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Research report

Dynamic patterns make the premotor cortex interested in objects: influence of stimulus and task revealed by fMRI

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Abstract

Research in monkey and man indicates that the ventrolateral premotor cortex (PMv) underlies not only the preparation of manual movements, but also the perceptual representation of pragmatic object properties. However, visual stimuli without any pragmatic meaning were recently found to elicit selective PMv responses if they were subjected to a perceivable pattern of change. We used functional magnetic resonance imaging (fMRI) to investigate if perceptual representations in the PMv might apply not only to pragmatic, but also to dynamic stimulus properties. To this end, a sequential figure matching task that required the processing of dynamic features was contrasted with a non-figure control task (Experiment 1) and an individual figure matching task (Experiment 2). In order to control for potential influences of stimulus properties that might be associated with pragmatic attributes, different types of abstract visual stimuli were employed. The experiments yielded two major findings: if their dynamic properties are attended, then abstract 2D visual figures are sufficient to trigger activation within premotor areas involved in hand-object interaction. Moreover, these premotor activations are independent from stimulus properties that might relate to pragmatic features. The results imply that the PMv is engaged in the processing of stimuli that are usually or actually embedded within either a pragmatic or a dynamic context.

Theme: Motor systems and sensorimotor integration

Topic: Cortex

Keywords: Premotor cortex; fMRI; Hand-object-interaction; Sensorimotor integration

1. Introduction

In accordance with primate research, imaging studies in man have found the ventrolateral premotor cortex (PMv) to respond to real objects. These activations have been demonstrated during object grasping [37], imagining object grasping [5,12], silent generation of manual object-related action words [32], looking at manmade tools [13], and during memorizing graspable objects [15]. Moreover, behavioral facilitation effects have been reported indicating object recognition priming based on grasp-specific object properties [4]. Together, these findings suggest that the monkey model of PMv function in transforming object perception into manual action, i.e. pragmatic representations [10,24,38,47], might also apply to the human brain.

However, these data also imply that the premises for premotor involvement in object processing are surprisingly unspecific, both with regard to the stimulus material and the cognitive task. Thus, the PMv is not only activated by the presentation of real natural or manmade objects, but also by the presentation of 3D objects from virtual reality, and by 2D line drawings from manufactured objects (Snodgrass figures; [61]). Likewise, the PMv is found to be engaged in objects not only in tasks that require real grasping, but also those which require to imagine, name, or memorize objects.

Moreover, recent fMRI findings have shown the PMv to be activated in a paradigm that did not require any object-directed-motion or motion imagery, and that used abstract geometrical figures that did not manifest any obvious pragmatic meaning [55,57]. Participants were asked to attend to sequential patterns of regular changes within one of three different stimulus properties. Interestingly, atten-

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tion to these dynamic object properties was reflected by PMv activations similar to those observed in object grasping (for comparison, see [55]), and which could be dissociated clearly from those which were activated by attention to dynamic spatial or dynamic temporal stimulus properties [54–56] and from those caused by attention to dynamic pitch properties [57].

From that it appears that not solely pragmatic object information, but also dynamic object properties can be reflected by PMv activation. In this context, the term 'dynamic' refers to any stimulus property which is subjected to a perceivable sequential pattern of changes over time. Proceeding on this idea, we used fMRI to test the assumption that cortical areas particularly prominent in the processing of pragmatic stimulus properties, the PMv, gets significantly activated also by tasks that require the processing of dynamic stimulus properties. To this end, a sequential figure matching task that required to attend to dynamic stimulus properties was contrasted with a nonsequential nonfigure control task (Experiment 1) and a nonsequential figure matching task (Experiment 2).

In order to investigate dynamic properties only, we had to control for influences of stimulus features that could somehow relate to pragmatic properties. To this end, we employed abstract visual stimuli of different quality in both Experiments 1 and 2. We presented stimuli as single item, as rotating twins, and as decomposable or nondecomposable pattern covering the entire presentation screen. In case that any pragmatic properties would be associated with these stimuli, we expected them to be different for these conditions. Thus, we took the single item condition to correspond to directly graspable entities, rotating twins to moving objects requiring fast, unpredictable manual adjustments, and patterns to stimuli hardly graspable at all, respectively.

In Experiment 1, we tested three different stimulus types in sequential matching conditions. As dynamic properties were the same for these conditions, but missing in the control condition, premotor activation should be not influenced by our manipulations of the physical stimulus properties if exclusively caused by the requirement to process dynamic properties. According to previous findings [55,57], we expected abstract geometrical figures to induce significant premotor involvement, provided that their dynamic properties are attended. However, an open question was whether this type of stimulus would also cause premotor involvement in the absence of dynamic patterns, i.e. in a nonsequential task. In Experiment 2, task and stimuli were therefore manipulated in a two by two design in order to confirm the independence of both factors, i.e. the experimental task and the physical stimulus features. As in Experiment 1, we expected significant premotor activations for the sequential tasks, as compared to the nonsequential tasks, corresponding to a main effect for the factor task. In contrast, we expected no main effect for the factor stimulus and no task by stimulus interaction, if activation would be exclusively caused by the requirement to process dynamic stimulus properties.

2. Materials and methods

2.1. Participants

Twelve healthy right-handed students (Experiment 1: four male, aged 20–26 years, mean 23.3 years; Experiment 2: five male, aged 22–31 years, mean 24 years) participated in the experiments. After being informed about potential risks and screened for contraindications 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.

2.2. Stimuli

Two types of stimuli were employed. The first type was composed of a black 25-mm circle (0.14° of visual angle). In Experiment 1, a slightly smaller geometrical form was placed in the center of this circle (see also Fig. 1). For six figures, this was a 14-mm square, and a 10-mm circle for the six other figures. The big circle and the small inlay were colored red, yellow, or blue, respectively, such that figures were always two-colored. In Experiment 2, the circle was filled with a vertical color-transition from one color at the left and the right side to the second color in the middle of the stimulus (see also Fig. 2). The other type of stimulus covered the entire presentation screen (17.1° of visual angle), and was either composed of multiples of one of the first stimulus type (Experiment 1), or color-transitions without contours or shape (Experiment 2).

2.3. Tasks

2.3.1. Experiment 1

Three sequential figure matching tasks Single Item (S1), Twins (T1), and Pattern (P1), and one control condition (C) were presented visually in a random trial design (see Fig. 1). Trials lasted 9.6 s, with an intertrial interval of 6.4 s. Forty-two trials were presented per condition. In all conditions, twelve pictures were presented subsequently for a mean duration of 800 ms each. In the sequential tasks, the first, second and third picture within each trial were repeated four times in proper order. Subjects were asked to attend to the sequential order of the presented pictures. In 40% of the trials, one picture was transferred from its proper place to the end of the trial, so that the sequential order of the pictures was violated. Such an omission occurred between the 4th picture (at the earliest) and 11th picture (at the latest), and on average 6 s after trial onset. In these trials, all pictures following the missing picture immediately moved up, so that no temporal gap

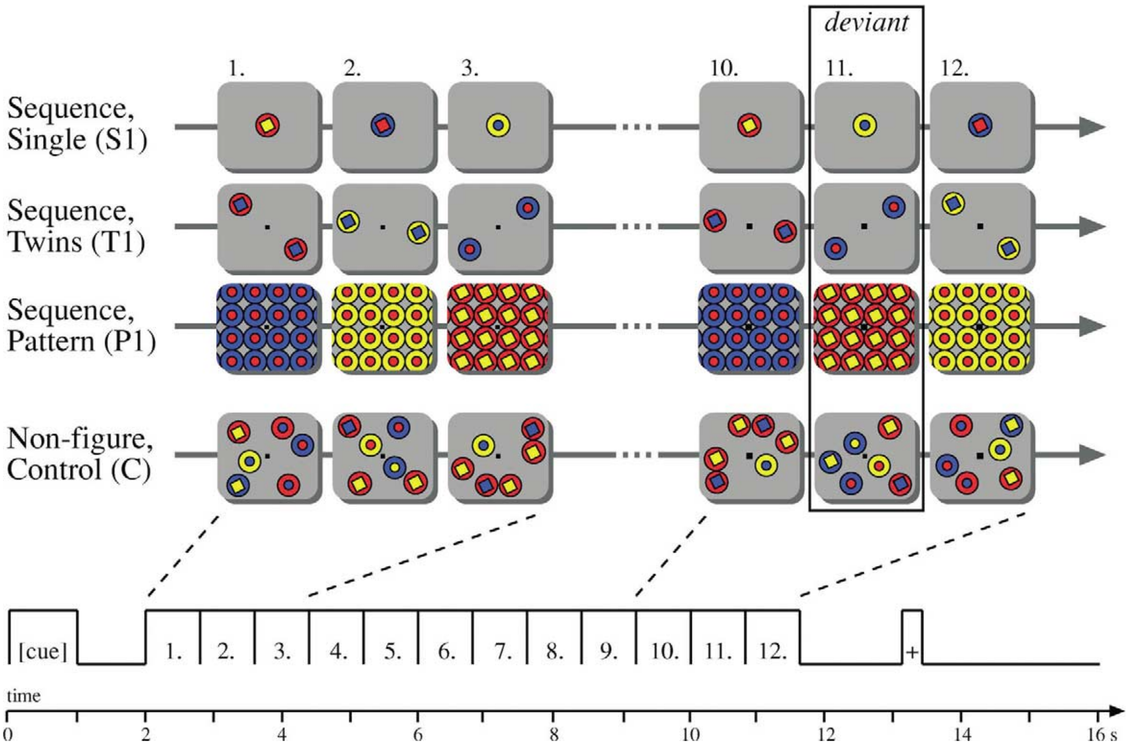

Fig. 1. Samples of stimuli presented in the three sequential matching conditions Single (S1), Twins (T1), and Pattern (P1), and the nonfigure control task (C) in Experiment 1. The lower panel shows the temporal schedule for one trial, comprising a task cue, a sequential stimulation of twelve frames, and response feedback. An example for a sequentially deviant stimulus is given in the first row, 11th picture.

was perceived. Subjects had to indicate a missing picture immediately by button press with the right index finger. Conditions S1, T1 and P1 differed only with regard to the visual stimuli presented. In the S1 condition, one single figure was presented at a time in the screen center. In the T1 condition, two identical figures were presented on each screen at opposite locations on a virtual circle, at 3.1° of visual angle to the screen center, resulting in 6.2° of visual angle for the entire circle. On the virtual circle, there were 32 possible locations at constant gaps of 11.25°, starting at 5° clockwise. As stimulus locations changed randomly from frame to frame, the presentation in this condition resulted in the impression of a rotating stimulus. In the P1 condition, multiples of one figure were presented, framing the fixation sign in the screen center, and forming a continuous pattern covering the whole screen (17.1° of visual angle). In both T1 and P1, the screen center was marked to facilitate constant visual fixation.

In the control condition (C), subjects were asked to indicate irregular changes of the fixation sign size while ignoring a sample of six figures presented at random screen locations changing from picture to picture. Regular changes of the fixation sign were defined as follows: small sign in the first three pictures, bigger sign in the subsequent three pictures, then again three times a small sign, and finally again three bigger signs in the last three pictures. The control condition exactly matched the figure conditions with regards to motor responses and preparatory effects of the go/no-go response mode. Moreover, the fixation size changes were the same in all conditions, though meaningless in the figure conditions.

2.3.2. Experiment 2

As shown in Fig. 2, four figure conditions were presented visually in a random trial design. Single figures were presented centrally in the Sequential Matching, Single Item (SS) and in the Individual Matching, Single Item (IS) condition, whereas patterns were presented in the Sequential Matching, Pattern (SP) and in the Individual Matching, Pattern (IP) condition. Number and length of trials, intertrial intervals, and presentation times of stimuli were the same as in Experiment 1. The two sequential matching tasks SS and SP differed from the tasks employed in Experiment 1 only with regard to the figure material. In the two individual matching tasks IS and IP, twelve different figures were presented within each trial in random succession. Subjects were required to indicate immediately by button press, if the figure shown at the beginning of a trial was presented a second time in the course of the same trial (40% of all trials).

2.4. Data acquisition

Data acquisition and analysis was identical in Experiments 1 and 2.

Participants underwent a 1-h training-session a few days

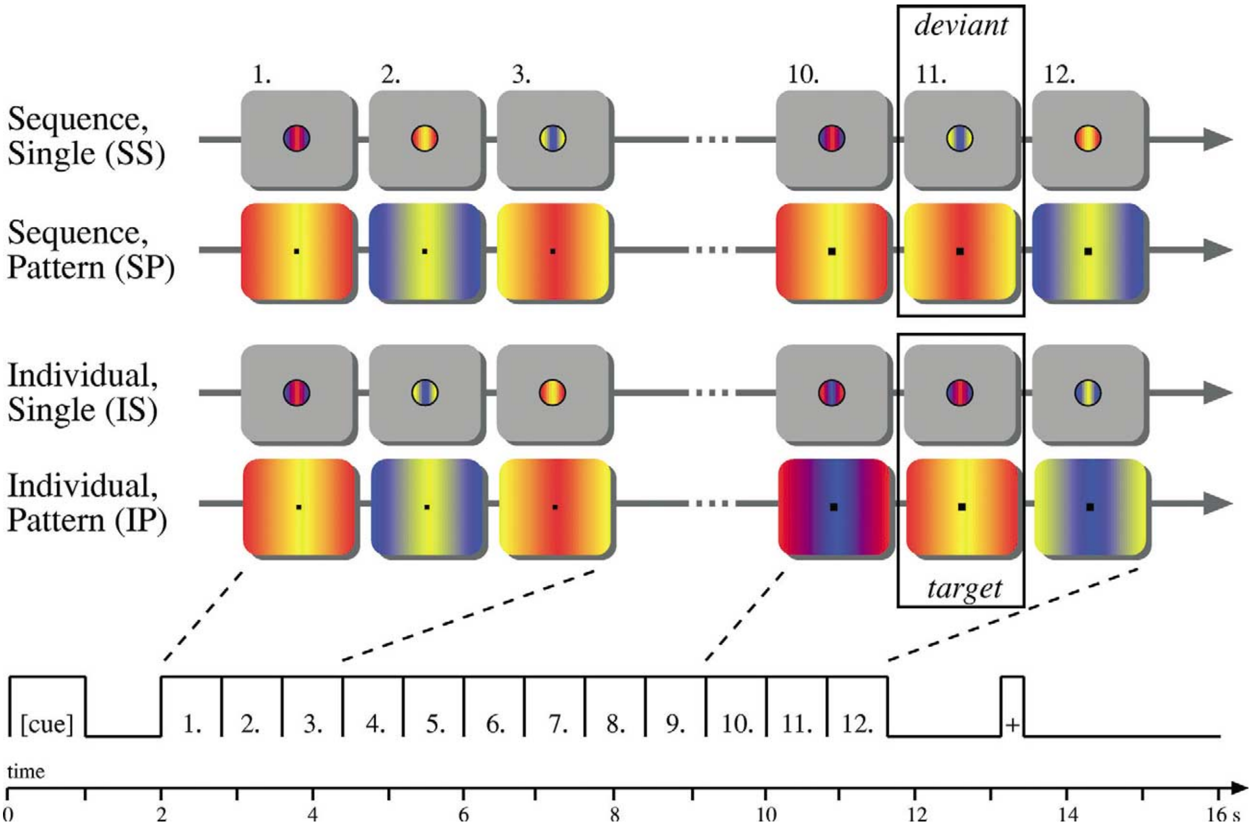

Fig. 2. Samples of stimuli presented in the two sequential matching conditions Sequential Matching, Single Item (SS) and Sequential Matching, Pattern (SP), and the two individual matching tasks Individual Matching, Single Item (IS), and Individual Matching, Pattern (IP) in Experiment 2. An example for a target stimulus in the individual figure matching conditions, defined as the repetition of the first stimulus within the same trial, is given in the third row, 10th picture.

before each main experiment. Imaging was performed at 3T on a Bruker Medspec 30/100 system equipped with the standard bird cage head coil. Subjects were supine on the scanner bed, and cushions were used to reduce head motion. Slices were positioned parallel to the bicommissural plane (AC–PC), with 16 slices (thickness 5 mm, spacing 2 mm) covering the whole brain. A set of two-dimensional anatomical images was acquired for each subject immediately prior to the functional experiment, using a MDEFT sequence (256×256 pixel matrix). Functional images in plane with the anatomical images were acquired using a single-shot gradient EPI sequence (TE= 30 ms, 64×64 pixel matrix, flip angle 90°, field of view 192 mm) sensitive to BOLD contrast. During each trial, eight 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 three-dimensional segmented MDEFT sequence covering the whole brain.

2.5. Data analysis

The fMRI data were processed using the software package LIPSIA [28]. In the preprocessing, low-frequency signals (frequencies due to global signal changes like respiration) were suppressed by applying a 1/130 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=2×64 s≈130 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 algorithm based on the Nyquist–Shannon theorem was employed [46]. 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) [65] 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 mm^3.

The statistical analysis was based on a least squares estimation using the general linear model (GLM) for serially autocorrelated observations [9,70,71]. The design matrix was generated with a boxcar function model and a response delay of 6 s. The brain activations of 8 s of the serial picture presentation of each condition and nogo-trial, starting from the first picture, were analyzed. As correct and incorrect nogo-trials revealed no significant activation differences in any condition, both were included in the analysis in order to enhance the overall signal-to-noise ratio. Go-trials were excluded from analysis. The last 1.6 s of the picture presentation were skipped in order to exclude the beginning of the intertrial interval. 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. Within this model, the temporal autocorrelation and the effective degrees of freedom were estimated. 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 ($Z \geq 3.09$) [22].

3. Results

3.1. Behavioral performance

3.1.1. Experiment 1

Behavioral performance was assessed by error rates. A repeated measures ANOVA with the three-level factor STIMULUS (Single, Twins, Patterns) indicated no significant main effect, with an error rate of 17.5% for Single, 12.1% for Twins, and 15.8% for Patterns. The two-level factor TASK (Figure, Control) showed a main effect ($F(1,11)=19.3$, $P<0.001$), indicating that performance was significantly better in the control condition (7.7% errors) than in all figure tasks together (15.5% errors).

3.1.2. Experiment 2

A repeated measures ANOVA with the two-level factors STIMULUS (Single, Pattern) indicated a main effect ($F(1,11)=51.5$, $P<0.0001$), showing that the pattern presentation was significantly more difficult (22.9% errors) than the single presentation (14.1% errors). The two-level factor TASK (Sequential, Individual) showed also a main effect ($F(1,11)=13.6$, $P<0.004$), indicating that performance was significantly better in the sequential tasks (16.7% errors) than the nonsequential tasks (20.7% errors). Moreover, there was a significant STIMULUS×TASK interaction ($F(1,11)=19.3$, $P<0.001$). Single *t*-tests revealed that this interaction was due to a nonsignificant difference of error rates between single item conditions SS and IS (14.1% errors in both) ($F(1,11)=0.0$, $P=1.0$), in contrast to a significant difference between pattern conditions SP (18.5% errors) and IP (27.3% errors) ($F(1,11)=57.6$, $P<0.0001$).

3.2. MRI data

3.2.1. Experiment 1

As listed in Table 1, all figure tasks S1, T1, and P1 elicited activations within premotor and other frontal as well as posterior areas, relative to the control condition C. As can be seen in the *Z*-maps displayed in Fig. 3, foci and intensities of activations within the left presupplementary motor area (preSMA), the PMv, the right superior frontal sulcus (SFS), the inferior frontal sulcus (IFS), and the left intraparietal sulcus (IPS) showed no remarkable differences between conditions. In contrast, more posterior parts of the IPS were activated only by S1-C and T1-C, whereas the fusiform gyrus (FG) was activated both by T1-C and P1-C. P1-C activated the left inferior occipital gyrus (IOG), and more posterior subregions of the calcarine sulcus (CAS) than both S1-C and T1-C. In addition, the frontal eye fields (FEF) were found to be activated by T1-C.

3.2.2. Region of interest analysis

In order to confirm premotor activations to be statistically comparable in all three figure conditions, lateral and medial premotor areas that were found to be significantly activated were subjected to a further post hoc analysis. More specifically, we tested whether the activation strength in regions of interest (ROIs) differed between conditions [2]. In each hemisphere, one sphere with a radius of 4 mm was defined as ROI within PMv, and one further within the left preSMA. The exact locations of the ROIs were established as follows. A new group *Z*-map was generated which resulted from contrasting the conditions S1, T1, and P1 against the C condition, so that all three experimental conditions of interest were represented in one *Z*-map (Fig. 4A). Each ROI was then centered at a local maximum of this *Z*-map. Thus, the locations of the ROIs did not differ across conditions or subjects. For all voxels of a ROI, a mean contrast was calculated for each subject and condition (for group averaged mean contrast values, see Fig. 4B). These mean values subsequently entered a repeated measures ANOVA with the three-level factors STIMULUS (S1, T1, P1) and ROI (left PMv, right PMv, left preSMA). Since the ROIs analyzed in this posthoc ANOVA already were shown to be significantly activated, α was set to $P=0.05$ with no further correction being necessary (see [2]). The ANOVA yielded no main effect

Table 1
Experiment 1: anatomical specification, hemisphere, mean Talairach coordinates and maximal Z scores (Z) of significantly activated voxels detected in each figure matching tasks versus control task

		Single-Control				Twins-Control				Pattern-Control			
		x	*y*	*z*	*Z*	*x*	*y*	*z*	*Z*	*x*	*y*	*z*	*Z*
PreSMA	L	−11	18	43	4.1	−11	19	43	4.1	−8	18	43	4.4
SFS	R	22	11	42	4.3	28	12	45	3.3	28	12	45	3.5
PMC	L	−41	2	29	4.3	−41	2	29	3.9	−41	2	29	4.2
	R	40	16	35	4.4	46	15	32	4.2	40	11	28	4.0
IFS	L	−44	26	24	4.0	−44	26	27	3.9	−44	26	24	4.1
	R					40	29	27	4.7	34	26	24	3.7
IPS	L	−38	−48	35	3.8	−41	−47	40	4.1	−38	−51	35	3.4
	R	43	−36	46	4.3	43	−36	46	3.8				
FEF	L					−29	−4	54	3.8				
	R					25	−8	49	3.3				
CAS	L	−20	−68	13	3.8	−23	−75	11	3.4				
	R	13	−63	12	4.0	13	−63	9	4.3				
	R									4	−82	7	5.8
IOG	L									−29	−86	−8	5.3
FG	L									−29	−55	−6	5.0
	R					22	−44	−14	4.8	28	−41	−12	5.5

PreSMA, presupplementary motor area; SFS, superior frontal sulcus; PMC, premotor cortex; IFS, inferior frontal sulcus; IPS, intraparietal sulcus; FEF, frontal eye field; CAS, calcarine sulcus; IOG, inferior occipital gyrus; FG, fusiform gyrus.

for STIMULUS ($F(2,22)=0.6$, $P>0.48$), and no interaction for STIMULUS×ROI ($F(4,44)=1.9$, $P>0.15$).

3.2.3. Experiment 2

As listed in Table 2, the contrast between single item tasks and pattern tasks, each collapsed over the sequential and the individual matching tasks [(SS, IS)–(SP, IP)], revealed different occipital activations for the single items (IOG) and for the patterns (CAS), respectively. No differences were found in any frontal or other parietal areas. However, the contrast between the sequential matching tasks and the individual matching tasks, each collapsed over single item and pattern stimuli [(SS, SP)–(IS, IP)], revealed the preSMA, the right and left lateral PMC, the right IPS, right SFS, and the caudate nucleus (CAU) to be significantly more activated during the sequential tasks, whereas no significant activation was found for the converse contrast. Corresponding Z-maps are shown in Fig. 5A. Finally, no significant activation or deactivation was found for the task by stimulus interaction contrast.

3.2.4. Region of interest analysis

In order to confirm premotor activations to be activated independently from the stimulus material, significant activations within the regions of interest were subjected to a posthoc analysis as in Experiment 1. Three ROIs were centered at the local maxima of the medial and the right and the left lateral PM activations of the Z-map contrasting sequential and individual matching. Mean values from each subject and condition entered a repeated measures ANOVA with the two-level factors STIMULUS (Single, Patterns), TASK (Sequential, Individual), and the three-level factor ROI (left PMv, right PMv, left preSMA). The ANOVA yielded neither a STIMULUS×TASK interaction ($F(1,10)=1.7$, $P>0.22$), nor a main effect for STIMULUS ($F(1,10)=0.78$, $P>0.4$), but a significant main effect for TASK ($F(1,10)=36.8$, $P>0.0001$). As can be seen in Fig. 5B, the main effect TASK was due to a global activation dominance of the sequential over the individual matching tasks within each ROI.

Together, results from both experiments yielded two main different groups of anatomical areas. Firstly, the lateral and the medial premotor areas, together with the right SFS and the IPS were activated by all sequential matching conditions in Experiments 1 and 2. In each condition, activations in these areas were independent from the stimulus material employed. Secondly, several occipital areas comprising the CAS, the FG, and the IOG were modulated differently by the stimulus material in the figure tasks, as indicated by the baseline contrasts in Experiment 1 and by direct contrasts between single item and pattern tasks in Experiment 2. Interested particularly in the premotor correlates of visual figure processing, we will in the following focus on the first of these two groups of regions, whereas findings related to the second group will be discussed elsewhere.

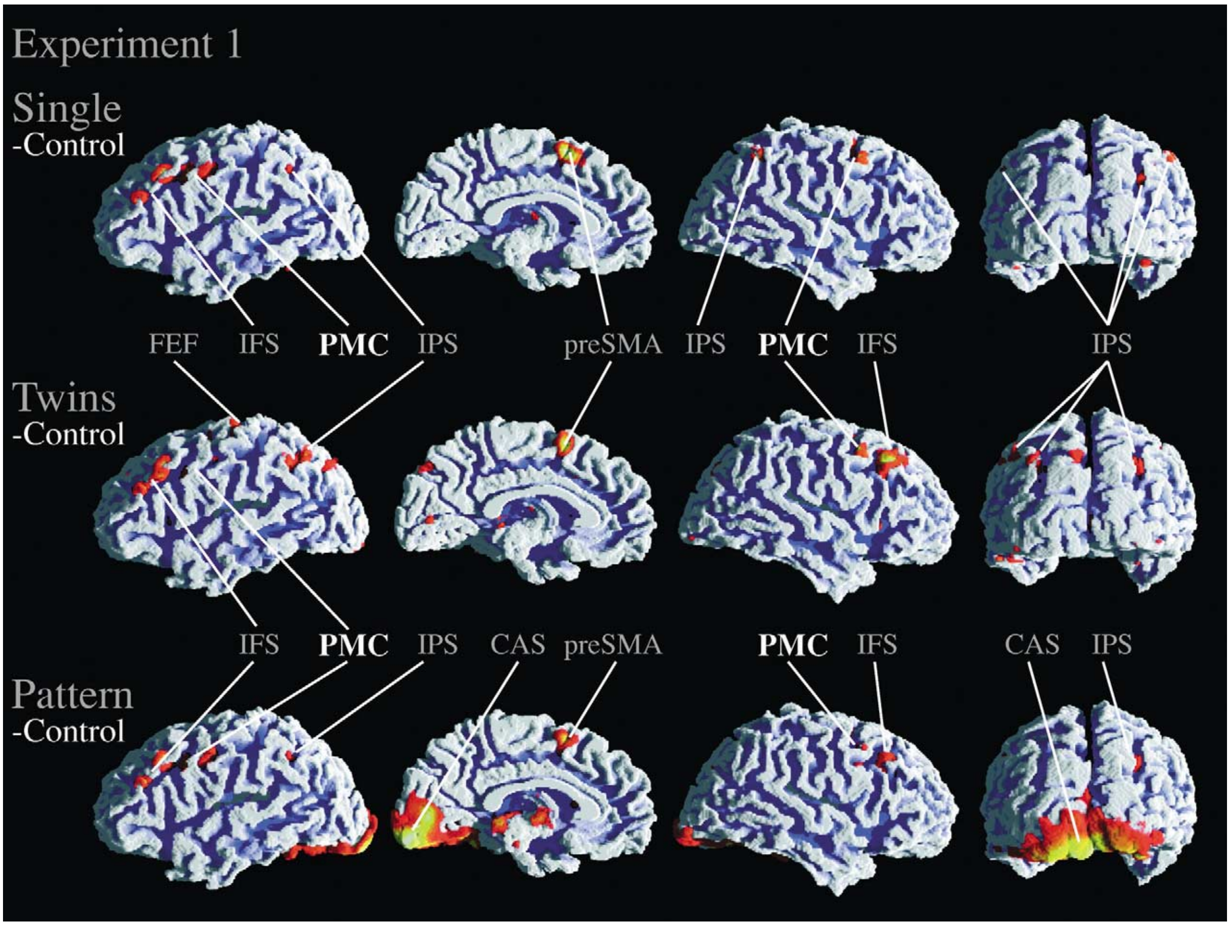

Fig. 3. Group averaged contrast maps ($n=12$) of Experiment 1 superimposed onto an individual brain scaled to the norm Talairach brain size [69]. The brain's gray matter (outermost 3–5 mm) is removed in order to show brain activations without anatomical distortion (white matter segmentation) [32]. Each of the three sequential matching tasks was contrasted with the control condition (upper panel: S1-C, middle panel: T1-C, lower panel: P1-C). Views show the left lateral hemisphere, the left median wall, the right lateral hemisphere, and the back of the brain (from left to right). Anatomical areas are abbreviated as follows: frontal eye field, FEF; inferior frontal sulcus, IFS; premotor cortex, PMC; intraparietal sulcus, IPS; presupplementary motor area, preSMA; calcarine sulcus, CAS.

4. Discussion

As expected, attention to dynamic properties of abstract visual stimuli caused significant activations within the PMv. This was the case in Experiment 1, where a sequential figure matching task was contrasted with a nonfigure baseline task, as well as in Experiment 2, where the same task was contrasted with a nonsequential matching task. Furthermore, this premotor activation was independent from manipulated stimulus features relating to potentially associated pragmatic attributes.

In the monkey, the PMv (Area F5) [35] has been related to object representation. Based on the finding that a certain class of F5 neurons respond not only selectively to grasping behaviors [10,24], but even in the absence of a motor preparation that refers to an attended object [47], a pure perceptual activation has been suggested [8,38]. A challenging interpretation of this finding is that attended objects are, regardless of any intention to grasp, translated into a potential grasping action in the observing animal. This potential action is suggested to reflect the pragmatic properties of the object, such as size, form, or weight. A number of fMRI findings now support the idea of premotor pragmatic representations in the human, as indicated by PMv involvement during both active grasping behaviors [37] as well as during perceiving [13], imagining [5,12], memorizing [15], and naming [32] graspable objects.

Accordingly, the present sequential matching paradigm revealed activation within areas related to the representation of pragmatic object features, the PMv. In addition, cortical areas that support or extent this function either with regard to action preparation, the preSMA, or with regard to object perception, the IPS, were found to be co-activated with the PMv. This was taken to reflect the

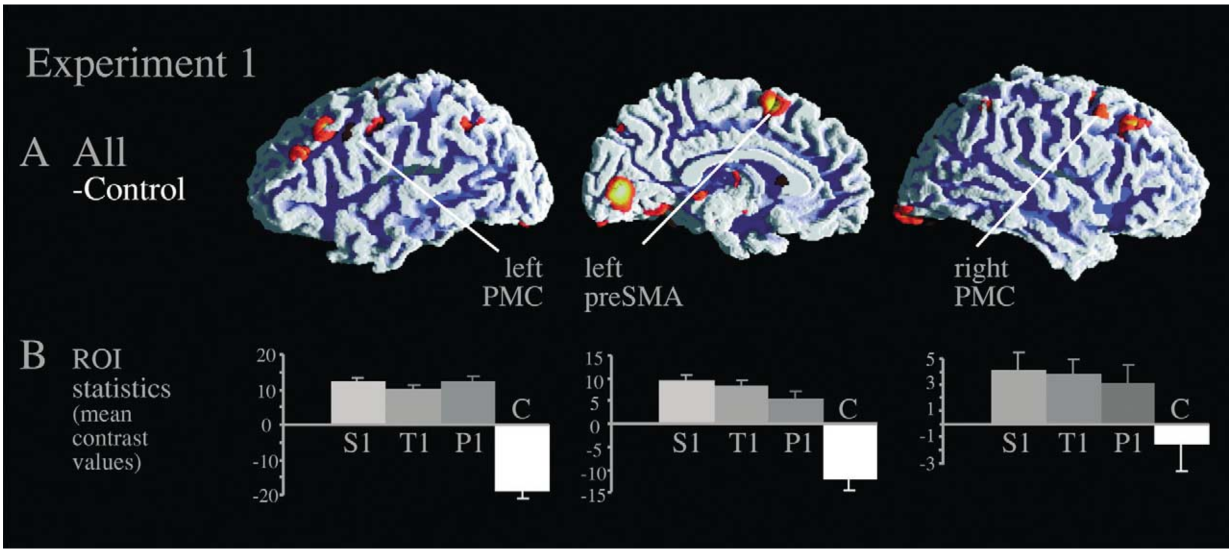

Fig. 4. (A) Group averaged *Z*-map contrasting all sequential matching conditions (S1, T1, and P1) versus the control condition C (Experiment 1), views from left, left median wall, right (left to right). (B) Group-averaged mean contrast values (absolute effect size) obtained from three regions of interest (left PMv, right PMv, left preSMA) in the posthoc ROI statistics.

intensive reciprocal projections between the preSMA and the vPMC [29,31] between the vPMC and the IPS [34,36], and between the IPS and the preSMA [31].

On the one hand, monkey research has indicated that the PMv and the anterior part of the IPS (aIPS) are involved in the transformation of object properties into manual action [38,39,48,53,64]. Likewise, the posterior IPS was reported to be involved in the coding of object size and shape [58]. Further evidence comes from a recent imaging study showing that object manipulation is reflected by activation within several areas of the prehension circuit, as found in the monkey, including the PMv and aIPS [1]. Accordingly, we suggest posterior as well as anterior IPS activation found in the sequential figure matching tasks to be due to requirements of visual stimulus processing. This interpretation is in line with the fact that IPS activations differed slightly between conditions and both experiments, as would be expected for varying object properties.

Table 2
Experiment 2: anatomical specification, mean Talairach coordinates and maximal *Z*-scores (*Z*) of significantly activated voxels detected in sequential versus individual matching tasks (SS/SP–IS/IP), and in single item versus pattern conditions (SS/IS–SP/IP) and vice versa (SP/IP–SS/IS)

		x	*y*	*z*	*Z*
Sequential-individual					
PreSMA	L	−5	1	50	4.4
	R	1	19	37	3.5
SFS	R	25	12	45	3.8
PMCd	L	−53	−4	37	3.4
	R	43	−6	43	3.7
PMCv	L	−56	5	17	4.3
	R	43	3	21	4.2
IPS	R	37	−40	44	4.1
	R	28	−61	46	4.2
CAU	R	13	5	0	3.7
Single item–pattern					
IOG	L	−32	−90	0	3.9
	R	31	−86	2	4.1
Pattern–single item					
CAS	L	−20	−57	8	5.2
	R	10	−55	4	5.2
	R	1	−83	4	5.9

CAU, caudate nucleus; other abbreviations as in Table 1.

On the other hand, involved in visually guided motor selection and control [6,16,45,62,68], the preSMA is known to project restrictively to the ventral subregions of the PMC [31]. This projection is conceived of serving the binding of goal selection of a movement to a target or grip selection [7]. Together with findings showing grasping and reaching activation in this area [3,30,66], global control functions over reaching–grasping actions are suggested to be supported by the preSMA [49,50]. Most importantly for the present findings, however, SMA and pre-SMA are crucially involved in sequencing multiple movements over time [20,21,44,59,60,67]. As the preSMA was found to be activated in all contrasts between the sequential matching and nonsequential tasks in Experiments 1 and 2, we take the learning of sequential information to have caused preSMA activation. This would be in line with the finding that a medial premotor sequencing function is not bound to motor output, but in contrast is also present in the learning of perceived sequential events [54].

Using a perceptual task and simple two-dimensional, abstract stimulus material, the present findings particularly confirm the idea that lateral premotor and related cortical areas that support object-directed behaviors can also be activated in the absence of the conscious intention, or even the possibility to grasp or manipulate the attended

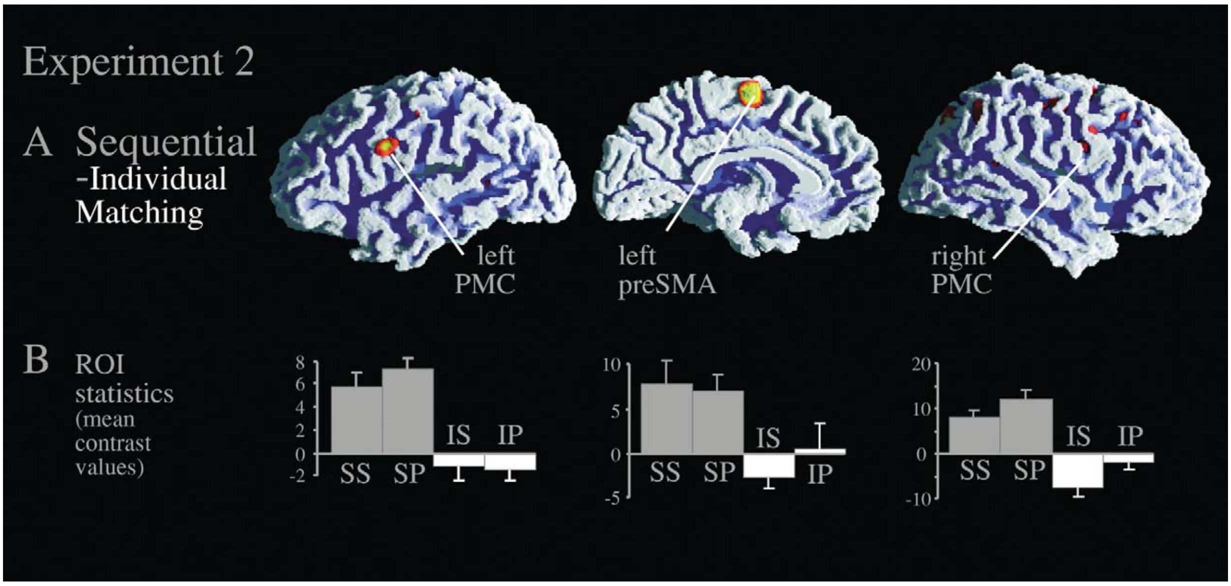

Fig. 5. (A) Group averaged *Z*-map contrasting all sequential matching conditions (SS, SP) versus all individual matching conditions (IS, IP) (Experiment 2), views from left, left median wall, right (left to right). (B) Group-averaged mean contrast values (absolute effect size) obtained from three regions of interest (left PMv, right PMv, left preSMA) in the posthoc ROI statistics.

stimulus. Accordingly, highly similar premotor activations are obtained during tasks that relate to pragmatic object properties, and during tasks that relate to dynamic stimulus properties, as in the present studies and prior investigations using the same paradigm (see Fig. 6). This finding raises the question why the PMC should respond not only to pragmatic object properties, but also to dynamic stimulus features, such as continuously changing patterns in an abstract figure sequence.

An answer might be gained from the wellknown premotor role in sequencing movements. Evidence for this function comes particularly from paradigms in which participants are asked to transform dynamic perceptual patterns into dynamic movement patterns, resulting in sensory guided sequential movements [7,17,18,40,69]. Whenever the guiding stimulus exposes a regular, and therewith predictable, dynamic, movements can get more and more independent from guidance by the stimulus due to a learning process. The premotor role in this sensorimotor transformation has been indicated by a number of imaging studies [11,14,19–21,23,26,42,51,52,67] using the serial reaction time paradigm (SRT) introduced by Nissen and Bullemer [41].

Based on these and previous findings [55,57], we suppose that, by its potential movement-guiding function, each dynamic stimulus feature can get a pragmatic mean-

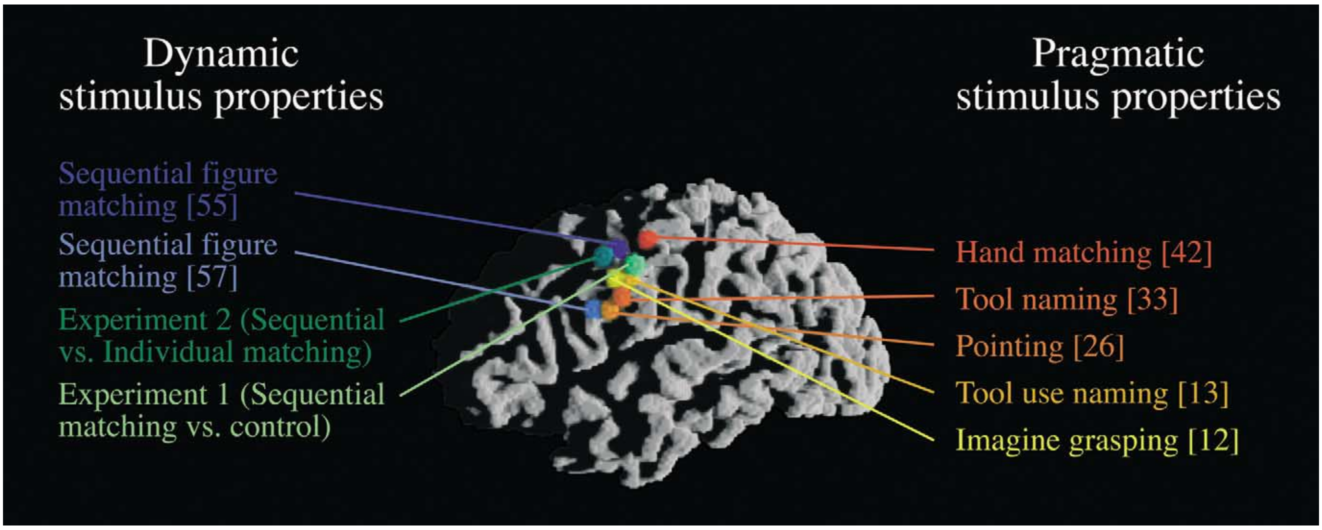

Fig. 6. Schematic comparison of activation foci obtained within other imaging studies investigating pragmatic or dynamic stimulus properties (references in brackets) and the present Experiments 1 and 2, plotted on an individual brain.

ing. For instance, in an SRT task, the left diode on a screen that lights up means, e.g. 'left hand button press', whereas the right diode lighting up means 'right hand button press'. Although as in this example, movements are usually spatially referenced onto a guiding stimulus in SRT tasks, the movement-guiding stimulus feature could in principle be also a temporal property (like e.g. rhythm in a melody) or an object property (like e.g. object form in a pulsing motion). First evidence for an anatomical dissociation of these three types of feature representation, i.e. spatial, temporal, and object-related, comes from fMRI [55], showing that temporal stimulus sequences causes activation within the most ventral region of the PMC in the vicinity of BA 44 (Broca's Area), whereas spatial stimulus sequences lead to activation in the most dorsal PMC, near to the FEF, and, between both, object stimulus sequences activates the superior part of PMv. We have proposed that this functional–anatomical pattern reveals an effector-based representation of attended dynamic stimulus sequences. This assumption of a rough somatotopical representation of attended stimulus features was replicated in a recent fMRI study [57]. As displayed in Fig. 6, the present activation foci obtained in the sequential figure tasks match very well the anatomical location of activation obtained in the prior object tasks. However, the present findings did not only support these prior interpretations, but indicate more specifically that it is the embedding within a dynamic context that makes the premotor cortex to be engaged in the processing of figure properties. Thereby the present data stress the influence of the task, i.e. the top-down modulations, on premotor activation during the perceptual processing of objects or abstract visual figures, and relativizes the influence of the stimulus properties, i.e. bottom-up modulations.

It has to be considered that the design of Experiment 1 suffered from the fact that the control condition also required a certain amount of sequential processing in the sense that regular changes of the fixation cross were to be monitored. One may argue that the difference of sequential processing requirements in the sequential tasks and the control condition would not have been significant enough to cause premotor activation differences. However, this alternative explanation can be ruled out by the findings of Experiment 2, where sequential tasks were compared with purely nonsequential tasks. Likewise, it could be argued that differences in task difficulty may obscure the interpretation that findings were caused by varied requirements of dynamic feature processing. However, as the control was easier than the experimental conditions in Experiment 1, and the experimental conditions easier than the controls in Experiment 2, this explanation can be ruled out as well.

Interestingly, modified applications of the SRT paradigm indicate that the premotor involvement does not depend on actual overt tracking movements, but is even present during mere perceptually tracking dynamic stimulus patterns [54–56]. Independently from actual situational demands, the PMC thus appears to respond to dynamic environmental features, probably in order to prepare for potential response requirements. Such a readiness for entities that are marked by a pattern or process of change has a direct vital meaning, as it optimizes the accuracy and speed of sensory processing, and it thereby facilitates the preparation of appropriate motor responses [25,27,43,72].

How is this interpretation compatible with the second finding of the present studies, that premotor activations were found to be uninfluenced by varying stimulus properties? In Experiment 1, this was indicated by comparable Z-scores of premotor activation foci in all figure conditions, and was also supported by the missing main effect of the factor STIMULUS in the posthoc ROI analyses within premotor regions. This finding was replicated in Experiment 2, where the direct comparison of single figure versus pattern conditions revealed no premotor activation. As in Experiment 1, no main effect for the factor STIMULUS was found in the posthoc ROI statistics in Experiment 2. Together, none of the stimulus properties that were manipulated in the present studies—the presentation as single item, rotating figure, decomposable and nondecomposable pattern— yielded any modulating influence on the resulting premotor responses. Although this result might be different for other manipulations as those employed in the present experiments, and missing effects cannot build the basis for any argumentation—we would like to discuss at least the theoretical implications for our interpretation.

Stimulus features that relate to pragmatic object properties such as e.g. how easily an object can be grasped, appears to be of significant influence on premotor involvement, as indicated by a number of imaging studies [1,32,33,63]. In contrast, stimuli that induced premotor activation in the present studies did not have any obvious pragmatic meaning. By manipulating the presentation in different ways, we tried to provoke pragmatic associations in order to test their potential influence. As indicated by missing stimulus effects in both experiments, however, there was no hint for any conceivable pragmatic properties influencing the present tasks. In contrast, we have argued that premotor activations were caused exclusively by attending to dynamic stimulus features, which are, in contrast to pragmatic properties, not bound to specific object features like size, form, or weight.

However, if attending to dynamical features gives rise to some kind of sensorimotor transformation within premotor cortices, then one might wonder which kind of movement-related representation there might be that could correspond to sequences of color-transitions, as for instance in the sequential pattern task in Experiment 2 (condition SP).

A preliminary answer might be that attending to sequential patterns that are defined by object-specific properties might give raise to manual movement representations in the PMv, because the hand is the motor effector best adapted onto objects. While this idea is straightforward for properties like object form, as corresponding to grip type, or object size, as corresponding to grip aperture, it is less so for object properties like color or surface structure, which do not correspond directly to a motor effector parameter. One can argue that, even if not each object feature might be relevant for restricting manual movement parameters in object grasping or manipulation, all the features together help us to recognize an object and activate appropriate object-related actions, that is, we do not ignore 'nonpragmatic' object properties. Conversely, some pragmatic object properties are in fact invisible, as for instance object weight, corresponding to grip force.

Most importantly, however, stimulus features within our reach that are subjected to relatively fast dynamic patterns of changes do usually have a pragmatic relevance and require fast, appropriate motor responses. In real life, changes of brightness or, as in the pattern conditions in Experiment 2, changes of color announce a moving target. According to this idea, premotor responses to dynamic stimulus features might reflect sensorimotor representations that are less specific than those that reflect pragmatic stimulus features, as they do not correspond to specific, over-learned hand movements. Nevertheless, due to the vital meaning of dynamic patterns, particularly in near space, the engagement of premotor areas involved in hand–object interaction might be a functional default modus that applies to all dynamic stimuli defined by object properties.

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