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Neural correlates of incongruous visual information An event-related fMRI study

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Abstract

Incongruous information is better remembered than ordinary information. This result has been attributed both to semantic incongruity and surprise. To determine the contribution of each factor, we performed a functional magnetic resonance imaging study in which participants viewed pictures depicting ordinary and incongruous objects (e.g., head of a wrench fused onto a sheep body). To maximize surprise we administered novel incongruent pictures infrequently in an initial scan. (This scan also included infrequent color-inverted pictures as a control for frequency.) To obtain a pure measure of the effect of incongruity we conducted a second scan in which participants viewed equal numbers of ordinary and incongruous pictures. Signal increases were greater for incongruous versus ordinary and oddball stimuli throughout the ventral and dorsal visual pathways, and in prefrontal cortex bilaterally. Signal decreases were larger for incongruous than for ordinary stimuli bilaterally in lateral parietal regions. A subset of regions near the right frontal operculum and extending laterally responded only to, or more strongly to, infrequent incongruous pictures. A second, purely behavioral, experiment involving a separate group of participants demonstrated that incongruous pictures were better recognized than ordinary pictures. We interpret our results as suggesting that, although correlates of a surprise response can be observed, better memory for incongruous visual information is attributable mainly to more processing and, consequently, better encoding.

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Introduction

Incongruity is the quality generated by the violation of norms and expectations built up over a lifetime. Multiple behavioral studies have shown a memory advantage for incongruous versus commonplace material (e.g., Riefer and LaMay, 1998). This result is commonly known as the “bizarreness effect.” To provide a better understanding of the neural correlates of this effect, we conducted a functional magnetic resonance imaging (fMRI) experiment directly

contrasting responses evoked by incongruous versus ordinary visual stimuli. A corresponding memory advantage was demonstrated for incongruous over ordinary stimuli in a behavioral recognition experiment.

Previous studies have established that semantically incongruous sentences (e.g., “The soldier licked the kittens”) are better recalled than ordinary sentences (e.g., “The man read a book”) (Cornoldi et al., 1988; Hirshman et al., 1989; McDaniel and Einstein, 1986; Nicolas and Marchal, 1996; Riefer and LaMay, 1998; Worthen and Marshall, 1996). Incongruity in these studies typically is induced by violating semantic consistency, for example, by attributing human actions to animals and artifacts or vice versa. Subjects typically are asked to read incongruous and ordinary sentences with attention to semantic content. A memory ad-

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vantage on subsequent testing for incongruous material has so far been reliably demonstrated mostly with recall (as opposed to recognition) tasks and with mixed (including incongruous and ordinary items) rather than pure lists.

Several mutually nonexclusive interpretations of the bizarreness effect are currently under debate (see, e.g., Worthen et al., 2000). One possibility is that incongruous stimuli elicit extra (more elaborated) processing because they are more difficult to make sense of in the context of expected properties and semantic norms (the elaboration hypothesis) (Merry, 1980; Wollen and Cox, 1981). According to this view, the extra elaboration given to incongruous items strengthens their memory trace much as deep, semantically elaborated tasks encourage memorization in standard memory paradigms (e.g., Craik and Lockhart, 1972; Craik and Tulving, 1975). Related to this is the finding that the memory benefits of incongruity are due in part to distinctiveness in the encoding context (Hunt and Elliot, 1980; McDaniel and Einstein, 1986). Another possibility is that incongruous stimuli elicit a surprise response due to the violation of expectations, which enhances contextual cues available for later recall (the surprise hypothesis; Hirshman et al., 1989).

The physiological basis of the bizarreness effect is incompletely understood. Relevant data derive from studies of electrophysiological responses to incongruous stimuli. The N400 potential is a central-parietal scalp negativity that peaks 400 ms after the presentation of (1) semantically incongruous words in the context of sentences (see Kutas and Hillyard, 1983), or (2) semantically unrelated words or pictures (see Holcomb, 1988, and McPherson and Holcomb, 1999). The N400 phenomenon is thought to be a correlate of the semantic conflict arising when perceived information is different from information expected based on prior context. Three recent fMRI studies (Kuperberg et al., 2000; Newman et al., 2001; Ni et al., 2001) have compared responses to semantic (e.g., “The man sailed the hotel to China”) versus syntactic (e.g., “The woman read the with letter attention”) anomalies. All three studies report functional anatomic differences in responses to semantic versus syntactic anomalies, but, in aggregate, do not provide a consistent picture of the specifically activated regions.

The physiological correlates of the surprise response proposed by Hirshman et al. (1989) have not been defined. The “surprise” may originate in an orienting response, which is usually evoked by unexpected stimuli and corresponds to a complex of processes including arousal, capture of attention, and memory formation (Sokolov, 1963). The electrophysiological phenomenon most associated with orienting is the P3 potential, i.e., scalp positivity peaking about 300 ms after infrequent (oddball) stimuli are presented (Johnson, 1986, 1993; Matt et al., 1992). Two P3 subtypes may be distinguished: Whereas the P3b is strongly modulated by stimulus task relevance and does not habituate, the P3a occurs in response to unexpected or context-violating events, exhibits a somewhat earlier latency and more ante-

rior scalp distribution, and habituates rapidly (Knight and Nakada, 1998; Knight and Scabini, 1998). Several fMRI correlates of the P3a have recently been reported suggesting that the hippocampus as well as the temporal, prefrontal, and parietal cortices contribute to the generation of this potential (Kirino et al., 2000; Knight, 1996; McCarthy et al., 1997; Strange et al., 2000).

In a series of two studies, we explored the neural and behavioral correlates of incongruous visual material to test whether such stimuli elicit extra elaboration and/or a surprise response. Incongruous pictures incorporating semantic violations concerning artifacts and living things were generated by combining incongruous parts (e.g., head of cat on body of lobster, kangaroo with the head replaced by the hose/nozzle assembly of a gasoline pump). One condition was designed to examine the response to incongruous materials under conditions usually used in previous behavioral memory experiments. In this condition (frequent incongruous, or Freq-Inc condition), incongruous and ordinary pictures were presented with equal frequency. Such a condition was expected to allow examination of additional encoding activity (if any) related to incongruity. Another condition (infrequent incongruous, or Inf-Inc condition) was designed to examine the surprise response (if any) associated with the perception of incongruous pictures. We tried to maximize the possibility of a surprise response by (1) presenting only few incongruous pictures among several ordinary pictures, and (2) always running this condition first so that these incongruous pictures were the first seen in the experiment. A small number of oddball stimuli (color inverted but otherwise ordinary pictures) were also included as a control for frequency effects.

Although firm predictions are not possible, the elaboration hypothesis tentatively predicts greater activity for incongruous pictures than for ordinary pictures in areas underlying the processing of these stimuli. This extra processing should occur independently of the frequency of the incongruous pictures. Accordingly, data supporting this hypothesis should show greater activity for incongruous pictures across our conditions in visual extrastriate cortex and prefrontal cortex, reflecting visual and semantic encoding (see Buckner et al., 1999; Fletcher et al., 1998; Tulving et al., 1994). The surprise hypothesis predicts greater activity for incongruous pictures than for ordinary pictures in areas underlying emotional responses such as the thalamus, the amygdala, and/or the frontal operculum (see Strange et al., 2000). This emotional response should be enhanced (or only appear) when incongruous stimuli are novel and infrequent (Inf-Inc condition).

In addition to the fMRI study, we conducted a separate experiment to examine the effect of stimulus incongruity on recognition memory. The study phase of this behavioral experiment was closely matched to the Freq-Inc condition of the fMRI experiment. A novel sequential recognition design was implemented that provided sensitive measures of recognition accuracy as well as a measure of recognition

confidence. We hypothesized that incongruous stimuli would be recognized more accurately and more quickly than ordinary stimuli.

Experiment 1: fMRI correlates of visual incongruity

Materials and methods

Participants

Twenty-four participants (13 females, mean age = 21.8 years) were recruited from the Washington University community. All participants had normal or corrected-to-normal vision, were native English speakers, showed a strong right-handed preference as measured by the Edinburg Handedness Inventory (Raczkowski et al., 1974), and reported no history of significant neurological problems. Participants were paid and provided informed consent in accordance with guidelines set by the Washington University Human Studies Committee.

Imaging procedures

Imaging was conducted on a Siemens 1.5 Tesla Vision System (Erlangen, Germany). Headphones were used to dampen scanner noise. Visual stimuli were generated on an Apple Power Macintosh G3 computer using Psyscope (Cohen et al., 1993) and were projected onto a screen positioned at the head of the magnet bore by an LCD projector. Participants viewed the stimuli by way of a mirror mounted on the head coil. They responded by using a fiber-optic light-sensitive keypress interfaced to a Psyscope Button Box (Carnegie Mellon University, Pittsburgh, PA). A pillow placed within the head coil and a thermoplastic face mask were used to minimize head movement.

Structural imaging included a high resolution ($1 \times 1 \times 1.25$ mm) sagittal T1-weighted MP-RAGE (TR = 9.7 ms, TE = 4.0 ms, flip angle = 10, TI = 20 ms, TD = 500 ms) and a T2-weighted fast turbo-spin echo (TSE) scan. Functional data were acquired using an asymmetric spin-echo echoplanar sequence sensitive to blood oxygenation level dependent (BOLD) (T2*) contrast (TR = 2.84 s, TE = 37 ms, 3.75×3.75 mm in-plane resolution). Whole-brain coverage was achieved with 21 contiguous 6-mm slices. Slice tilts and offsets were prescribed in relation to the AC-PC plane on the basis of fast automatic atlas registration of a low resolution (2 mm cubic voxel) pre-fMRI MP-RAGE scan. Each functional run included 105 whole-brain image acquisitions (approximately 5 min). The complete imaging session lasted approximately 1 h.

Stimuli

All stimuli were prepared from commercially available vector graphic drawings of common artifacts and living things. CorelDraw 10 (www.corel.com) was used to modify the pictures as necessary. Alphanumeric labels, if present, were removed. Depictions of single, whole objects made up

the ordinary stimuli (e.g., teapot, and tuna). The incongruous stimuli were generated by combining semantically unrelated parts (e.g., head of wrench fused onto the body of a sheep) and removing visual clues suggesting the presence of more than one object (Fig. 1). Care was taken to preserve the iconographic identity of the depicted parts, to generate an incongruous percept. This strategy is different than that of Kroll and Potter (1984) who created tracing composites in which the identity of the parts characteristically was obscured. Oddball stimuli were generated by inverting the color values of selected ordinary stimuli. Thus, the background of the ordinary and incongruous stimuli was white whereas for the oddballs it was black (Fig. 1). Ordinary stimuli were vertically flipped to create obviously upside-down pictures (see behavioral procedures below). No object part was depicted more than once over the entire stimulus set. As viewed by the subject during fMRI the vector-graphic stimuli subtended 8 to 11 degrees of visual angle.

fMRI protocol

The fMRI experiment was composed of two conditions, each administered during a separate fMRI run. In each condition 50 pictures were presented according to a rapid-presentation randomized event-related design (Burock et al., 1998). The two conditions differed only in the proportion of stimuli drawn from each category (ordinary, oddball, and incongruous). In the Inf-Inc condition (first fMRI run) 5 incongruous, 5 oddball, and 40 ordinary stimuli were presented. In the Freq-Inc condition (second run) 25 incongruous and 25 ordinary stimuli were presented. Stimulus duration was one fMRI time point (2.84 s). To vary the inter-stimulus interval, 50 presentations of a fixation crosshair (one fMRI time point duration) were randomly intermixed with the pictures.

Participants were instructed to detect upside-down pictures and respond by right-hand button press. The purpose of this task was to promote attention to the pictures. Only one upside-down picture was presented at the very end of each condition. Recording the detection responses provided a check on participant vigilance. These events did not contribute to the recovered hemodynamic response because of their late positioning in the run. False detection responses occurred occasionally during the runs (see results section below). These events were excluded from the hemodynamic response analysis.

After imaging and removal from the scanner participants rated the subjective incongruity of the stimulus set on a scale of 1 (“ordinary”) to 7 (“bizarre”). The rating questionnaire was filled out using pencil on color printed hard copy. Memory could not be assessed in this study without introducing confounds. For this reason, a second study using similar stimuli and study procedures was conducted to explore effects on memory as described below in Experiment 2.

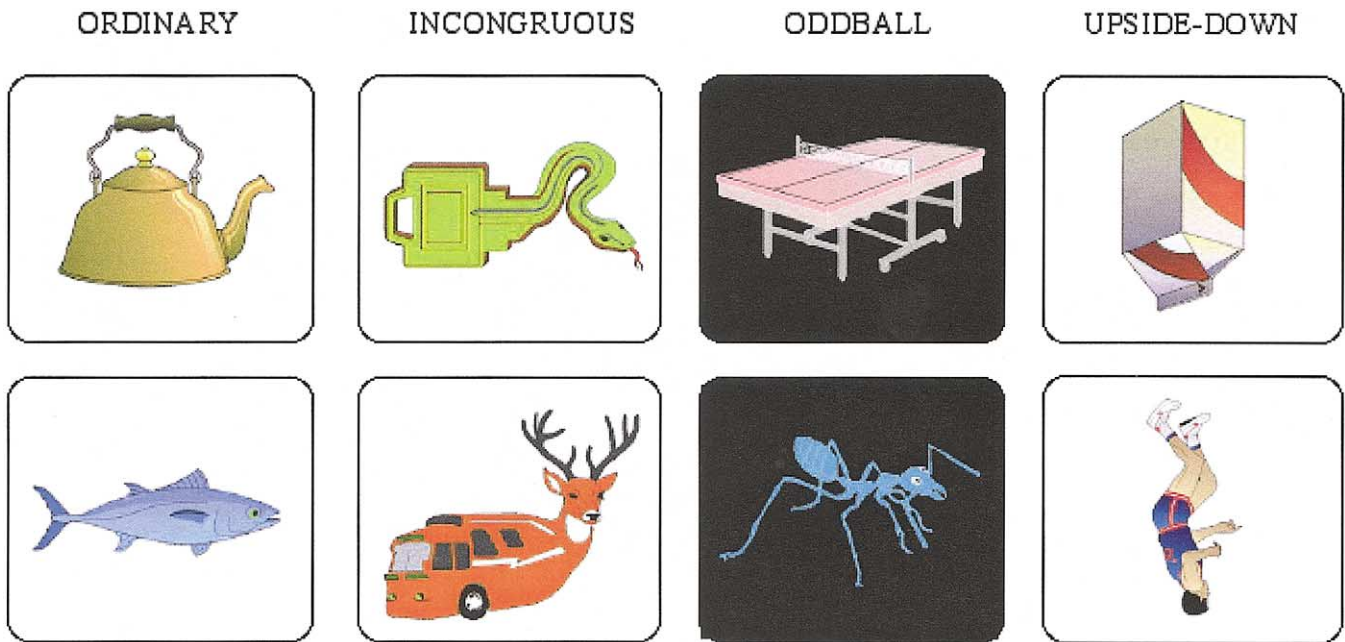


Fig. 1. Examples of ordinary, incongruous, oddball, and upside-down pictures.

fMRI data analysis

Preprocessing included (1) compensation for slice-dependent time shifts (136 ms/slice), (2) elimination of odd/even slice intensity differences due to interpolated acquisition, (3) realignment of all data acquired in each subject within and across runs to compensate for rigid body motion (Ojemann et al., 1997), and (4) intensity normalization to a whole-brain mode value of 1,000. The functional data were transformed into the stereotaxic atlas space of Talairach and Tournoux (1988) by computing a sequence of affine transforms (first frame EPI to T2-weighted TSE to MP-RAGE to atlas representative target), which were combined by matrix multiplication. Reslicing the functional data in conformity with the atlas then involved only one interpolation. For cross-modal (e.g., functional to structural) image registration, a locally developed algorithm was used.

The first four frames of each run were discarded to allow for stabilization of longitudinal magnetization. Linear trends in the time series were removed on a voxel-by-voxel basis (Bandettini et al., 1993). Event-related responses for each individual were extracted using the general linear model, with a set of seven delta basis functions covering the seven scanning frames after the presentation of each stimulus, and separate event types for each combination of stimulus type and condition (Miezin et al., 2000). Voxels corresponding to significant task-related modulations were determined by voxel-wise random-effects analysis of variance (ANOVA) with condition (Inf-Inc or Freq-Inc), picture type (ordinary or incongruous), and time point (1 to 7) as independent variables. In this analysis, regions that respond overall to the presentation of a stimulus will show a main effect of timepoint. To identify regions involved in processing the stimuli, the F -statistic map of the main effect of time

point was converted to equivalently probable Z values and thresholded at $Z > 4.5$ over at least 5 contiguous voxels. This threshold corresponds to a 5% multiple comparisons adjusted probability of falsely identifying one or more activated voxel clusters on the basis of Monte Carlo simulations and the Box correction for correlated data. This thresholded map was used to automatically define regions of interest (ROI) centered on loci of peak Z statistics. The ROI definition procedure ensured that ROI centers were separated by at least 15 mm. Voxels outside the thresholded main effect of the time point map were excluded. This procedure yielded 31 ROI. Estimated time courses for each participant for each event type were then averaged over each region and submitted to region-wise ANOVAs. Statistical significance was assessed after Bonferroni correction (multiplication by 31) applied to the computed F -ratio probabilities.

Results

Behavioral results

All but 1 of the 24 participants correctly responded to both upside-down pictures. One subject failed to detect the upside-down picture presented at the end of the Freq-Inc condition. We conclude that participants paid attention to the pictures. Participants made false detections on 0.66% of the trials only. Of the 11 incorrect button presses occurring in the Inf-Inc condition, 1 was in response to an incongruous picture, 2 were in response to color-inverted oddballs, and 8 in response to ordinary pictures. In the Freq-Inc condition, 4 false detections occurred, 2 in response to incongruous pictures and 2 in response to ordinary pictures. Thus, in-

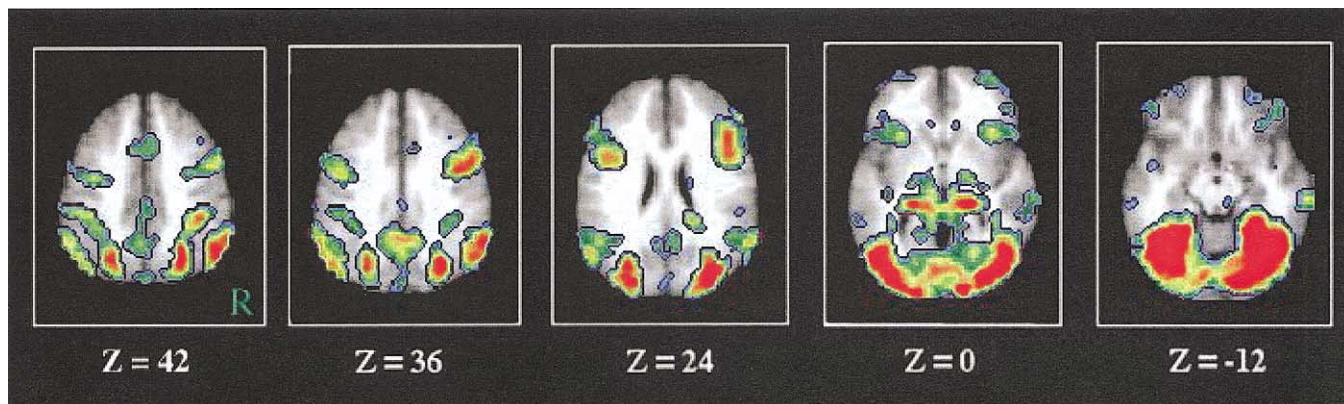


Fig. 2. Voxel-wise map of statistically reliable task-related BOLD modulation (main effect of time point). This test was collapsed over picture type (incongruous and ordinary), condition (frequent incongruous and infrequent incongruous), and over all 24 participants. The statistical map is superimposed on the structural T1-weighted image averaged over all participants.

congruous pictures were no more likely than ordinary pictures to elicit false upside-down target detection responses.

The rating questionnaire results were consistent with the a priori categorization of the pictures. On the scale of 1 (“ordinary”) to 7 (“bizarre”) mean ratings for ordinary, oddball, and incongruous pictures were 1.08 (SD = 0.24), 1.37 (SD = 0.78), 5.48 (SD = 0.66), respectively. An ANOVA conducted on these data showed a main effect of picture type, $F(2,58) = 4.16$, $P < 0.001$.

fMRI results

Regions that showed reliably modulated activity in response to picture presentation (main effect of time point in the voxel-wise ANOVA, irrespective of picture type or condition) are illustrated in Fig. 2. Partition of this map generated the 31 ROI listed in Table 1. This set of regions provided the basis for several ANOVA analyses examining stimulus- and condition-related effects. In the following presentation of ROI-based ANOVA results the quoted F and P values correspond to the least significant ROI in each ANOVA.

Effects of picture type across conditions

The map resulting from a picture type (incongruous vs. ordinary) \times time point voxel-wise ANOVA is shown in Fig. 3A. This map differed from the map showing all modulated activity (Fig. 2) primarily in excluding supplementary motor area (SMA), dorsal thalamus, and dorsal premotor areas. A modest degree of right hemisphere emphasis in the picture type \times time map was evident. This result was reinforced by ROI-based analysis combining data across both fMRI runs consisting of a 2 (Inf-Inc vs. Freq-Inc) \times 2 (incongruous vs. ordinary) \times 7 (time point) repeated measures (subject) ANOVA conducted on each region. A significant time point \times picture type interaction was obtained [$F(6,138) > 4.2$, $P < 0.0007$] in 26 ROI (Table 1, fourth column from the right). These regions covered a large portion of the occipital lobes bilaterally, including striate (BA

17) and extrastriate cortices (BA 18 and 19) with bilateral extension to temporal (BA 37) and parietal regions (BA 7). Similar results were observed bilaterally in frontal areas (BA 45/47 and 6/9/44) and posterior thalamus. A significant picture type \times time interaction for orbitofrontal cortex (BA 47 and 10) was found only on the right. In all ROI showing an effect of picture type the incongruous stimuli generated a greater response in comparison to the ordinary stimuli. This applies to positive (BOLD increase) as well as negative (BOLD decrease) responses as illustrated in Fig. 3B and C.

Eight regions showed a reliable three-way interaction between picture type, condition, and time point [$F(6,138) > 4.1$, $P < 0.0008$; Table 1, third column from the right]. In all eight regions the difference between incongruous and ordinary pictures was greater in the Inf-Inc condition versus the Freq-Inc condition. This pattern is illustrated in Fig. 4. ROI showing this three-way interaction included striate and extrastriate cortex on the left (ROI 2 and 11), intraparietal cortex on the right (ROI 18), thalamus bilaterally (ROI 10 and 26), SMA (ROI 13), and two inferior frontal regions (ROI 8 and 22). The interaction effect in the left frontal operculum (ROI 9) fell just below significance after Bonferroni correction.

Inf-Inc condition

Analysis of the data from the Inf-Inc condition alone (5 incongruous, 5 oddball, and 40 ordinary pictures) revealed a significant time point \times picture type interaction in a network of areas including much of the posterior occipital-temporal cortex, the intraparietal regions, and parts of frontal cortex (Table 1, second column from the right). Larger responses for incongruous versus ordinary pictures [$F(6,138) > 4.1$, $P < 0.0007$] occurred in 24 of 31 of the ROI. These encompassed parts of the ventral and dorsal visual pathways bilaterally, extending from occipital cortex to the inferotemporal and parietal regions. In anterior regions, greater responses for incongruous versus ordinary pictures were observed bilaterally in frontal operculum (BA

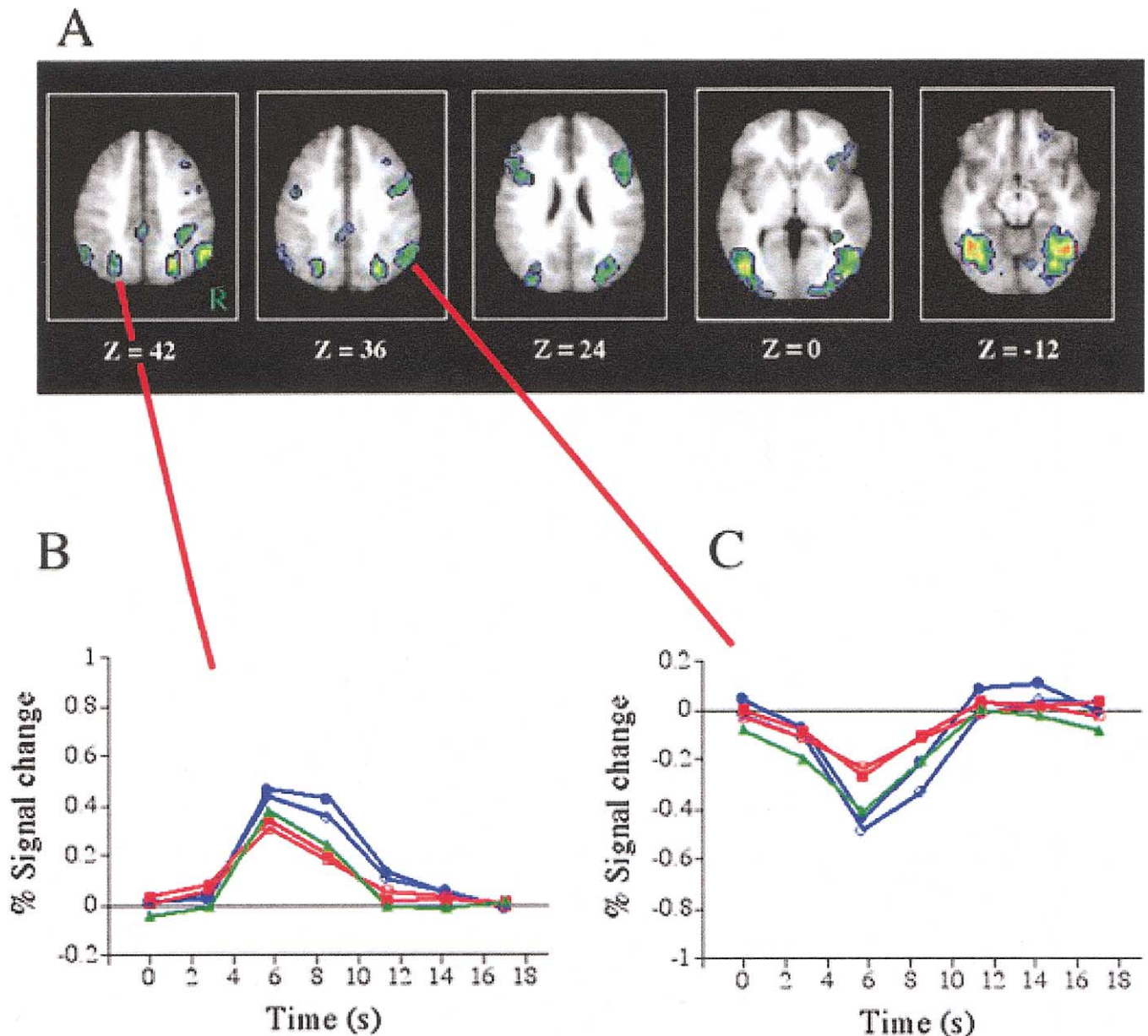


Fig. 3. Voxel-wise map of statistically reliable time point by picture type (incongruous versus ordinary) modulation. This test was collapsed over condition (frequent incongruous and infrequent incongruous) and over all 24 participants. The statistical map is superimposed on the structural T1-weighted image averaged over all participants. BOLD response time courses in two selected regions of interest are shown to illustrate both activation and deactivation responses to incongruous pictures. See Table 1 for additional statistical results.

47) and prefrontal cortex (BA 6/9/46) as well as in left inferior frontal gyrus (BA 45/46) and right orbitofrontal cortex (BA 47 and 10). Larger incongruous versus ordinary responses were observed bilaterally also in the thalamus.

Greater BOLD responses for oddball than for ordinary pictures occurred only in two regions of the occipital lobe, i.e., the right fusiform (ROI 16) and at midline in the pericalcarine region (ROI 11) [$F(6,138) > 4.1$, $P < 0.0007$].

Larger BOLD responses for incongruous versus oddball pictures occurred in four regions: right fusiform (ROI 16),

left ventral extrastriate cortex (ROI 2), pericalcarine cortex (ROI 11), and right frontal operculum (ROI 22).

Parts of the brain that characteristically exhibit BOLD signal decreases in response to task-related events (see Gusnard and Raichle, 2001) exhibited deactivation responses to all picture types (see ROI 27 to 31).

Freq-Inc condition

The Freq-Inc condition included presentation of 25 incongruous pictures and 25 ordinary pictures. Larger BOLD responses for incongruous versus ordinary pictures

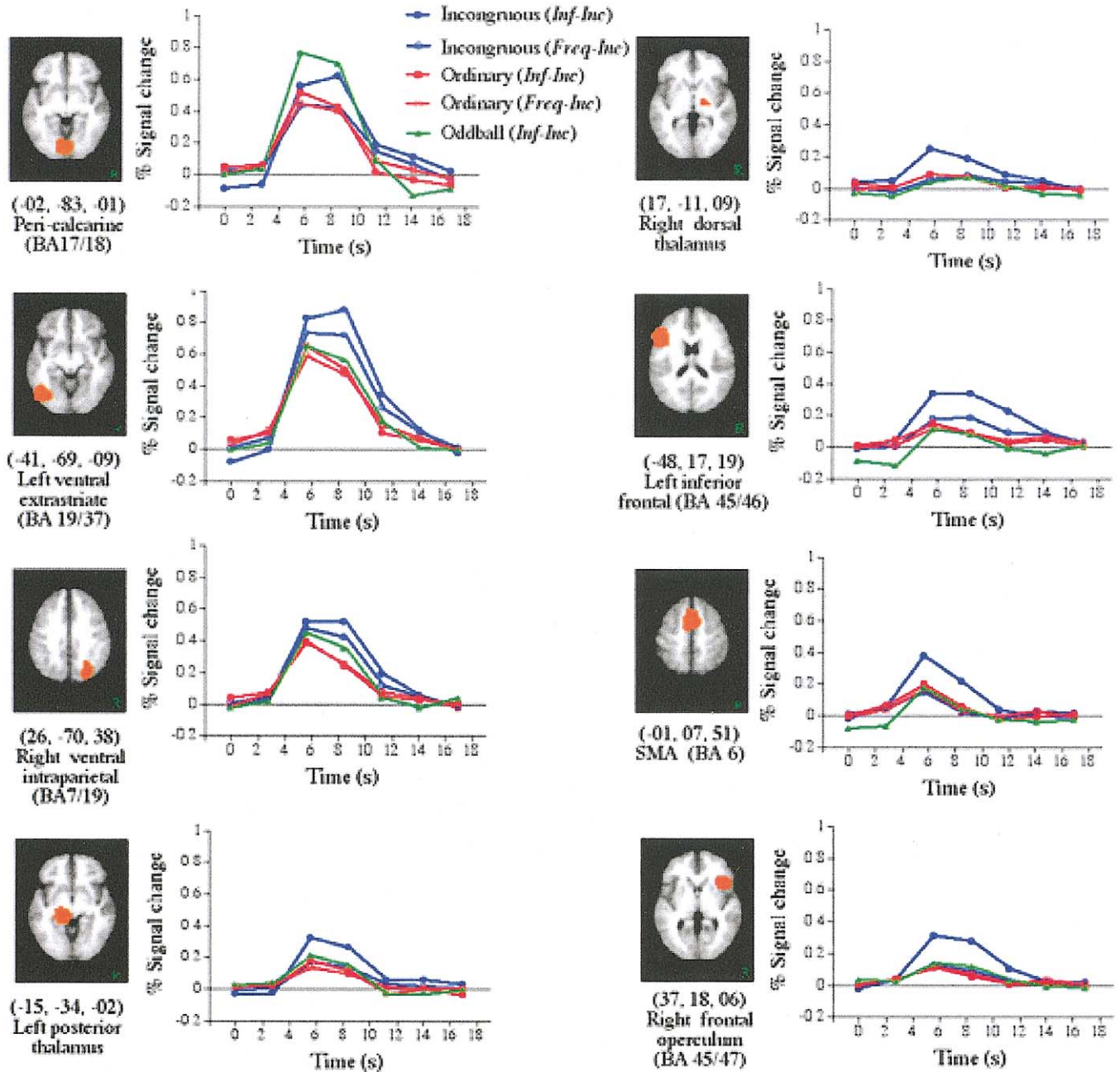


Fig. 4. Time course of the eight regions of interest (ROI) showing an “infrequent bizarreness effect” (infrequent incongruous condition). Single-slice depictions of each ROI are shown to the left of the response time courses. ROI labels and the Talairach coordinates of the ROI center are given under each slice diagram.

($F(6,138) > 4.7, P < 0.0003$) were found in 16 ROI (Table 1, rightmost column). This set of regions included most but not all ROI showing a significant effect of picture type in the Inf-Inc condition alone. ROI showing a significant effect of picture type in the Inf-Inc condition but not the Freq-Inc condition (Table 1, rightmost and adjacent columns) included the frontal operculum bilaterally, left inferior frontal gyrus, and right prefrontal cortex. This result was obtained despite relative loss of statistical power Inf-Inc condition due to fewer (5 vs. 25) incongruous stimuli.

All ROI showing a significant effect of picture type in the Freq-Inc condition but not the Inf-Inc condition exhibited de-

activation responses (greater for incongruous in comparison to ordinary pictures). These ROI included right medial temporal cortex (BA 21), bilateral lateral parietal cortex (BA 39/40), and posterior cingulate cortex (BA 23/31).

Discussion

Greater responses to incongruous compared to ordinary stimuli (the physiological bizarreness effect) were observed in a network of regions including visual, frontal, and parietal areas. This result suggests that incongruous stimuli receive distributed additional processing compared to ordi-

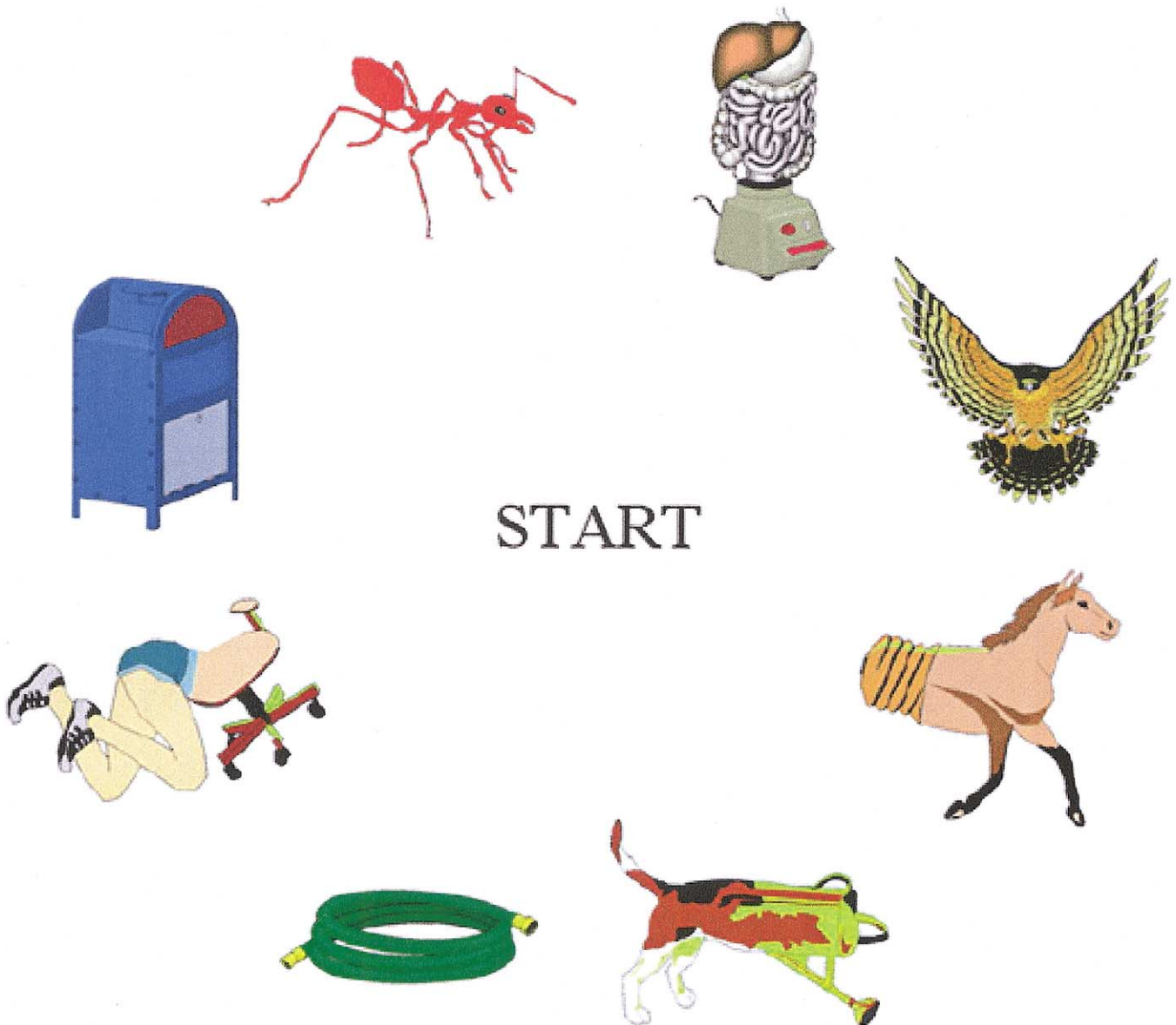


Fig. 5. Example of the display used in the recognition phase of Experiment 2. Of the eight pictures shown on the screen, four were studied (two incongruous and two ordinary) and four were nonstudied (two incongruous and two ordinary).

nary stimuli. A subset of regions showed augmented responses to infrequent incongruous stimuli in the first run (Infr-Inc condition). However, in many regions, a robust effect of picture type was present under conditions that excluded frequency effects (Freq-Inc condition). We hypothesized that stimuli producing this physiological bizarreness effect should also produce a behavioral bizarreness effect, i.e., better memory for incongruous than ordinary stimuli. This was tested in Experiment 2.

Experiment 2: recognition memory for incongruous pictures

Experiment 2 was designed to assess recognition memory for the stimuli used in Experiment 1. To exclude fre-

quency effects it was necessary to study a group of participants separate from those in the fMRI experiment. In accordance with standard practice, both the study and test phases of Experiment 2 included equal numbers of incongruous and ordinary pictures (as in the fMRI Freq-Inc condition). A recognition memory design with a novel response method was used.

Materials and methods

Participants

Thirty undergraduate students from Washington University (25 females, mean age = 19.33 years) participated in the study and received course credit for their participation. None had participated in the fMRI study. All had normal or corrected-to-normal vision and were native English speakers.

Table 1

For each ROI, the peak location is given in Talairach coordinates, accompanied by the location in terms of Brodmann's areas (BA) and anatomical label^a

ROI #	Coordinates			Location		Picture type × time	Picture type × time × condition	Picture type × time (Inf-Inc)	Picture type × time (Freq-Inc)
	X	Y	Z	BA	Anatomic label				
Activation responses									
1	-29	-88	9	18/19	Left	Dorsal extrastriate	*	*	*
2	-41	-69	-9	19/37		Ventral extrastriate	*	*	*
3	-32	-58	-16	37		Fusiform	*	*	*
4	-39	-44	45	7		Anterior intraparietal	*		
5	-25	-68	41	7/19		Ventral intraparietal	*	*	*
6	-32	-10	48	6		Dorsal premotor			
7	-43	3	29	6/9/44		Prefrontal cortex	*	*	*
8	-48	17	19	45/46		Inferior frontal gyrus	*	*	*
9	-34	16	3	45/47		Frontal operculum	*	*	*
10	-15	-34	-2	—		Posterior thalamus	*	*	*
11	-2	-83	-1	17/18	Midline	pericalcarine	*	*	*
12	-1	-70	49	7		Dorsal precuneus	*	*	*
13	-1	7	51	6		SMA		*	
14	32	-84	12	18/19	Right	Dorsal extrastriate	*	*	*
15	37	-79	-4	19/37		Ventral extrastriate	*	*	*
16	36	-63	-12	37		Fusiform	*	*	*
17	39	-40	47	7		Anterior intraparietal	*	*	*
18	26	-70	38	7/19		Ventral intraparietal	*	*	*
19	24	-60	52	7		Dorsal intraparietal	*	*	*
20	32	-6	48	6		Dorsal premotor	*		
21	45	5	30	6/9/44		Prefrontal cortex	*	*	*
22	37	18	6	45/47		Frontal operculum	*	*	*
23	44	36	-6	47		Lateral orbitofrontal	*		
24	33	51	-3	10		Anterior orbitofrontal	*		
25	17	-33	0	—		Posterior thalamus	*		
26	17	-11	9	—		Dorsal thalamus		*	
Deactivation responses									
27	0	-56	34	23/31	Midline	Posterior cingulate			*
28	-49	-63	32	39/40	Left	Lateral parietal	*		*
29	59	-44	5	22	Right	Medial temporal			
30	64	-31	-7	21		Medial temporal	*		*
31	51	-58	37	39/40		Lateral parietal	*		*

^a The fourth column from the right identifies region of interest (ROI) in which time courses were different for incongruous versus ordinary pictures in both conditions (Bonferroni corrected $P < 0.05$). The third column from the right denotes whether the contrast “incongruous minus ordinary” was statistically different in the Inf-Inc and Freq-Inc conditions (corrected $P < 0.05$). The final two columns denote whether the interaction between the factors time point and picture type was statistically reliable in the Inf-Inc and Freq-Inc conditions, respectively (corrected $P < 0.05$).

Materials

All 30 incongruous pictures used in the fMRI study plus 6 additional pictures of the same type were used. Thirty-six ordinary pictures were randomly selected from the 65 used in the fMRI study. Two equivalent sets, A and B, each consisting of 36 pictures (18 incongruous and 18 ordinary) were created.

Design and procedure

In the study phase, the stimuli were presented under conditions that closely matched the frequent incongruous (Freq-Inc) fMRI condition. Half the participants viewed picture set A and the other half set B. Each picture was shown for 2.84 s randomly intermixed with fixation crosshairs, exactly as in the fMRI experiment. Participants performed the same task (upside-down picture detection, right-hand button press response)

under the same instructions. Participants were asked to return in 2 weeks for recognition testing.

In the recognition phase all participants viewed both sets (A and B) of pictures while performing a forced choice new versus old discrimination task. The complete item set was divided randomly into 9 screens of 8 pictures. On each screen 4 pictures were old (2 incongruous and 2 ordinary) and 4 were new (2 incongruous and 2 ordinary) (Fig. 5). Each screen was presented for 8 s. Participants were asked to select by mouse click the 4 old pictures as quickly as possible. To reduce the tendency for sequential selection of neighboring pictures the participants clicked the “start” area in the display center before each response (Fig. 5). The location of incongruous and ordinary pictures as well as the location of old and new items within the displays was randomly varied across subjects.

Table 2
Performance statistics (in percentage) for Experiment 2 collapsed over selection order^a

	Incongruous pictures	Ordinary pictures
Hits	81.3 (24)	51.8 (18.8)
False alarms	28.5 (22.4)	17.6 (17.1)
Hits—false alarms	52.8 (39.8)	34.2 (27.3)

^a Standard deviations are in parentheses.

Results

Results are listed in Table 2. Hit rates as well as false recognition rates were higher for incongruous pictures than for ordinary pictures [$t(29) = 7.25$, $P < 0.01$, and $t(29) = 2.83$, $P < 0.01$, respectively]. Critically, recognition scores corrected for bias (i.e., hits minus false alarms) were higher for incongruous than for ordinary pictures [$t(29) = 4.16$, $P < 0.01$].

One attractive feature of our design was that the sequential order of picture selection could be recorded. This allowed testing for a possible attentional bias toward one or the other type of stimuli. This was done by computing a 2 (bizarre, ordinary) \times 4 (selection 1, 2, 3, or 4) ANOVA on the corrected recognition scores (hits minus false alarms). Results of this analysis are shown in Table 3.

The interaction of picture type and order of selection was statistically significant [$F(3,87) = 18.35$, $P < 0.001$]. Participants picked incongruous pictures preferentially in the first and second positions. Moreover, corrected recognition scores were higher for incongruous than for ordinary pictures for stimuli picked in first [$t(29) = 6.86$, $P < 0.01$] and second position [$t(29) = 3.22$, $P < 0.01$]. No significant difference was observed between incongruous and ordinary pictures for stimuli picked in third position [$t(29) = 1.87$, $P = 0.07$]. Finally, in the fourth position, more ordinary pictures were correctly recognized than incongruous pictures [$t(29) = 3.02$, $P < 0.01$].

Discussion

Experiment 2 demonstrated a behavioral bizarreness effect, i.e., better recognition memory for incongruous versus ordinary pictures. This result provides a basis for discussion

of the physiological responses observed in the Freq-Inc condition of the fMRI experiment in terms of recognition memory. As equal numbers of ordinary and incongruous stimuli were presented during the study phase, the recognition advantage for incongruous pictures is attributable to picture type as opposed to frequency effects.

Certain design features of this experiment are notable. First, a robust bizarreness effect was obtained using recognition, as opposed to recall. This outcome appears to be somewhat atypical (e.g., Cornoldi et al., 1988; Hirshman et al., 1989; McDaniel and Einstein, 1986; Nicolas and Marchal, 1996; Riefer and LaMay, 1998; Worthen and Marshall, 1996) but not unprecedented (Engelkamp et al., 1993). The long (2-week) interval between the study and test phases may also have contributed to the sensitivity of the present measure. Second, the response recording technique provided, in addition to hit/miss statistics, an extra dimension of temporal order. The data showed a strong relationship between picture type and order of selection: Incongruous stimuli tended to be selected early, whereas ordinary stimuli tended to be selected later. This could further reflect better memory for the incongruous stimuli, or it could reflect a bias to attend to the incongruous stimuli first during the recognition test.

General discussion

Neural and behavioral correlates of visual incongruity were explored to better understand how such information is processed and why it is remembered better than ordinary information. First, an extensive network of regions was differentially activated by incongruous pictures both during frequent and infrequent presentation contexts. Regions modulated by incongruous pictures spanned the ventral and dorsal visual pathways bilaterally, the frontal cortex along the inferior frontal gyrus, parietal areas, SMA, and the thalamus. Second, some regions, most notably the right frontal operculum (BA 45/47), responded significantly more to infrequent incongruous pictures, with minimal or no response to frequent incongruous pictures. Finally, better recognition was demonstrated for incongruous pictures studied under conditions that paralleled the fMRI study,

Table 3
Performance statistics (in percentage) for Experiment 2 tabulated by order of selection^a

	Incongruous pictures				Ordinary pictures			
	Order of selection				Order of selection			
	1	2	3	4	1	2	3	4
Hits	66.7 (20.8)	52.2 (24.6)	30.0 (16.5)	13.3 (12.2)	17.7 (12.6)	23.3 (15.3)	31.1 (16.8)	31.5 (20.6)
False Alarms	11.5 (16.1)	12.9 (16.8)	18.5 (14.4)	12.6 (14.5)	3.3 (8.8)	7.0 (8.9)	11.1 (14.6)	13.3 (14.9)
Hits—false alarms	55.2 (34.9)	39.3 (37.3)	11.5 (21.9)	0.7 (17.7)	14.4 (17.1)	16.3 (18.2)	20.0 (25.7)	18.1 (26.3)

^a Standard deviations are in parentheses.

suggesting a correlation between the neural correlates associated with the bizarreness effect and improved memory.

Support for the elaboration hypothesis

Previous studies have shown that specific frontal and temporal regions are associated with memory encoding. For example, numerous studies have noted increased responses in frontal cortex along the inferior frontal gyrus (near BA 45/47 and extending into BA 44) during intentional encoding and also during deep incidental encoding (Buckner et al., 1999; Fletcher et al., 1998; Tulving et al., 1994). Responses in these regions can even predict, on a trial-by-trial basis, whether participants will remember individual stimuli (Brewer et al., 1998; Wagner et al., 1998). Our results are concordant in showing an association between BOLD modulation and subsequent memory performance in highly similar cortical regions. In contrast to the above-mentioned studies, here item processing was directly manipulated by incorporating incongruity. The result was increased activity across a broad set of regions prominently including temporal and frontal regions previously implicated in the kinds of elaborative processing that lead to memory encoding.

The right prefrontal cortex regions, here modulated by incongruity independently of frequency effects, are conventionally identified as central to processes used by working memory tasks (e.g., Barch et al., 1997; Courtney, 1997; D'Esposito et al., 1998; Smith and Jonides, 1999). It is possible that working memory load and demands may increase for incongruous pictures as a result of deep elaboration processes taking place in other regions such as those in extrastriate cortex and inferior frontal gyrus to resolve the cognitive inconsistency.

These results support the elaboration hypothesis as a principal mechanism underlying the behavioral bizarreness effect. The elaboration hypothesis proposes that incongruous materials elicit increased processing that leads to more distinct and robust memory traces. Bilateral increases were larger for incongruous than ordinary pictures in the vicinity of the intraparietal sulcus. Similarly, decreases were larger for incongruous stimuli in lateral parietal cortex. This pattern may suggest differential activation by incongruous stimuli of systems mediating spatial attention and visual search (Shulman et al., 1997a, b). Within this possibility, attentional factors may have contributed to enhanced encoding. However, we cannot exclude the possibility that the incongruous stimuli elicited more eye movements. The contribution of visual search to the physiological bizarreness effect could be better defined in a future experiment using brief tachistoscopic presentation.

Although the present neuroimaging results indicate that physiological activity at encoding may account for at least part of the bizarreness effect, results from the behavioral study also suggest that retrieval stage processes may play an important role in some of the performance characteristics. In particular, Table 3 shows a substantially greater false rec-

ognition rate for incongruous items. Incongruous items were also selected earlier than ordinary items. A recognition bias for bizarre material has been previously noted; the underlying mechanism is under debate (Worthen and Wood, 2001). Enhanced orienting to incongruous pictures at retrieval would be expected to encourage more frequent and earlier selection of both false and true old incongruous pictures. Thus, the results from the behavioral study suggest that bizarre objects are recognized better than ordinary objects and also that the reasons for this performance benefit likely stem from both processes at encoding and retrieval.

Support for the surprise hypothesis

In the Inf-Inc condition, only a few incongruous pictures were presented in the context of mostly ordinary pictures and the experience of such stimuli was novel for the participant. We expected the element of surprise to be maximized under these circumstances. Among regions modulating preferentially in response to the first few incongruous stimuli were right frontal operculum, right dorsal thalamus, and SMA (Fig. 4).

Several studies have reported that unexpected or infrequent stimuli provoke activation of the right frontal operculum (Strange et al., 2000; Optitz et al., 1999) as in the present data. We note that activity in this region was higher for infrequent incongruous pictures than for equally infrequent oddballs (see below), which suggests that the salient feature was unexpected incongruity. This same region is activated by negative feedback in the Wisconsin Card Sorting task (WCST) (Konishi et al., 2002; Monchi et al., 2001). Fink et al. (1999) observed similar responses in a slightly more dorsal region by creating (with mirrors) conflict between the visual and proprioceptive senses. Interestingly, Strange et al. (2000) reported frontal operculum activation specifically in response to emotional oddballs compared to perceptual and semantic oddballs. The common theme appears to be information at variance with the current subjective assessment of reality, which, in turn, reflexively leads to a shift or alteration in the mode of interaction with the environment. In the WCST the notion of paradigm shift is explicit. Here, we suggest that the first few incongruent pictures caused participants to prepare for the possibility of encountering such stimuli, many of which are strange or disturbing.

Inf-Inc specific responses in ROI other than the right frontal operculum are consistent with the above interpretation. Thalamic responses to oddball stimuli have been reported in a few previous studies (Clark et al., 2000; Kiehl et al., 2001). These may be related to orienting or arousal linked with emotion. SMA is ubiquitously involved in any "preparation for action" (e.g., Clark et al., 2000). Its activation may be a response to the activity in the frontal operculum once a conflict between expectation and reality has been detected.

The design of our fMRI Inf-Inc condition does not allow

distinguishing between effects of frequency and of novelty. However, the existence of physiological responses specific to infrequent (or unexpected) incongruous stimuli lends indirect support to the surprise hypothesis, i.e., the notion that, under some circumstances, surprise during encoding may contribute to the behavioral effect in memory (Hirshman et al., 1989). We note that the memory advantage for incongruous material demonstrated in Experiment 2 was obtained using a study protocol designed to exclude surprise as a factor. Therefore, although surprise may contribute to the memory phenomenon, it is not required.

The fMRI bizarreness effect and the P3a

P3a (novelty P3) scalp potentials are elicited by unexpected “deviant” stimuli (Friedman et al., 2001). This electrophysiological response characteristically exhibits rapid habituation, typically within 5 repetitions (Knight and Nakada, 1998). Previous functional neuroimaging studies of the neural correlates of P3a have reported increased activity in temporoparietal and frontal cortex (Kirino et al., 2000; Knight, 1996; McCarthy et al., 1997; Optitz et al., 1999; Strange et al., 2000; Williams et al., 2000). As these characteristics match the present Inf-Inc incongruous stimulus BOLD responses, the P3a phenomenology might be expected to appear in an ERP version of Inf-Inc paradigm.

Oddball responses in the Inf-Inc condition

Oddball (color reversed) pictures elicited greater activation responses than ordinary pictures in the right fusiform (near BA 37) and the pericalcarine region (at or near BA 17/18) (Fig. 4). In the lateral parietal cortex, both oddball and incongruous pictures elicited deactivation responses of comparable magnitude, both being clearly greater than the deactivation responses to ordinary pictures (Fig. 3C). The existence of these responses indicates that the oddball stimuli functioned at least partly as intended, i.e., to serve as a control for pure frequency effects. The observed pattern of oddball-related responses suggests a distinct process unrelated to incongruity, possibly capture of visual attention on the basis of unexpected superficial features.

Oddball responses are difficult to study because of the limited statistical power due to the low number of stimuli used. These considerations apply especially to the color inverted oddballs used here, which may have been “deviant,” but arguably were less so than the Inf-Inc incongruous pictures. The absence of oddball responses in frontal or parietal areas or in the hippocampus may very well represent a type II error due to low sensitivity.

The present oddball results do not agree with the report of Zeki and Marini (1998) in which color inverted stimuli acted more like our incongruous pictures, i.e., activated right inferotemporal and prefrontal cortex. This difference may be attributable to different context effects or the fact

that our oddball stimuli were not intended to embody incongruity whereas Zeki and Marini (1998) designed their color inverted stimuli to be perceived as “abnormal.”

The fMRI bizarreness effect and the N400

Many cognitive neuroscientists would classify the type of incongruity in our pictures as semantic (e.g., Shallice, 1987). The relevance of this view to the present work is supported by the observation that incongruous sentence endings presented in either text or picture (i.e., rebus) format (Ganis et al., 1996; West and Holcomb, 2002) as well as single unrelated stimuli, words or pictures (Holcomb, 1988; McPherson and Holcomb, 1999), elicit similar evoked potentials in the N400 paradigm. As the presence of context (e.g., a sentence) appears crucial to the N400 phenomenon (Kutas and Hillyard, 1983), one may argue that a random sequence of stimuli, even if they are incongruous, should not elicit this response. However, our stimuli were designed to violate expectations embedded in the viewer’s background semantic knowledge about artifacts and living things. It is possible that such knowledge may act as a context, in which case a N400 might be produced in an Event Related Potential (ERP) version of both the Inf-Inc and Freq-Inc conditions.

The present findings are consistent with previous fMRI studies of sentential semantic violation, notwithstanding that these studies employed text input (spoken or written) and incomplete brain coverage (except for Newman et al., 2001). Both Ni et al. (2001) and Newman et al. (2001) reported left inferior frontal gyrus (probably BA 9/46) responses to semantic violations. Kuperberg et al. (2000) emphasized that semantic violations activate the left inferior temporal and fusiform cortex.

The above discussion taken together with our previous considerations regarding enhanced encoding due to perceived incongruity leads to the possibility that semantic violations should be especially well remembered. In fact, the available data indicate that words eliciting an N400, i.e., incongruous sentence endings, are less well recognized on subsequent testing than are expected endings (Neville et al., 1986). This result has been attributed to the idea that expected sentence endings lead to integrated cognitive units that are more elaborated and therefore better encoded. This theory may be correct but the principle is contrary to the present main findings. It remains to be seen whether this discrepancy is fundamental to the distinction between sentential versus pictorial incongruity, or relates to effects at the time of retrieval that were minimized in the present study by using a recognition procedure.

The electrophysiological phenomenon most consistently associated with better subsequent memory is late (350–800 ms latency) scalp positivity (e.g., Rugg et al., 1996). The correlation between late positivity and subsequent recognition holds for visual patterns as well as words (van Petten

and Senkfor, 1996). This ERP potential can be experimentally manipulated in parallel with subsequent recall by varying the “distinctiveness” of presented items (the von Restorff effect) (Fabiani et al., 1986; Otten and Donchin, 2000). Whether incongruous stimuli of the present type elicit late positivity remains a matter for future exploration.

Other behavioral and neuroimaging studies using similar visual stimuli

Several recent functional neuroimaging studies have used geometrically impossible or nonsense figures as controls for meaningful images. All but one of these studies reported that such stimuli elicited either comparable (Schacter et al., 1995; Martin et al., 1997) or less (Vuilleumier et al., 2002) activation of inferotemporal cortex in comparison to meaningful images. The study of Gerlach et al. (1999) bears a more complex relationship to our experiment. Participants judged whether images depicted real or nonreal objects. The nonreal images were of two types, i.e., (1) semantically unidentifiable nonsense objects, or (2) chimeric figures, e.g., head of panda on body of bull. Comparing chimeric figures to real objects led to greater blood flow than comparing nonsense objects to real objects in inferotemporal cortex. Comparison of this result to our data is confounded by the task. Specifically, the chimeric versus real judgment was more difficult as indexed by response time. However, the Gerlach et al. (1999) result is consistent with our observations even if their chimeric figures were not specifically designed to be incongruous. The above-discussed studies, in aggregate with our own data, suggest that mere nonreality does not differentially activate inferotemporal cortex. Rather, it appears that the salient property truly is incongruity.

In the present study, fused drawings of semantically unrelated parts were used to embody incongruity. These pictures functioned as intended, according to the rating questionnaire filled out by our fMRI participants. However, we have not as yet systematically examined incongruous stimuli that do not involve interacting objects. According to the interacting hypothesis (Wollen et al., 1972) memory is the most enhanced when studied materials are both bizarre and interactive. Wollen et al. (1972) assessed the relative contribution of these two variables to paired-associate learning and showed that bizarre pictures facilitated learning only to the extent that they also depicted interaction. This result suggests that the simultaneous presence of semantically incongruent objects is necessary but not sufficient to generate a bizarreness effect: The objects have to interact. It is unclear whether fusion qualifies as such an interaction. To assess the relative contribution to the bizarreness effect of semantic incongruity versus object interaction, future fMRI experiments are needed in which responses to fused, interacting, and separate objects are measured.

Conclusions

In summary, we investigated the functional anatomy associated with the perception of incongruous pictures to better understand why such material is especially well remembered. Our results lend primary support to the elaboration hypothesis, which states that incongruous percepts lead to the formation of more robust memory traces, in part, due to additional processing at the time of encoding. Structures differentially activated by incongruous pictures included regions associated with object identification (fusiform cortex), working memory (prefrontal cortex), and spatial attention (parietal cortex). We also found indirect support for certain aspects of the surprise hypothesis (Hirschman et al., 1989), which proposes that incongruous materials are better recalled because of enhanced availability of episodic cues triggered by surprise. However, our behavioral data demonstrate that superior memory for incongruous stimuli can be obtained under study conditions in which such items are neither novel nor infrequent, conditions that do not elicit the neural correlates of surprise.

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