The posterior cingulate cortex and planum temporale/parietal operculum are activated by coherent visual motion

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Abstract

The posterior cingulate cortex (PCC) is involved in higher order sensory and sensory-motor integration while the planum temporale/parietal operculum (PT/PO) junction takes part in auditory motion and vestibular processing. Both regions are activated during different types of visual stimulation. Here, we describe the response characteristics of the PCC and PT/PO to basic types of visual motion stimuli of different complexity (complex and simple coherent as well as incoherent motion). Functional magnetic resonance imaging (fMRI) was performed in 10 healthy subjects at 3 Tesla, whereby different moving dot stimuli (vertical, horizontal, rotational, radial, and random) were contrasted against a static dot pattern. All motion stimuli activated a distributed cortical network, including previously described motion-sensitive striate and extrastriate visual areas. Bilateral activations in the dorsal region of the PCC (dPCC) were evoked using coherent motion stimuli, irrespective of motion direction (vertical, horizontal, rotational, radial) with increasing activity and with higher complexity of the stimulus. In contrast, the PT/PO responded equally well to all of the different coherent motion types. Incoherent (random) motion yielded significantly less activation both in the dPCC and in the PT/PO area. These results suggest that the dPCC and the PT/PO take part in the processing of basic types of visual motion. However, in dPCC a possible effect of attentional modulation resulting in the higher activity evoked by the complex stimuli should also be considered. Further studies are warranted to incorporate these regions into the current model of the cortical motion processing network.

Keywords: Human, Motion perception, fMRI

Introduction

The majority of physiological and neuroimaging studies investigating visual motion stimuli have focused on the initial stages of motion perception, with less regard to the later stages of processing motion information. However, characterization of the response properties of individual brain regions to certain types of motion stimuli is a prerequisite for the proper integration of respective areas into the complex network of visual motion processing. The most intensively studied visual area related to motion perception is the human V5 (Zeki et al., 1991; for a recent review see: Born & Bradley, 2005). The temporal or permanent disruption of motion processing in this area results in akinetopsia (Beckers & Homberg, 1992; Shipp et al., 1994). Motion perception deficits, however, are also associated with a variety of subcortical and cortical lesions, and other neurological disorders that might cause disconnection(s) within the motion processing pathways (Nawrot, 2003).

The posterior cingulate cortex (PCC, Brodmann areas 23 and 31) and retrosplinal cortex (Brodmann areas 29 and 30) form the posterior cingulate gyrus including an extension into the cingulate sulcus. According to stroke and functional imaging studies in humans, this region is part of a network that mediates visuospatial orientation, navigation, and related memories (Berthoz, 1997; Kataoka et al., 2006; Vogt et al., 2006). Although PCC seems to be involved in the later stages of visuospatial and motor information processing, it exemplifies the problem of an area that is poorly characterized using basic types of motion stimuli. As a by-product of recent publications, it has been found to be activated by various visual motion stimuli (Braddick et al., 2001; Cornette et al., 1998a; Dieterich et al., 2003; Orban et al., 2003; Stebbins et al., 2004; Stiers et al., 2006; Sunaert et al., 1999). Most of these studies found that the PCC was activated by coherent motion in comparison to static patterns (Cornette et al., 1998a, 1998b; Orban et al., 2003; Sunaert et al., 1999) or to incoherent motion stimuli (Braddick et al., 2001). Furthermore, motion reversal resulted in stronger activation than continuous motion (Cornette et al., 1998b). Brandt et al. (1998) found that circularvection induced by large-field visual motion stimulation also activated the PCC. The dorsolateral part of PCC (dPCC) is known to be involved in

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higher-order information processing during cognitive tasks and visuospatial orientation and integration processing (for a review see: Vogt & Laureys, 2005; Vogt, 2005).

Like the PCC, the planum temporale/parietal operculum (PT/PO) was found to be activated in some fMRI studies using visual motion stimuli (Cornette et al., 1998b; Sadato et al., 2005) although this area is known to take part in auditory and vestibular integration processing (Eickhoff et al., 2006; Krumbholz et al., 2005). This region occupies the superior temporal plane posterior to Heschl's gyrus. Abnormal hemispheric lateralization of PT is observed in dyslexia and schizophrenia (Stein, 1994), frequently coinciding with abnormal motion processing. However, direct correlation of the anatomical abnormalities and the functionally altered motion processing is lacking. The PT/PO region is important in the perception of motion in acoustic space (Pavani et al., 2002); nevertheless, its functional role in visual motion perception and processing is yet unclear.

In general, the above-mentioned studies have used only one or two types of different visual stimuli (e.g., randomly moving or coherently moving dots versus static patterns) or complex moving patterns (e.g., movements of body parts). None of the studies addressed the question of which basic properties of different types of *simple* visual motion stimuli account for activations in these regions. Therefore, in the present study, we used basic types of visual motion patterns such as incoherent random motion as well as coherent motion patterns of different complexity, e.g., translational, rotational, and radial motion. These types of motion stimuli have already been used by several imaging studies (for a recent one see: Smith et al., 2006). Visual stimuli can be decomposed into these elementary motion types. Translation and rotation occurring in a plane perpendicular to an observer's visual axis are typical for an in-plane motion. Translation is mostly experienced as an object moves along a single given direction, whereas rotation is involved as an object moves around a fixed given point. Expansion and contraction along an observer's visual axis are typical for an in-depth motion. The aim of the present study was to identify and describe the properties of the dPCC and PT/PO of the human brain using fMRI with special emphasis on applying these basic types of visual motion stimuli. We hypothesized that incoherent motion would elicit less activation than coherent motion. Regarding the different coherent patterns, we considered the processing of radial

and rotational motion to be more demanding than simple translational movements, which should be reflected by differential amounts of activation.

Materials and methods

Subjects

Ten human adults (age range: 23–38 years, mean $\pm$ SD: 26.8 ± 4.4 years, three males) with normal or corrected-to-normal vision and no history of neurological or psychiatric disease, participated in the study which was approved by the Ethical Committee of the University of Göttingen. Written informed consent was obtained from all subjects. The study conforms to The Code of Ethics of the World Medical Association (Declaration of Helsinki).

Visual motion paradigms

To assess the characteristic responses to basic types of motion stimuli, subjects were shown five different kinds of white moving dot patterns on a black background (Fig. 1). Two tasks consisted of simple linear VERTICAL and HORIZONTAL moving dots, respectively. In addition, a more complex ROTATIONAL dot pattern, rotating around the center of the screen, and a RADIAL pattern, imitating in-depth motion, was used. These four coherent types of motion were complemented by an incoherent RANDOM moving dot pattern. All moving dot patterns reversed direction at a frequency of 0.7 Hz. The central 14° of the visual field was masked, leaving only a central stationary dot which the subjects had to fixate throughout the experiment. In the unmasked area of the screen, an average of 216 white dots (size: 0.04°) represented a randomly generated dot pattern. In order to create linear motion (VERTICAL or HORIZONTAL), these dots moved with a constant speed of 3.5°/s. ROTATION was constructed by rotating the whole pattern with a speed of 20° /s resulting in faster moving dots in the periphery compared to the more central aspects of the dot patterns. RADIAL motion was produced by moving the dots toward the center of the screen and vice versa. Again peripheral dots moved faster than more central dots but an average speed of 3.5°/s was achieved. The RANDOM pattern was constructed by

Fig. 1. Scheme of the five visual motion reversal dot patterns (top) and the stimulation paradigm employed (bottom). The arrows in the centre of the sketches indicate the kind of motion employed for the different movement types. Following an initial baseline condition, ten repetitions of visual stimulation with the respective moving and static dot pattern were applied.

displacing the single dots in randomly chosen directions at different speeds. Again an average speed of $3.5^\circ/\text{s}$ was used. Whenever dots crossed the peripheral or central mask border, they were replaced at the appropriate location, i.e., at the central mask or peripheral border, respectively.

In all tasks, 10 repetitions of the motion stimulation phases (12 s) were interleaved with control phases (18 s) consisting of a static version of the dot pattern, including additional control conditions at the beginning and at the end of one experimental run, resulting in a total measuring time of 5 min 18 s. With the use of “Presentation 9.00” (Neurobehavioral Systems, Albany, NY), stimuli were fed into a set of MR-suited LCD glasses (Resonance Technology, Northridge, CA) covering a visual field

of 20° in the vertical and 30° in the horizontal direction. The order of the five visual motion experiments was pseudo-randomized between subjects.

Fixation Accuracy

The fixation accuracy was controlled by eye tracking. Fig. 2 shows the group results from additional examinations of four subjects, revealing that the subjects fixated equally well during the different visual motion stimulation experiments. The supplementary experiments consisted of five runs with durations of 3 min each (one run per experimental condition). In the first minute, subjects had to track a moving dot within a 5×5 calibration matrix covering the

Fig. 2. Group results ($n = 4$) of the fixation accuracy experiments. Fixation probability maps (z-scores) for each of the five visual motion experiments and the group average are overlaid onto a scheme of the dot pattern used.

whole screen. During the remaining 2 min, subjects had to fixate a central dot, while phases of the peripheral moving and stationary dot patterns were presented (30 s each). Eye tracking data were acquired with an integrated video-oculographic system (Arrington Research Inc., Scottsdale, AZ) and analyzed using in-house software based on the MatLab program package (MathWorks Inc., Natick, MA). The following three step algorithm was applied to generate fixation probability maps (FPM) for each of the five experimental conditions: To identify and remove blinks the so-called pupil ratio was utilized. This ratio is a measure of the ellipticity—and thus also the goodness—of the pupil fit.

The nonlinear local distortion as well as the variance of the eye tracking system was quantified using the data from the calibration period. Around each point of the calibration matrix, a search area of $\pm 2^\circ$ visual angle horizontal and vertical was defined. Then, a two-dimensional (2D) normal (Gaussian) distribution $G(x, y)$ was estimated as follows:

$$G(x, y) = \frac{1}{2\pi\sqrt{|Det(C)|}} \times \exp\left(-\frac{1}{2}[x - \bar{x} \ y - \bar{y}]D^{-1}\begin{bmatrix} x - \bar{x} \\ y - \bar{y} \end{bmatrix}\right),$$

where C is the covariance matrix for all coordinate pairs x, y , and $\bar{x}, \bar{y}$ are the mean values of the x and y coordinates of the sampling points, respectively. The differences between the positions of the maximum of this model and the corresponding calibration point in x and y direction were calculated. These two values were allocated to the corresponding calibration position in the x and y distortion fields, respectively. The resulting distortion fields for the whole screen were then generated by interpolating between all 5×5 calibrations points using cubic splines.

Finally, a 2D rotationally symmetric Gaussian low pass filter using the following $m \times n$ Gauss operator $h_G(m, n)$ was calculated:

$$h_G(m, n) = \exp^{-(m^2 + n^2)/(2\sigma^2)},$$

where σ is the mean standard deviation of all 5×5 distributions and $m, n = 1 \dots 5$. The FPM for the remaining 2 min of each run was calculated by convolving the sampling point pattern of this period with the Gaussian low pass filter. The outcome of this procedure is a probability field $PF(x, y)$. Regarding a global probability of 1 for the whole field or screen, respectively, the final $FPM(x, y)$ was calculated as follows:

$$FPM(x, y) = \frac{PF(x, y)}{\sum_{x=1}^X \sum_{y=1}^Y PF(x, y)},$$

where X is the width and Y is the height of the stimulation screen (800×600 pixels). Finally, the factor between the probabilities of a random fixation of pixel (x, y) , which is $1/(800 \times 600)$, and the real value for pixel (x, y) in our FPM was calculated and the result overlaid atop our stimulation image.

Magnetic resonance imaging

MRI was performed at 3 Tesla (Siemens Magnetom Trio, Erlangen, Germany) using the standard eight-channel phased-array head coil. Subjects were placed supine inside the magnet bore and wore

headphones for noise protection. Vital functions were monitored throughout the experiment. Initially, an anatomical T1-weighted MR dataset covering the whole head at 1 mm^3 isotropic resolution was acquired (3D Turbo FLASH, repetition time (TR): 1950 ms, inversion time: 1100 ms, echo time (TE): 3.93 ms, flip angle: 12°). For functional imaging, a T2*-sensitive gradient-echo EPI technique with an in-plane resolution of $2 \times 2 \text{ mm}^2$ was used (TR: 2000 ms, TE: 36 ms, flip angle: 70° , acquisition matrix: 96×128). Sixteen consecutive sections of 4 mm thickness angulated in an axial-to-coronal orientation, covering the brain areas of interest, e.g., the occipital lobe and especially the posterior cingulate gyrus as well as the planum temporale and parietal operculum, were acquired. For each of the five different visual stimulation tasks, a total of 159 volumes were recorded.

Data analysis

In a first step, the functional data were analyzed on an individual basis using Brainshow (in-house software, Baudewig et al., 2003). This comprised a correlation analysis of the unfiltered original functional time-series with the respective box-car reference function of visual stimulation shifted by 4 s (2 volumes) to account for hemodynamic latencies. Activation maps were generated using the double threshold approach described previously (Kleinschmidt et al., 1995), which incorporates a conservative threshold to define activation centers ($p < 0.0001$) and a liberal one ($p < 0.05$) to identify the extension of activated regions. To assess the overall brain response to respective motion stimuli, the total number of activated pixels was calculated from each individual functional experiment. Furthermore, the number of activated pixels was calculated in the regions-of-interest (ROI) of the early visual areas surrounding the calcarine fissure (V1/V2) and V5 in the inferior temporal sulcus, as well as in the dPCC and the PT/PO, where the maximum percent signal change was also assessed. Coherences of the stimulus type and the number of activated pixels or the maximum percent signal change, respectively, were assessed using an analysis of variance (ANOVA) and, if applicable, subsequent pairwise comparisons using a paired Students t-test assuming equal variances at a significance level of $p < 0.05$.

Group analysis and visualization were achieved using Brain Voyager QX 1.6 (Brain Innovation, Maastricht, The Netherlands). Preprocessing included 3D motion correction, slice scan time correction, linear trend removal, and spatial smoothing with a Gaussian kernel (full width at half maximum $4 \times 4 \times 4 \text{ mm}^3$). Subsequently, functional datasets were co-registered to the anatomical dataset and transformed into Talairach space. A fixed-effect group analysis was performed using the multi-study, multi-subject approach of the general linear model. Different movement types were regarded as the different predictors. Global activation maps of the respective motion stimuli were separately computed and a conjunction analysis incorporating all predictors was performed. Furthermore, the functional contrast of coherent (VERTICAL, HORIZONTAL, ROTATION, RADIAL) versus incoherent (RANDOM) motion was calculated and overlaid onto the mean anatomical dataset of all participants. The obtained p -values were corrected for multiple comparisons using the False Discovery Rate approach ($q(\text{FDR}) < 0.05$) described previously (Genovese et al., 2002).

The dPCC and the PT/PO were identified bilaterally using gross anatomical landmarks, following the descriptions by Vogt et al. (2006) and the assignment provided by a neuroanatomical atlas, respectively. In short, the dPCC was defined on the mid-

sagittal plane as the portion of the dorsal bank of the cingulate gyrus extending from 10 mm anterior to the vertical of the posterior commissure to the vertical of the posterior aspect of the splenium. The PT was identified on the superior surface of the superior temporal gyrus posterior to the transverse temporal gyri. Regarding the PO, only the posterior part directly opposing the PT was included, omitting the more frontal aspects.

Results

Single condition activation maps as well as the conjunction analysis revealed that all stimuli activated a distributed cortical network including well-known regions such as striate and extrastriate visual areas, as well as several occipito-temporal, parietal, and frontal regions. The total activation sizes across subjects were (mean $\pm$ SD, in cm^3) 22.3 ± 15.1 for VERTICAL, 28.4 ± 13.8 for HORIZONTAL, 35.6 ± 18.1 for ROTATION, 42.5 ± 17.3 for RADIAL, and 28.0 ± 9.8 for RANDOM motion. The ANOVA revealed a difference in the mean number of activation sizes due to motion stimuli ($n = 10$, $F = 2.7$, $p = 0.04$). Subsequent post-hoc comparisons demonstrated that simple coherent (VERTICAL [$p = 0.002$], HORIZONTAL [$p = 0.01$]), and incoherent (RANDOM [$p = 0.006$]) motion stimuli revealed fewer activations as compared to RADIAL stimulation. There was no significant difference between simple coherent (VERTICAL, HORIZONTAL) and incoherent (RANDOM) motion stimuli.

Fig. 3 shows the dPCC involvement in a representative subject. The dPCC was activated by the different coherent visual motion stimuli (VERTICAL, HORIZONTAL, ROTATION, and RADIAL) but no significant response to the incoherent motion stimulus (RANDOM) was found. Correspondingly, the ANOVA of activation volumes in the dPCC of all subjects revealed a significant influence of the motion stimulus ($n = 10$, $F = 5.7$, $p < 0.001$). Subsequent pairwise comparisons demonstrated that RANDOM motion activated less than the coherent motion stimuli (RANDOM versus VERTICAL [$p = 0.008$], HORIZONTAL [$p = 0.002$], ROTATION [$p < 0.001$], RADIAL [$p < 0.001$]) (Fig. 4). Furthermore, complex coherent motion evoked more activation than simple coherent motion (ROTATION/RADIAL versus VERTICAL/HORIZONTAL [$p = 0.002$]). There was no significant difference between VERTICAL and HORIZONTAL as well as between ROTATION and RADIAL motion stimuli. Therefore, regarding activation size, the order incoherent $<$ simple coherent $<$ complex coherent motion became apparent. Comparing maximum percent signal changes evoked by the different motion stimuli revealed similar tendencies, however, with only the pairwise comparisons of the incoherent RANDOM motion to some of the coherent motion types showing significant effects (RANDOM versus VERTICAL [$p = 0.03$], HORIZONTAL [$p = 0.31$], ROTATION [$p = 0.02$], RADIAL [$p = 0.01$]).

In contrast to the dPCC, the PT/PO revealed no significant differences in activation size for different coherent motion types.

Fig. 3. Brain activations (red) in a representative subject resulting from the different visual motion stimuli compared to a static dot pattern. The activations are overlaid onto three consecutive sections (s5–s7) from the original fMRI dataset running through the dorsal posterior cingulate cortex (dPCC).

Fig. 4. Boxplots (boxes were constructed using the quartiles, whiskers represent the 5% and 95% percentiles, $n = 10$) of the activation volumes resulting from the different visual motion stimuli compared to a static dot pattern in the dorsal posterior cingulate cortex (dPCC).

Solely pairwise comparisons of the incoherent RANDOM motion to the different coherent motion types revealed that coherent motion activated the PT/PO stronger (RANDOM versus VERTICAL [$p = 0.02$], HORIZONTAL [$p = 0.07$], ROTATION [$p = 0.01$], RADIAL [$p = 0.02$]). Further statistical comparisons revealed no significant differences between the coherent motion stimuli. Again, comparing maximum percent signal changes evoked by the different motion stimuli revealed similar tendencies, however, without statistical significance (RANDOM versus VERTICAL [$p = 0.06$], HORIZONTAL [$p = 0.28$], ROTATION [$p = 0.14$], RADIAL [$p = 0.07$]).

V1/V2 showed significant differences in activation size for the simple coherent (VERTICAL and HORIZONTAL) and incoherent (RANDOM) motion types, as well as for the simple coherent and complex coherent (ROTATION and RADIAL) motion types. Correspondingly, the ANOVA of activation volumes in V1/V2 of all subjects revealed a significant influence of the motion stimulus ($n = 10$, $F = 3.3$, $p = 0.02$). Subsequent pairwise comparisons demonstrated that RANDOM motion activated less than simple coherent motion (RANDOM versus VERTICAL/HORIZONTAL [$p = 0.008$]) and that simple coherent motion activated less than complex coherent motion (VERTICAL/HORIZONTAL versus ROTATION/RADIAL [$p = 0.002$]). In V5, no significant differences in activation size for different motion types were detected.

Contrasting coherent (VERTICAL, HORIZONTAL, ROTATION, RADIAL) versus incoherent (RANDOM) motion reveals strong bilateral activation in dPCC and PT/PO (Fig. 5). This is also reflected by corresponding time-courses, indicating that the coherent motion types induce strong increases of the MR-signal, while the incoherent motion results in only a minor positive deflection. The corresponding Talairach coordinates and activation volumes of these regions are given in Table 1. The mean coordinates of the left- and right-hemispheric activations reveal a rather symmetrical location in dPCC and PT/PO, respectively.

Discussion

In the present study, we used five visual motion stimuli with different grades of coherence and complexity, ranging from incoherent random dot motion via simple translational up to complex rotational and radial motion patterns. In agreement with previous neuroimaging reports, our study identified a widespread network

of motion responsive areas in the human brain extending beyond the dorsal pathway, including distinct parietal and frontal areas engaged in the processing of different motion types (Orban et al., 2003; Sinaert et al., 1999; Vanduffel et al., 2002). To further evaluate the plausibility of our results, we compared the findings in well-studied brain regions like early visual areas V1/V2 and V5 to previously published reports. In particular, for V1/V2 our results were in line with most of the findings reported previously (Cheng et al., 1995; Martinez-Trujillo et al., 2005; McKeefry et al., 1997; Morrone et al., 2000; Paradis et al., 2000). The literature regarding the behavior of V5 in response to different visual motion stimuli is partly controversial (e.g., compare Cheng et al., 1995; Martinez-Trujillo et al., 2005; McKeefry et al., 1997; Paradis et al., 2000; Rees et al., 2000; Smith et al., 2006). Several studies (Rees et al., 2000; Braddick et al., 2001) have documented the sensitivity of the human V5/MT complex to motion coherence. However, we did not find that coherent motion yields stronger activity than random motion in V5. Although this conflicts with the above studies, it is in agreement with the findings of McKeefry et al. (1997), Smith et al. (2006), and Paradis et al. (2000), who compared responses to coherent and incoherent motion using PET and fMRI, and found that responses to incoherent motion were as large as those in coherent motion. Similarly, Martinez-Trujillo et al. (2005) using similar motion stimuli, did not find significant difference between translation evoked and gradient motion evoked activation in V5.

With respect to the dPCC and PT/PO, we found these areas activated by the different visual motion stimuli to a varying degree: bilateral activations in the dPCC were evoked using coherent motion stimuli irrespective of motion direction (VERTICAL, HORIZONTAL, ROTATION, RADIAL). Greater responses were produced by complex stimuli (ROTATION, RADIAL) compared to translation. In contrast, the PT/PO responded equally well to all of the different coherent motion types. Incoherent (RANDOM) motion yielded significantly less activation both in the dPCC and in PT/PO area. Below, the involvement of these regions in visual motion processing is discussed in more detail.

Dorsal posterior cingulate cortex

One of our main focuses was the characterization of the motion responsiveness in the dPCC. We found activation for all five

Fig. 5. Group analysis ($n = 10$) shows differential activations resulting from contrasting coherent (VERTICAL, HORIZONTAL, ROTATION, RADIAL) versus incoherent (RANDOM) visual motion in (A) the dorsal posterior cingulate cortex (dPCC) and (B) the planum temporale/parietal operculum (PT/PO) overlaid on the averaged anatomical data and respective time-locked averaged signal intensity time-courses (red—VERTICAL, green—HORIZONTAL, blue—ROTATION, black—RADIAL, yellow—RANDOM). The stimulation period is indicated by the solid bar.

Table 1. Activations in the dPCC and the PT/PO resulting from contrasting coherent versus incoherent visual motion

Region	Hemisphere	Talairach Coordinate (mm)			Activation Size (mm ³)	Peak Activation (<i>t</i> -Value)
		<i>x</i>	<i>y</i>	<i>z</i>		
dPCC	R	10	-28	42	499	5.0
	L	-12	-24	39	886	7.8
PT/PO	R	49	-29	24	2194	6.2
	L	-50	-33	20	5196	7.1

coherent: VERTICAL, HORIZONTAL, ROTATION, RADIAL; incoherent: RANDOM.

dPCC: dorsal posterior cingulate cortex; PT/PO: planum temporale/parietal operculum.

L: left; R: right.

motion stimuli employed. Furthermore, coherent motion induced a stronger activation as compared to the incoherent random dot pattern. Characterization of the dPCC regarding its responsiveness to the various visual motion stimuli resulted in the tentative order incoherent $\ll$ simple coherent $<$ complex coherent motion, with most prominent differences for incoherent $<$ coherent (see Fig. 4).

It is important to mention that most of the previous fMRI studies that reported activation for visual motion stimuli did not separate the dorsal part of the PCC but mentioned this brain area as posterior cingulum or cingulate cortex (Brandt & Dieterich, 1999; Dieterich et al., 2003; Sunaert et al., 1999). However, anatomical and fMRI results show that the human PCC has structural and functional dichotomy: while dPCC is involved in the processing of visual information and orientation of the body in space, its ventral part participates in the processing of self-relevant emotional and non-emotional information as well as self-reflection (Vogt et al., 2006). Even though there are quite a number of publications that mention activation of the PCC or dPCC region (Braddick et al., 2001; Brandt et al., 1998; Büchel et al., 1998; Cornette et al., 1998a, 1998b; Gulyas et al., 1994; Indovina et al., 2005; Pekkola et al., 2006; Stebbins et al., 2004; Sunaert et al., 1999), e.g., when viewing motion stimuli, the corresponding discussions rarely address this finding. Braddick et al. (2001) have described bilateral cingulate activity for vertically moving coherent dots versus random noise patterns; however, according to the Talairach coordinates, the activated brain area is closer to the anterior than the posterior part of the cingulate cortex. One fMRI and two PET studies (Brandt et al., 1998; Cornette et al., 1998a, 1998b) have also found left PCC activation for single axis motion onset versus static random dot pattern presentation and clockwise motion. It was suggested that PCC responds specifically to motion onset and is involved in the processing of eye-movement-related signals. Corresponding activations were also reported after stimulation with apparent radial moving circles in patients with Parkinson's disease (Stebbins et al., 2004). Our findings are in line with these reports, as we found activation for all five motion stimuli employed. Furthermore, coherent motion induced a stronger activation as compared to the incoherent random dot pattern.

We did not run any types of task to attempt to control for attention. Therefore, we have no direct evidence that the results are not partly due to differences in how much transient attention might

be drawn to different stimulus types. Nevertheless, in the present study, as well as in several others dealing with visual motion, the attention level was expected to be the same during the whole experimental session, as the subjects were instructed to simply fixate the dot in the centre of the screen. Additionally, the order of visual stimulation experiments was randomized between sessions to prevent order-related attentional influences on our results. Our findings likely show the sensitivity of dPCC to the global structure of the visual motion stimuli; however a possible effect of attentional modulation on this activity should be kept in mind. The posterior cingulate region has been shown to be activated under conditions of sustained attention (Braddick et al., 2001; Büchel et al., 1998; Carter et al., 1999) and to reveal greater activation when attention was directed to a radial moving dot pattern (Büchel et al., 1998). These results may suggest a role for the dPCC in encoding stimulus "attractiveness" taking into account that different kinds of moving stimuli evoke different degrees of attention (Franconeri & Simons, 2003). According to this, in our case, expanding fields probably induced higher attention than simple translation, while random motion was the less "attractive" compared to other stimuli. However, it was suggested by a previous study that, at least in V5, attentional modulation of some 900% would be required to explain the difference between complex motion and translation (Smith et al., 2006). Although estimates of attentional modulation in V5 are no guarantee for other regions, particularly for higher order cognitive areas; according to previous results and our own data, the dPCC seems to be an area involved more in multiple functions, one of which is the processing of the basic aspects of visual motion information.

Planum temporale/parietal operculum

We found bilateral activation of the PT/PO to translation, rotation, and radial motion while random motion resulted in little or no activation, which reflects the basic characteristics of the dPCC. Interestingly, the PT/PO area responded equally well to all of the different coherent motion types in contrast to the dPCC. In previous studies, the PT was found to be activated by sound location and motion in the acoustic space (Krumbholz et al., 2005; Pavani et al., 2002), by mouth movement (Sadato et al., 2005), and by visual speaking gestures (Pekkola et al., 2006), but its activation by visual motion was not yet described. The neighboring PO seems to be involved in vestibular processing (Eickhoff et al., 2006); however, the adjacent posterior insula is often activated when coherent motion is compared with static patterns (Claeys et al., 2003; Dupont et al., 1994; Orban et al., 2003; Sunaert et al., 1999) or a blank screen (Luks & Simpson, 2004). Decreased activation of this area was evoked by inducing perceived self-motion (Brandt et al., 1998; Dieterich et al., 2003; Kleinschmidt et al., 2002) suggesting that this region represents, at least in part, a portion of the parieto-insular vestibular cortex usually found activated by caloric vestibular stimulation and regarded as an integration center for multisensory vestibular function (Brandt & Dieterich, 1999; Eickhoff et al., 2006). The results suggest that the functional segregation of these cortical areas (PT, PO, posterior insula) using different types of sensory stimuli is probably often impossible because this complex is indeed involved in visual-vestibular-auditory integration, protects us from vestibular-visual mismatches (Brandt et al., 1998), and represents the human equivalent of the monkey parieto-insular vestibular cortex, described recently (Eickhoff et al., 2006). Here, we add new aspects to the already existing results, namely, that the PT/PO is involved in the processing of

different types of simple visual motion stimuli that represent the basic elements of the optic flow.

General aspects

In contrast to previous studies, we used visual stimuli that were omitted in the central aspect of the visual field in order to prevent passive tracking of motion by the eyes and to avoid stimulating the part of the visual field that is less sensitive for motion perception. It is known from previous studies, that the central and peripheral visual field aspects have different motion sensitivities; generally the motion sensitivity is increasing with eccentricity (Solomon & Sperling, 1995; Turano et al., 2005).

As it was not possible to record the eye-position during the fMRI experiments, we performed eye tracking measurements in additional experiments using the same stimulus material outside the MR-scanner. These experiments revealed that subjects fixated equally well during the different visual motion conditions. Nevertheless, theoretically there remains the possibility that our results reflect differential patterns of eye-movements. However, (1) subjects were instructed to fixate during the sessions and none of them reported fixation problems. (2) As stated above, the central 14° of the visual field were omitted in order to avoid passive tracking of the motion. (3) Rotation and expansion-contraction do not cause a problem for eye stability (Smith et al., 2006). Therefore, in our opinion, the present results are unlikely to reflect eye-movement related effects.

In summary, we aimed to identify and describe the properties of the dPCC and PT/PO of the human brain using fMRI with special emphasis on applying basic types of visual motion stimuli. Unlike in earlier reports (e.g., Sunaert et al., 1999), we were able to detect activation of the dPCC and the PT/PO in every single subject. We grouped the five stimuli employed into coherent and incoherent motion with the hypothesis that motion coherence would yield stronger activations and this was indeed observed. However, regarding the different coherent patterns, we considered the processing of radial and rotational motion to be more demanding than simple translational movements. While the dPCC exhibited increasing activation in line with the grade of stimulus complexity, PT/PO responded equally well to all of the different coherent motion types. This suggests that dPCC might play an important role for differentiating between complex coherent visual motion types, whereas PT/PO seems to encode motion-coherence per se.

In the last 10 years, neuroimaging studies have revealed an extensive network of motion-sensitive areas throughout the human brain, in addition to the already highly studied MT/V5 complex and thereby verifying and extending psychophysical and electrophysiological findings. However, a more detailed characterization of the basic properties of these motion-sensitive areas such as the dPCC and PT/PO described in the present study could help further understanding of the feed-forward and feed-back circuits in the processing of visual motion. Lesions and temporary or permanent disconnections of these circuits might result in malfunction of motion processing independently from the functional state of the classical motion-related dorsal stream. The relationship between different types of anatomical lesions related to these structures and neurological or psychiatric disorders associated with motion perception deficits such as dyslexia, schizophrenia, Alzheimer's disease, remains to be determined. Further studies using more complex types of visual motion stimuli, such as biological motion patterns are needed to identify the specific roles of the dPCC and the PT/PO in motion processing.

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