’), incorrect (‘-’) or missing (‘0’).

2.4. Scanning procedure

Imaging was performed at 3 T on a Bruker Medspec 30/100 system equipped with the standard bird-cage head coil. In order to reduce movements of the head, stabilizing cushions were used. Slices were positioned parallel to the bicommissural plane (AC-PC), with 14 slices (thickness 6 mm, spacing 2 mm) covering the entire brain. Two sets of two-dimensional anatomical images were acquired for each participant immediately prior to the functional experiment, using an MDEFT and an EPI-T1 sequence (256×256 pixel matrix, respectively). Functional images in plane with the anatomical images were acquired using a single-shot gradient EPI sequence (TR=1000 ms, TE=30 ms, 64×64 pixel matrix, flip angle 90°, field of view 192 mm) sensitive to BOLD contrast. One functional run with 2030 time points was measured, with each time point sampling over all 14 slices.

2.5. Data analysis

The fMRI data were processed using the software package LIPSIA [30]. To correct for movements, the images of the fMRI time series were geometrically aligned using a matching metric based on linear correlation. To correct for the temporal offset between the slices acquired in one image, a sinc-interpolation algorithm based on the Nyquist Shannon-Theorem was employed. In the pre-processing, low-frequency signals (frequencies due to global signal changes like respiration) were suppressed by applying a 1/105 Hz highpass filter. The filter length was calculated as 1.5 times the length of one complete oscillation, i.e., maximal interval between two trials of the same experimental condition (1.5×70 s=105 s). Because low frequencies were removed, temporal filtering also effected the signal baseline correction. The increased autocorrelation caused by the filtering was taken into account during statistical evaluation by an adjustment of the degrees of freedom. Spatial smoothing was performed using a Gaussian kernel with a sigma of 0.8.

To align the functional images onto a 3D stereotactic coordinate reference system, a rigid linear registration with six degrees of freedom (3 rotational, 3 translational) was



Fig. 1. Examples of the movies for conditions *correct action*, *object error*, *movement error*, and *baseline*. For each example, one image from the beginning, the middle and the end of the movie is shown from left to right. In *correct action*, an alarm clock is set. In *object error*, brown shoe cream is chosen for the black shoe. In *movement error*, a coin is held transversally to the opening of a piggybank. In *baseline*, a Scotch tape roll is moved 'thoughtlessly'.

performed. The rotational and translational parameters were acquired on the basis of the MDEFT respectively EPI-T1 slices to achieve an optimal match between these slices and the individual 3D reference data set. Furthermore, each individual transformation matrix was scaled to the standard talairach brain size ($x = 135$, $y = 175$, $z = 120$ mm) [53] by linear scaling. Finally, these normalized transformation matrices were applied to the individual functional raw data. Gaps between slices were scaled using a trilinear interpolation, generating output data with a spatial resolution of 3 mm.

The statistical analysis was based on a least squares estimation using the general linear model (GLM) for serially autocorrelated observations [1,20,55,56]. The pre-processed data were globally scaled. Using an epoch-related approach, the design matrix was generated with a boxcar function model and a response delay of 6 s. For

smoothing the design matrix and the data, a Gaussian kernel of dispersion of 4 s FWHM was applied. As the results for trials with correct responses and those with incorrect responses did not differ for neither condition, trials with correct and incorrect responses were collapsed for the analysis. For each condition, the 4 s of the respective movie, excluding the 2 s of the frozen image presentation, were analyzed. In the following, contrast maps, i.e., estimates of the raw-score differences of beta coefficients between specified conditions, were generated for each subject. As the individual functional datasets were all aligned to the same stereotactic reference space, group analyses were subsequently performed. One-sample *t*-tests of contrasts across subjects were computed to indicate whether observed differences between conditions were significantly distinct from zero ($Z \geq 3.09$, uncorrected, random effects model) [27]. In order to allow an exact

Table 1
Description of stimulus material employed in the three experimental conditions and the baseline

| Correct action | Object error (appropriate object, inappropriate object) | Movement error (inappropriate movement) | Baseline |
|----------------------------------|--|--|---|
| fold napkin | set the table (plate, pan) | correct text with white-out (slip off text line) | roll |
| cut apple | stir coffee (teaspoon, table spoon) | open can (not pressing hard enough, can opener not stuck in can) | knife |
| lace shoe | stamp a letter (appropriate size stamp, too big stamp) | punch holes in A4 size paper (set hole puncher to punch holes in A5 size paper) | cup |
| fold laundry | prepay letter (stamp, airmail sticker) | pack suitcase (lay garment on edge of suitcase and close suitcase) | eraser |
| cut piece of paper with scissors | put lid on plastic box (appropriate size lid, too big lid) | stick band-aid on wound (stick partially beside wound) | marker |
| put bookmark in book | put lid on pot (appropriate size lid, too small lid) | tear out page with picture on it from magazine (tear out half the picture) | ruler |
| paint fingernail | insert whisk into left mixer opening (left whisk, right whisk) | clean glasses with cloth (rub fingers on glasses) | hand lotion |
| screw top off bottle | cut bread (appropriate bread knife, too small bread knife) | open letter with a letter opener (slip off so that letter is not opened at its edge) | corkscrew |
| put on gloves | put refill into ball pen (appropriate size refill, too big refill) | assemble jigsaw puzzle (place last piece so it does not fit) | pear |
| fasten with safety pin | put cap on green pen (green cap, red cap) | write text with ballpoint pen (forget to make the ballpoint pen ready to write) | sponge |
| set alarm clock | put on second sock (brown sock, green sock) | put on ring (put on the wrong finger) | calendar |
| unzip backpack | butter slice of bread (slice of bread, piece of cake) | put on wristwatch (put on the wrong way around) | stop watch |
| cut hair | staple a batch of paper (appropriate size stapler, small stapler) | put money in piggybank (hold the coin transverse to the piggybank opening) | vase |
| wipe floor | sweep floor (broom, mop) | mark place on city map (slip off the place to be marked) | passport |
| take cookie out of box | thread a needle (sewing needle, pin) | light a candle (holding flame too far away from wick) | egg cup |
| mix cards | cut fingernails (nail scissors, too big scissors) | put on sandal (entangling toes in slings of shoe) | bandage |
| peel orange | add cocoa to milk (cocoa, coffee) | stick text on noticeboard (text facing the noticeboard — not readable) | sweetener |
| turn on heating | screw a screw (slotted pan-head screw, crossed pan-head screw) | pour water into glass (pour some of the water slightly beside glass) | purse |
| sew by hand | add sugar to coffee (sugar, salt) | put flowers in vase (some flower stems stick out of the vase) | money/ bottle of shampoo magazine/ book |
| open can (cola) | add milk to tea (milk, buttermilk) | open bag of sweets (bag not opened enough so that no sweets can be taken) | glass/bottle of mineral water |
| use sand paper | put frozen food in freezer (ice cream, milk) | switch on a fan (switch pressed not hard enough) | pen/scissors tin/pepper |
| erase text | open bottle of wine (corkscrew, bottle opener) | peel banana (pull upwards instead of downwards) | fountain pen/scissors tin/pepper |
| take butter with knife | put pot of water on stove (water, orange juice) | sweep dirt onto dust pan (sweep beside sweeper) | |
| zip jacket | unlock door (appropriate size key, too big key) | open bottle of beer (slip off) | alarm clock/ CD |
| dry hair | put lotion on hands (hand lotion, hair wax) | cut piece of meat (knife pressed not hard enough to cut meat) | tomato/ carrot |
| close window | screw bulb in mounting (appropriate size bulb, too small bulb) | pick flower (pick only part of the blossom) | dish towel /plate |

Table 1. Continued

| Correct action | Object error (appropriate object, inappropriate object) | Movement error (inappropriate movement) | Baseline |
|------------------------------|---|--|-----------------------------|
| dial telephone number | perfume oneself (perfume, hair spray) | unlock bicycle lock (hold the key transverse to the lock) | pliers/ hammer |
| wash hands | pour coffee in cup (cup, glass) | put on belt (put on belt inside out) | cap/sun glasses |
| clean window | put shoe cream on black shoe (black shoe cream, brown shoe cream) | fax letter (insert sheet of paper asew in the fax machine) | thermos/ teaspoon |
| spray cream next to cake | pack picnic basket (bread, hair dryer) | copy text (lay sheet of paper wrong way around in copy machine) | spirit level/ spatula |
| play dominos | wipe up dirt with cloth (cloth, washrag) | close door (forgetting to press down doorhandle) | stapler/ staple |
| rinse cup | fizzy tablet in glass (fizzy tablet, cap of package) | string beads (letting the beads fall off other end of the string) | elastic band/ sharpener |
| typing on the computer | peel potato (peeler, big knife) | shave leg (holding the shaver upside down) | scarf/ bathing suit |
| wipe tiles | throw coin into cigarette automat (appropriate size coin, too big coin) | play dice with shaker (not closing the opening of the shaker so dice fall out of shaker) | Scotch tape/ paper block |
| pull up blinds | cut flower stem with shears (appropriate size shears, too small shears) | put toothpaste on toothbrush (not pressing hard enough to get toothpaste out of tube) | bookmark/ book |
| drop newspaper in letter box | mix cake mixture (sugar, pepper) | take piece of cake with fork (not pressing hard enough to separate an eatable piece of the cake) | cigarette/ ashtray |

anatomical localization of activation peaks in individual subjects, z -maps were generated for each subject using t statistics.

3. Results

3.1. Behavioral performance

Behavioral performance was assessed by error rates and by reaction times of correct responses. A repeated measures ANOVA with the factor CONDITION (*correct*

action, *object error*, *movement error* and *baseline*) indicated a main effect for error rates ($F(3,33)=14.6$, $P<0.0001$) and reaction times ($F(3,33)=32.44$, $P<0.0001$) (Fig. 2). Single t -tests with a Bonferroni α -level correction revealed that, compared to the classification of correct actions and erroneous actions, the movement classification was significantly easier (*correct action*, $F(1,11)=14.97$, $P<0.003$; *object error*, $F(1,11)=49.67$, $P<0.0001$; *movement error*, $F(1,11)=26.15$, $P<0.0003$) and faster (*correct action*, $F(1,11)=39.39$, $P<0.0001$; *object error*, $F(1,11)=29.73$, $P<0.0002$; *movement error*, $F(1,11)=35.52$, $P<0.0001$). Moreover, classifications of correct

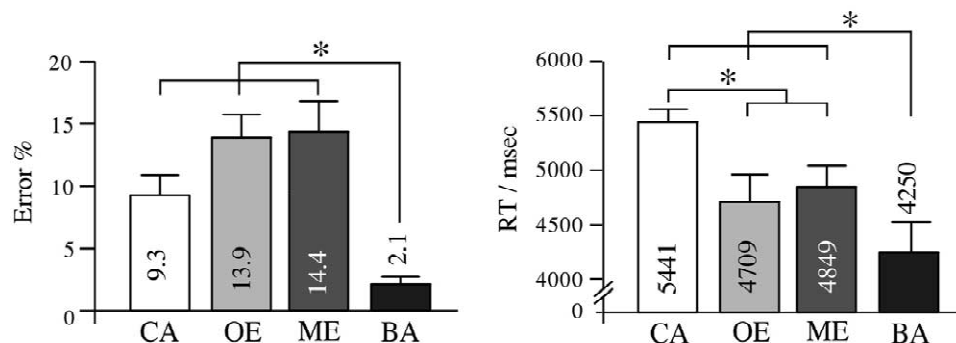


Fig. 2. Behavioral performance. Error rates and reaction times of the correct responses for the four conditions *correct action* (CA), *object error* (OE), *movement error* (ME) and *baseline* (BA).

actions took significantly longer than those of action slips (*object error*, $F(1,11)=26.27$, $P<0.0003$; *movement error*, $F(1,11)=32.67$, $P<0.0001$).

3.2. FMRI data

Several brain areas showed significant activations during the observation of correct actions, actions with object violation, and actions with movement violation. All conditions caused activations within the left vPMC, the frontal eye fields (FEF), the posterior intraparietal sulcus (pIPS), the left pre-supplementary motor area (preSMA), and the motion area (MT), relative to baseline (Table 2 and Fig. 3). Additionally, conditions *correct action* and *movement error* yielded activations within the right vPMC, the supramarginal gyrus (SMG) extending into the aIPS, and the caudal cingulate zone (CCZ).

In order to quantify the hemispheric distribution of activation in *correct action* and *movement error* within (a) the vPMC and (b) the aIPS, spherical regions of interest

(ROIs) were defined bilaterally for the vPMC and the aIPS according to the respective conditions. ROIs were defined as spheres with a radius of 6 mm. Their exact locations were established as follows. A new group z -map was generated which resulted from contrasting the conditions *correct action* and *movement error* against the *baseline*, so that the experimental conditions of interest were represented in one z -map [8]. ROIs were then centered at the local maxima of this z -map within right and left vPMC and aIPS, respectively. Thus, the locations of the ROIs did not differ across conditions or subjects. For all voxels of a ROI, mean contrast values were computed for each contrast and subject. These mean values subsequently entered a repeated measures ANOVA.

This ANOVA with the factor HEMISPHERE (left, right) indicated, firstly, that the vPMC activation was significantly stronger in the right hemisphere than in the left hemisphere for *correct action* and *movement error* (*correct action*, $F(1,11)=24.02$, $P<0.0005$; *movement error*, $F(1,11)=8.04$, $P<0.016$) and, secondly, that the aIPS

Table 2
Baseline contrasts: *Correct action* (CA), *object error* (OE), or *movement error* (ME) versus *baseline* (BA)^a

| Anatomical area | CA-BA | | | | OE-BA | | | | ME-BA | | | | |
|-----------------|-------|-----|-----|----|---------|-----|-----|----|---------|-----|-----|----|---------|
| | | x | y | z | Z-score | x | y | z | Z-score | x | y | z | Z-score |
| vPMC | L | -49 | 0 | 32 | 4.1 | -46 | 6 | 23 | 4.3 | -43 | 0 | 29 | 4.8 |
| | R | 46 | -2 | 32 | 4.9 | -40 | -5 | 38 | 4.3 | 46 | -2 | 32 | 4.6 |
| CCZ | | 1 | 0 | 29 | 4.3 | -4 | 0 | 32 | 3.8 | 4 | 3 | 29 | 4.5 |
| FEF | L | -25 | -8 | 44 | 5.2 | -22 | 3 | 50 | 4.7 | -25 | -8 | 44 | 4.8 |
| | R | 28 | -2 | 53 | 5.1 | 25 | -2 | 47 | 4.2 | 22 | -2 | 47 | 4.7 |
| preSMA | L | -7 | 21 | 53 | 3.6 | -4 | 16 | 55 | 3.9 | -4 | 15 | 55 | 3.5 |
| | R | 10 | 6 | 50 | 4.3 | | | | | | | | |
| MFG | L | | | | | -43 | 27 | 26 | 3.2 | | | | |
| SMG | L | -58 | -26 | 32 | 4.4 | | | | | -58 | -35 | 38 | 4.6 |
| | R | -58 | -38 | 38 | 3.9 | | | | | 58 | -32 | 41 | 3.9 |
| aIPS | R | 40 | -35 | 41 | 4.3 | | | | | 31 | -41 | 41 | 3.5 |
| pIPS | L | -31 | -47 | 47 | 4.4 | -28 | -50 | 47 | 4.8 | -25 | -50 | 47 | 4.5 |
| | R | -16 | -68 | 50 | 4.5 | -19 | -68 | 47 | 5.1 | -25 | -77 | 32 | 5.1 |
| MT | L | 22 | -74 | 38 | 5.0 | 28 | -80 | 41 | 4.4 | 25 | -80 | 41 | 5.2 |
| | R | 22 | -56 | 55 | 5.0 | 22 | -56 | 53 | 4.2 | 10 | -53 | 58 | 5.1 |
| MTG | L | -43 | -68 | 0 | 5.4 | -40 | -68 | 0 | 5.0 | -43 | -65 | 0 | 5.2 |
| | R | 46 | -53 | 0 | 4.2 | 49 | -50 | -3 | 3.6 | 52 | -65 | 8 | 4.8 |
| INS | L | 40 | -65 | 20 | 3.8 | | | | | 40 | -65 | 20 | 4.2 |
| | R | | | | | -25 | 21 | -3 | 4.1 | -28 | 18 | 0 | 4.1 |
| FG | L | -37 | -5 | 17 | 4.1 | -19 | -47 | 0 | 4.9 | -28 | -50 | -3 | 4.4 |
| | R | 37 | -2 | 23 | 4.0 | -19 | -47 | 0 | 4.9 | -28 | -50 | -3 | 4.4 |
| CAU | L | -19 | -47 | 0 | 5.1 | -19 | -47 | 0 | 4.9 | -28 | -50 | -3 | 4.4 |
| | R | 28 | -56 | 0 | 4.0 | 25 | -44 | -5 | 3.6 | 34 | -38 | 0 | 4.1 |
| THA | L | 4 | 9 | 11 | 3.9 | -7 | 6 | 11 | 3.7 | -4 | 3 | 11 | 4.2 |
| | R | | | | | 4 | 6 | 11 | 4.5 | 7 | 9 | 8 | 4.2 |
| | L | | | | | | | | | -4 | -14 | 5 | 4.4 |
| | R | | | | | | | | | 4 | -14 | 5 | 4.2 |

Anatomical areas are abbreviated as follows: aIPS anterior intraparietal sulcus, CAU caudate nucleus, CCZ caudal cingulate zone, FEF frontal eye field, FG fusiform gyrus, MFG middle frontal gyrus, INS insula, MT motion area, MTG middle temporal gyrus, pIPS posterior intraparietal sulcus, preSMA pre-supplementary motor area, SMG supramarginal gyrus, THA thalamus, vPMC ventrolateral premotor cortex.

^a Mean location [56] and Z-score of peak activations from group statistics ($N=12$).

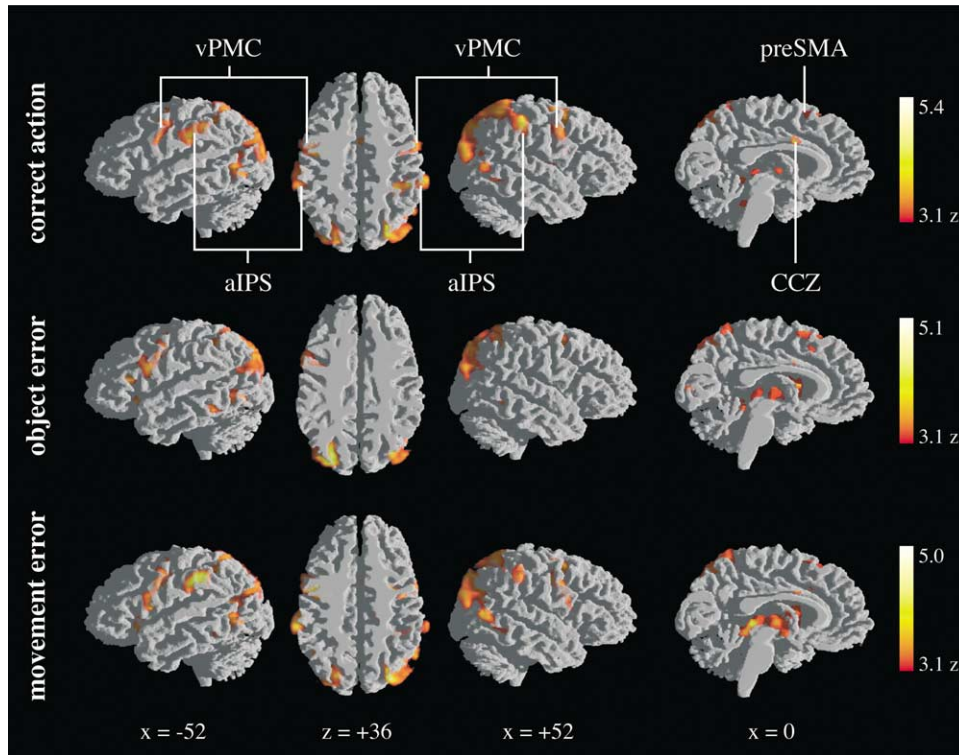


Fig. 3. Brain activations during *correct action* and *object/movement errors*. Group statistics ($N=12$) indicating significant activations during observation of *correct action*, *object error* and *movement error*, relative to the object manipulation baseline were superimposed onto a T1-weighted individual brain. In order to show activations without anatomical distortion, the outermost 3 to 5 mm of the brain were removed using a white matter segmentation. The first column shows the brain from the left side (x -coordinate = -52 [53]), the second column shows the top-view (z -coordinate = $+36$), the third column shows the right side (x -coordinate = $+52$), and the fourth column shows the medial perspective (x -coordinate = 0). Activation was noted in *correct action* and *movement error* bilaterally within the ventrolateral premotor cortex (vPMC), whereas in *object error* activation was noted only within the left vPMC. The bilateral activation of the anterior part of the intraparietal sulcus (aIPS) was noted only in *correct action* and *movement error*.

activation was significantly stronger in the left hemisphere than in the right hemisphere for *movement error* ($F(1,11)=17.84$, $P<0.001$). Accordingly, the ROI analysis yielded a right hemisphere dominance within the vPMC for *correct action* and *movement error*, and a left hemisphere dominance for aIPS activation for *movement error*.

4. Discussion

The present study investigated whether the observable components of action, i.e., employed objects and performed movements, are processed differently within the PMC. To this end, each component was manipulated distinctly in an error detection paradigm. Our findings revealed vPMC activation during the observation of correct actions, and during the observation of both movement-related and object-related violations, relative to baseline. However, conditions *correct action* and *movement error* induced stronger activations within the right vPMC, whereas condition *object error* induced stronger activations within the left vPMC.

Premotor activations during action observation are in line with findings reported in monkeys [21,38] and in

humans [9,13,24–26]. Particularly, the vPMC is reported in studies that investigated the observation of manual actions, as e.g. grasping food [21,22,38], grasping a cup and raising it to the mouth as well as the pantomime of this action [9], opening a bottle presented as a pantomime [13,25], grasping objects with precision grip [24] and manipulating small objects [26].

Premotor involvement in action observation is taken to reflect a system that matches observed actions onto corresponding motor representations [45]. The prerequisite for this matching process is a triggering of the action schema within the premotor cortex that corresponds to the observed action. It has been suggested, that this matching process underlies our ability to recognize observed actions. Moreover, the same matching processes might also underlie the learning of actions by means of imitation.

In the present study, the vPMC was activated within both hemispheres during observation of correct actions and movement errors, and the activation was dominant in the right hemisphere, as evident from the ROI statistics. During observation of object errors, in contrast, the left vPMC was activated exclusively.

Note that Z-scores of group-averaged data in *movement error* (Table 2) did not reflect this effect. However, this

lack of consistence can be explained by the fact that the interindividual spatial variance of local activation maxima was higher within the right PMC (Table 3). Moreover, right hemisphere dominance in movement error was also reflected by individual Z-scores (Table 3).

Thinking about possible explanations for this finding, we propose that the hemispheric lateralization might reflect a bias towards one of two possible levels of information processing, relating to coordinate ('global') and categorical ('local') representations. As proposed by Kosslyn and colleagues [28], categorical representations capture general properties of a stimulus without making commitments to specific properties that are likely to change from instance to instance. This also applies to the observation of *object errors* in the present study, which were determined by the combination of two or more objects inappropriate to achieve an action goal. In contrast, coordinate representations capture locations of a stimulus or parts of it in terms of metric units. This applies to the observation of *movement errors* in the present study, which were determined by the way that an object or tool is moved or manipulated in relation to another. The processing of coordinate and categorical representations have been suggested to be lateralized, i.e., within right-handers, coordinate representations are processed dominantly within the right hemisphere, whereas categorical representations are processed dominantly within the left hemisphere [28]. This

has been indicated by a number of clinical and experimental studies [15,28,40,54]. In line with these findings, event-related potential studies and imaging studies have revealed lateralized activation patterns based on coordinate and categorical processing of information, using, e.g., compound letter stimuli [17,42] or visuospatial polygon patterns [32].

Along with these findings, we suggest that left hemisphere dominance in the *object error* condition could reflect the processing of categorical representations, and right hemisphere dominance in the *movement error* condition the processing of coordinate representations, respectively.

Like *movement errors*, however, the *correct action* condition also revealed dominantly right hemisphere activation. This could be due to the fact that both conditions were rather similar in that both required to monitor the entire sequence of movements performed on an object in order to decide whether the action was correctly performed until the end of the movie. In order to test this hypothesis, a post-hoc behavioral study was conducted. Sixteen subjects had to classify trials showing *correct actions*, *object errors* and *movement errors* in a speeded choice paradigm, i.e., the answer was required during the movie presentation. As a result, both the classification of correct actions (2630 ms) and that of movement errors (2677 ms) took significantly longer than the classification of object

Table 3
Baseline contrasts: *Correct action (CA)*, *object error (OE)*, or *movement error (ME)* versus *baseline (BA)*^a

| Subject | CA-BA | | | | | OE-BA | | | | | ME-BA | | | | | |
|---------|-------|-----|----|----|---------|-------|-----|----|----|---------|-------|-----|----|----|---------|------|
| | | x | y | z | Z-score | BA | x | y | z | Z-score | BA | x | y | z | Z-score | BA |
| 1 | L | -41 | 2 | 21 | 5.2 | 6 | -44 | 2 | 21 | 7.4 | 6 | -47 | 2 | 24 | 4.6 | 6 |
| | R | 43 | 7 | 20 | 5.1 | 6 | 46 | 10 | 19 | 4.0 | 6 | 43 | 8 | 23 | 5.5 | 6/44 |
| 2 | L | -47 | 6 | 22 | 5.6 | 6 | -47 | 10 | 24 | 5.1 | 6 | -44 | 8 | 16 | 5.2 | 6 |
| | R | 46 | 3 | 20 | 6.2 | 6 | 46 | 3 | 23 | 3.7 | 6 | 46 | 3 | 20 | 6.6 | 6 |
| 3 | L | -47 | 10 | 28 | 7.7 | 6 | -47 | 13 | 27 | 8.3 | 6 | -47 | 10 | 28 | 7.0 | 6 |
| | R | 49 | 13 | 27 | 8.1 | 6 | 46 | 11 | 23 | 6.6 | 6/44 | 49 | 13 | 27 | 7.3 | 6 |
| 4 | L | -53 | 5 | 29 | 4.9 | 6 | -41 | 6 | 20 | 5.7 | 6 | -47 | 8 | 31 | 5.8 | 6 |
| | R | 52 | 4 | 26 | 7.3 | 6 | 49 | 5 | 29 | 4.4 | 6 | 52 | 4 | 26 | 7.0 | 6 |
| 5 | L | -38 | 13 | 10 | 4.0 | 44 | -38 | 19 | 23 | 4.7 | 44 | -41 | 12 | 7 | 3.5 | 44 |
| | R | 49 | 10 | 11 | 4.3 | 6 | 46 | 18 | 20 | 3.8 | 44 | 43 | 7 | 11 | 4.4 | 6 |
| 6 | L | -44 | 3 | 33 | 7.6 | 6 | -41 | 1 | 25 | 5.6 | 6 | -41 | 1 | 27 | 5.8 | 6 |
| | R | 49 | 7 | 23 | 6.2 | 6 | 43 | 0 | 22 | 2.3* | 6 | 55 | 12 | 19 | 5.8 | 6 |
| 7 | L | -62 | 4 | 21 | 4.5 | 6 | -53 | 5 | 24 | 6.1 | 6 | -59 | 1 | 22 | 5.8 | 6 |
| | R | 52 | 5 | 24 | 4.3 | 6 | 37 | 4 | 21 | 2.3* | 6 | 49 | 0 | 19 | 4.8 | 6 |
| 8 | L | -50 | 4 | 15 | 4.6 | 6 | -53 | 6 | 13 | 4.0 | 6/44 | -50 | 3 | 12 | 5.6 | 6 |
| | R | 52 | 2 | 21 | 5.9 | 6 | 55 | 8 | 8 | 2.7* | 44 | 52 | 5 | 21 | 6.4 | 6 |
| 9 | L | -46 | 0 | 39 | 5.5 | 6 | -35 | 4 | 24 | 4.9 | 6/44 | -47 | 3 | 21 | 5.1 | 6 |
| | R | 43 | 1 | 24 | 5.6 | 6 | 34 | -1 | 25 | 4.0 | 6 | 46 | 0 | 22 | 7.5 | 6 |
| 10 | L | -47 | 2 | 30 | 6.8 | 6 | -44 | 4 | 23 | 8.1 | 6 | -47 | 2 | 30 | 8.1 | 6 |
| | R | 49 | 2 | 30 | 7.7 | 6 | 43 | -1 | 25 | 6.3 | 6 | 49 | 2 | 30 | 5.9 | 6 |
| 11 | L | -50 | 5 | 27 | 4.4 | 6 | -47 | 5 | 27 | 5.7 | 6 | -47 | 3 | 18 | 4.8 | 6/44 |
| | R | 49 | 0 | 13 | 6.7 | 6 | 43 | 0 | 19 | 6.3 | 6 | 46 | 0 | 16 | 5.1 | 6 |
| 12 | L | -44 | 13 | 25 | 4.2 | 6 | -38 | 12 | 23 | 6.6 | 6 | -44 | 13 | 25 | 4.7 | 6 |
| | R | 46 | 13 | 25 | 5.4 | 6 | 31 | 12 | 23 | 5.3 | 6/44 | 40 | 5 | 21 | 5.3 | 6 |

* Non-significant Z-score.

^a Mean location [56] and Z-score of peak activations within the premotor cortex (including the corresponding Brodmann area, BA) of individual subjects.

errors (2240 ms) (*correct action*, $F(1,15)=17.72$, $P<0.0008$; *movement error*, $F(1,15)=46.53$, $P<0.0001$). We take this result to indicate that participants tended to reassure precisely that correct actions did not contain any deviant movement.

A slightly different explanation comes from imaging studies that reveal exclusively left PMC involvement [11,36] and dominantly left PMC involvement [48] during presentation of objects. Accordingly, a left hemisphere preference for objects could be the cause for the left premotor dominance in observation of *object errors* in the present study. This could be taken to reflect that when attention was attracted by the erroneously chosen object, action schemata related to this inappropriate object could have been triggered in addition to that triggered by the appropriate object. Hence, one would expect an increase of activation within the areas that prepare and represent action schemata of the hand that manipulates the inappropriate object, i.e., the left PMC, as corresponding to the right hand.

A further alternative explanation of the hemisphere effect is that the initial analysis of the observed action is made by the left hemisphere, whereas a more detailed analysis of movements is carried out by the right hemisphere [25]. As the initial analysis of the observed action is sufficient to classify object errors, a left hemisphere dominance would be expected. In contrast, for correct actions and movement errors a detailed analysis of movements has to be made additionally, leading to a right hemisphere involvement. According to this view, if the initial action analysis precedes detailed movement analysis, the effect in question could be due to a different responsiveness of left and right hemisphere to early versus late segments of observed actions. To test this, a post-hoc analysis was carried out. The early phase of action observation was contrasted with the late phase for each single condition. As a result, no significant activation differences were found within the PMC between early and late action analysis. Likewise, baseline contrasts, computed separately over the early phase and the late phase of movie presentation each, revealed the same patterns of activation as the analysis of the entire presentation phase. Therefore, both analyses did not support the notion of a preferred responsiveness of the left hemisphere to early segments of actions, and of the right hemisphere to late segments of action, respectively. In contrast, we propose that categorical and coordinate information processing underlies different involvement of the left and the right hemisphere.

In monkeys, the cortical area suggested to realize a matching system for action observation and action execution is area F5 [45]. It has been suggested that the human homologue is located within BA 44 in the frontal opercular cortex (FOP). This suggestion was based on functional, anatomical, and cytoarchitectonic findings concerning both cortical areas [39,41,43]. In contrast, premotor activations in the present study were focused within the ventrolateral

part of the premotor cortex in BA 6. Based on the present findings and other imaging studies [9,24], it could be suggested that activation within ventral BA 6 during observation of hand actions corresponds to that found in monkey area F5. However, BA 44 and BA 6 are not only closely adjacent areas, but also expose a high interindividual variance. Accordingly, it is difficult to straightforwardly ascribe group averaged activations to one of these areas.

Therefore, we determined the anatomical location of ventral premotor activation within each single subject for the baseline contrasts of *correct action*, *object error*, and *movement error* (Table 3 and Fig. 4). Within the left hemisphere, ventrolateral premotor activation was located in BA 6 within 11 subjects for *correct action*, but only within 1 subject in BA 44. For *object error*, 9 subjects showed activation in BA 6, 2 subjects in BA 6/44, and 1 subject in BA 44. Finally, for *movement error*, 10 subjects revealed activations in BA 6, 1 subject in BA 6/44, and 1 subject in BA 44. If we take the inferior precentral sulcus as a landmark separating BA 6 and BA 44, our findings indicate that ventrolateral premotor activation was dominantly in BA 6 rather than in BA 44. Generally, it has been mentioned that it is difficult to separate Brodmann Areas from each other on the basis of anatomical landmarks, because cytoarchitectonically distinct areas can sometimes transverse anatomical structures [2]. However, the inferior precentral sulcus appears to be a rather reliable border between BA 6 and BA 44, as opposed to other anatomical landmarks, such as e.g. the ramus ascendens separating BA 44 and BA 45 [2]. Moreover, our single subject analysis demonstrates that ventrolateral premotor activation during action observation was dominantly located within the ventral precentral gyrus. Interindividual and intraindividual (condition-related) variation of premotor activation location was surprisingly small. Together, our findings indicate that during the observation of actions, not Broca's area (BA 44), but rather ventral BA 6 is dominantly involved.

However, one may object that, for determining the anatomical location of premotor activations, the movement baseline was subtracted from the experimental conditions. However, since both the baseline as well as the experimental conditions presented *proximal* and *distal* movements (reaching and manipulation), subtraction should not have biased activation in favor of either type of movement. This is important because distal movements have been suggested to be represented more anteriorly/inferiorly than proximal movements in monkey BA 6 [23].

From a broader perspective, there are two functional interpretations concerning BA 6 and BA 44, that might be interesting to consider here. Firstly, there is evidence that the perceptual analysis of dynamic object patterns involves BA 6 [48,50]. Accordingly, the *analysis* of both observed actions and observed dynamic object patterns might involve a common cognitive process reflected by BA 6 activation. This could be the prediction of the expected

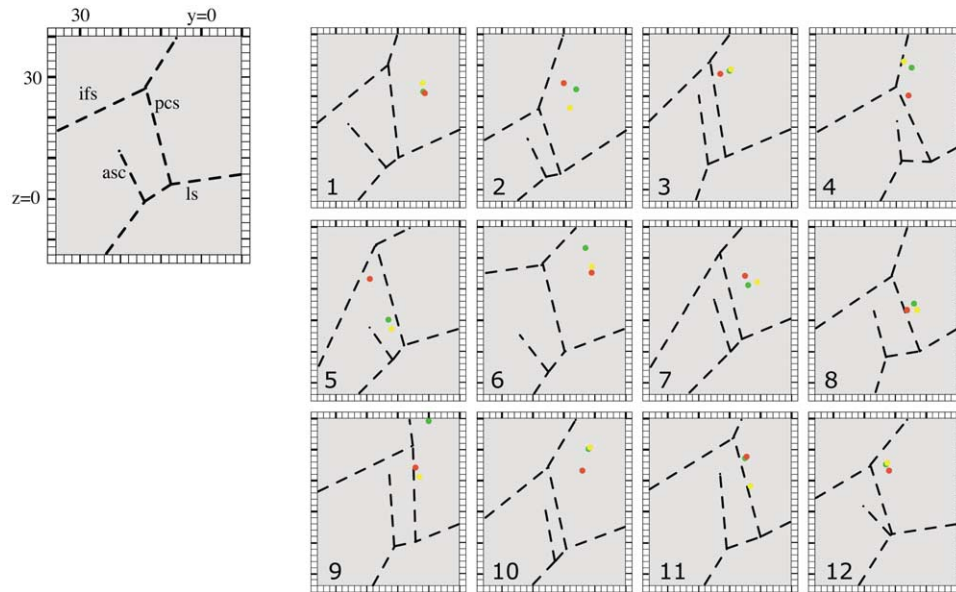


Fig. 4. Mean location [53] of peak activations within the left ventrolateral premotor cortex (vPMC) of individual subjects for all baseline contrasts. Dot colors correspond to conditions: *correct action* (green), *object error* (yellow) and *movement error* (red), respectively.

course of movements caused by both non-living and living entities. Both BA 6 and BA 44 have been reported to be involved in the detection of violation in expected events. Thus, several studies indicate that BA 44 is activated when syntax errors are detected in perceived language [10,12,19,37]. Likewise, fMRI studies report BA 6 to be activated when sequential errors are detected in target motion [48–50]. From that one may suggest that the cortical region around BA 6 and BA 44 is crucial in the detection of structure violations.

An area comprising the aIPS and SMG was activated bilaterally, relative to baseline. The activation extended from the SMG into the aIPS with a local maximum within the SMG, and did not show hemispheric lateralization. Both regions, the aIPS [4–6] and the SMG [7,24,29] have been discussed as possible human functional homologues of the AIP/PF-area in the monkey. This area is closely linked with the vPMC both anatomically and functionally [31,33,34], especially with regard to sensorimotor mapping functions [16,22]. Particularly, both monkey PF [18,22] and human SMG [7,9,24] were reported to be involved during action observation, whereas both monkey AIP [47] and human aIPS [4–6] were suggested for grasping and tactile exploration of objects. These areas are taken to be involved within two parallel premotor-parietal circuits relevant for action, the one suggested to match observed actions onto motor representations, the other involved in solving object affordances.

Therefore, even though the parietal activation we found did not clearly separated into two distinct activation foci, one might suggest them to reflect different functional subprocesses. Accordingly, activation within SMG might be caused by an object-related analysis during action

observation, whereas aIPS activation might be related to object affordances themselves.

This interpretation would also be in line with the finding that the activation was bilateral, since bimanual actions were presented. Moreover, in contrast to *correct action*, the observation of *movement error* yielded a statistically significant activation bias towards the left hemisphere. This might indicate that the finger movements of the right hand were analyzed more intensively in this condition, as the movement error occurred in this hand, and thus, attention was focused on the dominant hand. Accordingly, a direct correspondence between the amount of attention paid to the analysis of finger movements concerning one specific hand might be reflected by a lateralized aIPS activation. This would comply with the fact that the parietal cortex exhibits contralateral dominant connections concerning effectors similar to the PMC [4,35].

With regard to the aIPS role in observed actions and its interpretation, conflicting findings have been made. In a study by Bonda and coworkers [7] aIPS activation reflected the observation of manual actions as compared to body motions. Both conditions were realized by a light point display. This implicates that it is not necessary to observe an actual object employed in the action. In contrast, observing a pantomime of an action did not elicit an aIPS activation in a study by Buccino and co-worker [9]. The authors, therefore, suggested that an actual object has to be present in an observed action to evoke aIPS activation. In the present study, we presented real objects employed in manual actions. However, objects were also presented in the baseline and were unintentionally moved by hands. Therefore, our results suggest that aIPS gets involved not due to actual object presentation or a move-

ment directed towards an object, but rather due to goal-directed object-related movements, i.e., movements in the context of an action.

5. Conclusion

The present findings support the view that the vPMC (BA 6) and its parietal input zone are crucial for the observation of actions in humans. Moreover, we demonstrated that by attracting attention to either objects or to movements in action observation it is possible to examine how different components of this premotor-parietal network within each hemisphere contribute to action analysis.

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