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Brain Areas Involved in Rapid Categorization of Natural Images: An Event-Related fMRI Study

Denis Fize,* Kader Boulanouar,† Yvan Chatel,† Jean-Philippe Ranjeva,†
Michèle Fabre-Thorpe,* and Simon Thorpe*

**Centre de Recherche Cerveau and Cognition (UMR 5549, CNRS-UPS), Faculté de Médecine de Rangueil, 133 route de Narbonne, 31062 Toulouse, France; and †INSERM Unité 455, Hôpital de Purpan, Toulouse, France*

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Event-related fMRI was used to investigate brain activation during a visual go/no-go categorization task based on colored photographs of natural scenes, similar to a previous ERP study by Thorpe *et al.* (1996, *Nature* 381: 520–522). Subjects had to press a key when an animal was present in the display. Stimuli were flashed for 33 ms using an intertrial interval of 5 s and a design that carefully balanced targets and distractors in a pseudo-random sequence. Activation produced by targets and distractors was compared with two different techniques, one based on correlations with the stimulation pattern, the other using simple *t* score statistics to compare selected scans. The contralateral primary motor cortex and the ipsilateral cerebellum were both more active following target trials than following distractors, thus confirming the sensitivity of the method. Differential activity was also seen in the posterior cingulate cortex, the fusiform, and the parahippocampic gyri. Activity in such structures could underlie the differential evoked-potentials reported previously in the same task. Surprisingly, in these visual structures, the signal was stronger following distractor trials than target ones. This result could be due to more prolonged processing on distractor trials. Alternatively, it could be that target detection induces strong activation of a small proportion of neurons, which, because of competitive inhibitory mechanisms, could result in a decrease in activity for the population as a whole. We suggest that this kind of mechanism could also account for the decreases in signal observed in perceptual priming experiments. © 2000 Academic Press

Key Words: **event-related fMRI; natural scenes; extra-striate visual cortex; categorization; competitive inhibition; attentional processes.**

INTRODUCTION

In a previous study, we described a go/no-go categorization task in which subjects were asked to decide whether or not briefly displayed color photographs (natural scenes as well as man-made environments) contain an animal (Thorpe *et al.*, 1996). Despite the high demands on the visual system imposed by such a task, subjects performed accurately and rapidly. In addition, simultaneously recorded event-related potentials (ERPs) revealed an early ERP difference between target and distractor trials that started roughly 150 ms after stimulus onset. The effect was particularly visible on frontal electrodes, but the sources of this differential response were unclear.

To help locate the brain areas involved in generating this differential electrical response, we tested human subjects with the same sort of task in a study using functional magnetic resonance imaging (fMRI), which measures local changes in blood oxygenation and provides good spatial resolution. Our approach involved the use of event-related fMRI, a methodology that has become increasingly popular in recent years (Buckner *et al.*, 1996; Schacter *et al.*, 1997; Zarahn *et al.*, 1997; Burock *et al.*, 1998; Friston *et al.*, 1998; Rosen *et al.*, 1998). Such methods allow the use of paradigms that depart from the standard "blocked" testing procedures normally used in fMRI and PET studies by making it possible to isolate brain responses to individual trials. Its flexibility allows different types of trials to be intermixed in a random sequence, a feature that is vital for the go/no-go categorization task used here. A number of empirical studies have made these developments possible by showing that the hemodynamic response sums roughly linearly over trials (Boynton *et al.*, 1996; Dale and Buckner, 1997), and by measuring signal changes in response to brief visual stimuli as short as 34 ms (Savoy *et al.*, 1995). Here we used natural images briefly flashed for 33 ms and an intertrial interval of 5 s; both the interstimulus and presentation durations were in the range of values known to elicit a detectable hemodynamic response related to each stimulus. The relatively short intertrial interval minimized interference from irrelevant cognitive processes, a problem that can occur when long intervals are used to

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TABLE 1

Behavioral Results

Subject	Age	Sex	Hand	RT ms	Global (% error)	Targets (% error)	Distractors (% error)
cc	19	f	l	546	10.7	12.7	8.8
cm	45	f	l	449	3.4	3.9	2.9
gr	45	f	r	520	14.7	20.6	8.8
bj	30	m	l	580	14.7	17.6	11.8
df	27	m	r	470	12.5	16.7	8
ec	28	m	r	466	12.2	19.6	4.5
Mean	32.3			505	11.4	15.2	7.5

Note. For each of the six subjects indicated by their initials, the table provides their sex (m/f), their age, the used (preferred) hand (r/l), and the mean reaction time for the correct go responses (RT expressed in ms). The table also provides the global percentage of errors (Global % error), and separately the percentage of errors on targets (Targets % error) and the false positives on distractors (Distractors % error).

allow the complete decay of the hemodynamic response.

In the present experiment, we first designed a carefully balanced sequence of target and distractor trials to handle the overlaps between hemodynamic responses and cancel out the effects of surrounding stimuli. To assess the reliability and the sensitivity of the methods used in this study, cerebral activation induced by the motor response was tested separately for left- and right-handers at both individual and group levels. We then focused on the brain structures that were differentially activated during this particularly demanding go/no-go visual categorization task and could be the source of the differential ERP response reported previously.

MATERIALS AND METHODS

Six subjects (three females and three males, three right- and three left-handed subjects, see Table 1) aged between 19 and 45 (mean age: 32.3 years) volunteered in this experiment. Subjects were asked to press the button of a computer mouse when photographs containing an animal were displayed. The stimuli were selected from a very large set of available scenes (4300 color photographs from the Corel photolibrary) that had already been used in previous visual categorization studies in humans and monkeys (Thorpe *et al.*, 1996; Fabre-Thorpe *et al.*, 1998). The photographs containing animals were very varied and included a wide range of species (birds, mammals, reptiles, and fish) in their natural environments. The number of animals, their size and the viewing angle varied widely across the stimulus set. The distractors included pictures of natural scenes as well as man-made environments, and were also very varied in terms of color saliency, spatial frequency and luminance (see examples in Fig. 1). The earlier ERP study showed that VEP components up to 150 ms did not differ significantly between targets and distractors, making it unlikely that there was a systematic difference between the two types of stimulus in terms of low-level factors such as contrast or luminance. Each stimulus was presented once and for each subject the data analysis was based on a minimum of 204 images in 3 blocks of 68 photographs (5 mn 40 s per run). Six different blocks of images were used, none of which was seen by all the subjects. The photographs were flashed in color for 33 ms through a pair of fMRI video goggles (Resonance Technology Inc., California) that provides a visual field of 30°.

Stimuli were flashed every 5 s for the task to be as close as possible to the reference go/no-go task used in the ERP study mentioned above. Reaction times (RT) were recorded with a nonmagnetic mouse linked to a Macintosh computer. Imaging was performed on a 1.5 T MRI system (Siemens Magnetom Vision); each echoplanar scan (EPI) was composed of 12 noncontiguous slices (slice thickness: 6 mm, interslice gap: 1.2 mm, echo time: 64 ms, repetition time: 2.5 s, image size: 128 $\times$ 128, field of view: 200 mm). Each set of slices took about 1.3 s to acquire, and during a run, data were continuously collected every 2.5 s, i.e., at delays of roughly 1.5 and 4 s after the onset of the stimulus (Fig. 2A). Because of constraints due to the stimulation sequence described below, image acquisition began after the fifth stimulus.

Stimulation Sequence

The 68 stimuli in each run were presented in a sequence in which targets and distractors were equiprobable. Although the sequence was unpredictable for the subject, it was carefully designed to minimize any possible bias introduced by the overlap of hemodynamic responses due to surrounding stimuli. It was designed so that all combinations of 2 to 5 consecutive stimuli (targets and distractors) were equally represented (Figs. 2B and 2C). Thus any stimulus was not only labeled as a target or distractor but was also characterized by the preceding and subsequent 1–4

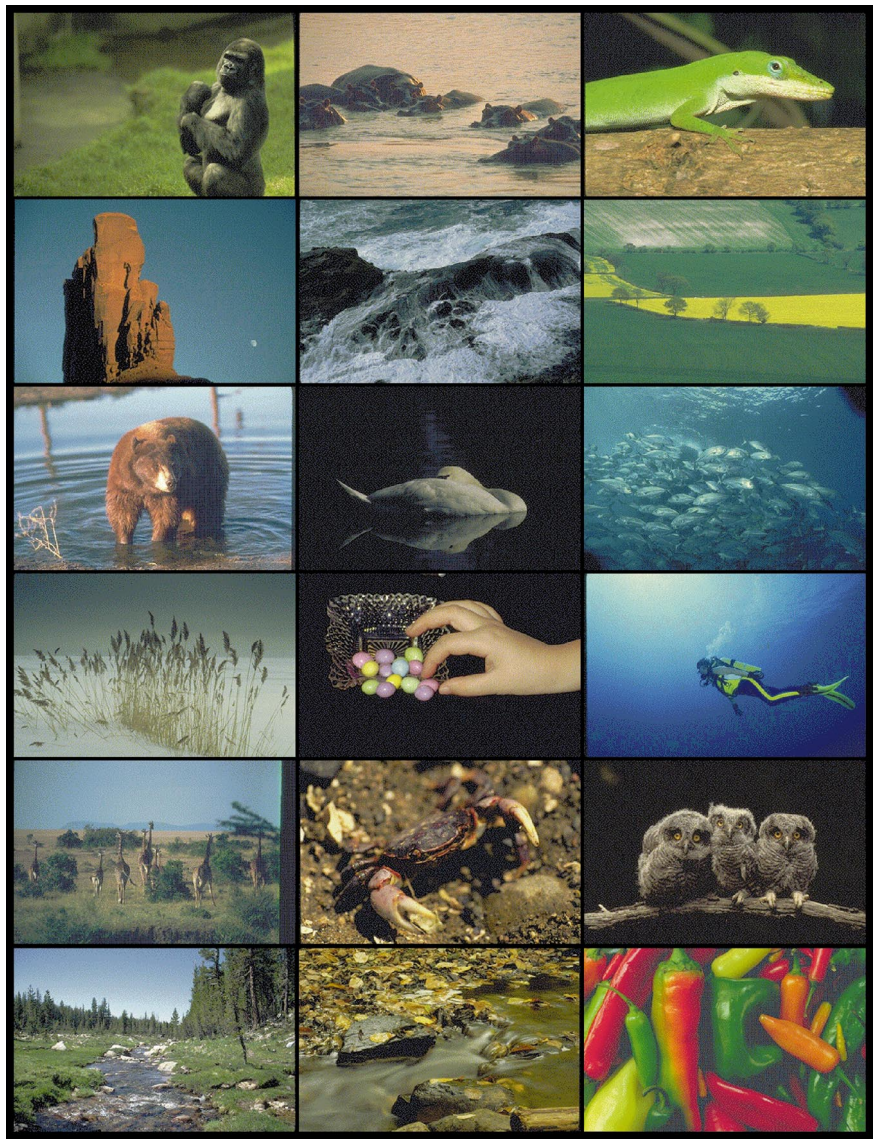

FIG. 1. Examples of stimuli. The 204 color photographs were displayed for 33 ms every 5 s using nonmagnetic video goggles and were presented once. The target scenes contained at least one animal (human beings were considered as distractors). Colors, luminances, and spatial frequencies were very varied for both targets and distractors.

stimuli. Scanning started after the presentation of the fifth stimulus to allow appropriate labeling of the trials. Such a design allowed the mean signals elicited by target and distractor trials to be compared, since any combination surrounding a given trial was equally represented in both target and distractor conditions.

fMRI Data Analysis

The first two scans were discarded to allow signal stabilization, and the remaining 126 scans of each run were realigned to correct for head movement, then normalized and smoothed by a gaussian kernel (10 mm FWHM). After this preprocessing, two different methods of analysis were used. The first involved the detection of differentially activated pixels with the general linear model as implemented in SPM software (Friston *et al.*, 1995). The linear model used low frequency (>120 s) variable adjustment and two covariates for target and distractor activations that were generated by convolving the stimulus pattern with a poissonian hemodynamic response peaking at 6 s delay. The second method was based, as in ERP analysis, on the comparison of scans selected on the basis of correct (go and no-go) trials. Scans were first labeled target or distractor depending on the nature of the preceding trial; the two sets of selected images were then compared with *t* score statistics using the AFNI (Analysis of Functional NeuroImages) software package (Cox,

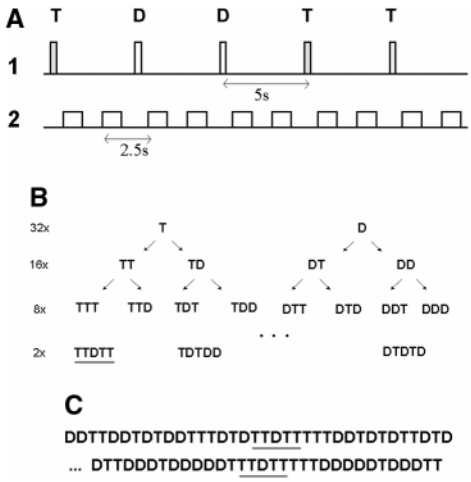

FIG. 2. Stimulation and image acquisition design. (A) In the sequence of stimulation (1), target (T), and distractor (D) stimuli appeared quasi randomly. MRI scans (2) were synchronously acquired 1.5 and 4 s after each stimulus display. (B) The stimulation sequence was designed to equalize the number of target and distractor stimuli and any subsequences composed of 2 to 5 stimuli. It included 32 targets and distractors, 16 subsequences composed by TT, DD, TD, and DT, and 2 subsequences for every possible combination of 5 targets and/or distractors. One of them, TTDTT is underlined for clarity in the sequence (C). (C) The complete stimulation sequence was composed of 68 trials, and MRI acquisitions were performed after the presentation of the fifth stimulus.

1996). The use of *t* test statistics on selected sets of images was made theoretically possible by the design of the sequence of stimulation since, on average, the effects of surrounding stimuli were cancelled.

The first method that measures the correlation between the recorded data and an expected pattern of response signal is used in most neuroimaging studies. Using this method, we first analyzed separately the data recorded in right- and left-handed subjects in order to assess the sensitivity of the event related fMRI protocol to motor activations. Using the same method, we then performed a group study that included all the subjects (regardless of their hand preference) in order to localize other sites with task-related activity. Finally, the robustness of the results was assessed by comparing individual data obtained using both correlation analysis and *t* score statistics on selected scans.

RESULTS

Behavioral Results

Despite the physical constraints of the fMRI situation, the subjects performed this challenging task very well. The mean RT was 505 ms on targets, and 568 ms for false detections (Table 1) for a percentage of correct responses that reached 88.6% by run. The subjects were less accurate and less fast than in our previous study (94% correct for a mean RT of 471 ms), but the MRI environment, the subject's position, the use of goggles for stimulus presentation as well as image definition and contrast could all contribute to these differences.

fMRI Results

The results of the analyses performed separately for the right- and left-handed subjects showed an increase in signal strength following target trials in the contralateral motor cortex and ipsilateral cerebellum for the two groups (Figs. 3A and 3B). Similar motor activations were obtained when considering the individual cerebral activations shown by each subject using the two different methods of analysis (Table 2).

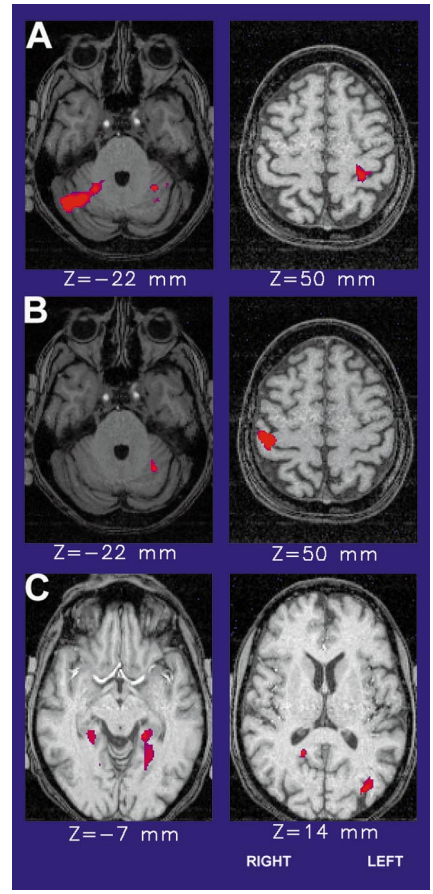

FIG. 3. Statistical parametric maps of correlation analyses performed on groups of subjects using SPM96. Statistical parametric maps are thresholded at $P < 0.001$ for peak height and $P < 0.05$ (corrected) for spatial extent. (A and B) Results of the analysis of 3 right-handed subjects (A) and 3 left-handed subjects (B) performed to assess the sensitivity of the protocol. Activations after target trials (T − D contrasts) were only observed in contralateral Brodmann area 4 and in the cerebellum ipsilateral to the dominant hand. (C) Results from analysis including all 6 subjects. A higher signal was observed after distractor trials when compared to target trials (D − T contrast) in right cingular gyrus near occipitoparietal sulcus (BA 31), left fusiform gyrus (BA 19/37), bilateral parahippocampic gyri, and medial occipital gyrus (BA 19).

TABLE 2

Differentially Activated Areas between Target and Distractor Conditions from Individual and Group Studies

	T − D > 0									D − T > 0								
					Tc									Tc				
Subjects (hand)	Size	*Z*	*t*	Lat.	x	y	z	Areas	R/L	Size	*Z*	*t*	Lat.	x	y	z	Areas	R/L
CM	102	6,79	5,6	4 s	36	−22	50	BA 4	R	27	4,97	−3,8	9 s	44	−30	7	BA 41/42	R
(L)	57	6,33	5,5	4 s	−24	−52	−22	Cerebellum	L	250	4,96	−3,4	9 s	6	−45	7	(BA 29)	R
											4,15	−3,1	9 s	10	−35	0	Parahipp.	R
											4,53	−3,3	9 s	4	−64	29	BA 31/18	R
											3,34	ns		−6	−76	29	BA 18	L
											3,86	ns		2	−76	22	BA 18	R
										25	4,69	−2,9	9 s	44	−14	7	BA 22	R
GR	152	4,44	4,3	4 s	−36	−42	50	BA 1,2	L	72	4,26	−4,9	6.5 s	−10	−60	7	BA 31	L
(R)	53	3,94	3,2	4 s	−42	−38	43	BA 40	L	18	4,06	−4,6	6.5 s	−36	−74	7	BA 19	L
	34	3,73	2,8	4 s	−36	28	29	Prefrontal	L									
	23	4,37	3,4	4 s	16	−64	−7	Cerebellum	R									
BJ	105	4,52	4,1	4 s	40	−24	50	BA 4	R	25	4,34	−3,2	6,5 s	−12	−82	−7	BA 18	L
(L)										28	3,82	−3,0	6,5 s	10	−86	14	BA 19	R
										23	3,68	ns		30	42	36	BA 9	R
CC	69	5,90	3,4	4 s	−26	−66	−22	Cerebellum	L	109	5,90	−4,1	4 s	−24	−56	14	BA 37	L
(L)											5,47	−4,1	4 s	−22	−52	−7	BA 19	L
										215	4,74	−3,8	6.5 s	−28	−78	36	BA 19	L
										59	5,31	−3,2	4 s	−28	−8	43	BA 6	L
EC	94	5,45	3,7	4 s	−32	−60	−29	Cerebellum	L	118	4,71	−4,1	9 s	12	−58	14	BA 31	R
(R)	21	4,65	2,9	4 s	−32	−26	50	BA 4	R	28	4,21	−4,1	9 s	−4	−62	7	BA 31	L
	62	4,10	2,5	4 s	36	−58	−29	Cerebellum	L	24	4,26	−2,9	6.5 s	−54	−12	−7	BA 22	L
	55	3,84	3,0	4 s	40	8	7	BA 6	R	34	3,94	ns		40	−10	7	BA 22	R
DF	67	4,74	3,6	6.5 s	−50	−34	50	BA 1,2	L	71	3,58	−3,1	9 s	0	−85	22	BA 18	
(R)	51	5,19	4,5	6,5 s	16	−50	−22	Cerebellum	R	14	3,37	ns		46	52	−7	BA 37	R
										23	3,35	ns		−22	34	43	BA 8 (FEF)	L
Left-handed subjects (CM, BJ, CC)										Six subjects								
	112	6,54			36	−16	50	BA 4	R	59	5,21			14	−58	14	BA 31	R
	27	4,26			−24	−52	−22	Cerebellum	L		5,09			12	−54	7	BA 31	R
											4,43			18	−35	−7	Parahipp.	R
Right-handed subjects (GR, EC, DF)										68	5,17			−18	−35	−7	Parahipp.	L
											4,94			−22	−60	−7	BA 19	L
	27	4,34			−26	−28	50	BA 4	L	52	5,05			−30	−82	14	BA 18/19	L
	125	5,30			28	−56	−22	Cerebellum	R		3,74			−26	−80	29	BA 19	L
											3,72			−28	−72	36	BA 19	L

Note. Individual results are presented for each subject indicated on the left by their initials and preferred hand. The results from the group studies (six subjects) are shown in the bottom part of the table (left- and right-handed subjects are considered separately for the activation of the motor structures). The left column lists areas for which the signal difference was observed to be higher after target stimuli (T − D > 0). The right column lists areas for which the signal difference was observed to be higher after distractor stimuli (D − T > 0). In both columns, the results obtained with the two different methods of analysis are presented. The size (number of pixels) of the areas and their maximum *Z* values were both obtained by SPM analyses run on the overall data of each subject. Within the same areas, the maximum *t* values and their latency in seconds (*t* lat.) were obtained with selective comparisons (see Materials and Methods), using only the scans for which the preceding stimulus was correctly categorized. The Talairach coordinates (Tc) of the maxima, the corresponding areas, and the activated hemisphere (L/R) are also indicated. Note that motor structures were more activated after target trials (left column), whereas visual structures were more activated after distractor trials (right column) and generally with a longer latency than motor areas.

Although motor structures were found to be more activated following target trials than following distractors, some visual areas were found to be more activated by distractor trials. These differentially activated structures included the extrastriate visual cortex and the hippocampal gyri (Fig. 3C summarizes the overall results obtained with the six subjects). Four main areas with differential activations can be seen from this group study; they include Brodmann Area 31 (BA 31) in the right occipitoparietal sulcus, the posterior parahippocampic gyri on both sides, a large part of BA 19/37 in the left fusiform gyrus and BA 19 in the median occipital gyrus. This pattern of differential activation was also seen at the individual level of analysis (Table 2) and with the two different methods of analysis. However, some individual differences could be noted; for example, in subjects CM and EC additional differential activity could be seen in BA 22.

In order to determine the temporal course of the responses to distractors and targets in visual areas, we performed *t* test comparisons between images acquired at 1.5 and 4 s poststimulus for targets and distractors separately. As shown in Fig. 4 for subject CM, both targets and distractors elicited robust increases in occipital areas including primary and extrastriate visual cortex. However, further analysis aimed at localizing structures with significantly different levels of activation in response to targets and distractors showed that the main effect, namely a larger signal on distractor trials, was not seen until later (see Fig. 4C).

Figure 5A illustrates the group average signal around target and distractor trials for a differentially activated region in the median occipital gyrus (BA 19). It can be seen that both target and distractor trials induced an initial increase in signal after stimulus presentation with, as a consequence, a modulation of the signal at the presentation rate. But the interesting feature is the divergence between the average response to targets and distractors that lasts for a period of up to 10 s, with distractors producing more activity than targets. Note that both curves are initially roughly equal since the first point on each curve corresponds (thanks to the balanced experimental design) to an equal mix of target and distractor trials. The same sort of averaging was also performed on the differentially activated motor area BA 4. Figure 5B shows that, in this case, signal values in this area increased only around target trials (i.e., when there was a go-response), whereas the signal following distractor trials decreased back to a value below the baseline. This makes sense, given that the baselines were effectively the average of target and distractor signal values. Note that since there was no systematic motor activation on both target and distractor trials, there is no modulation of the signal at the presentation rate.

Figures 5C and 5D show that the differential visual and motor effects have different time-courses: in visual areas the difference in signal lasts longer and reaches its maximum later than in motor cortex.

DISCUSSION

The most surprising result of the present study was that in a go/no-go visual categorization task, extrastriate visual areas, including the right occipitoparietal sulcus, the posterior parahippocampic gyri on both sides, the left fusiform gyrus and the median occipital gyrus are more activated following distractor trials than target ones. The second result concerns the reliability of an event-related fMRI protocol that includes short stimulus presentations and relatively short intertrial intervals, in a counterbalanced sequence of stimuli to handle biases resulting from overlapping hemodynamic responses. This study shows that such protocols allow reliable results to be obtained not only at a group level but also in the case of individual studies.

Protocol

The reliability of the event-related protocol used in this study is clearly demonstrated by the group analysis performed on right and left handed subjects. The results showed clear motor activations (contralateral BA 4 and ipsilateral cerebellum) related to the finger movement required by the task in response to target stimuli. Similar results were obtained with the two different methods, using a linear model and t-tests on selected sets of images. It should be emphasized that this type of design is able to provide a sufficient signal-to-noise ratio (not estimated here), since the pattern of activity resulting from a single subject is close to the pattern exhibited by the group study: motor activations were observed in individual subjects, and differential effects seen in visual areas were also found in anatomically similar sites in different individuals.

The modulations in MR signal elicited by the trials were found to be generally in the range 0.07–0.1% around the mean values and the differential effects between the target trials and distractors were in the range 0.1–0.3%. These small amplitudes may be partly due to the relatively short and fixed intertrial period used here since the overlap between the hemodynamic responses due to preceding stimuli will increase baseline values and lower signal variations (Burock *et al.*, 1998). There are other studies with short ISIs that have reported larger amplitude fluctuations than those reported here, but they randomized the intertrial interval with a third neutral stimulus, a technique that increases the size of signal variations (Buckner *et al.*, 1998; Clark *et al.*, 1998). Another factor may well be the use of very short stimulation durations that prevented any visual exploration of the stimuli. Comparisons of the signal in occipital cortex at 1.5 and 4.5 s poststimulus clearly showed that briefly displayed photographs of both targets and distractors produce statistically significant visual activation. But as Savoy *et al.* (1995) reported, brief 33 ms visual stimulation only produces a relatively small response (less than 1% from the baseline in their case).

Another aspect of the stimulation design is the use of a counterbalanced sequence of stimuli involving up to five successive target and distractor trials. The results suggest that such sequences successfully equated the baselines for target and distractor trials, and the overlap of hemodynamic responses to surrounding stimuli. This is supported by the fact that the averaged signals computed before and 10 s after stimulus presentation are virtually identical for both target and distractor conditions. Such designs can therefore overcome the biases encountered in other rapid mixed designs that use random mixing. For example, Buckner *et al.* (1998)

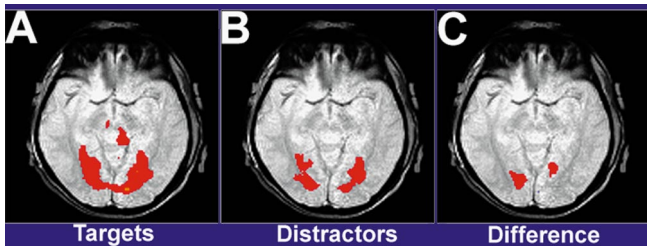

FIG. 4. Results of t tests performed on subject CM at $Z = -7$ mm. (A and B) t score maps between 1.5 and 4 s poststimulus after correct target trials (A) and after correct distractor trials (B). A large involvement of occipital cortex can be seen for both stimuli types during this period ($t > 2.87$; uncorrected $P < 0.005$; $df = 246$). (C) Differential activations in visual areas were seen in this subject at 9 s poststimulus ($|t| > 2.83$; uncorrected $P < 0.05$; $df = 244$). These visual areas present a higher signal for distractor than target trials (D − T > 0).

have argued that counterbalancing should involve several successive trials. While 30 trials are generally thought to be sufficient to balance a series containing just two types of trial, the number required to equate the four different combinations of two successive trials would be very much longer if it depended on random mixing. In our case, this problem was avoided by defining sequences that balanced target and distractor strings up to fifth order, but remained unpredictable for the subjects.

Taken together, these balanced stimulation designs and the available range of processing methods mean that fMRI studies can be conducted with single-trial protocols very similar to those used in psychophysics and electrophysiological studies.

Relation to the Differential Evoked Potentials

The design of the protocol used in this fMRI experiment is very similar to that used in the ERP study by Thorpe *et al.* (1996) that demonstrated strong differential activity to target and distractor trials starting roughly 150 ms after stimulus presentation. Subsequent source analysis using BESA has shown that this pattern of differential activity is consistent with two dipole sources located in occipitotemporal regions (Fize *et al.*, 1998, and in preparation). These regions are very close to the visual areas BA 19/31 in the fusiform and cingulate cortex that were differentially activated in the present study. The fusiform gyrus has been implicated in the processing of various categories of visual stimuli by a number of recent imaging studies (Martin *et al.*, 1996; Price *et al.*, 1996). For example, the fusiform gyrus contains regions that are strongly activated by faces (Kanwisher *et al.*, 1997; McCarthy *et al.*, 1997; Clark *et al.*, 1998), and recent studies suggest that similar regions are also activated by photographs of animals (Chao *et al.*, 1999a, b). The regions activated by animal photographs were shown to be located in the lateral fusiform gyrus. In contrast, the differentially activated regions reported here appear more medial and anterior, extending as far forward as the parahippocampal region. However, direct comparisons between these different studies is made difficult since we used a categorization task that is clearly different from the passive viewing, matching and naming tasks used in these two studies.

The ERP source analysis also showed clear differential activity in the contralateral motor cortex that started considerably later (250–350 ms). ERPs sources would thus fit with the localization of differential visual and motor fMRI responses seen in the present study.

Underlying Mechanisms

Many visual areas are activated by both target and distractor trials. However, the results show that some of these areas, mainly BA 19 and BA 31, are differentially activated by target and distractor trials and that the signal is smaller in response to targets. When comparing two experimental conditions, many studies have also reported decreases in signal that have been interpreted as reflecting either inhibitory mechanisms of irrelevant sensory modalities (Haxby *et al.*, 1994), suppression of habitual responses during difficult cognitive tasks (Shulman *et al.*, 1997; Vandenberghe *et al.*, 1997), or attentional involvement during simple fixation (Orban *et al.*, 1997). Unlike these studies, our result seems to reflect ongoing visual processing mechanisms during the task since the increases in signal were shorter in duration following the presentations of target stimuli than after distractor ones, and seem to reflect a different kind of dynamic to the more conventional differential activity observed in motor cortex.

What kind of mechanisms could explain the greater signal after distractor trials than following targets? One possibility is that processing lasts longer on distractor trials. This hypothesis is consistent with results from visual-search paradigms that show that subjects have shorter reaction times when a target is present than when the display only contains distractors (Treisman and Gelade, 1980). This has often been explained by supposing that search is a serial process that ends as soon as a target is found, whereas with nontarget displays, analysis has to run to completion. If this were true in the present task, then this might explain why the signal is stronger on distractor trials. But the speed with which both humans and monkeys can perform this task suggests that target detection involves mainly parallel processing (Thorpe *et al.*, 1996; Fabre-Thorpe *et al.*, 1997, 1998). Furthermore, the onset of the differential ERP response did not vary with reaction time. However, it may be that processing related to target search continues for longer when the

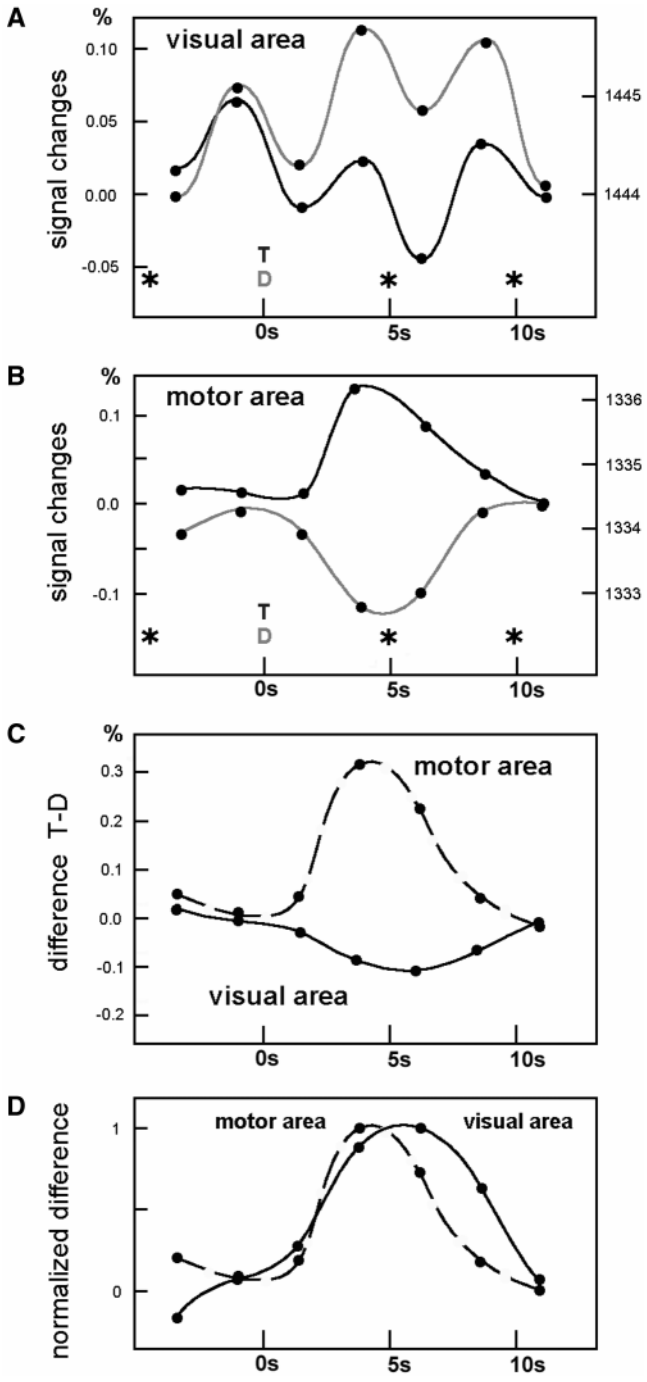

FIG. 5. Timecourses of signal changes from group studies. The marks on the x-axis correspond to stimulus presentations. At time 0 s either a distractor (D) or a target (T) is displayed, whereas for preceding and subsequent stimulations (*), targets, and distractors are equiprobable. In between stimulations, each acquisition of a set of slices is indicated on the result curves by a dot (●). (A) Average of voxels (for which z score >2.5) in the visual area BA 19. The signal increases after target (black line) and distractor trials (grey line) displayed at $t = 0$ s, but this area shows higher activation for distractors than for targets. Note that baselines in (A) and (B) average the responses of the two types of trials. (B) Average of voxels (for which z score >2.5) in the motor area BA 4 in left-handed subjects. This area shows higher signal after target trials (black line), whereas the signal after distractors decreases below the baseline. (C) Average differences between voxel values (targets − distractors) for the data in (A) and (B). Note the larger amplitude difference in motor structures (dashed line) and the change in polarity between motor and visual areas (solid line). (D) Normalized signal differences from (A) and (B). Note that the differential effect lasts longer in the visual area than in the motor one.

stimulus is a distractor, and this could explain the current result.

An alternative explanation might involve the existence of long-lasting competitive inhibition following the detection of a target. This mechanism would also explain why the signal on distractor trials was stronger than with targets. Suppose that within a cortical visual area, the percentage of neurons activated by a particular visual stimulus is relatively small, and that the activation of these neurons provokes a widespread inhibition of the other neurons in the same area, as suggested by a number of experimental studies (Nelson, 1991; Motter, 1994; Maunsell, 1995; Duncan *et al.*, 1997; Borg-Graham *et al.*, 1998; Kastner *et al.*, 1998). Suppose that in addition, when the stimulus is a target, top-down facilitatory processes mean that the relevant neurons have been "primed" before the start of the trial. As a consequence, the responses of the neurons related to the target might be enhanced, which in turn could result in even stronger competitive inhibition (Luck *et al.*, 1997; Caputo and Guerra, 1998; Desimone, 1998). Note that, if the proportion of neurons related to the target is small (5–10%), the *net* effect on the whole population could be an inhibition of overall firing, a result consistent with our finding that the fMRI signal is smaller following targets. Interestingly, if the competitive inhibitory mechanisms activated following the detection of a target were long-lasting, this could explain why the peak difference was only seen at 6.5–9 s after the presentation of the stimulus, much later than the motor related activation, which presumably involves mainly excitatory effects. This sort of prolonged inhibition within the cortex following target detection might well be related to the attentional blink phenomenon, described by a number of recent studies (Chun, 1997; Vogel *et al.*, 1998). It is clear that the temporal resolution of the current experiments is limited and that further studies will be required to determine whether the time-course of posttarget inhibitory effects is consistent with behavioral phenomena such as the attentional blink and single-unit studies of inhibitory mechanisms.

The same sort of mechanism could also account for the somewhat paradoxical finding that perceptual priming, which typically results in increased accuracy and shorter behavioral reaction times, is associated with decreases in signal both in the case of fMRI and electrophysiological studies (Desimone, 1996; Schacter

and Buckner, 1998; Wiggs and Martin, 1998). Here again, an enhanced response in a subset of neurons following priming could potentially result in a decrease in activity for the population as a whole.

Conclusion

Event-related fMRI was used in a go/no-go categorization task adapted from an ERP protocol: complex natural scenes were briefly flashed for 33 ms and subjects were asked to respond when an animal was present in the displayed photograph. Stimuli were presented every 5 s in a carefully counterbalanced intermixed sequence of targets and distractors designed to avoid biased overlaps of hemodynamic responses. We have shown that both correlation analysis using the general linear model and *t* test comparisons close to ERP methods produce similar results: robust activations in motor cortex in response to targets in this active task and large occipital recruitment for both target and distractor stimuli.

Although visual processing of both targets and distractors involved extensive parts of the occipital cortex, only some extrastriate visual areas and parahippocampic gyrus were differentially activated. We propose that these visual areas, which include the fusiform gyrus and cingulate cortex, could be the sources of the early differential effect previously reported using ERPs. Surprisingly, the fMRI signals in these areas were found to be stronger on distractor than on target trials. One interpretation of this result would consider that target detection involves strong activation of a subpopulation of neurons which, because of competitive inhibitory mechanisms, could lead to a reduction in *net* activity across the whole population.

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