

Understanding non-biological dynamics with your own premotor system

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The human premotor cortex (PM) appears to subserve a variety of cognitive and motor functions, including the prediction of non-biological dynamics. In the present study we directly tested the correspondence of premotor correlates of predicting different non-biological dynamics and imagining different actions by means of functional magnetic resonance imaging. Prediction tasks on either spatial, object or rhythmic dynamics were expected to draw on premotor areas involved in motor imagery tasks for arm, hand and mouth movements, respectively. Firstly, the results confirmed comparable dorsal-to-ventral distributions of property effects (in prediction) and movement effects (in motor imagery) in PM. Secondly, even more direct correspondences were observed for mouth movement imagery and rhythm prediction in inferior ventral PM and for arm movement imagery and spatial prediction in dorsal PM. Hand movement imagery and object prediction led to activations in closely adjacent areas in left superior ventral PM. Together, the present findings support the notion that to-be-predicted stimulus dynamics and motor effectors are coupled in lateral PM according to a pragmatic default. Beyond that, the results add further support to the notion that the human PM is involved in the prediction of many if not all kinds of dynamics.

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Introduction

The dynamics we constantly perceive in our environment and their future states that we anticipate are of different pragmatic relevance for actions performed with different limbs. Reaching movements, for instance, call for spatial attention rather than for object attention, whereas the opposite is true for grasping movements. Meanwhile reaching causes the spatial properties in our environment to change and some reachable and graspable entities in the world are in motion themselves. Hence if we plan a reaching movement, we also anticipate and predict the spatial dynamics we cause ourselves and those which are caused externally. Previous functional magnetic resonance (fMRI) findings suggest that the lateral premotor cortex (PM) is crucially

involved in the prediction of non-biological (abstract) stimulus sequences (Schubotz and von Cramon, 2001, 2002a,b,c; Schubotz et al., 2003; Wolfensteller et al., 2004). This raised the question as to how these findings fit with the PM's classical role in planning, imagining and observing actions (Buccino et al., 2001; di Pellegrino et al., 1992; Ehrsson et al., 2003; Gentilucci et al., 1988; Sakreida et al., 2005). Recent evidence from cognitive psychology, neuropsychology and neurophysiology suggests an isomorphism between action and perception (Craighero et al., 1999; Prinz, 1990; Rizzolatti et al., 1987; Schubotz et al., 2003; Wilson, 2001). However, the nature of this isomorphism remains elusive. Based on fMRI data, the Habitual Pragmatic Body Map account recently proposed that the PM codes spatial dynamics in the arm field (dorsal), object dynamics in the hand field (superior ventral) and rhythmic dynamics in the vocal field (inferior ventral) (Schubotz et al., 2003). However, the focus of former studies was on either the premotor correlates of actions or on the premotor correlates of non-biological predictions. Hence the question remains as to how both functions relate to each other anatomically: is there an anatomical correspondence indicating a pragmatic default mapping of arm actions and spatial prediction, hand actions and object prediction and mouth actions and rhythm prediction, respectively? To directly test these assumptions in the present study, we employed three non-biological serial predictions tasks (spatial, object and rhythm) on the one hand and three motor imagery tasks on intransitive movements (arm, hand and mouth) on the other hand. The serial prediction task (SPT, Schubotz, 1999) allows investigating non-biological prediction without confounding motor planning while motor imagery of intransitive movements allows investigating motor actions without a confounding attentional focus on an external goal stimulus. Thus the experimental procedure aimed at investigating the premotor correlates of action and prediction as purely as possible in the same experimental group. Prediction conditions served as localizer tasks in order to identify premotor fields that were activated relatively more for a specific prediction condition, i.e., fields showing specific property effects for space, object and rhythm. Motor imagery conditions served as localizer tasks in order to identify premotor fields that were activated relatively more for a specific motor imagery condition, i.e., fields showing specific movement effects for arm, hand and mouth. Our question of interest

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was whether premotor property effects in prediction correspond to premotor movement effects in motor imagery (and vice versa). Here, the term *correspondence* will be used to refer to two patterns. First, it refers to the expected general dorsal–ventral distribution of differential premotor activations in both serial prediction and motor imagery tasks. Second, it refers to the direct comparison of property effects and movement effects in premotor regions of interest as described above. Note, however, that this does not necessarily imply congruency of the absolute locations of corresponding property-related and movement-related activations in PM.

Materials and methods

Participants

We obtained written consent from 16 participants (9 female, mean age 25 years, range 21–33) prior to the scanning session. All participants were right-handed, had normal or corrected-to-normal vision and were native German speakers. No participant had a history of neurological, major medical or psychiatric disorder; none was taking medication at the time of measurement.

Training

One to three days before the experimental session all participants took part in a training session. Three to-be-imagined

movements were instructed (cf. Fig. 1, lower part). To assess performance in motor imagery, ten movement times were recorded for each movement during imagery and execution, respectively. Participants pressed a button once they started to execute or imagine a movement and again once they had finished. None of the subjects showed overt movements during imagery. Subsequently, the six experimental tasks (see below) were trained until the critical performance level of 85% was reached. Immediately before scanning the movement times for movement execution movement imagery were recorded again for ten trials per condition.

Tasks

During the experimental session, participants performed six experimental tasks in a random trial design. We introduced two types of tasks: serial prediction tasks (SPT, Schubotz, 1999) for three stimulus properties and motor imagery tasks for three movements (cf. Fig. 1). To enhance the temporal resolution at which the BOLD signal was sampled, variable initial fixation intervals of 0, 500, 1000 or 1500 ms were inserted prior to the task cue at the beginning of each trial. The task cue (500 ms) was followed by a fixation period (500 ms). Thereafter, in serial prediction trials visual stimulation was given which lasted for 5700 ms. Correspondingly, the period in which subjects had to imagine the instructed movement in motor imagery trials had a

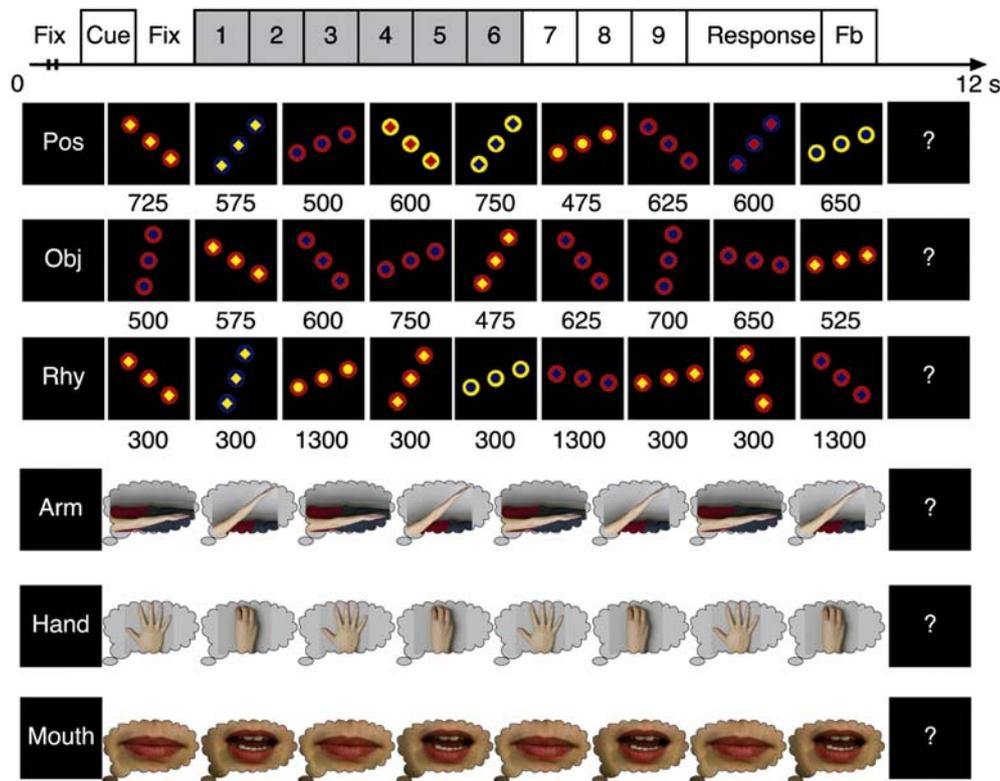


Fig. 1. Experimental paradigm. The broken line prior to the cue indicates the variable fixation interval. The analyzed epoch is indicated by a gray background color in the uppermost panel. The numbers below each frame show the duration of presentation in milliseconds. Serial prediction trials are depicted in the upper three panels. “Pos” indicates that serial prediction should be made on the basis of spatial positions; “Obj” indicates that serial prediction should be made on the basis of object features, and “Rhy” indicates that serial prediction should be made on the basis of rhythms. Motor imagery trials are depicted in the lower three panels. Note that participants had to fixate the cross that was presented in the center of the black screen. The instructed movements are shown here for illustration only.

length of 5700 ms. Following this, the response cue was presented and remained visible until the response was delivered (maximally 1500 ms). The response was immediately followed by a valid feedback (500 ms). Due to varying initial fixation and response intervals, the intertrial interval ranged from 1600 ms to 4800 ms. The experimental session comprised 24 trials per experimental condition, i.e., 144 experimental trials in total, and 24 resting baseline trials, during which only a fixation aid was presented in the center of the screen. All visual stimuli were presented with VisuaStim (Magnetic Resonance Technologies, Northridge, CA) over two small thin film transistor monitors placed directly in front of the eyes, simulating a distance to a normal computer monitor of ~1000 mm.

Serial prediction task

The serial prediction task requires participants to detect a sequential pattern within a series of stimuli and to predict its further course. The visual stimuli were composed such that they concurrently provided spatial, object and rhythmic information (cf. Fig. 1). We employed twelve different visual items that will be referred to as objects hereafter. Each object consisted of a large circle ($d=21$ mm) with either a smaller circle or a diamond ($d=12$ mm) embedded in its center. The two parts of an object differed in color (red, yellow or blue). Three identical objects were presented at once, one in the center of the screen and two at opposite locations on a virtual circle ($d=64$ mm) around the center of the screen. These locations, hereafter referred to as positions, were equidistantly arranged (distance 13°), starting at 13° , skipping 0° , 90° , 180° and 270° . Nine rhythms were induced by varying the duration of three successive stimuli (300, 600, 1000 and 1300 ms), which added up to 1900 ms. At the beginning of each trial, the task cue indicated, whether participants should attend to the positions, objects or the rhythms of the stimuli. Note that the sequential pattern of a given trial referred to the instructed stimulus property only, whereas the to-be-ignored, i.e., irrelevant stimulus properties were randomly varied. Following the task cue and fixation, nine stimuli were presented successively without temporal gap. In order to test the participants' prediction performance, a sequential violation was induced in 50% of all SPT trials. This was done by transferring the 7th or 8th stimulus to the end of the trial or by replacing the 9th stimulus with the 7th stimulus. The following pictures were presented in normal succession, so that no temporal gap was perceived. At the end of each trial, participants had to indicate by button press whether or not the sequential pattern had been violated.

Motor imagery task

In motor imagery trials, the task cue indicated whether participants should imagine an arm, hand, or mouth movement. In the arm condition, participants imagined lifting the outstretched right arm to an angle not exceeding 30° and lowering it back to the starting position. In the hand condition, participants imagined spreading and contracting all fingers of the right hand. In the mouth condition, participants imagined opening and closing the mouth as if vocalizing the German letters "MAM". Participants were instructed to fixate on the crosshair presented in the center of the screen and to repetitively imagine the instructed movement until the response cue was presented. Subsequently, they had to indicate by button press whether or not they had succeeded in concentrating on the to-be-imagined movement.

Scanning procedure

Participants lay supine on the scanner bed, with index finger and middle finger of the left hand positioned over the two buttons of a response box. Participants' hands were carefully stabilized, and form-fitting cushions were used to prevent arm, hand, and head motion. To attenuate scanner noise, participants were provided with earplugs.

Imaging was performed at a 3 T scanner (Siemens TRIO, Erlangen, Germany) equipped with the standard birdcage head coil. Twenty-two axial slices (64×64 pixel matrix, field of view 192 mm, thickness 4 mm, spacing 0.8 mm) positioned parallel to the bicommissural plane (AC–PC) were acquired using a single-shot gradient echo-planar imaging (EPI) sequence (TE 30 ms, flip angle 90° , repetition time 2000 ms). In total, 1014 functional images were acquired in a single run. Prior to the functional run, 22 two-dimensional anatomical images (256×256 pixel matrix, MDEFT sequence) and T1-weighted EPI images were acquired.

Data analysis

Functional data were motion-corrected online with the Siemens motion correction protocol (Siemens, Erlangen, Germany). Further processing of the fMRI data was performed using the software package LIPSIA (Lohmann et al., 2001). In the pre-processing, low-frequency components of the signal (i.e., baseline drifts) were suppressed by applying a 1/160 Hz high-pass filter. A spatial smoothing was performed using a Gaussian kernel with a standard deviation of 0.8. With a voxel size of 3 mm, this is equivalent to a full width at half maximum (FWHM) of 5.65 mm.

To correct for the temporal offset between the slices acquired in one image a sinc-interpolation algorithm based on the Nyquist–Shannon sampling theorem (Press et al., 1992) was employed. Subsequently, functional data sets were aligned with the high-resolution three-dimensional (3D) reference data sets (160 slices, 1 mm thickness) by rigid linear registration with six degrees of freedom (three rotational, three translational). These rotational and translational parameters were acquired by registering the two-dimensional MDEFT and EPI-T1 with the individual 3D reference data set. Subsequently, the rotational and translational parameters were transformed to standard size (Talairach and Tournoux, 1988) by linear scaling. Transformed parameters were then used to align the functional slices with the stereotactic coordinate system by means of trilinear interpolation, thus generating output data with a spatial resolution of $3 \times 3 \times 3$ mm (27 mm^3).

The statistical analysis was based on a least squares estimation using the General Linear Model (GLM) for serially autocorrelated observations (random effects model, Friston et al., 1995). The design matrix was generated with a boxcar function, convolved with the hemodynamic response function, including a delay of 6 s. The analyzed epochs (cf. Fig. 1) had a length of 3800 ms, starting 1000 ms after the onset of the task cue. Incorrectly answered SPT trials and unsuccessfully performed motor imagery trials were excluded from the analysis. In order to account for the temporal autocorrelation of the data (Worsley and Friston, 1995), the model equation, including the observation data, the design matrix and the error term, was convolved with a Gaussian kernel of dispersion of 4 s FWHM. In the following, nine contrast images, containing the estimated raw-score differences between specified conditions, were generated for each participant. Each of the three serial prediction conditions was contrasted with the other two (position (P) vs.

object (O) and rhythm (R); O vs. P and R; R vs. O and P). In the same manner each of the three motor imagery conditions was contrasted with the other two (arm (A) vs. hand (H) and mouth (M); H vs. A and M; M vs. A and H). Additionally, each serial prediction condition and each motor imagery condition were contrasted with the resting baseline. As all individual functional data sets were aligned with the standard stereotactic reference space, a second-level group analysis could be performed subsequently. This group analysis consisted of a one-sample *t*-test across the contrast images of all participants that indicated whether observed differences between conditions were significantly distinct from zero. Subsequently, *t* values were transformed into *Z*-scores.

Combining a voxel-based threshold with a minimum cluster size has been argued to be a good approach to protect against false-positive activations (e.g., Forman et al., 1995). We used this double-threshold approach, considering an area to be activated only if it comprised at least 10 contiguous voxels (270 mm³). Given the specific anatomical hypotheses, the individual voxel height threshold for premotor regions in the direct task contrasts in serial prediction and motor imagery was set to $Z > 2.58$ ($p = 0.005$, uncorrected). Activations in brain regions for which we had no a priori hypotheses were thresholded at $Z > 3.09$ ($p = 0.001$, uncorrected) and required to exceed a volume of 270 mm³. Furthermore, the general engagement of lateral PM during serial prediction and motor imagery was confirmed in the resting baseline contrasts ($Z > 3.09$, minimum cluster size = 270 mm³). In order to quantify the overlap between property effects and movement effects in PM, conjunction analyses using the logical combination method, which has been suggested by Joseph et al. (2002), were performed (P vs. O and $R \cap A$ vs. H and M; O vs. P and $R \cap H$ vs. A and M; R vs. P and $O \cap M$ vs. A and H). Again, the height threshold was set to $Z = 2.58$. Another set of conjunction analyses (e.g., P vs. $O \cap P$ vs. R) verified the premotor regions of interest as identified in the direct task contrasts (e.g., P vs. O and R).

Additionally, we analyzed the signal change in several functionally defined premotor regions of interest (ROIs). An ROI was defined as the peak voxel of a premotor area that was activated either relatively more for a specific prediction condition (property effect) or relatively more for a specific motor imagery condition (movement effect). Within each ROI, the percentage signal change was calculated in relation to the mean signal intensity across all time steps. Resting baseline signal change was subtracted from the signal change in the experimental conditions. Subsequently, the maximal percentage signal change was obtained for the period 4 to 11 s after cue onset separately for each condition and participant.

Results

Behavioral results

The SPT trials with and without sequential violation did not differ in terms of error rates ($p > 0.05$). Therefore, they were collapsed in the following analyses. Separate ANOVAs were carried out with repeated measures on to-be-attended PROPERTY in serial prediction (position, object, rhythm) or MOVEMENT in motor imagery (arm, hand, mouth), respectively. In serial prediction tasks, the to-be-attended PROPERTY exhibited a main effect on error rates ($F_{(2,30)} = 3.85$, $p = 0.032$). This was due to the participants making significantly fewer errors in position SPT ($M = 7.6\%$) than in object SPT ($M = 14.6\%$, $p = 0.004$). In motor

imagery tasks, the MOVEMENT did not influence error rates ($F_{(1,4,21)} = 0.73$, $p = 0.492$).

Movement times recorded outside the scanner were collapsed across the two sessions and entered into an ANOVA with repeated measures on within-subject factors movement MODE (executed vs. imagined) and MOVEMENT (arm, hand, mouth). The analysis revealed a main effect for MOVEMENT ($F_{(1,2,18)} = 62.08$, $p < 0.001$) and a MOVEMENT by MODE interaction ($F_{(2,30)} = 11.47$, $p < 0.001$), but no main effect for movement MODE ($F_{(1,15)} = 0.68$, $p = 0.423$). Mean movement times are depicted in Fig. 2. Paired *t*-tests revealed that execution and imagery of mouth movements were done fastest followed by hand movements which were done significantly faster than arm movements (all $t_{(15)} > 2.59$, $p < 0.05$). Moreover, mouth movement imagery took longer than execution ($t_{(15)} = 2.25$, $p = 0.040$), whereas the opposite held for arm movements ($t_{(15)} = 3.49$, $p = 0.003$). Hand movement times did not differ between imagery and execution ($t_{(15)} = 0.83$, $p = 0.42$). Moreover, for all motor effectors the movement times for execution and imagery were highly correlated (Pearson's $r = 0.77$ – 0.88 , $p < 0.001$).

Imaging results

Contrasting serial prediction against the resting baseline revealed engagement of lateral PM for all prediction tasks (cf. Table S1). The SPT trials with and without sequential violation did not differ in terms of premotor activation and were therefore collapsed in the following analyses. Direct task contrasts showed that prediction of positions specifically engaged the dorsal PM bilaterally, prediction of objects specifically engaged left superior ventral PM, and prediction of rhythms specifically engaged the inferior ventral PM bilaterally (cf. Fig. 3 and Table 1). Moreover, position SPT specifically engaged bilateral inferior and superior parietal cortex laterally and medially, including precuneus and cuneus. The object SPT specifically involved left lateral prefrontal areas and the intraparietal sulcus in both hemispheres. Additionally, bilateral extrastriate visual areas, including fusiform and lingual gyrus, were relatively more involved during object as compared to position and rhythm prediction. Finally, the rhythm SPT specifically engaged the supplementary motor area (SMA) and pre-SMA and the posterior part of the inferior frontal gyrus, bilaterally, corresponding to Brodmann areas (BA) 44 and 45 extending into the anterior insula.

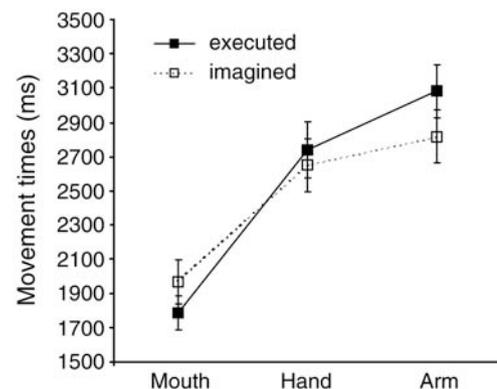


Fig. 2. Movement times for motor execution and motor imagery. The participants were instructed to indicate the beginning and ending of each executed and imagined movement by button press. Mean movement times averaged across the two recording sessions are shown. Bars indicate standard errors.

Furthermore, areas in right anterior prefrontal cortex, right parietal cortex and in the right temporal cortex covering large parts of the superior temporal sulcus were engaged relatively more in rhythm SPT than in object and position SPT.

Contrasting motor imagery against the resting baseline revealed activation in lateral PM and in the posterior part of the inferior frontal gyrus (BA 44) in both hemispheres for all imagery conditions (cf. Table S2). Direct task contrasts (cf. Fig. 4 and Table 2) revealed that arm motor imagery specifically engaged the left dorsal PM, while hand motor imagery specifically engaged the left dorsal PM and the left superior ventral PM. Note that the latter area was more strongly engaged during hand imagery as compared to arm motor imagery but not as compared to mouth motor imagery (cf. Fig. 5). Mouth motor imagery specifically engaged the inferior

ventral PM, bilaterally (cf. Fig. 4). Outside the lateral PM, right arm movement imagery specifically involved the superior part of the left postcentral gyrus and the precuneus. Right hand imagery specifically involved left primary somatosensory cortex and secondary somatosensory cortex (parietal operculum). Finally, mouth movement imagery specifically involved bilateral sensorimotor mouth areas, the posterior SMA and the cerebellum.

Signal change analyses in premotor regions of interest

The maximal percentage signal change values (for details, see the Materials and methods section) were entered into paired *t*-tests. Note that *t*-tests comparing motor imagery conditions were conducted for ROIs that had been identified by a property effect in direct serial prediction contrasts (cf. Fig. 3). Accordingly, *t*-tests

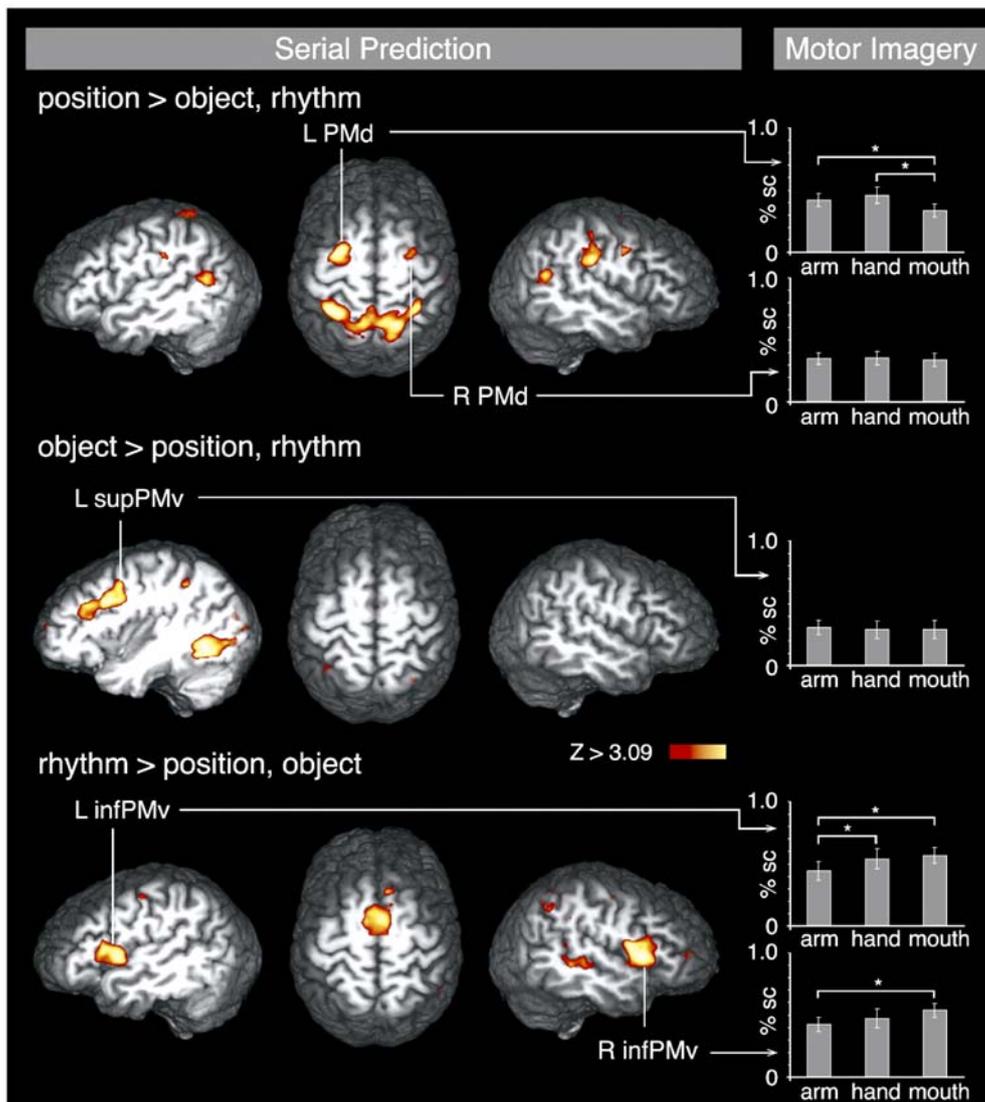


Fig. 3. Property effects in serial prediction. Group-averaged cerebral activations which were relatively stronger for a specific stimulus property in serial prediction are shown on the left. Areas within the premotor cortex were considered as activated if they comprised at least 10 contiguous voxels exceeding a Z-score of 2.58. Areas outside lateral PM were considered as activated if they comprised at least 10 contiguous voxels exceeding a Z-score of 3.09 (for details see Materials and methods section). From the premotor areas showing property effects in serial prediction (for Talairach coordinates see Table 1) the maximal percentage signal change values were extracted for the three motor imagery tasks. These values are shown in the bar graphs on the right together with corresponding standard errors. Significant differences ($p < 0.05$) are indicated by asterisks. Abbreviations: % sc percentage signal change, *infPMv* inferior ventral premotor cortex, *PMd* dorsal premotor cortex, *supPMv* superior ventral premotor cortex.

Table 1
Property effects in serial prediction

Anatomical specification		mm ³	x	y	z	Z
<i>Position > object, rhythm</i>						
Superior precentral sulcus (PMd)	R	2866	25	-4	53	4.8
	L	6089	-22	-4	50	4.7
Precentral gyrus (PMv)	R	546	50	-4	34	3.6
Parietal operculum	R	1448	50	-25	29	4.3
Superior parietal lobule, precuneus	B	8696	-26	-49	61	4.9
Temporoparietooccipital transition cortex	R	2283	41	-55	9	4.9
	L	1688	-41	-58	17	4.0
Inferior precuneus	R	1651	2	-58	15	4.4
STS, horizontal posterior segment	L	344	-35	-76	32	3.9
Cuneus	R	1175	11	-91	15	3.8
<i>Object > position, rhythm</i>						
Middle frontal sulcus	L	627	-26	50	11	4.2
Anterior superior insula	R	491	34	20	-1	4.2
Middle frontal gyrus	L	4812	-37	14	29	4.7
Inferior precentral sulcus (superior PMv)	L	l.m.	-37	2	40	4.1
Cingulate sulcus	R	815	8	23	38	3.7
Intraparietal sulcus, horizontal branch	R	1314	26	-61	41	4.1
	L	3573	-28	-58	41	5.1
Parieto-occipital fissure	R	296	23	-61	14	4.8
Collateral sulcus	R	5428	28	-58	-1	4.9
Lateral occipital gyrus	R	5006	31	-85	14	4.9
	L	13153	-28	-85	-3	4.9
<i>Rhythm > object, position</i>						
Anterior inferior frontal sulcus	R	329	43	44	6	3.9
Precentral gyrus/IFG (inferior PMv)	R	10271	49	8	6	5.4
	L	8325	-49	5	6	4.7
SMA/pre-SMA	L	3056	4	-1	61	4.6
Precentral gyrus (MI)	L	308	-46	-13	46	3.9
Superior temporal sulcus	R	1871	55	-43	15	4.2
Angular gyrus	R	500	44	-55	40	3.8
Putamen	R	729	26	5	12	4.3

Anatomical specification, hemisphere (L, R), Talairach coordinates (x, y, z), volume (mm³) and maximal Z-scores of brain areas showing property effects in serial prediction. All reported activations comprised at least 10 voxels (270 mm³) that exceeded a Z-score of 2.58 ($p < 0.005$) within lateral premotor cortex or a Z-score of 3.09 ($p < 0.001$) outside lateral premotor cortex. Local maxima (l.m.) are distinct maxima that were separated by at least 10 mm. Abbreviations: *B* bilateral, *IFG* inferior frontal gyrus, *L* left hemisphere, *MI* primary motor cortex, *PMd* dorsal premotor cortex, *PMv* ventral premotor cortex, *pre-SMA* pre-supplementary motor area, *R* right hemisphere, *SMA* supplementary motor area, *STS* superior temporal sulcus.

comparing serial prediction tasks were conducted for ROIs as identified by a movement effect direct motor imagery contrasts (cf. Fig. 4). By doing so, we tested for movement effects in premotor areas showing property effects and vice versa. The contrast in which an ROI was identified is given in brackets.

In left dorsal PM ($P > O$, R), arm and hand imagery elicited stronger activation than mouth imagery ($t_{(15)} > 2.30$, $p < 0.05$). In left inferior PM ($R > P$, O), mouth and hand imagery elicited stronger activation than arm imagery ($t_{(15)} > 3.04$, $p < 0.05$). In right inferior PM ($R > P$, O), mouth imagery elicited stronger activation than arm imagery ($t_{(15)} = 2.31$, $p = 0.04$). In right dorsal PM ($P > O$, R) and left superior ventral PM ($O > P$, R), the three motor imagery tasks did not differ ($t_{(15)} < 0.51$, $p > 0.61$).

Within the two ROIs in left dorsal PM showing movement effects ($A > H$, M and $H > A$, M), the prediction of positions elicited stronger

activation than prediction of objects and rhythms ($t_{(15)} > 2.13$, $p \leq 0.05$). In the left superior ventral PM ($H > A$), object and position prediction showed a tendency towards greater activation than rhythm prediction ($t_{(15)} > 1.86$, $p < 0.08$, cf. Fig. 5). In left inferior PM ($M > A$, H), prediction of rhythms showed a tendency towards greater activation than prediction of positions and objects ($t_{(15)} > 1.99$, $p < 0.07$). Within right inferior PM ($M > A$, H), prediction of rhythms elicited stronger activation than position prediction ($t_{(15)} = 2.27$, $p = 0.04$) and showed a tendency towards greater activation than object prediction ($t_{(15)} = 1.86$, $p = 0.08$).

These results were supported by a conjunction analysis performed on direct task contrasts on serial prediction and direct task contrasts on motor imagery. The analysis revealed an overlap for position prediction and arm movement imagery in left PMd. Furthermore, overlap of rhythm prediction and mouth movement imagery was observed for the inferiormost part of the PMv including precentral gyrus and the posterior part of the inferior frontal gyrus bilaterally (cf. Table 3).

Discussion

It has been shown that the PM subserves many different motor and cognitive functions, including the prediction of non-biological stimulus sequences (Schubotz and von Cramon, 2001, 2002a,b,c; Schubotz et al., 2003). The question of interest here was how the latter function relates to the classical role of PM in action planning. To address this question, we compared the premotor correlates of serial prediction tasks on non-biological stimulus sequences (spatial, object and rhythm) with the premotor correlates of motor imagery (arm, hand and mouth). On the basis of the Habitual Pragmatic Body Map account (Schubotz et al., 2003) we hypothesized that the pragmatic default mapping of stimulus properties and motor effectors would be reflected by corresponding property effects (in serial prediction) and movement effects (in motor imagery) in lateral PM. As a result, the prediction of spatial, object-related and rhythmic properties was associated with activation in PMd, superior PMv and inferior PMv, respectively. This was a direct replication of previous findings on non-biological prediction (Schubotz and von Cramon, 2001). A corresponding dorsal-to-ventral distribution was confirmed for premotor fields that were relatively more activated for arm, hand or mouth motor imagery tasks, respectively. Hence, first of all the present data confirm a general correspondence between to-be-predicted stimulus properties and imagined movements in terms of the dorsal-to-ventral distribution of premotor activation. But there are even more direct correspondences of movement effects and property effects in PM as confirmed by ROI and conjunction analyses. Arm and hand movement imagery engaged the left PMd most strongly, which was relatively more activated in spatial prediction. Conversely, spatial prediction engaged areas in left PMd most strongly, which were relatively more activated for arm imagery and hand imagery. A parallel pattern was observed for rhythm prediction and mouth movement imagery in inferior PMv. We did not observe such direct overlap for object prediction and hand movement imagery in superior PMv. Rather, these tasks specifically engaged closely adjacent areas in left superior PMv, located in the precentral sulcus for object prediction, and slightly more posteriorly on the lateral surface of the precentral gyrus for hand imagery. This latter finding is in line with the notion of an anterior–posterior gradient of attentional to motor processes as proposed by Boussaoud and co-workers for the dorsal premotor cortex (Boussaoud, 2001; Simon et al., 2002).

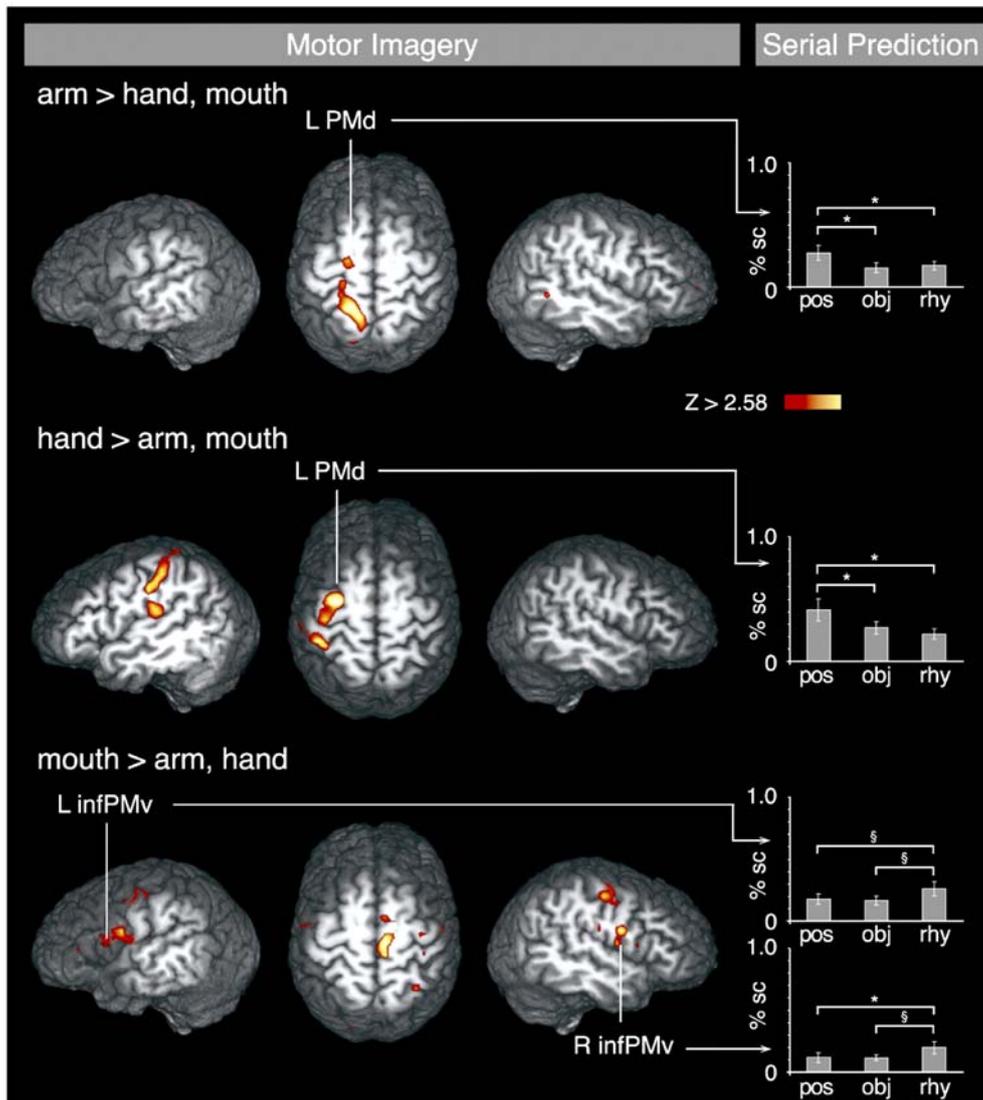


Fig. 4. Movement effects in motor imagery. Group-averaged cerebral activations that were relatively stronger for a specific movement in motor imagery are shown on the left. From the premotor areas showing movement effects in motor imagery (for Talairach coordinates see Table 2) the maximal percentage signal change values were extracted for the three serial prediction tasks. These values are shown in the bar graphs on the right together with the corresponding standard errors. Significant differences ($p < 0.05$) are indicated by asterisks, differences in the range of a statistical trend towards significance are indicated by “§”. Abbreviations: *obj* object, *pos* position, *rhy* rhythm. All other conventions as in Fig. 3.

Together, the present results suggest that the correspondences of non-biological prediction and motor imagery in human PM reflect a pragmatic default. On the basis of neurophysiological findings in monkeys and behavioral data in humans, Rizzolatti and co-workers have suggested a correspondence of spatial attention and action in dorsal PM (Premotor Theory of Attention, Rizzolatti et al., 1987; Rizzolatti et al., 1994). Extending the original scope of the theory, it has been proposed that a similar mechanism holds for object-related attention and grasping actions (visuo-motor priming, Craighero et al., 1999; Craighero et al., 2002). The present study provides fMRI evidence for this notion and shows moreover that it applies to three dimensions: to the prediction of spatial dynamics and arm (and hand) movements in PMd, to the prediction of object dynamics and hand movements in superior PMv and to the prediction of rhythm dynamics and mouth movements in inferior PMv. The lateralization of movement effects in motor imagery is perfectly in line with what

has been reported in the literature (for a review see e.g., Schubotz and von Cramon, 2003). As for the serial prediction tasks, the bilateral activations for rhythm and the left hemispheric activation for object dynamics correspond to a representation of these properties according to their best adapted motor effectors. The bilateral activation for spatial prediction fits with the view that the best adapted effectors are arms and eyes. Hence, as we have argued before, perceptual attention, particularly when anticipatory, appears to be a consequence of activation of brain regions which are also involved in the transformation of perceptual information into action and vice versa (Schubotz et al., 2003). As to the functional relevance of this pragmatic default mapping of action and prediction, from a traditional point of view, it may reflect the role of lateral PM in sensory-guided action (Goldberg, 1985). Alternatively, it could reflect the preparation of actions in terms of their anticipated perceptual effects as suggested by recent psychological theories

Table 2
Movement effects in motor imagery

Anatomical specification		mm ³	x	y	z	Z
<i>Arm > hand, mouth</i>						
Precentral gyrus (PMd)	L	1.m.	-17	-13	61	3.5
Superior parietal lobe, precuneus	L	1529	-16	-46	62	4.5
<i>Hand > arm, mouth</i>						
Precentral gyrus (PMd)	L	6829	-26	-10	61	4.7
Precentral gyrus (superior PMv) ^a	L	336	-50	-1	41	3.3
Postcentral gyrus (SI)	L	2019	-38	-34	52	4.2
Inferior postcentral sulcus	L	1.m.	-50	-19	34	3.6
Parietal operculum (SII)	L	357	-44	-25	20	4.4
<i>Mouth > arm, hand</i>						
Precentral gyrus (inferior PMv)	R	587	52	-4	20	3.9
	L	1.m.	-56	2	18	3.4
Paracentral lobule/posterior SMA	R	369	7	-22	56	3.9
Precentral gyrus (MI)	R	610	43	-13	49	3.8
	L	554	-46	-13	43	3.8
	L	313	-50	-10	15	4.4
Cerebellum	L	649	-22	-55	-10	3.8
	L	1.m.	-5	-55	-6	3.7

Anatomical specification, hemisphere (L, R), Talairach coordinates (x, y, z), volume (mm³) and maximal Z-scores of brain areas showing movement effects in motor imagery. Abbreviations: *L* left hemisphere, *MI* primary motor cortex, *PMd* dorsal premotor cortex, *PMv* ventral premotor cortex, *R* right hemisphere, *SI* primary somatosensory cortex, *SII* secondary somatosensory cortex, *SMA* supplementary motor area.

^a This activation was observed in the direct contrast of hand and arm movement imagery. All other conventions as in Table 1.

(Common Coding, Prinz, 1990; Theory of Event Coding, Hommel et al., 2001).

It has been argued that the PM is specifically involved in transitive, i.e., goal-related actions (Gallese, 2000; Umiltà, 2004). However, recent rTMS (Fadiga et al., 1999; Fadiga et al., 1995) and fMRI findings (Sakreida et al., 2005) in humans indicate the

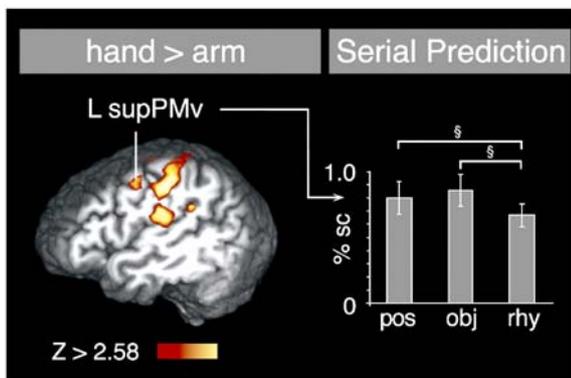


Fig. 5. Hand vs. arm movement imagery. Group-averaged cerebral activations that were relatively stronger during hand movement imagery as compared to arm movement imagery are shown on the left. The maximal percentage signal changes for the three serial prediction tasks were extracted from superior ventral PM (supPMv, for Talairach coordinates see Table 2). The values are shown in the bar graphs on the right together with corresponding standard errors. Differences in the range of a statistical tendency towards significance are indicated by “§”. Abbreviations: *obj* object, *pos* position, *rhy* rhythm. All other conventions as in Fig. 3.

Table 3
Overlap of property effects and movement effects in lateral PM

Anatomical specification		mm ³	x	y	z	Z
<i>Position ∩ arm</i>						
Precentral gyrus (PMd)	L	243	-20	-12	60	3.0
<i>Rhythm ∩ mouth</i>						
Precentral gyrus (inferior PMv)	R	162	52	0	18	3.0
Inferior frontal gyrus, pars opercularis (BA 44)	R	162	49	9	12	3.0
	L	324	-56	12	15	3.2

Anatomical specification, hemisphere (L, R), Talairach coordinates (x, y, z), volume (mm³) and maximal Z-scores of premotor areas showing corresponding property effects and movement effects. Direct task contrasts for serial prediction and direct task contrasts for motor imagery were subjected to a conjunction analysis. All reported activations exceeded a Z-score of 2.58 ($p < 0.005$).

observation that intransitive movements suffice to engage motor and premotor cortex in a roughly somatotopic manner. Here we employed highly overlearned, simple and intransitive movements for the motor imagery tasks. Our findings are generally in line with studies showing that motor imagery suffices to engage PM and lend further support to the notion of a restricted somatotopy for observed and imagined movements in lateral PM (e.g., Dechent et al., 2004; Ehrsson et al., 2003; Gerardin et al., 2000; Hanakawa et al., 2003; Meister et al., 2004). Arm and mouth motor imagery exposed fairly clear-cut activations in dorsal and inferior ventral premotor areas. In contrast, hand motor imagery showed two premotor foci of activation, one in PMd and one in superior PMv. The large extent of hand representation in the precentral gyrus and its overlap with arm and mouth representations may be the reason for this particular finding. Involvement of the hands in reaching, grasping and transport to the mouth is reflected by the presence of highly specialized premotor neurons distributed along the way from dorsal to ventral areas in the PM of the monkey (Murata et al., 1997; Raos et al., 2003, 2004; Rizzolatti et al., 1988). Some animal models suggest that primary motor cortex and premotor cortex contain several hand representations, which are differentiated by their specific workspaces, such as hand-to-mouth transport, hand-to-chest transport and defensive gestures with hand and arm over the head region (Graziano et al., 2002). In a recent study, Dum and Strick (2005) have shown that both dorsal and ventral premotor areas project to the digit representation in primary motor cortex. On a more conceptual level, Schieber has argued that biomechanical interdependencies of limbs could explain a limited somatotopy in the frontal motor cortices (Schieber, 2001). Whereas mouth and arm movements are biomechanically independent of each other, both of these effectors closely interact with the hand, such as in hand-to-mouth transport or reaching-and-grasping. Hence, the hand representation would be suggested to extend into the representations of both the arm and the mouth. Together, these data provide a plausible explanation for the finding that hand imagery caused a less focused activation than either mouth or arm imagery. This in turn might partly account for the finding that object prediction and hand imagery were not linked as closely as spatial prediction and arm and hand movement imagery, or rhythm prediction and mouth movement imagery, respectively. However, it does not fully explain why object prediction was not engaging the two premotor hand foci strongest and hand imagery was not engaging the premotor object focus strongest. In fact, the less direct link between object prediction and hand imagery might be

due to two aspects: firstly, the multiple representations of the hand and, secondly, the relative abstractness of the object properties (color–shape combinations) used for serial prediction. This leads to the question as to what would happen if true objects were used. In doing so, it might be possible to increase the overlap between object prediction and hand movements. However, this raises two potential problems: one being that real objects are easier to verbalize and the other being that real objects might automatically be presented in terms of object affordance (see Gentilucci, 2002; Tucker and Ellis, 1998).

Based on single-cell recording in non-human primates multiple premotor–parietal loops have been shown to code for different pragmatic features of actions (see e.g., Geyer et al., 2000; Matelli and Luppino, 2001; Rizzolatti and Matelli, 2003). In line with that, in the present study we observed activation in the superior parietal lobule for spatial prediction and arm imagery, in the intraparietal sulcus for object prediction and in primary and secondary somatosensory cortex for hand imagery. The importance of intact fronto-parietal circuits for the kind of non-biological prediction we investigated here has been corroborated by a clinical study showing that prediction is impaired not only in patients with premotor lesions but also in patients with parietal lesions (Schubotz et al., 2004). However, the property effects in parietal cortex appear to depend on the stimulus modality as they were only observed with visual stimuli (Schubotz and von Cramon, 2001). Auditory stimuli did not differentially engage parietal areas but rather temporal areas (Schubotz et al., 2003). In contrast, the property effects in lateral PM were not influenced by stimulus modality. Hence, the premotor cortex appears to code biological dynamics, i.e., actions and to-be-predicted non-biological dynamics in a modality-unspecific manner subserving a pragmatically driven attentional categorization of the environment.

How do our results fit with findings on the so-called “mirror neuron system”? Mirror neurons in the lateral PM of the macaque respond to both performed and observed action. They are suggested to play a role in understanding actions by mapping observed movements onto own action representations, thereby allowing the action goal (Gallese et al., 1996) or the motor intention (Jacob and Jeannerod, 2005) to be inferred. The observing animal probably automatically sets up several possible action outcomes on the basis of forward models which run in parallel and which are fed by both observation and own motor abilities (Wolpert et al., 2001). However, little is known about the neural basis of these processes. In humans, Broca’s area (BA 44 or BA 44/45) is suggested to correspond to the area of mirror neurons in the macaque (F5, Rizzolatti and Craighero, 2004), which in turn is suggested to subserve the inference of the action goal or its representation (Rizzolatti et al., 1998; Umiltà et al., 2001). On the other hand, action observation engages the entire lateral PM (BA 6) in a roughly somatotopical manner depending on the limb involved in the observed action (Buccino et al., 2001; Sakreida et al., 2005). Based on findings on action execution and action observation in both humans and monkeys, the “mirror system” in PM has been argued to subserve social cognition (Decety and Grezes, 2006; Iacoboni et al., 2005, but see Jacob and Jeannerod, 2005). However, understanding others’ behavior is only one of the factors which are pragmatically relevant to a person’s future behavior. In fact we have to understand the dynamics of animate and inanimate entities in our environment. The notion of a “Habitual Pragmatic Body Map” in the lateral PM claims that any dynamic event draws on the lateral PM as long as prediction is required (Schubotz et al., 2003). Thereby it may enable the

anticipation of the consequences these changes will have on own actions and vice versa. The present findings of correspondence for (imagined) action and non-biological prediction in human lateral PM fit in more generally with the exploitation of forward models for higher cognitive functions (Grush, 2004; Wolpert and Flanagan, 2001). From the view of embodied cognition one may further speculate that the correspondence of premotor activations in non-biological prediction and motor imagery reflects an isomorphism arising from motor simulation of the non-biological dynamics (Wilson, 2001, 2002). While this is an exciting hypothesis, it cannot explain why even very abstract stimulus dynamics as for instance color transition patterns without any obvious pragmatic meaning elicit selective ventral premotor responses (Schubotz and von Cramon, 2002b). So far, we see several alternative explanations for the pragmatic default correspondence between movements and predictable stimuli in PM: it could (1) arise from coding the stimulus dynamic in terms of the most appropriate movement, (2) from coding the movement in terms of the most relevant (goal-defining) stimulus property (see also Awh et al., 2006) or (3) from simulating the stimulus dynamics with the most appropriate limb representation in PM.

Critical considerations

Finally, we would like to address some critical considerations that might come to the interested reader’s mind. The serial prediction tasks and the motor imagery tasks we employed were not symmetric in terms of visual stimulation, namely there was visual stimulation in prediction but only a fixation cross in motor imagery. However, such global differences did not affect our data as the results we discuss here are based on direct task contrasts in both prediction and motor imagery conditions, i.e., we always refer to relative differences in premotor activation. In terms of visual stimulation, one might argue that an action observation task would have been more comparable to the prediction task than a motor imagery task. However, we sought to investigate the premotor correlates of non-biological prediction and movements as purely as possible. The problem with an action observation condition is that we would concurrently introduce the confounding factor of stimulus attention for instance directed towards a to-be-grasped object either by directly showing that object or less directly in pantomimed actions. The same problem arises with goal-directed motor imagery. Moreover, it has been argued that perceiving an object automatically activates the motor program describing how to act upon it (object affordance, Tucker and Ellis, 1998). Accordingly, overlap between serial prediction task and such goal-directed action observation or goal-directed motor imagery tasks would have been less informative because the premotor activation could have been attributed to attentional modulation in both types of tasks.

Another issue refers to the motor imagery tasks. Unfortunately, implicit procedures that provide trial-by-trial behavioral data on the participants’ imagery performance exist for hand movements only (e.g., Johnson, 2000). However, we believe that the present functional and behavioral data confirm that participants really performed motor imagery. Anatomically, the movement effects in the sensorimotor and parietal cortex are consistent with previous findings on arm (Rushworth et al., 1997; Scott et al., 1997), hand (Stippich et al., 2004, 2005; Young et al., 2004) and mouth movements (Hesselmann et al., 2004; Lotze et al., 2000). Behaviorally, the movement times recorded outside the scanner differed consistently between the three motor effectors during

movement execution and motor imagery and the movement times for execution and imagery were highly correlated. Hence the claim that movement imagery and movement execution should follow the same biomechanical constraints appears to be fulfilled (Decety and Michel, 1989; Jeannerod, 1995, 1999; Jeannerod and Decety, 1995).

Finally, one has to consider whether prediction and motor imagery tasks influenced each other. However, as the results on prediction fit with previous results that were obtained in sessions without imagery tasks (Schubotz and von Cramon, 2001; Schubotz et al., 2003), and the results on motor imagery fit with previous results that were obtained in sessions without prediction tasks (see e.g., Ehrsson et al., 2003; Schubotz and von Cramon, 2003), this appears to be rather unlikely.

Conclusion

The present study confirmed direct correspondences between motor effectors in motor imagery and stimulus properties in prediction for several premotor fields. Hence the present findings shed new light on how the anticipation of dynamics in our environment and action planning are mapped onto each other in human PM. They support the Habitual Pragmatic Body Map account which claims that to-be-attended stimulus properties and motor effectors are represented in human lateral PM according to a default sensorimotor mapping (Schubotz et al., 2003) linking a given motor effector with the pragmatically most relevant stimulus property. Furthermore the present data further underline the functional relevance of the premotor cortex for non-motor processes in general and more specifically for non-biological anticipatory processes that are not devoted to understanding another person's behavior.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2007.03.040](https://doi.org/10.1016/j.neuroimage.2007.03.040).

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