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## Auditory what, where, and when: a sensory somatotopy in lateral premotor cortex

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Recent findings have demonstrated that attention to visual events engages the lateral premotor cortex even in the absence of motor planning. Here, we used functional magnetic resonance imaging to explore acoustically triggered activations within the lateral premotor cortex. Temporal (*when*), object-related (*what*), and spatial (*where*) auditory patterns were to be monitored for violations in a serial prediction task. As a result, we found a modality-dependent modulation for auditory events within the inferior ventrolateral premotor cortex, an area engaged in vocal plans. In addition, however, auditory activations were distributed within the entire premotor cortex depending on which stimulus property was attended to. Attention to where patterns was found to engage fields for gaze and reaching (dorsolateral premotor cortex), what patterns to engage fields for hand movements (superior ventrolateral premotor cortex), and when patterns to engage fields for vocal plans. Together, the findings confirm the idea of a sensory somatotopy in lateral premotor cortex, according to which a perceptual pattern triggers representations within that motor effector which would be most appropriate to generate it as an action effect.

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### Introduction

The lateral premotor cortex functions in the adaptation of planned movements onto perceptual events, i.e., sensorimotor mapping (Wise, 1985). Until recently, this was suggested to be achieved by a stepwise transformation of sensory information within parietal cortices into motor representations within premotor cortex. However, evidence for sensory responses within monkey premotor cortex in the absence of any movement preparation (Fogassi et al., 1996; Graziano et al., 1999; Graziano and Gandhi, 2000) has begun to challenge this functional dichotomy in favor of a more distributed sensorimotor representation in both premotor and parietal areas.

Recent fMRI studies have shown that sensory responses also exist in the human premotor cortex (Schubotz et al., 2000; Schubotz and von Cramon, 2001a, 2001b, 2002a, 2002b, 2002c). In order to induce attention to sensory events without motor planning, we have introduced the

serial prediction task (SPT) (Schubotz, 1999). As a perceptual counterpart of the classical serial reaction task (SRT) (Nissen and Bullemer, 1987), the SPT requires subjects to extract and predict repetitive sensory patterns within sequentially presented stimuli. In contrast to SRT, however, SPT does not require motor coproduction. Instead, performance in sensory pattern prediction is tested after stimulation by a forced choice judgment on the occurrence of a pattern violation. Most importantly, in SPT no movements toward the stimulus are required and the task is to predict upcoming patterns within the attended sensory dimension.

As a most important and robust result, we found the location of premotor activation to be significantly modulated by the stimulus property that is attended to. The premotor cortex responded differently for attending to object-related patterns (*what*), temporal patterns or rhythm (*when*), and spatial patterns or trajectories (*where*), respectively. Together, the specific correspondences between attended stimulus property and anatomical location of premotor cortex activation strongly suggest what may be referred to as a *sensory somatotopy*. That is, whenever we attend to sensory patterns, these are mapped onto somatotopically corresponding motor patterns following the rough body map we know from monkey premotor cortex (Preuss and Gold-

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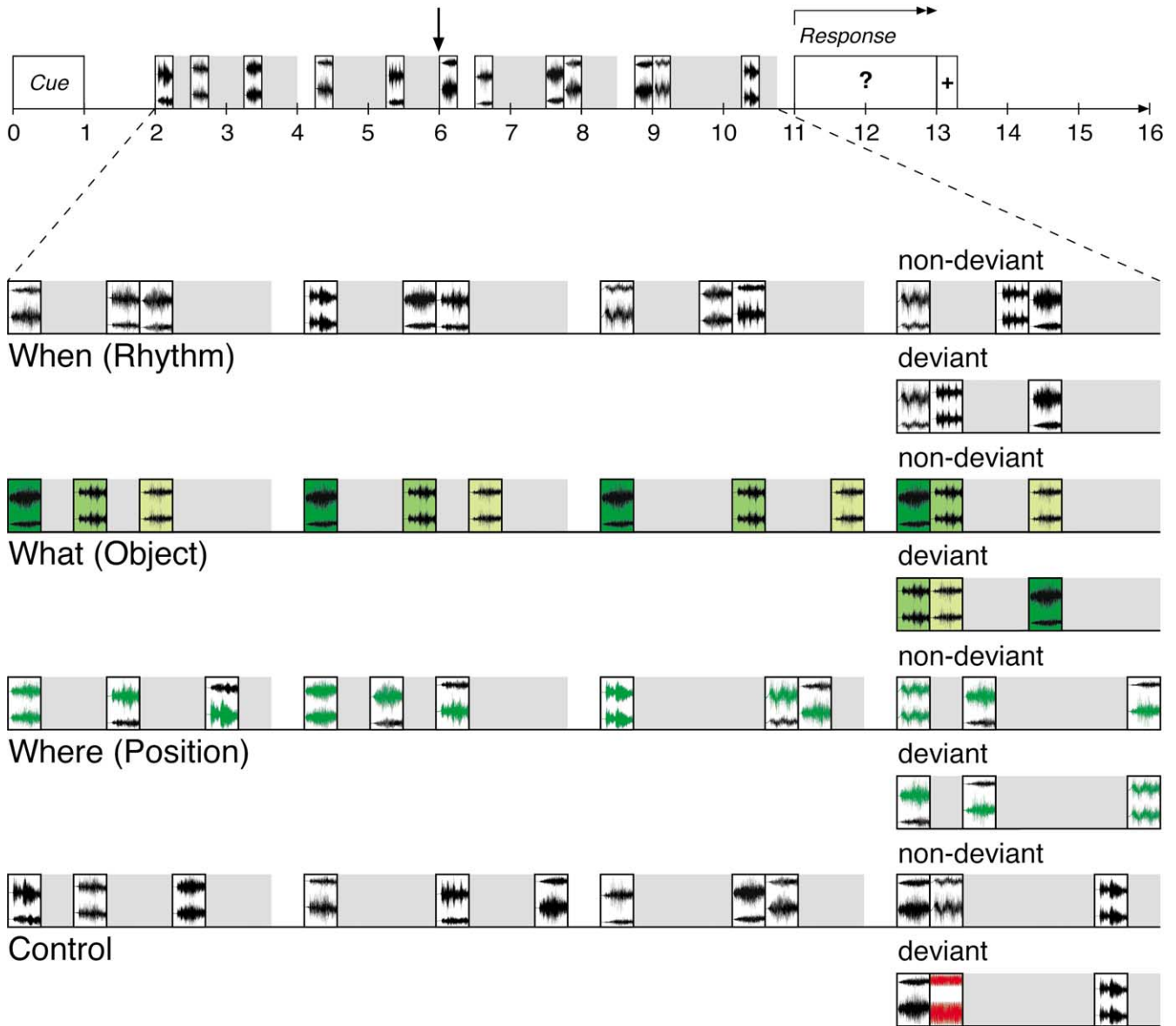


Fig. 1. Experimental conditions. Trial examples are plotted for the serial prediction tasks (SPT) and the control condition. Subjects were provided with patterns within the temporal (*when* condition), object-related (*what* condition), and spatial domain (*where* condition), respectively. Examples show trials both with and without pattern violations occurring on either the third last or the second last stimulus within the attended stimulus property. Different green tones indicate different types of sounds in the *what* condition, i.e., sound qualities, whereas the green-marked dominant channel in the *where* condition indicates the spatial location of a sound's source. The target within the control condition differed from all stimuli within the experiment, as indicated in red. The arrow on the timescale indicates the event on which serial prediction could start on the basis of preceding stimuli, and which was taken as reference for comparing activations between conditions.

man-Rakic, 1989; Preuss et al., 1996; Godschalk et al., 1995; Graziano et al., 2002). In particular, temporal and pitch patterns engaged premotor vocal fields, object-related patterns engaged premotor manual fields, and spatial patterns engaged premotor fields for gaze and reaching. In simple terms, events appear to trigger responses in those effector fields which are best adapted to interact with the attended sensory pattern. According to the same logic, however, it could be expected and was found that in addition to any property-specific activations, the premotor field for

manual configurations was always activated by attention to visual patterns.

Together, the data point to truly sensorimotor representations in the lateral premotor cortex. We find both (1) a top-down modulation by attention to property, and (2) a bottom-up modulation by sensory modality. Accordingly, if the property-dependent modulation account is correct, then (1) the modulations of lateral premotor activations for attending to *when*, *where*, or *what* within sensory patterns should be the same no matter whether

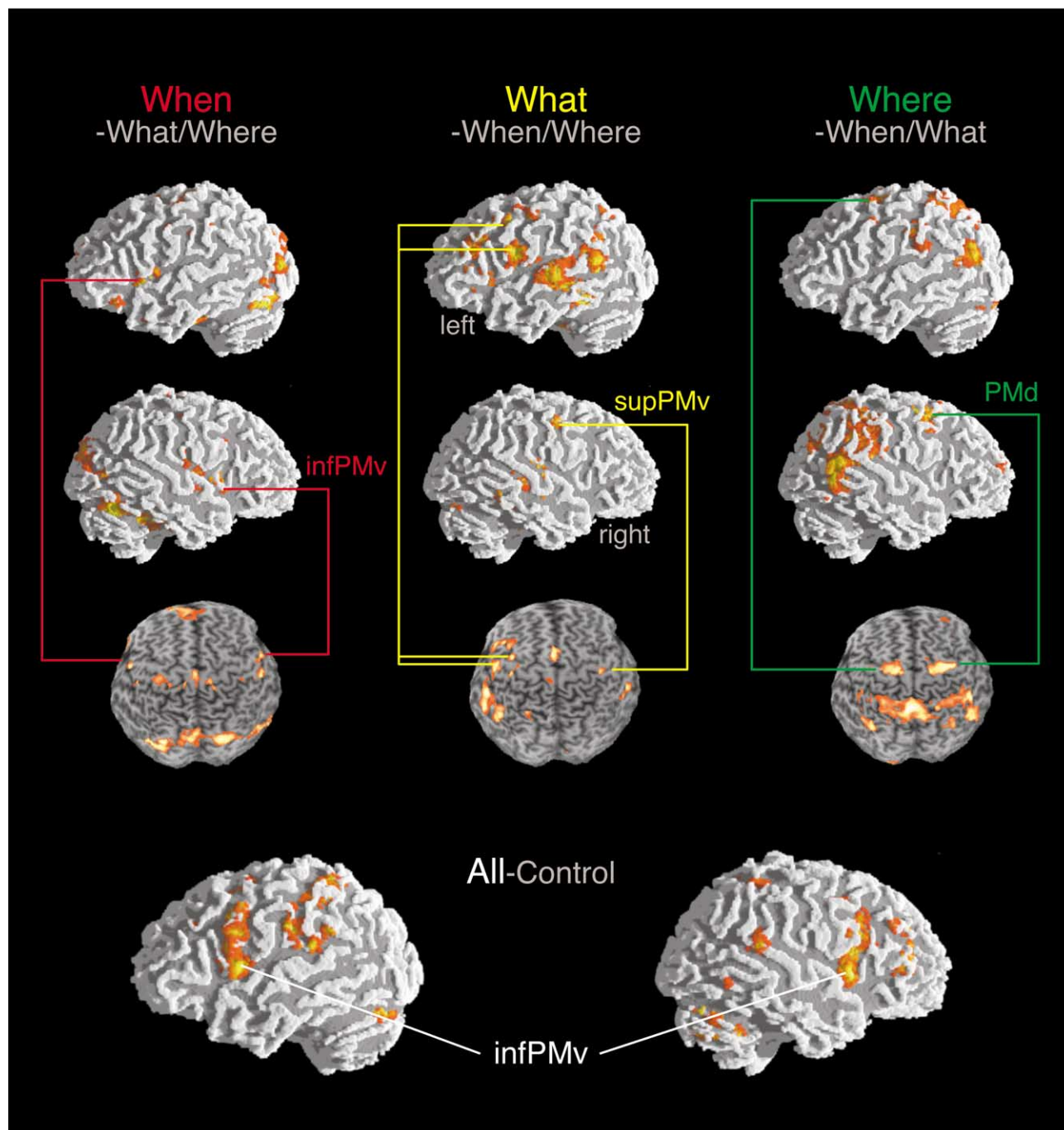


Fig. 2. Group-averaged brain activation ( $n = 16$ ) exceeding a threshold of  $Z = 3.01$  are superimposed onto a T1-weighted individual brain that underwent a white matter segmentation with partially filled sulci. In addition, activations are shown on intersection flat maps (third panel) (Lohmann et al., in preparation). (Top) Results for testing the property-dependent modulation hypothesis (see also Fig. 3). Activation during predicting *when*, *what*, and *where* patterns were directly contrasted against each other. Maximal premotor activations were found within inferior ventrolateral premotor cortex (infPMv) for *when* patterns, within superior ventrolateral areas (supPMv) for *what* patterns, and within dorsolateral areas for *where* patterns, respectively. (Bottom) Results for testing the modality-dependent modulation hypothesis (see also Fig. 4). Activation during predicting auditory patterns of collapsed experimental conditions, relative to the control task. Maximal activations were located within the right and left inferior ventrolateral premotor cortex.

they are provided by vision or audition. Think of blind subjects who certainly have a representation of pragmatic object properties, and have been shown to not be impaired in mental rotations of objects (Kerr, 1983; Marmor and Zaback, 1976) or mental imagery of object shape

triggered by sounds of familiar objects (De Volder et al., 2001). (2) If the modality-dependent modulation account is correct, then attention to auditory objects should, in addition to any property-dependent activations, generally induce activations within effectors best adapted onto gen-

erating auditory patterns, i.e., premotor fields for vocal patterns.

Whole-brain functional magnetic resonance imaging (fMRI) was used to test these two hypotheses—property-dependent modulation and modality-dependent modulation—which both derive from the assumption of a sensory somatotopy of the premotor cortex. Parallel to the preceding visual experiment (Schubotz and von Cramon, 2001a) we employed three SPT conditions providing auditory temporal, spatial, and object-specific patterns, respectively. The modality-dependent modulation hypothesis was tested by contrasting all auditory SPT conditions with a auditory control task, in addition to an effect stability analysis, whereas the property-dependent modulation hypothesis was tested by contrasting *when*, *where*, and *what* SPT against each other.

## Materials and methods

### Participants

Sixteen right-handed, healthy volunteers (8 female, 8 male, age range from 21 to 28 years, mean age 24.5 years) participated in the study. After being informed about potential risks and screened by a physician of the institution, subjects gave informed consent before participating. The experimental standards were approved by the local ethics committee of the University of Leipzig. Data were handled anonymously.

### Stimuli and tasks

Auditory stimulation was designed in order to allow a comparison between the present study and a recently published visual experiment (Schubotz and von Cramon, 2001a). Since abstract geometrical figures were employed as visual stimulus material, we employed abstract, i.e., artificial and meaningless, sounds as auditory stimuli in the present study. The stimulus material consisted of 96 different sounds. Stimuli were generated from natural sounds, e.g., a car braking, the shutting of a door, or flowing water, which were distorted artificially such that they could no longer be attributed to natural events. Participants reported that the stimuli sounded like odd machine noises. Sounds had a mean pitch of 8625 Hz (range from 6000 to 12,000 Hz), and each sound had a duration of 250 ms.

Three experimental tasks and one control task were presented in a random trial design and announced by visual cues. Thirty-six trials were presented per task. Each trial lasted 8750 ms, and the intertrial interval was 7250 ms. Within each trial, 12 stimuli were presented successively with varying temporal gaps, preceded by a task cue at the beginning of each trial, and followed by a visual response feedback (see Fig. 1).

The presentation of three successive stimuli, including

two interstimulus intervals, always added up to 2000 ms. Due to varying interstimulus intervals, three successive stimulus onsets built 1 of 18 different rhythm types, like 250–500–1250 ms, 250–750–1000 ms, 500–500–1000 ms, 1500–250–250 ms, etc. Sounds were presented binaurally, with the virtual source in front of the face (0°) or from the left (−90°) or the right side (+90°) of the head.

Within each trial of the experimental tasks, one of three stimulus dimensions (*when*, *where*, or *what*) was task-relevant, whereas the remaining two were task-irrelevant. Irrelevant stimulus properties always varied randomly from stimulus to stimulus. In contrast, the task-relevant stimulus dimension always varied in an orderly manner, such that each third sound of the trial was identical with respect to the task-relevant property. Thereby, a perceptual pattern was generated with respect to *when*, *where*, or *what* was heard. Subjects were instructed to encode the task-relevant features of the first three stimuli, i.e., the relevant sensory pattern, and look if it recurred three further times until the end of the same trial.

Performance was tested in a forced-choice response mode. In 50% of the trials, one of the task-relevant properties was transferred from its proper place (stimulus 10 or 11) to the end of the trial (stimulus 12), so that the sensory pattern was violated within the task-relevant dimension. Participants were asked to indicate if such a violation on the task-relevant dimension occurred (press button 1 with the right index finger) or not (press button 2 with the right middle finger). The response was required at the end of the stimulus presentation, as indicated by a question mark.

In the *what condition*, subjects had to attend to the qualitative pattern provided by the first three stimuli, i.e., what sounds were presented, and indicate whether a violation occurred on the order of the stimuli in the last pattern repetition. In the *where condition*, subjects had to attend to the spatial locations of the sounds in the starting sequence, and indicate whether a violation occurred on the pattern of stimuli's spatial locations in the last set repetition. In the *when condition*, subjects had to attend to the temporal durations of the starting sequence, i.e., the rhythm of the sounds, and indicate whether a violation occurred on the stimuli's temporal durations (rhythm violations) in the last set repetition. Finally, a *control condition* was employed in which subjects had to attend to a prelearned target stimulus that differed qualitatively from all stimuli within the experiment. Since a target was not defined by the sequence of preceding stimuli within the trial, in contrast to the experimental conditions, the control task did not require subjects to attend to any stimulus patterns. A target detection had to be indicated at the end of the trial by pressing button 1 with the right index finger, or no target by pressing button 2 with the right middle finger. Note that regarding the target sound in the control task, it is principally not possible to define a target that has neither temporal, nor spatial, nor qualitative properties. The target was defined qualitatively—this was the easiest way to

get participants not to consider sequential information in a control condition trial. Hence, the important difference between this task and the experimental *what* task (and the other sequential tasks) was that there was no sequential information to be processed in the control task.

### Procedure

Participants were instructed and trained a few days before the MRI experiment. Training was performed until a learning criterion of 80% (16 of 20 preceding responses correct). In the MRI session, subjects were supine on the scanner bed with their right index and middle fingers positioned on the response buttons. In order to prevent postural adjustments, the subject's arms and hands were carefully stabilized by tape. In addition, form-fitting cushions were used to prevent arm, hand, and head motion. Participants were provided with earplugs to attenuate scanner noise. Immediately prior to the functional imaging session, subjects spent 20 min in the scanner, so that they could acclimate to the confinement and sounds of the MR environment.

### Data acquisition

Imaging was performed at 3T on a Bruker Medspec 30/100 system equipped with the standard birdcage head coil. Slices were positioned parallel to the bicommissural plane (AC–PC), with 16 slices (thickness 5 mm, spacing 1 mm) covering the whole brain, except for the most ventral cerebellar cortex. A set of 2D anatomical images was acquired for each subject immediately prior to the functional experiment, using an MDEFT sequence ( $256 \times 256$  pixel matrix). Functional images in plane with the anatomical images were acquired using a single-shot gradient EPI sequence (TE = 30 ms,  $64 \times 64$  pixel matrix, flip angle  $90^\circ$ , field of view 192 mm) sensitive to BOLD contrast. During each trial, 8 images were obtained from 16 axial slices each at the rate of 2 s per image (16 slices). In a separate session, high-resolution whole-brain images were acquired from each subject to improve the localization of activation foci using a T1-weighted 3D segmented MDEFT sequence covering the whole brain.

### Data analysis

The fMRI data were processed using the software package LIPSIA (Lohmann et al., 2001). In the preprocessing, low-frequency signals were suppressed by applying a 1/120 Hz highpass filter. This filter length was calculated in the following way: twice the length of one complete oscillation, i.e., minimal gap between two trials of the same experimental condition =  $2 \times 60 \text{ s} \approx 120 \text{ s}$ . Because low frequencies were removed, temporal filtering also effected a signal control correction. To correct for the temporal offset between the slices acquired in one image, a sinc-interpolation algo-

rithm based on the Nyquist Shannon Theorem was employed. To correct for movements, the images of the fMRI time series were geometrically aligned using a matching metric based on linear correlation. The anatomical registration was done in three steps: first, the anatomical slices geometrically aligned with the functional slices were used to compute a transformation matrix, containing rotational and translational parameters that register the anatomical slices with the 3D reference T1 data set. In a second step, each individual transformation matrix was scaled to the standard Talairach brain size ( $x = 135$ ,  $y = 175$ ,  $z = 120$  mm) (Talairach and Tournoux, 1988) by applying a linear scaling. Finally, these normalized transformation matrices were applied to the individual functional raw data. Slice gaps were scaled using a trilinear interpolation, generating output data with a spatial resolution of  $3 \text{ mm}^3$ . The statistical analysis was based on a least-squares estimation using the general linear model (GLM) for serially autocorrelated observations (random effects model) (Friston, 1994; Worsley and Friston, 1995; Zarahn et al., 1997). The design matrix was generated with a synthetic hemodynamic response function (Friston et al., 1998; Josephs et al., 1997). For each trial, the event was set 4 s after stimulus sequence onset, corresponding to the fifth or the sixth stimulus (see also Fig. 1). Preexperimental testing had shown that only after this point, a three-element stimulus sequence could be successfully recognized. That is, in a nontrained test group of 10 subjects, performance increased from 65% correctly answered trials that required a deviant detection on the seventh, eighth, or ninth stimulus to 77.4% correctly answered trials that required a deviant detection thereafter ( $F(1,9) = 8.6$ ,  $P < 0.016$ ).

Only correctly answered trials entered the analysis. It is important to note that the participants' responses were recorded 5 to 7 s after the analyzed event. Although this interval is large enough to minimize possible confounds between serial prediction and the motor response given at the end of each trial, we controlled for this effect additionally by balancing the type and number of required motor responses between all contrasted conditions. By doing so, effects related to the button press were subtracted out.

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, contrast maps, i.e., estimates of the raw-score differences between specified conditions, were generated for each subject. As the individual functional datasets were all aligned to the same stereotactic reference space, a group analysis was subsequently performed. A one-sample *t* test of contrast maps across subjects was computed to indicate whether observed differences between conditions were significantly distinct from zero. Taking into consideration our hypothesis that was restricted to voxels within the lateral premotor cortex, we could have adjusted, i.e., lowered, the statistical threshold according to the volume of interest. However, we preferred a conservative testing of our results,

Table 1  
Correlates of *what*, *where*, and *when* patterns (direct task contrasts)

Area	Hemisphere	x	y	z	Z score
<i>when</i> vs. ( <i>what</i> , <i>where</i> )					
Inferior ventrolateral premotor cortex	L	-44	-1	8	4.3
	R	40	0	13	3.8
Anterior collateral sulcus	L	-23	-52	1	5.5
	R	36	-36	-7	5.3
Pregenuar anterior cingulate cortex	L	-5	29	12	5.1
Posterior insula	R	30	-14	19	4.6
Superior occipital gyrus	L	-38	-83	11	4.6
Hippocampal formation	L	-26	-20	-12	4.5
Intraparietal sulcus	R	22	-86	26	4.1
<i>what</i> vs. ( <i>when</i> , <i>where</i> )					
Superior ventrolateral premotor cortex	L	-42	4	32	4.1
	L	-57	-2	19	4.4
	R	47	-9	40	3.7
Superior temporal gyrus	L	-60	-26	6	5.1
Presupplementary motor area	L	-5	9	55	4.6
Superior temporal gyrus	L	-57	-53	14	4.4
<i>where</i> vs. ( <i>when</i> , <i>what</i> )					
Dorsolateral premotor cortex	L	-21	-7	52	4.7
	R	21	-6	51	4.2
Anterior superior precuneus	L	-6	-58	52	5.4
Supramarginal gyrus	R	53	-36	24	4.9
Posterior middle temporal gyrus	R	57	-59	8	4.6
Parieto-occipital transition area	L	-47	-70	18	4.4
Postcentral sulcus	L	-27	-43	42	4.0
	R	34	-41	41	3.7

Note. Talairach coordinates and Z scores of peak activations from group average data ( $n = 16$ )

and therefore took  $Z \geq 3.09$  as statistical threshold (Holmes and Friston, 1998).

In order to allow for a statistical comparison between the present findings from auditory correlates and previously found data from visual correlates (Schubotz and von Cramon, 2001a), the latter data were reanalyzed using the same preprocessing procedure and the same statistical account as that employed in the present study. Subsequently, we performed an effect stability analysis on the auditory experiment and on the visual experiment, respectively. To this end, voxels which were consistently activated above threshold ( $Z > 3.09$ ,  $P < 0.001$ ) for each of the three auditory pattern tasks were identified by a simple counting algorithm implemented in LIPSIA (to be updated in Lohmann et al., 2001). Resulting effect stability maps show only those voxels which were activated in each of the three contrasts of the auditory experiment and of the visual experiment, respectively.

Activations were analyzed throughout the entire brain. However, except for a listing of all significant activations (see Table 1), the report of the results and their discussion will be restricted to activations within brain areas that our hypotheses focused on, i.e., those within the lateral premotor cortex.

## Results

### Behavioral performance

Performance was assessed by error rates. A repeated measures ANOVA with the two-level factor TASK (Pattern, Control) indicated no significant main effect, with an error rate of 9.3% for SPT conditions and 8.1% for the control condition. A repeated measures ANOVA with the three-level factor DIMENSION (*what*, *where*, *when*) indicated a significant main effect ( $F(2,30) = 148.0$ ,  $P < 0.004$ ), with an error rate of 6.4% for the *when* condition, 9.2% for the *what* condition, and 12.5% for the *where* condition.

### MRI data

#### Property-dependent modulations by auditory *When*, *Where*, and *What*

In order to identify property-specific differences, direct task contrasts were computed. To this end, we contrasted condition *when* with collapsed conditions *what* and *where*, condition *what* with collapsed conditions *when* and *where*, and condition *where* with collapsed conditions *what* and

when, respectively. As a result, contrasts revealed a significant functional–anatomical dissociation between three premotor subregions (see Table 1 and Fig. 2). *When* patterns elicited significantly higher activation within the inferior ventrolateral premotor region. *What* patterns caused significantly higher activations within the superior ventrolateral premotor cortex. *Where* patterns yielded significantly higher activations within the dorsalmost premotor cortex. Further significant activations of the three direct task contrasts are also listed in Table 1.

In order to confirm that significant activations that were found in the direct task contrasts were not caused by deactivations of the subtracted conditions, we additionally analyzed the percentage signal change for each experimental condition and the control condition in both the auditory and the visual experiment. Results are shown in Fig. 3B. As already implicated by the *z* maps, highest signal changes were found in the inferior ventrolateral premotor cortex for the *when* patterns, in the superior ventrolateral premotor cortex for the *what* patterns, and in the dorsolateral premotor cortex for the *where* patterns.

#### *Modality-dependent modulations by auditory patterns*

In order to identify the general neural network underlying the prediction of auditory events, relative to the non-predictive control condition, conditions *when*, *what*, and *where* were collapsed and contrasted with the control condition. As evident from Fig. 2 (bottom panel), all auditory patterns elicited significant activations within the ventrolateral premotor cortex, peaking within its inferior portion. Hence, although conditions differed with regard to the location of their maximal premotor activation, they showed a significant overlap within the area that was most significantly activated by the *when* patterns. This was further confirmed by an effect stability analysis. The resulting effect stability map shows only voxels that are significantly activated within each contrast: *when* vs. control, *what* vs. control, and *where* vs. control, respectively. Results showed that the overlap between *when*, *what*, and *where* patterns was restricted to inferior ventrolateral premotor cortex within both hemispheres (Fig. 4, bottom panel).

#### *Modulations by auditory patterns and visual patterns*

For comparison of property-dependent modulations, activation foci found in corresponding experimental conditions in the present auditory and in the preceding visual study (Schubotz and von Cramon, 2001a) are plotted in Fig. 3A. Note that visual coordinates were taken from a statistical reanalysis that was absolutely parallel to that of the present study. Maximal activation foci in premotor cortex are indicated within both hemispheres for each condition, relative to control condition, for the auditory (Fig. 3A, left) and the visual study (Fig. 3A, right). As evident from the figure, foci for *when*, *what*, and *where* patterns distributed along the ventral–dorsal extension of the right and left

lateral premotor cortex for both auditory and visual events, respectively.

For comparison of modality-dependent modulations, activation maxima obtained from the all SPT vs. control contrast in comparison to activation maxima obtained from the visual study are schematically plotted in Fig. 4 (middle panel). As for the auditory experiment, we performed an effect stability analysis on the visual experiment. Both effect stability maps are shown in Fig. 4, with the lower panel showing the significant overlap between the auditory SPTs, and the upper panel derived from the visual SPTs. Peaks of auditory activation were located about 19 mm inferiorly to the visual activation peaks, within both hemispheres (see Table 2).

## Discussion

We used fMRI to test two core hypotheses that were derived from the assumption of a sensory somatotopy within human lateral premotor cortex. We investigated whether in the absence of motor requirements (1) auditory patterns engage a common area within the ventral premotor cortex, regardless of the property that is attended to (modality-dependent modulation hypothesis), and (2) the prediction of *when*, *what*, and *where* patterns in auditory signals is reflected by activation within inferior ventral, superior ventral, and dorsolateral premotor cortex, respectively (property-dependent modulation hypothesis). Our results confirmed both hypotheses, thereby consistently replicating previous findings from a corresponding visual version of the experiment (Schubotz and von Cramon, 2001a). Most importantly, this is the first time that the lateral premotor stripe can be segregated into three subareas specialized for information domains provided by auditory stimuli.

In the following, we will discuss why these results provide evidence for somatotopical organization principles that apply to premotor representations triggered by mere perceptual prediction. We will argue that the considered premotor subregions are known to be involved in the preparation and sensorimotor adaptation of vocal, hand, and arm/eye movements, respectively, and action effects of these motor effectors produce temporal, object-related, and spatial sensory patterns in our environment.

#### *When patterns—inferior ventrolateral premotor cortex*

As expected, predicting auditory rhythm elicited higher activations than predicting quality or location of sounds within inferior ventrolateral premotor cortex. Hence, though each SPT condition elicited activation within this area in contrast to the control task, this area was shown to be activated significantly stronger by the temporal than by any other SPT. Findings confirm data from previous fMRI investigations indicating rhythm prediction to rely on inferior ventrolateral premotor cortex and adjacent BA 44 (Schubotz

et al., 2000; Schubotz and von Cramon, 2001a, 2001b). As in the present study, activation induced by rhythm SPT in these studies spread across the most inferior part of the inferior precentral sulcus, the structure which separates inferior BA 6 from BA 44 (though it extends into the Sylvian fissure in only 24% of healthy human brains; Ono et al., 1989). As far as this may point to an extension of premotor function from inferior 6 into a part of BA 44, it is in line with the view that BA 44 may be, at least partly, the human homologue of monkey's premotor field F5 (Rizzolatti et al., 2002). These areas function in the representation of vocal configurations (Tonkonogy and Goodglass, 1981; Dronkers, 1996; Fox et al., 1996; Wise et al., 1999; Fadiga et al., 2002). In the present study, correlates of the *when* condition extended from BA 6 inferiorly into the frontal opercular cortex adjacent to the anterior insula. This so-called precentral operculum (Peters and Jones, 1985) contains a face representation. In combination with the inferior ventrolateral premotor cortex, it is taken to be related to the organization of complex behaviors related to the face and mouth. Activations found in this region were reported for rhythmic pattern production like singing (Perry et al., 1999; Riecker et al., 2000) as well as for rhythmic pattern rehearsal in speech (Riecker et al., 2002). In line with these findings, we take activation within inferior ventrolateral premotor cortex and the adjacent precentral operculum to reflect a short-term model of an abstract vocal sequence.

Consider that we do not intend to propose, conversely, that rhythm generation exclusively involves vocalization areas. One might think of rhythm generation in drumming or dancing, which certainly relies on other motor effectors as well. Likewise, a perceived rhythm may be mapped onto rhythmic output of a variety of motor effectors. However, evidence for the interpretation that rhythm reception may particularly engage the anatomical correlates for vocal production comes from the finding that this area is also significantly responsive to pitch sequences (Schubotz et al., 2000; Schubotz and von Cramon, 2002a; Platel et al., 1997; Maess et al., 2001; Gandour et al., 2000) and has been suggested in mapping sound onto pronunciation in vocal imitation (Skoyles, 1998; Kuhl and Meltzoff, 1982). As we found the same or very similar anatomical areas to respond to pitch and rhythm, and vocal effectors are the only areas available for pitch pattern production, we take this to indirectly support our present interpretation. This view has to be further validated, for instance by comparing rhythm reception directly with, say, vocal, manual, and perhaps foot rhythm generation.

#### *What patterns—superior ventrolateral premotor cortex*

In contrast to both temporal and spatial patterns, predicting object-related patterns particularly engaged the superior ventrolateral premotor cortex. Accordingly, anticipatory attention to *what* patterns elicited BOLD responses within the premotor field that is known to be engaged in manual

planning, as evident from humans (Decety et al., 1994; Martin et al., 1995; Matsumura et al., 1996; Grafton et al., 1996) and monkeys (Jeannerod et al., 1995; Rizzolatti et al., 1988). Moreover, findings confirmed prior results indicating this premotor field to be engaged in object-specific patterns determined by form (Schubotz and von Cramon, 2001a), size (Schubotz and von Cramon, 2002a, 2002b), or color patterns (Schubotz and von Cramon, 2002c). However, it is especially noteworthy that in the present study, superior ventrolateral premotor cortex was activated for *what* patterns provided by (1) auditory and (2) abstract events.

With regard to the auditory modality (1), premotor representations of hand–object interaction thus appear to apply not only to objects presented in the visual domain, but even to something we could denote as auditory objects. Recently, Kubovy and van Valkenburg (2001) proposed to extend the everyday notion of a (visual) object to audition, while others prefer to avoid the term of “auditory objects” in favor of that of “auditory events” (Blauert, 1997). No matter how we refer to object information provided by audition, however, a specific pathway and neural representation for auditory object information, parallel to the visual *what* system, are suggested by both behavioral (Wynn, 1977; Deutsch and Roll, 1976) and neurophysiological data (Clarke et al., 2000; Anourova et al., 2001; Maeder et al., 2001). The present finding confirms this view, suggesting that premotor areas reflect object properties no matter whether provided by vision or audition.

Regarding the abstractness of stimuli (2), the material employed in the present study was designed to match that used in the preceding visual study, and hence to avoid, as in the visual study, silent verbalization. One may expect that, if sensory patterns are transformed into sensorimotor patterns in premotor and associated parietal sites, then only (patterns of) properties provided by real objects would allow a transformation onto specific (patterns of) grip types or other manipulations. Obviously, however, object abstractness did not impede object-specific premotor activation. Based on findings in two fMRI studies investigating object-related premotor activations, we have argued that due to their vital meaning, dynamic stimulus patterns, particularly in near space, may engage premotor areas involved in hand–object interaction as a functional default mode that applies to all dynamic stimuli defined by object properties (Schubotz and von Cramon, 2002a). Present findings reconfirm this interpretation, showing that attentive anticipation to patterns of what we hear or see—no matter where and when—may be the common prerequisite for engaging lateral premotor regions for hand–object interaction.

#### *Where patterns—dorsolateral premotor cortex*

In contrast to *when* and *what* patterns, predicting patterns of spatial sources in abstract stimulus sequences elicited highest activations within dorsal premotor cortex. This finding confirms results provided by visuospatial SPT



(Schubotz and von Cramon, 2001a, 2001b). Generally, dorsal premotor regions mediate arm–eye coordination in reaching (Georgopoulos et al., 1982; Kurata and Tanji, 1986; Caminiti et al., 1991; Johnson et al., 1996). The present activations were composed of bilateral symmetrical spots within the junction of the superior frontal sulcus and the dorsal precentral sulcus, and a more lateral spot within the right hemisphere. Bilateral superior activations most probably correspond to the frontal eye fields (Paus, 1996), located within an area that supports both saccade generation and covert spatial attention (Corbetta et al., 1998; Nobre et al., 2000; Beauchamp et al., 2001). A separation of the human frontal eye field from lateral adjacent dorsal premotor regions is controversial with respect to both anatomical and functional properties. A tendency toward a rough dichotomy of reaching to be mediated by dorsolateral premotor cortex as in contrast to gaze mediated by the frontal eye field is suggested in monkeys (Fujii et al., 2000) and humans (Connolly et al., 2000; Desmurget et al., 2001). As within ventrolateral premotor cortex, sensory or context-dependent processes have been stressed for reaching in dorsolateral premotor cortex (Shen and Alexander, 1997; Wise et al., 1997). Accordingly, the dorsolateral premotor cortex and associated parietal projection sites are supposed to build up a task-dependent reference frame for coding target location as well as for coordinated gaze and arm movements (for a review, see Boussaoud and Bremmer, 1999; Joffrais and Boussaoud, 1999). Note, however, that dorsolateral premotor responses may sometimes also reflect a coding of target position in terms of head (turning) movements, which can accompany large saccades (Paus, 1996).

Since eye movements were not controlled in the present study, we cannot exclude that frontal eye field activation was induced by saccades toward the virtual location of the auditory target in the *where* task. Conversely, however, we cannot exclude that activations reflect a suppression of saccades, which is also suggested to be a frontal eye field function (Guiton et al., 1985; Law et al., 1997; Petit et al., 1999). Moreover, frontal eye field activation has been reported in a study that controlled for eye movements during the perception of auditory targets in virtual space (Griffiths and Green, 1999). Similar activations were also found for working memory of auditory localization when eye movements were not controlled (Martinkauppi et al., 2000). Accordingly, we take frontal eye field activation to reflect either overt or covert spatial attention to the spatial target location.

#### *Conceptual implications—predicting sensory patterns according to a body map*

Sites of premotor activations corresponding to auditory patterns, relative to the control task, are plotted in the left panel of Fig. 3A. Evidently, premotor correlates corresponding to each attended stimulus property were distributed in a parallel fashion for the auditory and for the visual

paradigm, respectively. Furthermore, we found the left and right ventrolateral premotor cortex to respond independently of the attended stimulus domain, both in the present auditory paradigm and in the corresponding visual study (Schubotz and von Cramon, 2001a). As evident from the effect stability analysis plotted in Fig. 4, however, visually induced activations were located more superiorly within the ventrolateral premotor cortex, whereas present auditory stimulation engaged the inferior portion of the ventrolateral premotor cortex (see also Table 2). The same distribution of ventral premotor activation was found for auditory pitch and visual size sequences (Schubotz and von Cramon, 2002a). In contrast to this study, however, the present is the first to employ *when*, *where*, and *what* SPTs that parallel those employed in the preceding visual study, and therefore allows for a comparison between vision and audition without confounding attended sensory property.

Together with data obtained from the visual experimental version, the present results suggest that premotor sites are modulated both bottom-up according to the sensory input modality and top-down according to the attended stimulus property. Both modulations point to a sensorimotor representation; that is, premotor areas respond to prediction of sensory patterns in a body-centered manner. We take premotor activations to reflect the involvement of sensorimotor areas activated by setting up a model of serial patterns. This model is on the one side determined top-down by the attended stimulus property, such that prehension fields map object properties, vocalization fields map rhythm and pitch, and finally fields for gaze and reaching map spatial patterns, no matter whether they are provided by vision or audition. On the other side, the model appears to be determined bottom-up by sensory modality such that areas underlying prehension get engaged when concerned with visual patterns, and areas underlying vocalization get engaged when concerned with auditory patterns.

However, while the former property dependence is directly demonstrated in both our data and within the preceding visual study, the influence of the modality, in contrast, is suggested on the basis of a descriptive comparison between the present auditory and the preceding visual study. Alternative interpretations for the modality effect are certainly available.

One is that areas underlying prehension get engaged when concerned with visual patterns only because the processing of their object features is not suppressed. Likewise, areas underlying vocalization may get engaged when concerned with auditory patterns only because the processing of their rhythmic features (though presented randomly within the *what* and *where* conditions) is not suppressed. According to this interpretation, premotor modulations by sensory modality would just be an indirect expression of their property dependence. This issue remains to be tested, for instance by congruency manipulations of unattended rhythm properties and attended other stimulus properties in an auditory SPT paradigm.

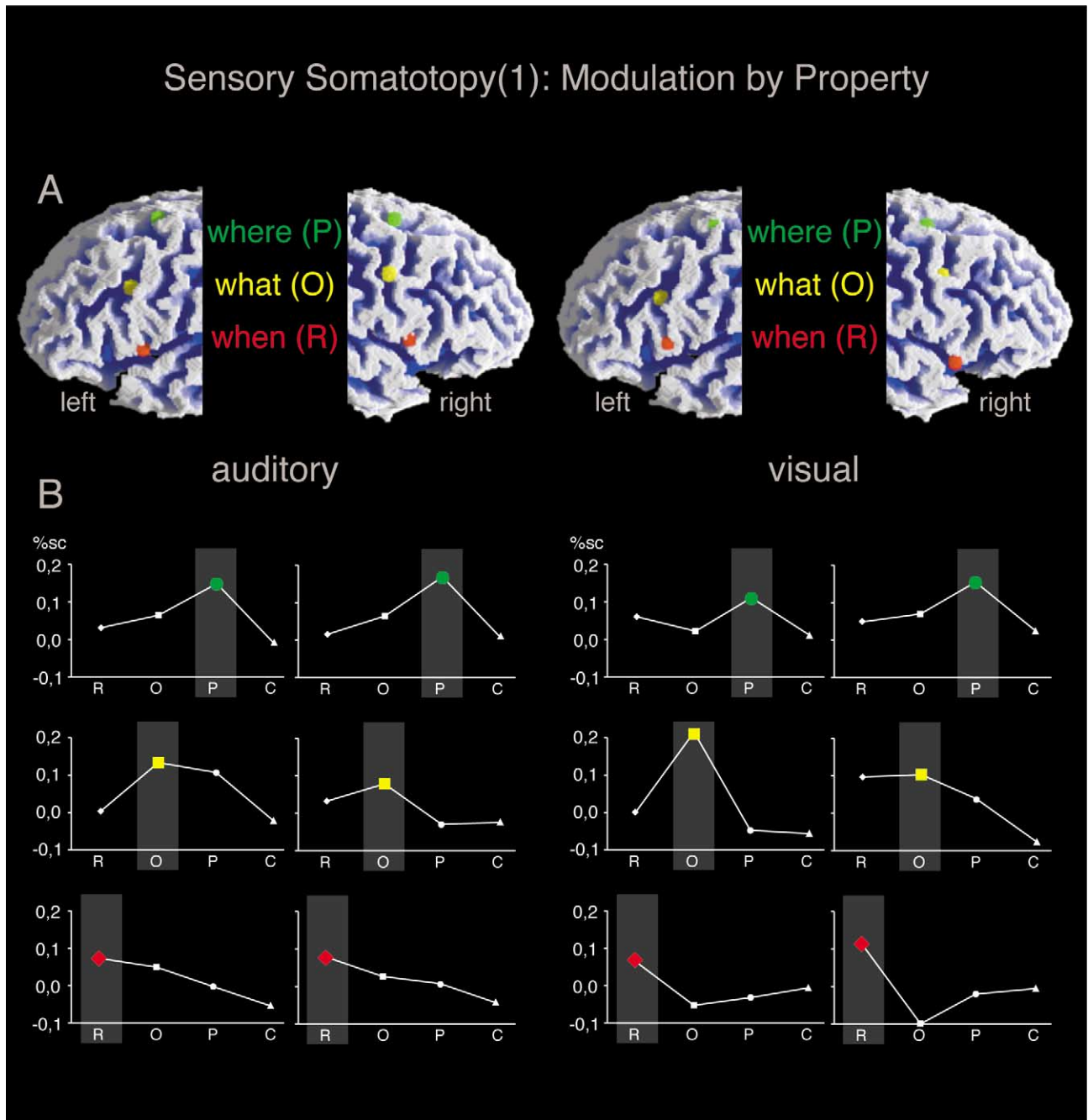


Fig. 3. Effects of property-dependent modulation. (A) Spherical markers for activation foci for *when* (red), *what* (yellow), and *where* (green) conditions of pattern prediction (direct task contrasts), plotted on the white matter segmentation of an individual brain. The comparison shows the strikingly parallel distribution between the present auditory stimulation (left) and the visual stimulation (right) from a preceding implementation of the serial prediction task (Schubotz and von Cramon, 2001a). (B) Maximal percentage signal changes of *when* (Rhythm, R), *what* (Object, O), *where* (Position, P), and the Control condition (C), respectively. Signal changes were extracted from the maximal activated voxels of the direct task contrasts, as indicated by the spherical markers in panel A. The four graphs in the upper row correspond to the green spherical markers in A (dorsolateral premotor cortex), with auditory data on the left side and visual data on the right. Here, highest signal changes are found in the *where* conditions, as indicated by green tags. The middle row shows highest signals in the *what* conditions, corresponding to the yellow labels in A (superior ventrolateral premotor cortex). Finally, graphs in the lowest row correspond to the red-labeled coordinates in A (inferior ventrolateral premotor cortex), with dominant signal changes in the *when* conditions.

Another interpretation is that some other features other than only the sensory modality differed between the visual and the auditory SPTs. First, auditory stimuli were presented for shorter intervals than the visual stimuli. Based on

pilot studies, this was done in order to adjust the task difficulty between the auditory and the visual task, and thereby induce comparable effort or attentional arousal within both modalities. Second, we had employed a go–no

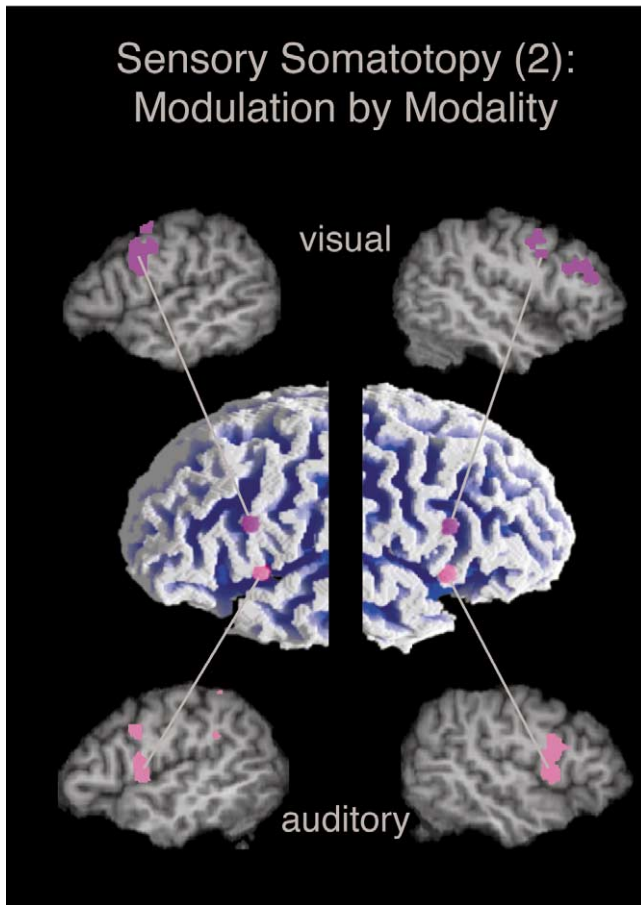


Fig. 4. Effects of modality-dependent modulation. Spherical markers of activation foci for collapsed conditions of auditory pattern prediction vs. control condition (pink), as compared to those obtained from collapsed visual pattern prediction vs. control (lilac). The top panel shows the corresponding effect stability map of the visual SPTs, the bottom panel that of the auditory SPTs (left side shows views onto the left hemisphere). The right and left hemisphere peaks of common activation for the auditory SPTs were located about 19 mm inferiorly to those for the visual SPTs (see Table 2).

go response mode in the visual paradigm (see also Schubotz et al., 2000; Schubotz and von Cramon, 2002c). Though we controlled in these studies for effects of responses by balancing their type and number between compared conditions, we decided to employ a forced choice response in the auditory paradigm. The forced choice task has several advantages for our purpose, for instance the late motor response at the end of the trial, the possibility to assess

behavioral performance by error rates instead of  $Pr$  scores, and the improved homogeneity of trial difficulty. Up to now, however, we found no hints in the literature that point to an effect that could explain for the specific differences between inferior and superior ventrolateral premotor activation during either go–no go or forced choice response paradigms. Nevertheless, this issue will have to be tested directly in order to exclude confounds caused by the experimental paradigm.

A challenging concept that may be applied to our present and related findings is the common coding theory (Prinz, 1990). It suggests that perception and action require a common representational medium, and that actions are planned in terms of their intended sensory effects, rather than in terms of a specific movement. Hence, a motor plan represents a sequence of sensory events effected by the body. Conversely, when the system expects to perceive a sensory event on the basis of a serial sensory pattern, as in an SPT, this may induce motor representations appropriate to generate these events.

Our findings provide evidence for a functional–anatomical architecture of the human premotor cortex that parallels the one determined in the monkey. Monkey premotor cortex is suggested to house sensorimotor or “hybrid” representations rather than purely motor or sensory ones (Wise et al., 1997; Burnod et al., 1999), and these representations are addressable either by perception or internally by action planning (Fadiga et al., 2000). These data have resulted in the theoretical concept of a premotor theory of attention (Rizzolatti et al., 1987) that suggests spatial attention to be a consequence of an activation of brain areas which are also involved in the transformation of spatial information into action. A related model is the motor theory of speech perception (Lieberman et al., 1967; Lieberman and Mattingly, 1985). Suggesting a kind of default “echolalic” mechanism, the theory suggests that motor speech areas may subserve speech perception. However, based on the present and preceding findings, we suggest that evidence for both the premotor theory of attention and the motor theory of speech perception issues from one and the same characteristic of premotor function. Perceptual attention, particularly when anticipatory, is a consequence of activation of brain regions which are also involved in the transformation of perceptual information into action and vice versa. The present findings may further contribute to the view that the premotor cortex

Table 2

Talairach coordinates of premotor activation derived from collapsed auditory patterns and collapsed visual patterns, respectively, each against its control condition

Hemisphere	Auditory Patterns vs Control			Visual Patterns vs Control		
	<i>x</i>	<i>y</i>	<i>z</i>	<i>x</i>	<i>y</i>	<i>z</i>
L	−50	0	7	−53	3	26
R	49	6	6	52	6	25

is the site where perceptual anticipation and pragmatic planning coincide.

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