

Posterior Parietal Cortex Activity Reflects the Significance of Others' Actions During Natural Viewing

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Abstract: The posterior parietal cortex (PPC) has been associated with multiple stimulus-driven (e.g., processing stimulus movements, providing visual signals for the motor system), goal-directed (e.g., directing visual attention to a target, processing behavioral priority of intentions), and action-related functions in previous studies with non-naturalistic paradigms. Here, we examined how these functions reflect PPC activity during natural viewing. Fourteen healthy volunteers watched a re-edited movie during functional magnetic resonance imaging (fMRI). Participants separately annotated behavioral priority (accounting for percepts, thoughts, and emotions) they had experienced during movie episodes. Movements in the movie were quantified with computer vision and eye movements were recorded from a separate group of subjects. Our results show that while overlapping dorsomedial PPC areas respond to episodes with multiple types of stimulus content, ventrolateral PPC areas exhibit enhanced activity when viewing goal-directed human hand actions. Furthermore, PPC activity related to viewing goal-directed human hand actions was more accurately explained by behavioral priority than by movements of the stimulus or eye movements. Taken together, our results suggest that PPC participates in perception of goal-directed human hand actions, supporting the view that PPC has a special role in providing visual signals for the motor system (“how”), in addition to processing visual spatial movements (“where”). *Hum Brain Mapp* 35:4767–4776, 2014. © 2014 Wiley Periodicals, Inc.

Key words: behavioral priority; fMRI; human parietal cortex; vision for action; spatial processing

Contract grant sponsor: aivoAALTO project, Aalto University;
Contract grant sponsor: Academy of Finland; Contract grant number: 138145

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Received for publication 23 May 2012; Revised 31 December 2013;
Accepted 17 March 2014.

DOI 10.1002/hbm.22510

Published online 5 April 2014 in Wiley Online Library
(wileyonlinelibrary.com).

INTRODUCTION

The posterior parietal cortex (PPC) is well positioned between sensory and motor areas to integrate sensory-motor signals and generate intentional goal-directed behavior [Bisley and Goldberg, 2010]. Visual spatial information is conveyed to PPC via the dorsal visual stream [see, Ungerleider and Mishkin, 1982] and PPC contains, for example, neurons that carry information about spatial loci and movements of stimuli [Bisley and Goldberg, 2010; Rizzolatti and Matelli, 2003; Robinson et al., 1978]. Previous studies have further demonstrated spatial processing deficits in patients with PPC dysfunction [Vallar et al., 2007], enhanced PPC activity when participants view moving stimuli [Silver and Kastner, 2009], and when focus of attention is directed from one location to another [Corbetta and Shulman, 2002; Salmi et al., 2007].

While the spatial processing (i.e., “where”) theory [Ungerleider and Mishkin, 1982; see also Kravitz et al., 2011] explains PPC function rather well, motor signals have been observed to additionally modulate PPC activity [Goodale and Milner, 1992; see also Perenin and Vighetto, 1988], giving rise to the so-called “how” theory of PPC function that emphasizes the role of PPC in merging visual with motor information. PPC has also been shown to respond both to visual stimulus and related motor action, suggesting that the PPC is a part of the so-called “mirror-neuron” system [Culham and Valeyar, 2006; Fabbri-Destro and Rizzolatti, 2008]. Mirror neurons are single nerve cells that increase their firing both when visually observing actions and when performing the corresponding actions [Nishitani et al., 1999; Rizzolatti et al., 1996] and have been suggested to play a major role in, for example, eye-hand coordination, imitation and understanding of others’ actions [Iacoboni and Dapretto, 2006]. In neurophysiological studies, dorsal PPC areas have been reported to be involved in visuo-motor transformations and ventral PPC areas have been observed to code specific motor actions such as movements of the arms, hands, face, and eyes [Fogassi and Luppino, 2005]. There are also studies suggesting that the left PPC is involved in motor processing and the right PPC in visuospatial processing [Rushworth et al., 2003]. The most notable difference between the “where” and “how” theories is that, unlike the latter, the “where” theory does not make predictions about effects of stimulus content/task beyond the information about spatial location.

Previous studies have mainly used non-naturalistic paradigms with repetitive stimulus presentation to test one or two hypotheses at a time. The ecological validity (i.e., the degree to which the stimuli and task approximate the real-world phenomenon that is being studied) of the previous studies can also be questioned, as there is accumulating evidence suggesting that paradigms using simplified tasks and stimuli are limited in describing brain function even in lower-level sensory areas [Carandini et al., 2005; David et al., 2004, 2009; see also Hasson et al.,

2010]. In higher-level associative areas such as PPC, this problem might be accentuated given that neurons receive larger number of, and more distributed, inputs (for a demonstration of heterogeneous nature of PPC neurons) [see Premereur et al., 2011]. Since PPC might be involved in multiple functions, and findings from previous studies may be difficult to generalize to more naturalistic conditions, it is important to study the relative sensitivity of PPC to each of the putative PPC functions in naturalistic stimulus conditions.

Over the last few years, there has been an emergence of human brain imaging studies with naturalistic stimuli and tasks [Bartels and Zeki, 2005; Carandini et al., 2005; Hasson et al., 2004, 2010; Jääskeläinen et al., 2008; Lahnakoski et al., 2012; Malinen et al., 2007; Nummenmaa et al., 2012; Salmi et al., 2013; Ylipaavalniemi et al., 2009]. These studies have demonstrated that human brain activity elicited by movies is highly replicable across subjects [Hasson et al., 2004; for a review see Hasson et al., 2010] and, further, that brain activity can be associated with stimulus features or subjective experiences contained in the movies [Bartels and Zeki, 2004, 2005; Hasson et al., 2004; Lahnakoski et al., 2012; Malinen et al., 2007; Nummenmaa et al., 2012; Ylipaavalniemi et al., 2009]. As an example, Hasson et al. [2004] showed that peaks in the across-subjects averaged mid-postcentral sulcus activity co-occurred with seeing film characters use their hands to perform various motor tasks. Further, Bartels and Zeki [2004] observed PPC activity in the superior parietal lobule/intraparietal sulcus (SPL/IPS) during movie episodes that included human bodies, and Bartels et al. [2008] demonstrated that specific PPC regions are associated with variations in local and global motion in a movie. Finally, Nummenmaa et al. [2012] reported that activity in PPC was modulated by subjectively experienced arousal during observation of emotional video clips.

Since human hand actions [Culham and Valeyar, 2006], other stimulus movements [Silver and Kastner, 2009], viewer’s intentions [Bisley and Goldberg, 2010; Corbetta and Shulman, 2002], eye movements [Goldberg et al., 2006], and relative size of the stimulus [Cavina-Pratesi et al., 2007], each modulate PPC activity and are often interdependent, characterization of the relative sensitivity of PPC to different functions during natural viewing requires detailed modeling of the stimulus as well as recording of the viewers’ subjective experiences and eye movements. Tentatively, a study combining these factors could significantly increase understanding of the role of PPC in real-life conditions.

Here, we collected 3-Tesla functional magnetic resonance imaging (fMRI) data while 14 healthy participants freely watched a re-edited feature movie (see Materials and Methods). To segregate between putative PPC functions, we modeled stimulus content, magnitude of stimulus movement, relative stimulus size, viewers’ eye movements, and their subjectively experienced behavioral priority (see Fig. 1). Extraction of these features allowed us

to simultaneously test several alternative hypotheses about the role of PPC in natural vision. We hypothesized that if PPC activity is characterized by the extent of spatial movements, as predicted by the “where” theory, a significant increase in PPC activity is observed during episodes containing any type of spatial movements (i.e., during all annotated stimulus categories) and that this activity is dependent on the magnitude of the stimulus and/or eye movements. Alternatively, we hypothesized that if the “how” theory characterizes PPC function better than the “where” theory, PPC activity is enhanced especially during episodes containing human hand actions (i.e., using hands in goal-directed behavior). Furthermore, we

hypothesized that if PPC represents “a priority map of intentions” rather than stimulus movements or related gaze patterns [Bisley and Goldberg, 2010], PPC activity is explained by subjectively experienced behavioral priority better than by stimulus features or eye movements. Hence, our design enabled us to test the relative sensitivity of PPC to different types of stimulus contents, as well as stimulus-driven vs. intentional processes, under natural viewing conditions.

MATERIALS AND METHODS

Participants

Sixteen healthy volunteers (3 females; 2 left handed; age 22–43 years, and mean 28 years) with neither hearing impairments, nor neurological or psychiatric history, and with normal vision participated in the experiment. Two of the participants were not included in the final data analyses, as one of them felt drowsy during the experiment, and the other had movement related spikes in the BOLD signal. Of the 14 included subjects, 12 completed behavioral priority annotation. Eye movements were collected from 11 additional healthy subjects (right handed men, age 20–47 years, and mean 29 years) in a separate session. All participants gave a written informed consent prior to participation in accordance with the Ethical Committee of Hospital District of Helsinki and Uusimaa.

Stimulus and Experimental Procedure

For the purposes of this fMRI study, a Finnish movie “The Match Factory Girl” edited by Aki Kaurismäki, 1990 was re-edited by a film director and coauthor (PT). The main storyline and individual scenes were left untouched while several supportive scenes were removed. The stimulus

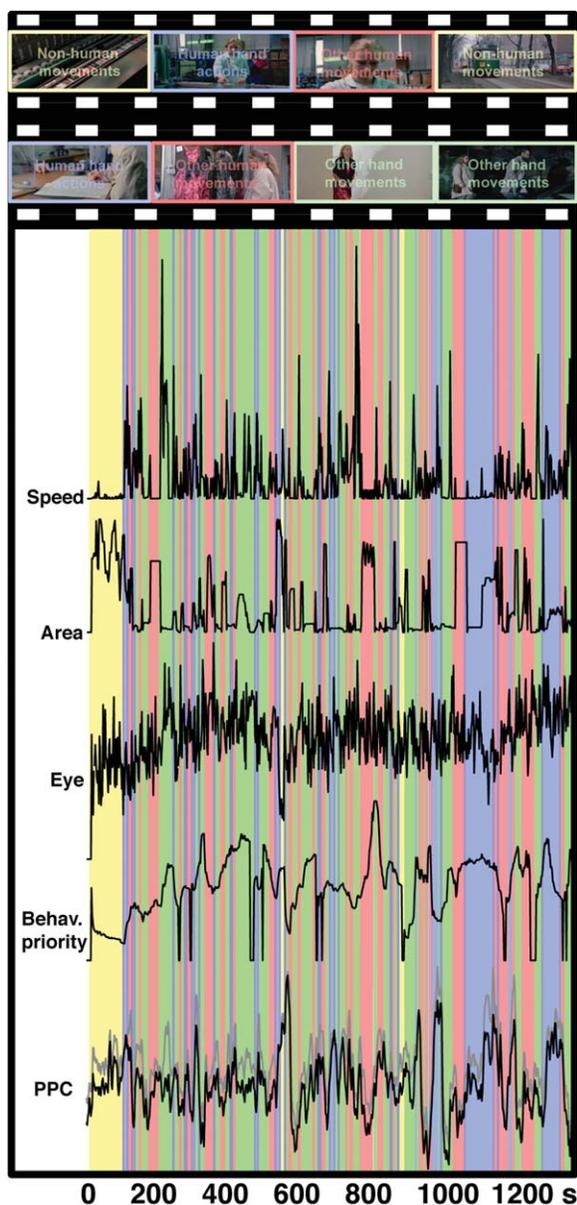


Figure 1.

In this study, we examined how alternative theories explain PPC activity during natural viewing. Multiple types of stimulus contents were annotated from a narrative film that was shown to 14 participants during functional magnetic resonance imaging (fMRI). Examples from each stimulus content category are shown on top of the figure. Colored (yellow, blue, red, and light green) columns at the bottom part of the figure indicate the presence of these stimulus content categories during the movie. Furthermore, fMRI signal was modeled with stimulus object movement (Speed), relative stimulus object size (Area), eye movements (Eye), and subjectively evaluated relative importance of the scene (Behav. priority). The time courses of these dynamic features are plotted with the black lines in the bottom part of the figure. The time courses at the very bottom depicts the average PPC activity across all subjects (black line = the activity in right PPC; gray line = the activity in left PPC). (Reproduced with permission from Aki Kaurismäki, “The Match Factory Girl,” 1990, © Sputnik Oy. All Rights Reserved.)

material involved social interaction between two or more people, music, environmental sounds, views from a scenery, and other typical real-life events. The re-edited version of the film shown during fMRI included 376 s of human hand actions (e.g., peeling an orange, brushing hair, opening a box or a letter, grasping objects, placing objects, manipulating objects), 502 s of other human hand movements not involved in goal-directed behavior (e.g., associated with walking or dancing), 292 s of other types of human movements (e.g., close-ups from the head or upper body), and 114 s of non-human movements (e.g., machine movement related to match assortment, placing, or moving of objects, a moving car or a tram, see Fig. 1); 46 s of the scenes did not contain any local movement (still images of buildings) and 60 s of the contained global movements (camera movement). Due to varying amount of trials in each condition, we used relative signal changes rather than direct comparisons of the model parameter estimates when making comparisons between episodes with different types of contents (see Fig. 3).

The subjects watched the movie in the scanner for 23 min (duration of the original movie is 68 min). They were instructed to watch the movie as they normally would, but without moving their head. The movie was projected on a semitransparent screen behind the participant's head using a 3-micromirror data projector (Christie X3, Christie Digital Systems, Mönchengladbach, Germany). The distance to the screen was 34 cm via a mirror located above their eyes (visual angle 12°, binocular view width 24 cm). The audio track of the movie was played to the subjects with an UNIDES ADU2a audio system (Unides Design, Helsinki, Finland) via plastic tubes through porous EAR-tip (Ety-motic Research, ER3, IL) earplugs.

Annotation of the Local Movements

Local stimulus/perceptual object movements were annotated with an in-house developed computer vision tool. In this tool, tracked objects are first manually identified. In the algorithm the images are first Gabor-filtered to create an edge and boundary representation. This template is then matched with the Gabor-response of the next frame to find the new location of the tracked object. The output of the tracking includes exact timing, spatial position, height, and width of the defined objects for each frame. Relative stimulus object size (height \times width) and movement (movement of the object centroid in time) were calculated and the resulting measures were scaled between 0 and 100. After this the annotation data was convoluted with the assumed shape of the HRF function (SPM default double gamma function with shape parameters 6, 16, and length 29 s) and downsampled to one sample per volume using a moving average. Samples containing several overlapping local stimulus/object movements within the same category were weighted with the maximum value in a given frame. Finally, annotations were divided into

following categories: (1) human hand actions, (2) other human hand movements, (3) other human movements, and (4) nonhuman movements. Given that obtaining these ratings (i.e., the initial step of manually defining all of the to-be-tracked objects for each frame where a new object emerged) was laborious and time consuming, these ratings were not obtained from the experimental subjects, but were carried out by author KJ. Partial testing of inter-rater reliability at initial stages of the analysis indicated values very close to one, which confirmed that at least in the case of the film material that was used in the present study the manual selection step of this semiautomated annotation procedure was unambiguous and operator-independent.

Annotation of the Behavioral Priority

Dynamic ratings of the subjectively experienced behavioral priority were collected with an annotation tool. Immediately after the fMRI scanning session each participant watched the film again and simultaneously evaluated the subjective importance of a given scene by moving a slider up or down with a mouse. The instruction of the rating was as follows: "View the film and simultaneously evaluate the relative priority of the ongoing scene (priority evaluation should account for your percepts, thoughts and emotions). When the relative priority increases during the film, lift the sliding controller up (using a mouse), and when the relative priority decreases, put the sliding controller down." Thus, the behavioral priority rating in the present study differed from estimates of behavioral priority that are sometimes obtained with indirect measures such as eye-movements/fixations on specific objects in a visual scene. During the rating, there was a scale on the right that showed the concurrent rating value relative to the maximum and minimum values.

After measurement, behavioral priority ratings were averaged across the subjects, convoluted with the same function as the stimulus annotations, downsampled to one sample per volume using a maximum value, and divided to same categories as local stimulus object movements. Supporting Information Figure 2 shows the reliability of the behavioral priority ratings across subjects. Across-subjects averaged data were used in modeling the fMRI-signal, since these data were collected in a separate measurement (evaluation of the film contents is very difficult at first view and it could have made the viewing unnatural), and because interpretation of the varying interactions between individual rating values and film contents would have been difficult [see Nummenmaa et al., 2012; Viinikainen et al. 2012].

Acquisition and Analysis of Eye-Tracking Data

Eye movements of a separate group of subjects were acquired with SMI MEye Track long-range eye tracking system (Sensomotoric Instruments GmbH, Germany),

based on video-oculography and the dark pupil-corneal reflection method. The coordinate data containing the speed of eye movements were averaged across the subjects, convolved with HRF function, downsampled to one value per volume using a maximum value, and divided to same categories as local stimulus object movements and behavioral priority annotations. The use of across-subjects averaged data was due to the same reasons as in the case of behavioral priority ratings.

MRI Data Acquisition and Analysis

Functional brain imaging was carried out with a 3.0 T GE Signa Excite MRI scanner (GE Medical Systems) using a quadrature 8-channel head coil. The imaging area consisted of 29 functional gradient-echo planar axial slices (thickness 4 mm, between-slices gap 1 mm, in-plane resolution $3.4 \times 3.4 \text{ mm}^2$, voxel matrix 64×64 , TE 32 ms, TR 2000 ms, flip angle 90°). Functional images (total 689) were acquired continuously during the experiment. In addition, a T1-weighted inversion recovery spin-echo volume was acquired for anatomical alignment (TE 1.9 ms, TR 9 ms, and flip angle 15°). The T1 image acquisition used the same slice prescription as the functional image acquisition, except for a denser in-plane resolution (in-plane resolution $1 \times 1 \text{ mm}^2$, matrix 256×256) and thinner slices (1 mm, no gap).

Preprocessing of the fMRI data was performed with the tools implemented in the Functional Magnetic Resonance Imaging of the Brain Centre (FMRIB) software library (FSL, release 4.1.6 www.fmrib.ox.ac.uk/fsl) [Smith et al., 2004]. To allow for the initial stabilization of the fMRI signal, the first 10 volumes of the session were excluded from the analysis (during this time a blank screen was presented). The data were motion corrected (McFlirt) and nonbrain matter was removed (BET). Spatial smoothing was conducted with a Gaussian kernel of 6 mm (FWHM), and high-pass filtering with 100 s cutoff. The data were coregistered (FLIRT) first to anatomical image allowing 7 DOF and then to MNI152 standard space (Montreal Neurological Institute) allowing 12 DOF.

GLM analysis was performed using fMRIB Improved Linear Model (FILM). Explanatory variables were derived from the stimulus annotations (relative object size and relative object speed), average behavioral priority ratings, and average eye movements (Fig. 1). The high-pass filtering applied to the model was the same as the one applied to the data.

Due to natural stimulation, behavioral priority ratings, average eye movements, and stimulus annotations were not strictly balanced between the episodes containing different contents (both the re-edited movie and annotation time courses are available from the authors upon request). Means and standard errors of mean for each dynamic signal are reported in Table I and their potential effect on the results is dealt with in the Discussion section. In addition

to the reported parameters, we have also annotated overall luminance changes, contrast edges, and global optic flow from the film.

The group analysis was performed using FMRIB's Local Analysis of Mixed Effects. Statistical inference was carried out using Gaussian random field theory and cluster-based thresholding, using a cluster-forming Z threshold ($Z > 4.0$) and a corrected cluster significance threshold ($P < 0.01$). It is possible that naturalistic stimulation with no repetition of the same exact stimulus, provides more reliable and efficiently encoded responses than repetitive isolated stimuli [Chechik et al., 2006; Vinje and Gallant, 2000; Weliky et al., 2003]. Due to, on one hand, reliable and possibly large responses, and however, a stimulation and paradigm that is not in repetitive use by multiple research units (however, see [Glerean et al., 2012; Lahnakoski et al., 2012] for studies using the same stimulus and partially overlapping data) we selected relatively strict thresholds for statistical testing.

RESULTS

A general linear model (GLM) analysis examining the effect of stimulus content shows that the presence of human hand actions, other hand movements, and non-human movements were all associated with activity in parietal and visual cortices. The statistical parametric maps showing this, thresholded at $Z > 4$ and cluster-level corrected at $P < 0.01$, are plotted in Figure 2. More specifically, during episodes containing human hand actions PPC activity covered widespread areas of SPL, IPS, and IPL. In contrast, during episodes containing other hand movements and nonhuman movements statistically significant PPC activity was observed but it was restricted to relatively small areas in SPL and IPS (Fig. 2).

While all stimulus contents significantly activated visual cortical areas V1, V2, V3, V3a, V5, and V7, the pattern of effects across the visual cortical areas was at least partially opposite to that seen in PPC areas, as there was more widespread activity during episodes with non-human movements than during episodes containing hand actions and other hand movements (Fig. 2). These results hence provide evidence of a functional dissociation at different stages of processing in the visual pathway, with the distribution of brain activity moving from lower level visual areas (V1–V5) to higher level PPC areas when the stimulus content changes from nonhuman movements to human hand actions.

Supporting Information Figure 1 shows statistical parametric maps of those brain areas that are not seen in the surface renderings. During human hand actions these areas included the ventromedial prefrontal cortex and thalamus; during other hand movements dorsomedial prefrontal cortex, cuneus, parahippocampal areas, and thalamus; and during other human movements V1, and superior temporal gyrus/sulcus (NB we failed to see any significant

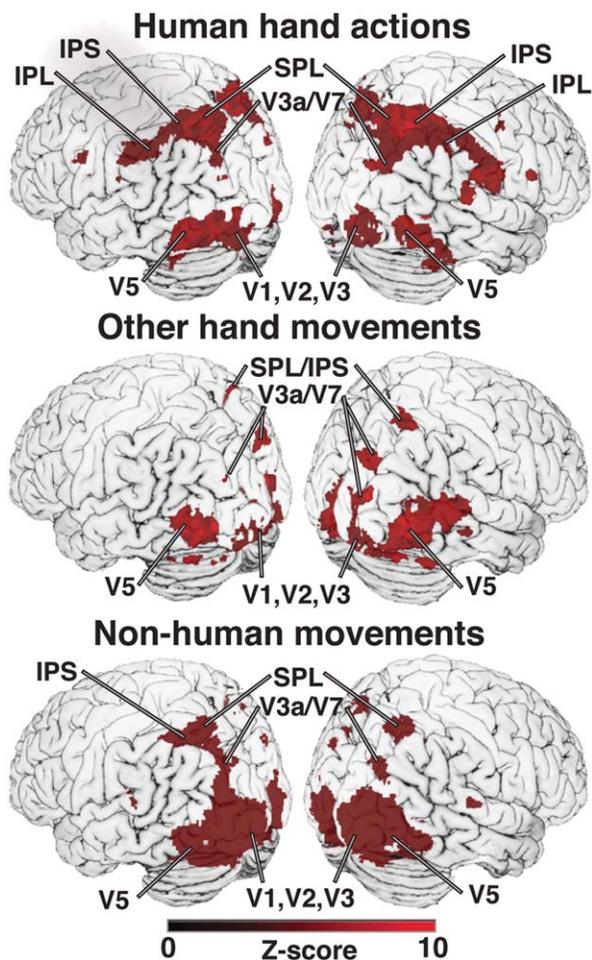


Figure 2.

Shown are the effects of stimulus content (human hand actions, other hand movements, and nonhuman movements) across all dynamic features as statistical parametric maps derived with a GLM analysis thresholded at $Z > 4.0$ and cluster corrected at $P < 0.01$. Abbreviations: IPS: intraparietal sulcus; IPL: intraparietal lobule; SPL: superior parietal lobule; V3a/V7: visual areas #3a/7; V5: visual area #5; V1: visual area #1; V2: visual area #2; V3: visual area #3. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

activity during episodes containing nonhuman movements in brain areas beyond those visible in the surface renderings shown in Fig. 2).

Given that the inspection of the extent of statistically significant activation in PPC (as seen in Fig. 2) does not directly answer the question of whether BOLD activity was stronger during episodes containing hand actions than in the other episodes, a region-of-interest (ROI) analysis was used to compare strength of BOLD responses (i.e., percent MR signal changes) elicited by the different stimulus contents in PPC (Fig. 3). This ROI included all PPC areas that were significantly activated by any of the

stimulus contents to avoid biasing the analysis towards any specific type of events. As can be seen Figure 3, BOLD activity in PPC was significantly stronger in both hemispheres during episodes containing human hand actions than during other episodes, including other hand movements, thus confirming that the differences seen in the extent of activation across PPC areas in Figure 2 were not due to statistical thresholding (e.g., activity in one

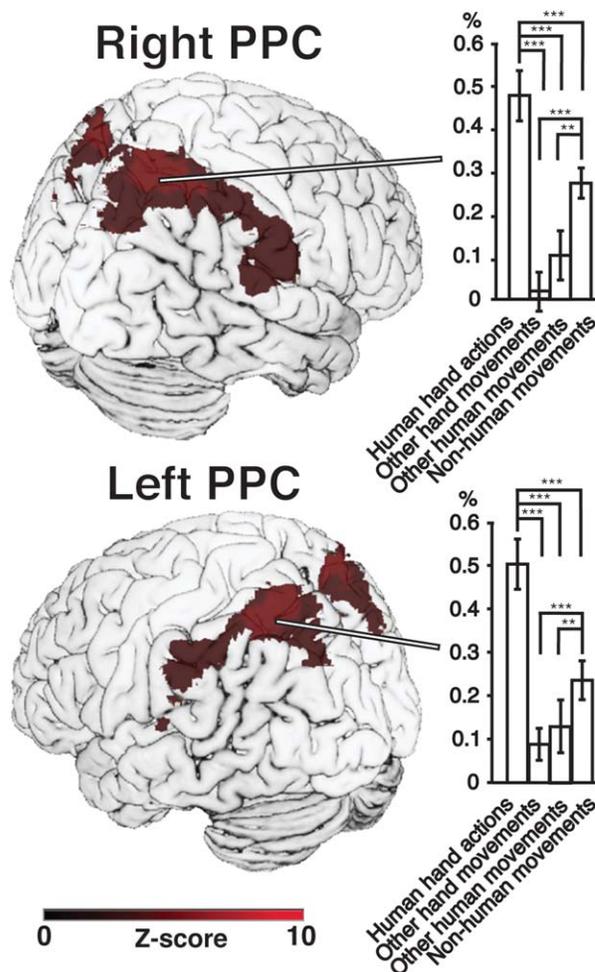


Figure 3.

Shown are the results of comparisons of average signal change in posterior-parietal cortex (PPC) regions of interest (ROI) between human hand actions, other hand movements, other human movements, and nonhuman movements using ANOVA. PPC ROIs (left) are defined based on the activity ($Z > 4.0$, cluster corrected $P < 0.01$) across all stimulus contents and dynamic features. ROI data were binarized before the analysis; hence, weighting based on Z values was not used. Bars at the right show the percentage of signal changes in left and right PPC ROIs for different stimulus contents. *** $P < 0.001$, ** $P < 0.01$. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

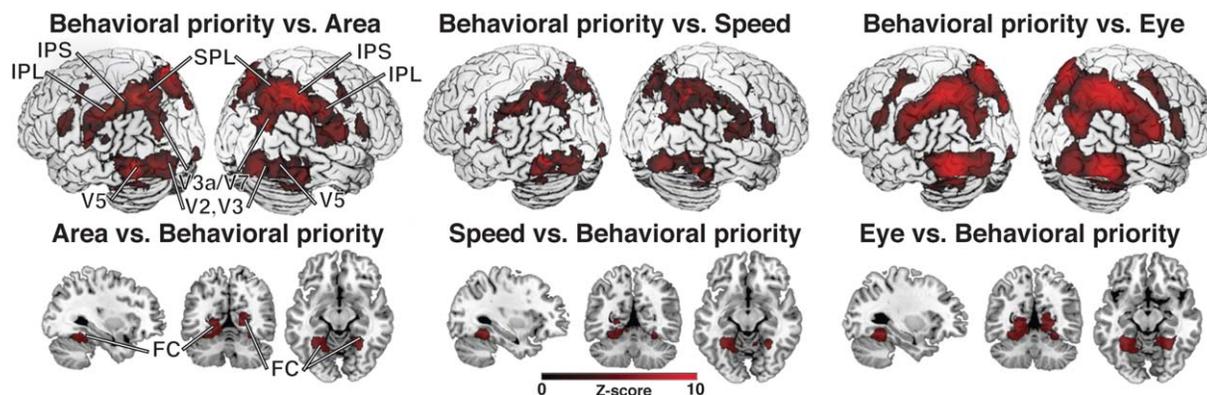


Figure 4.

GLM analysis contrasting brain activity modeled with behavioral priority versus the three other dynamic features (Area = relative stimulus object size, Speed = stimulus object movement, and Eye = eye movements, see Fig. 1 for the visualization of the dynamic features) during episodes containing human hand actions (threshold at $Z > 4.0$, cluster corrected $P < 0.01$). The upper part of the figure shows brain regions wherein the subjectively experienced behavioral priority explained brain activity better than the other dynamic features. As can be seen, these

condition barely exceeding the threshold vs. barely falling below the threshold in another condition). Note that the second-largest activation seen in Figure 3 was elicited by non-human movements. This effect was seen in both the left and right hemisphere PPC, suggesting that human movements other than hand actions are not preferred stimuli for activating PPC and, conversely, that there is something specific about observing human hand actions that preferentially activates the PPC.

Next, we studied with GLM how well behavioral priority, stimulus object movements, object size, and eye movements explained PPC activity during natural viewing. This was achieved by comparing the goodness-of-fit between these dynamic features and PPC activity. Hence, as in several other previous studies using naturalistic stimulation [e.g., Bartels et al., 2008; Lahnakoski et al., 2012; Malinen et al., 2007; Nummenmaa et al., 2012] we modeled the BOLD responses in each voxel using stimulus models that have realistic temporal dynamics (accounting for sluggishness of the BOLD signal). Since PPC activity was relatively low during other types of episodes except human hand actions (see Figs. 2 and 3), we limited the analysis to these events. As can be seen in the upper part of Figure 4, pairwise comparisons of the models show that behavioral priority explains PPC activity better than relative object size ("Area"), object movement ("Speed"), or eye movements ("Eye") during episodes containing human hand actions. These effect was observed across all the three contrasts in a relatively large area that covered both ventral and dorsal aspects of PPC, including SPL, IPS, and IPL, with the most widely

included PPC and visual cortical areas. The lower part of the figure shows brain regions wherein the other dynamic features explained brain activity better than behavioral priority, which was observed in temporo-occipital fusiform cortex. Abbreviations: IPS: intraparietal sulcus; IPL: intraparietal lobule; SPL: superior parietal lobule; V3a/V7: visual areas #3a/7; V5: visual area #5; V1: visual area #1; V2: visual area #2; V3: visual area #3; FC: temporo-occipital fusiform cortex. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

spread and most statistically significant effects in the behavioral priority vs. eye movements comparison.

In addition to PPC areas, behavioral priority explained activity in the bilateral ventral and dorsal motor cortex and visual areas V1–V5 significantly better than the other three dynamic variables during episodes containing hand actions (see the upper part of Fig. 4). In each of the three opposite contrasts shown in the bottom part of Figure 4, the other dynamic features explained hemodynamic activity significantly better than behavioral priority in the temporo-occipital fusiform cortex during episodes containing hand actions. Hence, there was a functional dissociation between the PPC and visual areas V1–V5, where behavioral priority explained the hemodynamic activity significantly better than the other dynamic features that were tested, and the temporo-occipital fusiform cortical areas wherein the other dynamic features explained the hemodynamic activity better than behavioral priority, during episodes containing hand actions.

DISCUSSION

PPC activity was associated with observing multiple types of spatial movements (Figs. 2 and 3), supporting previous studies that have indicated involvement of PPC in the spatial ("where") processing stream [Bartels et al., 2008; Silver and Kastner, 2009; Ungerleider and Mishkin, 1982]. Among many sorts of episodes containing stimulus movements (for instance, social interaction between two or more people, dancing, movement of the vehicles, and many other

typical real-life events) viewing goal-directed human hand actions was, however, associated with the most widespread and robust enhancement in PPC activity. This activity was not explained by spatial movements of the stimuli or synchronized eye movements (as suggested by significantly higher activity during observation of hand actions vs. these other categories, see Fig. 3), and we failed to see higher behavioral priority ratings during human hand action episodes than during other types of episodes.

Categories “human hand action” and “other human hand movement” differed only with respect to the goal of the action, suggesting that PPC activity was rather specifically elicited by viewing goal-directed behavior. PPC activity associated with goal-directed vs. non goal-directed hand movements has been reported in previous brain imaging studies with non-naturalistic stimuli [for a review see Caspers et al., 2010; Culham and Valeyar, 2006], and was also observed by Hasson et al. [2004] under natural viewing conditions. The important role of PPC in vision for action (i.e., “how”) is possibly explained by the anatomical connections of this area with both visual and motor systems [Fabbri-Destro and Rizzolatti, 2008; Goodale and Milner, 1992]. Neurophysiological evidence suggesting that the same dorsal stream circuits are involved in visual processing, motor execution, and visuo-motor transformations has also accumulated recently [Bisley and Goldberg, 2010; Buccino et al., 2001; Fabbri-Destro and Rizzolatti, 2008; Fogassi and Luppino, 2005; Goldberg et al., 2006]. Furthermore, several recent studies have highlighted the role of “mirror neurons” in increasingly complex PPC functions such as perception of language and/or social interactions [for a review see Iacoboni and Dapretto, 2006]. The present study provides preliminary evidence that the mirror neuron system can be studied also during natural vision. However, to confirm the role of mirror neurons specifically in such conditions one would need an additional task containing overt hand actions by the experimental subjects that could be then compared with the effects elicited by observing hand actions carried out by others, given that mirror neurons by definition are neurons that respond similarly during action execution and observation of actions by others.

The present results suggest that observed human hand actions activate a large set of areas in PPC encompassing also IPL and somato-motor cortex, while processing of other stimulus/object movements is more restricted to dorsomedial PPC areas (Fig. 2). These findings might parallel previous non-human primate findings suggesting that while a specific dorsal PPC area (the lateral intraparietal area) is involved in targeting eye movements and spatial attention [Goldberg et al., 2006], there is a specific ventral PPC area (the anterior intraparietal area) that is associated with orienting towards action [Murata et al., 2000]. Similar dissociation between the dorsal and ventral PPC functions has been also observed in human brain imaging studies on action perception [Culham and Valeyar, 2006], and neuroimaging studies have provided evidence for a more

domain-independent role of dorsal PPC [Esterman et al., 2009; Fox et al., 2005; Salmi et al., 2007]. Thus, it seems that the “how” theory well describes ventral PPC function and the “where” theory is more valid for dorsal PPC.

Nonhuman primate studies have advocated the behavioral priority model of PPC [Bisley and Goldberg, 2010], however, the role of behavioral priority in explaining human PPC function is less clear. In our study, the differences between processing of observed goal-directed vs. non goal-directed actions in PPC suggests that PPC is more involved in goal-directed than stimulus-driven processing. In this study, subjectively rated behavioral priority explained PPC activity better than either synchronization (or speed of) eye movements or spatial movements of the stimulus (Fig. 4). These findings agree with studies demonstrating robust top-down effects in PPC [Behrmann et al., 2004; Corbetta and Shulman, 2002; Mesulam, 1981; Riddoch et al., 2010]. Since PPC activity was relatively low during other types of episodes except human hand actions (see Figs. 2 and 3), we limited inspection of the stimulus-driven vs. goal-directed effects to these events. Notably, comparisons between dynamic signals and PPC activity were carried out with continuous intensity models where relative amplitude changes play less significant role than in a conventional boxcar modeling. Furthermore, each continuous intensity model was standardized to remove potential bias due to overall magnitude differences.

The sensitivity of PPC to different stimulus categories and behavioral priority differed from that in the lower-level visual cortical areas. First, the analysis focusing on sensitivity of voxel-wise brain activity to different stimulus contents demonstrated that the activity in the visual areas is relatively stronger to nonhuman than human movements (Fig. 2). We see two possible explanations for this: It is possible that the spatial and temporal distribution of nonhuman movements was different than the corresponding distribution of human hand actions, leading to differential activation of the visual cortex areas since they are sensitive to less complex visual features [Silver and Kastner, 2009] and accumulate information over shorter temporal receptive windows [Hasson et al., 2008] than the higher-level areas. Second, the prominent activity in parietal cortex could be associated with enhanced goal-directed attention during episodes containing human hand actions [see Bisley and Goldberg, 2010; Corbetta and Shulman, 2002]. However, our results (Fig. 4) suggested that the effect of behavioral priority influenced not only the PPC but also areas V1–V5 during episodes containing hand actions. Indeed, only one brain area in the vicinity of FC showed stronger activation to the visual stimulus features than to self-rated behavioral priority.

Although brain activity (also in PPC) is highly synchronized across subjects during natural viewing, some movies synchronize the brains of subjects better than others, possibly reflecting how well the director is able to guide the viewers [Hasson et al., 2010]. Thus, it is possible that individual viewing patterns affect PPC activity during natural

viewing. Due to the potential interactions between stimulus content and individual viewing patterns during natural viewing, accurate modeling of behavior and experiences is highly important. When using natural viewing conditions, it is challenging to distinguish between all possible factors that could affect the results (for example, distinction between sensory, emotional, and higher-level cognitive processes is not always clear even at the level of subjective experience). Keeping these hurdles in mind, we are nonetheless confident that the natural viewing paradigm provides an important complementary approach for studying PPC functions that enables, for instance, contrasting predictions of established theories that have been based on studies with non-naturalistic tasks and stimuli.

CONCLUSIONS

Our results suggest that both processing of spatial information and vision for action contribute to PPC activity during natural viewing. However, relative to the other categories, PPC was observed to be most sensitive to seeing human hand actions, which supports the “how” and “mirror neuron” theories of PPC function. Furthermore, behavioral priority predicted changes in PPC activity during hand action episodes, indicating that the sensitivity of PPC to changes in behavioral priority is high when viewing others' actions. These findings suggest that PPC supports human intentional behavior in addition to the other functions associated with this structure such as spatial processing. Being able to perceive the significance of others' actions enables one to predict intentions of others, which is also crucial for planning and choosing one's own actions [see Desmurget et al., 2009]. Taken together, our findings support views according to which PPC harbors “a priority map of intentions” that can be dynamically utilized in perceiving the significance of others' actions [Bisley and Goldberg, 2010].

ACKNOWLEDGMENTS

Special thanks to Ms Marita Kattelus for her help in collecting the MRI data, Ms Heini Heikkilä for helping with extracting the annotations, and Mr Jerem Tonteri for assistance in re-editing the movie.

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