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Rapid categorization of foveal and extrafoveal natural images: Associated ERPs and effects of lateralization

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Abstract

Humans are fast and accurate at performing an animal categorization task with natural photographs briefly flashed centrally. Here, this central categorization task is compared to a three position task in which photographs could appear randomly either centrally, or at 3.6° eccentricity (right or left) of the fixation point. A mild behavioral impairment was found with peripheral stimuli with no evidence in support of hemispheric superiority; but enlarging the window of spatial attention to three possible stimuli locations had no behavioral cost on the processing of central images. Performance in the central categorization task has been associated with a large difference between the potentials evoked to target and non-target correct trials, starting about 150 ms after stimulus onset on frontal sites. Present results show that this activity originates within extrastriate visual cortices and probably reflects perceptual stimuli differences processed within areas involved in object recognition. Latencies, slopes, and peak amplitudes of this differential activity were invariant to stimulus position and attentional load. Stimulus location uncertainty and lateralization did not affect speed of visual processing.

Keywords: Human performance; Categorization; Natural scenes; ERP; Extrafoveal vision; Lateralization

1. Introduction

When collecting visual information in our surrounding world we usually make a succession of saccades to bring various points of interest into foveal vision where detailed visual analysis can be performed. But human subjects are able to extract the meaning of briefly presented scenes very rapidly (Biederman, 1972; Keysers, Xiao, Foldiak, & Perrett, 2001; Potter, 1976). They are highly accurate at detecting particular categories of objects such as animals (Thorpe, Fize, & Marlot, 1996) or means of transport (Van Rullen & Thorpe, 2001b), without exploratory eye movements, in briefly flashed photographs of natural scenes that had never been seen before. They are also remarkably fast: shortest response latencies were well below 300 ms. This speed of behavioral performance sets a temporal constraint on the underlying brain processing necessary to perform the task. But these constraints are even more severe when analyzing the event-related potentials (ERPs) associated with task performance: the ERPs averaged separately on target and non-target correct trials diverged clearly on all frontal electrodes from around 150 ms after stimuli onset. Moreover, this very short latency was found to be

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similar for both biological and non-biological objects (Thorpe et al., 1996; Van Rullen & Thorpe, 2001a).

However, in all these studies, stimuli were always presented centrally and since they were obtained from commercial sources, one could argue that most targets will have been centered by the photographer and would naturally fall near to the fovea, rendering the use of saccades unnecessary. The ability to perform this categorization task at large eccentricities has been recently assessed behaviorally (Thorpe, Gegenfurtner, Fabre-Thorpe, & Bülthoff, 2001): the authors showed that the accuracy decreased linearly with eccentricity. At 15° eccentricity a mild impairment of accuracy (4%) and speed (20 ms) was observed. The present experiment used a similar superordinate animal/non-animal categorization task with stimuli presented at a smaller eccentricity onto the left or right of the fixation point (outer edge at 7°). It was designed to investigate both human performance and brain activity using ERPs, and to determine the source localization of the observed differential activities.

The localization of the sources from which this early differential activity in such categorization tasks originates is certainly a central issue: as subjects were engaged in a go–no go response in which they had to respond only to targets, these differential ERP responses seen at frontal sites were originally thought to reflect frontal inhibition of the motor response on distractor trials (Thorpe et al., 1996). However, there is also evidence that they might reflect perceptual decisions (Van Rullen & Thorpe, 2001a). Here also, frontal sites may be important, given recent data that have involved prefrontal neurons in visual categorization (Freedman, Riesenhuber, Poggio, & Miller, 2001). On the other hand, one could reasonably expect that the early differential activity is generated in regions in the temporal lobe (Sigala & Logothetis, 2002; Vogels, 1999). With lateralized presentations of a brief 20 ms stimulus, visual inputs should be initially restricted to contralateral occipital cortex; this feature might help distinguishing between frontal and occipito-temporal sources of the early differential activity.

Secondly, comparing the latencies and amplitudes of the ERPs associated with stimuli presented at different locations in the visual field can shed light on the cerebral mechanisms underlying central and peripheral processing of natural scenes. Although reduced performance in peripheral vision is often explained by poor spatial scaling or a loss in contrast sensitivity, the concept of size scaling fails to explain experimental results in a number of more complex tasks that include reading (Rubin & Turano, 1994), interpretation of sentences (Latham & Whitaker, 1996), position of image components (Bennett & Banks, 1987), digit recognition (Strasburger, Rentschler, & Harvey, 1994), and classification of compound Gabor patterns (Juttner & Rentschler, 1996). Moreover, to ensure position invariant object representations, some authors have proposed a dynamic routing for remapping selected portions of an input array into an object-centred reference frame (Olshausen, Anderson, & Van Essen, 1995). If this is the case, we might well expect an increase in processing time when stimulus position is uncertain and lateralized.

Finally, lateralized brief stimulus presentations are ideal to tackle the question of hemispheric specialization in the processing of natural scenes. Partial results of the current study have been published in a preliminary form (Fabre-Thorpe, Fize, Richard, & Thorpe, 1998).

2. Material and methods

2.1. Subjects, tasks, and stimuli

A group of 13 right-handed subjects (5 females and 8 males) aged 22–55 years (mean: 35 years) volunteered twice for the experiment. They all gave informed consent and reported normal or fully corrected vision.

Subjects were sat in a dim room, 1.10 m away from a computer monitor with a small central white cross as fixation point (0.1×0.1 deg). The subjects had to perform a go–no go categorization task in which they had to detect whether a briefly (20 ms) flashed photograph (6.7° by 4.5°, either horizontally or vertically oriented) contained an animal (Fig. 1). To start a trial, the subjects pressed on a computer mouse and were asked to respond only when a scene contained an animal. This go response consisted in a button release within 1 s after stimulus onset, otherwise the next trial started within a 1.5–2.5 s random interval. Subjects were asked to respond as fast and as accurately as possible.

During a session, subjects performed on successive blocks of 100 trials (about 4 mn). During the 3-position task (3-P) blocks, stimuli were presented randomly centrally, or at an eccentricity of 3.6° to the left or right of the central fixation point. The 1-position task (1-P) blocks were similar to previous studies already cited, in which stimuli were always presented centrally. The 1-P or 3-P blocks were randomly alternating with a larger proportion of 3-P task blocks as three different trial locations had to be considered separately for analysis, however, subjects were always clearly informed about which task they would be required to perform. Because of the unpredictable location of the stimulus in the 3-P task, subjects were obliged to widen the span of their attention to include a region of the visual field that was just over twice the size of the area in the 1-P position task. Following ethical rules, subject could decide on the length of the session, they were tested on a mean of 10 blocks (range 7–14 blocks) in the 1-P task and on a mean of 19 blocks (range 16–21 blocks) in the 3-P task.

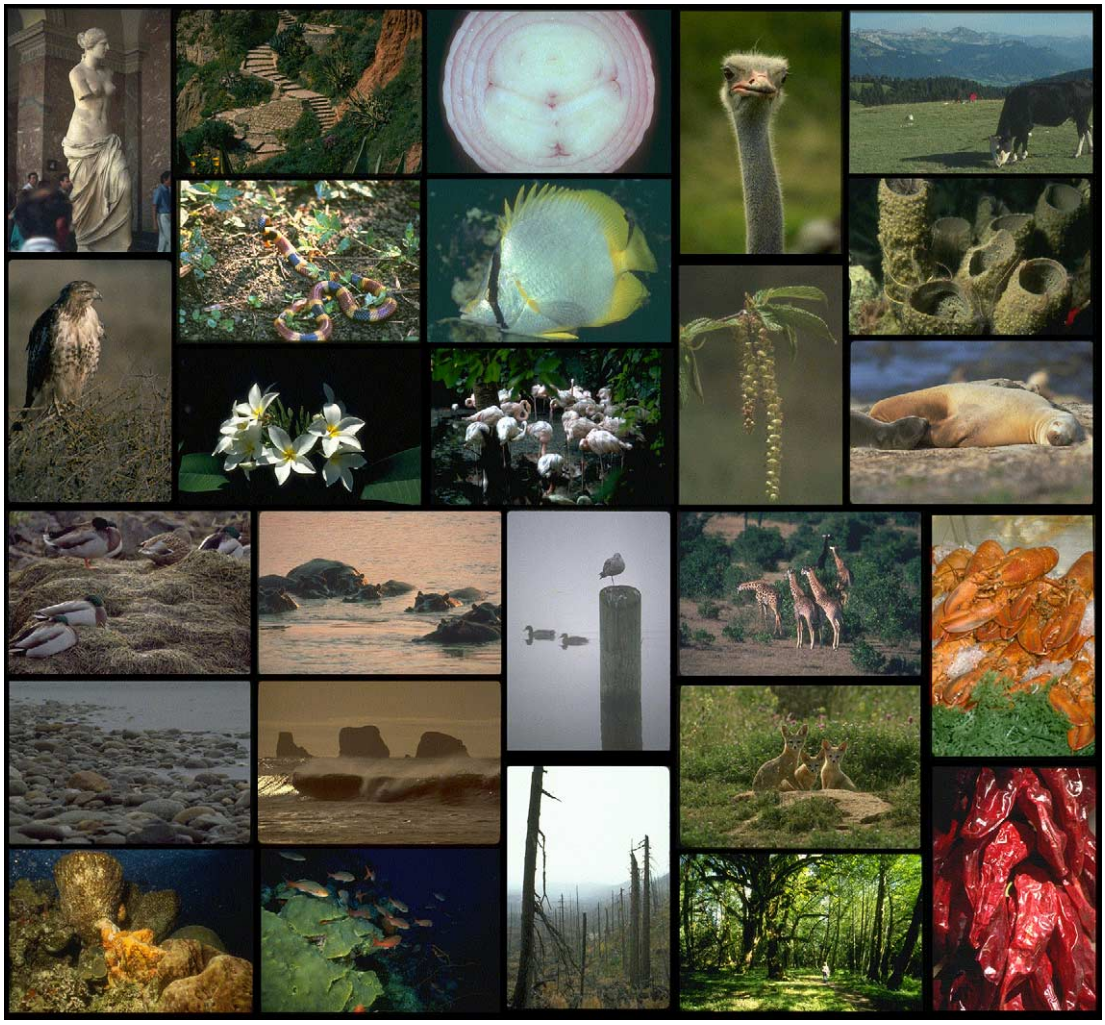

Fig. 1. Examples of natural photographs used in the categorization task. Each stimulus was briefly flashed during 20 ms and shown only once to the subjects. About 1500 photographs were seen by each subject.

Stimuli have already been described elsewhere (Fabre-Thorpe, Delorme, Marlot, & Thorpe, 2001; Thorpe et al., 1996; Van Rullen & Thorpe, 2001b). Briefly, the pictures presented were natural scenes taken from a large commercial CD-ROM library (Corel Stock Photo Library, see Fig. 1), with a mixture of general views and close-ups, very varied in terms of color saliency, spatial frequency and luminance so that the categorization task could not be based on the detection of a single low level feature. Targets contained one or more animals from partial close-up to far views that could be partially occluded; they included fish, birds, mammals, reptiles, and insects presented in their natural environments. Subjects had no a priori information concerning the number or types of animals to look for, their size, viewing angle or position in the image. Distractors included landscapes, trees, buildings, flowers, fruits, and man-made objects. Photographs were never seen before by the subjects and were presented unmasked; each stimulus was only presented once in order to avoid learning. Examples are presented in Fig. 1.

2.2. Behavioral data

Behavioral performance was analyzed in terms of accuracy (proportion of correct trials) and speed (reaction time distributions for correct and incorrect go responses). Statistical comparisons between all different conditions of image presentations were done using chi-square tests for accuracy and two-tailed *t* tests or paired *t* tests for reaction time (RT) distributions. Results from non-parametric paired Wilcoxon tests are also given to strengthen the results from the paired *t* tests.

The latency of the fastest correct responses for which visual processing must have been completed was defined as the shortest reaction time for which the number of responses to targets significantly outnumbers responses to distractors. Given that targets and distractors are equally probable, any response made before this time can be considered as the result of a guess. The RT histograms for correct and incorrect responses were analyzed per 10 ms bin, and the first of successive bins which showed significant differences with a random

distribution (chi-square tests, $p < .05$) will be described as "Minimal Reaction Time" in the results section. Cumulative d′ curves were also computed to track for any differences in performance over time between conditions.

2.3. ERP recordings

Event-related potentials were recorded using a 32-electrode Electrocap bonnet connected to a SynAmps system (Neuroscan Inc., USA) with frontal ground and linked ears as reference. The EEG was amplified (bandpass 0.01–100 Hz) and digitized at a sampling rate of 1 kHz. To avoid blinks or eye movements artifacts, trials for which signal values exceeded [−50; 50] μV on FP1 or FP2 electrodes during the epoch duration (from −100 to 400 ms post stimulus) were rejected off-line using SCAN 4 software (Neuroscan Inc., USA). For each given condition, incorrect trials were ignored and ERPs were separately averaged on animal and non-animal correct trials for each electrode and for each subject. ERPs on target and non-target trials were then averaged for each electrode over all 13 subjects. Finally, the differential brain activity that developed between animal and non-animal trials was computed, with particular attention being paid to its onset latency and magnitude across the different conditions. Onset latencies were evaluated using the statistical criteria proposed by Rugg, Doyle, and Wells (1995): at least 15 consecutive *t* test values had to exceed 0.05 level of significance. The increase of scalp recording sites from 20 to 32 since the original study (Thorpe et al., 1996) allowed a more accurate investigation of the cerebral origin of this differential activation.

2.4. Source analysis

Source analyses were performed on the differential activation that resulted from subtracting the average ERP on distractor trials from the average ERP on target trials. To look for sources, ERPs were re-referenced to the average of the 32 electrode sites and the difference waveforms between animal and non-animal trials were first qualitatively analyzed using voltages maps. Source analysis was done using BESA software (MEGIS Software GmbH, Germany), which calculates the forward solution of a given dipole model assuming an idealized head model (Scherg & Berg, 1991). The head model also assumes uniform scalp thickness, which could well explain the relatively poor fit at the inion (electrode IZ) for most of dipole models. For this reason, that site was turned off during source analysis. Minimum residual variance between dipole model and data was obtained using an energy criterion set to 20% to reduce interactions among dipoles. Separation criterion was not set since fits were restricted to short periods of time (25 ms).

The visual processing of natural images involves so many parameters that searching for all the various brain sources that underlie the overall recorded evoked potentials would be exceptionally complex. However, by using the differential ERP that is obtained by subtracting distractor trials ERPs from target trials ERPs, we can tackle very specifically the question of which brain structures could generate the differential activity associated with our categorization task. Analyses were thus performed on short intervals from the latency at which the differential activities reached statistical significance until the peak that follows a linear increase of the differential responses (model of ascending slope).

The procedure used to look for ERP sources was the following: for initial steps, only position parameters (not dipoles orientations) were fitted using orientation-free dipoles by the minimization algorithm. At first, a single source was tested, that diverged out of the brain from any initial position. Two sources constrained to be located symmetrically in each hemisphere were then tested from various initial positions including parietal, frontal, occipital, and temporal ones. All of these symmetric solutions converged to the temporal location described in Section 3. The relaxation of the constraint of symmetry did not bring another assumption: solutions that converged were all located near previous locations in temporal lobes and were less stable. Thus the two sources symmetrically constrained were finally fitted for dipole orientation. Both positions and orientations were very stable and replicable for the two main symmetric conditions tested (1-P and 3-P center). Without fitting, the 1-P solution did account for 3-P center data with a large amount of variance (more than 80%), and vice versa. These solutions were further tested on the asymmetric conditions (3-P left and right presentations) with and without orientation fitting, and did account for a large amount of the variance as mentioned in Section 3. This cautious approach was used to rule out any major contribution of other cortical region than temporal at the latency range of 190–215 ms of ERP signal. Due to the ongoing rough spatial resolution of ERP sources, no finer localization was hypothesized than the ventrolateral recruitment of the temporal lobes.

3. Results

Three main types of results will be described: (1) categorization performance and ERPs for central stimuli will be compared in the 1-P and the 3-P task; this analysis will show how little the rapid categorization of natural scenes is affected by monitoring an increased number of locations, thus by sharing attention across a wider region of the visual field, (2) categorization performance and ERPs will be compared for central and lateral stimuli in the 3-P task, in order to determine to which extent extrafoveal presentation influence performance and brain activity, (3) categorization performance and ERPs will be considered separately for stimuli presented in the left and the right hemifield, to look for possible hemispheric specialization.

Results were computed from a total of 5671 trials performed during the 1-P task and 11,116 trials performed during the 3-P task (3802 trials from central presentations and 7314 from lateral ones). A small proportion (around 1%) of trials evenly distributed on all subjects had to be rejected for technical reasons.

3.1. Categorization of the central stimuli in the 1-P and 3-P tasks

The results presented here compare the trials performed in the 1-P task with the third of the 3-P task trials in which the natural scenes were flashed centrally around the fixation point.

3.1.1. Behavioral performance

In the 1-P task, the group of 13 subjects averaged 95% of correct responses with a median RT of 417 ms (mean RT: 430 ms, Fig. 2A). In the 3-P task that used centrally presented stimuli randomly interleaved with equiprobable presentations in the other two lateral locations, subjects averaged 94.8% correct responses for central stimuli with a 419 ms median RT (mean RT: 432 ms). This 2 ms increase in mean or median RT observed in the 3-P condition (see Table 1) was not statistically significant (*t* test nor Wilcoxon test). The Minimal Reaction Time (see Section 2) occurs at similar latencies in the 1-P task (270–280 ms) and in the 3-P task (280–290 ms). Cumulative d′ curves (Fig. 2D) clearly illustrate the similarity in the performance over time when subjects are categorizing central photographs in both the 1-P and in the 3-P conditions. Response strategy or stimulus detectability is thus not affected by monitoring an increased number of locations compared to the control 1-P task.

These data show that the behavioral cost of sharing attention between three different locations in the visual field is obviously very limited. There is no effect on accuracy or speed of response.

3.1.2. ERPs related to the attentional constraints

The increased attentional demand in the 3-P task was clearly observed as an amplitude enhancement for the

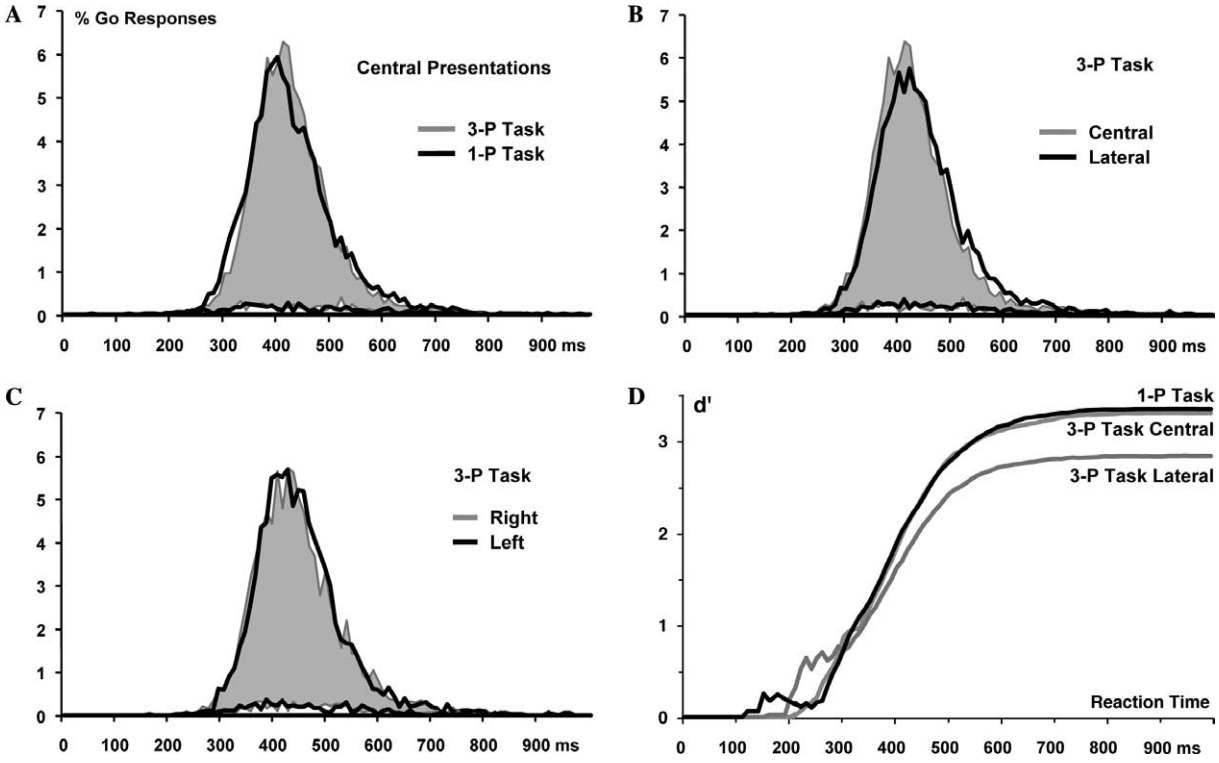

Fig. 2. Task and reaction time distributions. (A–C) Reaction time distributions of correct and incorrect go-responses (expressed as a percentage of the total number of go responses by 10 ms bin) for central photograph presentations in the 1-P and the 3-P tasks (A) for central and lateral presentations in the 3-P task (B) and for right and left lateral presentations in the 3-P task (C). In (A–C), reaction time distributions are shown for correct (top lines) and incorrect (bottom lines) go-responses. Shaded histograms and thin lines for 3-P central presentation in A and B and for right presentation in C. Black lines for 1-P presentation in A, lateral presentations in B, and left presentations in C. (D) A plot of how the sensitivity index d′ improves as a function of time for foveal 1-P condition (black line), the foveal 3-P condition (grey line) and for extrafoveal stimuli (thick grey line). The d′ was calculated from the formula $d' = z_n - z_s$, where z_n is chosen such that the area of the normal distribution above that value is equal to the false-alarm rate and z_s is chosen to match the hit rate. The d′ curves are similar for the foveal stimuli regardless of the task, and while it is clear that d′ is lower for extrafoveal stimuli, the earliest behavioral responses are found at the same latencies. Note that in A, B, and C, the Minimal Reaction Time to perform the task accurately is defined by the time at which the correct responses to targets start to significantly outnumber the responses to distractors (false positives).

Table 1
Reaction times

Subjects	Mean C1P	Mean C3P	C1P vs. C3P	Mean Lat	C3P vs. Lat	Mean L	Mean R	L vs. R
12 (F-45)	439	450	<.05	456	ns	458	455	ns
13 (F-40)	401	403	ns	412	ns	422	402	<.02
14 (F-55)	462	447	<.02	477	<.0001	476	477	ns
23 (M-27)	394	402	ns	406	ns	408	403	ns
26 (M-26)	482	472	<.04	497	<.0001	500	495	ns
27 (F-45)	418	442	= .0001	449	ns	452	446	ns
28 (M-28)	410	413	ns	422	ns	420	424	ns
30 (M-22)	375	374	ns	409	<.000ZZ1	415	402	ns
35 (M-42)	424	437	ns	457	<.01	466	449	= .05
37 (M-25)	444	441	ns	449	ns	449	450	ns
38 (M-22)	491	489	ns	504	<.03	496	512	ns
39 (M-25)	425	423	ns	427	ns	432	421	ns
57 (F-46)	424	418	ns	430	<.04	423	437	<.05
Overall trials	430	432		446		447	444	
Paired *t* test			ns		.0003			ns
Paired Wilcoxon			ns		.0015			ns

For each subject (from 12 to 57), the identification number is followed in brackets by their gender (male or female) and age. The Mean Reaction Time for correct go-responses is indicated for the central position in the 1-P task (mean C1P), for the central position in the 3-P task (mean C3P), for all laterally presented stimuli (mean Lat) and separately for stimuli presented on the left (mean L) or on the right (mean R). Results from statistical tests on reaction time distributions are given for different comparisons: central presentation in the 1-P and the 3-P tasks (C1P vs. C3P), central and lateral presentations in the 3-P task (C3P vs. Lat), left and right presentations in the 3-P task (L vs. R). To compare reaction time distributions for individual subjects *t* tests have been used. To compare the performance obtained in different conditions, paired *t* tests and paired Wilcoxon tests were performed using the mean results of the individual subjects.

N1 (in the 130–200 ms latency range, $p < .05$ from 131 ms, see Fig. 3) component in both target and distractor trials, when comparing 3-P task central trials to 1-P task (central) ones. In contrast, the early P1 (80–130 ms) did not show any statistical differences in either amplitude or latency to peak (168 ms).

An increased P1 and N1 component is known to reflect the early influence of spatial selective attention on visual processing (Heinze & Mangun, 1995; Hillyard & AnlloVento, 1998; Hillyard, Teder-Salejarvi, & Munte, 1998). Numerous studies have shown that visual stimuli presented at an attended location (vs. unattended location) usually result in an increased amplitude for *both* P1 and N1 deflections in the occipital ERPs (Gomez Gonzalez, Clark, Fan, Luck, & Hillyard, 1994; Hillyard & AnlloVento, 1998). Remarkably in the present study where all locations were attended, no effect was seen on the amplitude of the P1, whereas the N1 did show a larger amplitude when the window of spatial attention was enlarged, probably reflecting a stronger attentional load. A differential effect on N1 and P1 has only been reported rarely (Luck, Heinze, Mangun, & Hillyard, 1990) and only when comparing attended vs. non-attended locations.

3.1.3. ERPs related to the categorization task

The responses were averaged on all seven frontal electrodes (FP1, FP2, F3, F4, F7, F8, and FZ) and computed separately for animal and non-animal trials in the 1-P and 3-P tasks. A differential activity between these two conditions was clearly seen on these electrodes, as reported in the original study (Thorpe et al., 1996). It showed a significant onset from 176 ms (individual range 154–204 ms) in the 1-P task and from 175 ms (individual range 150–214 ms) in the 3-P task. No statistical difference could be found when comparing the two difference curves averaged for the whole group of subjects, or when comparing individual latencies of both curves for each subject of the group with a paired *t* test (Table 2). The results are illustrated by the grand average frontal ERPs on animal and non-animal trials (Fig. 4A) and by their difference curves calculated between the two conditions (Fig. 4B).

A differential activity of inverse polarity was also seen at similar latencies on occipital and temporal electrodes. In these regions, the variety of recording sites where this differential activity was observed led to large variances in amplitudes and waveform signals that were not suitable for averaging. Topographic maps are shown Fig. 5, with simple dipole models that account for data at these latencies (next paragraph).

The ERP data thus confirm that increasing the number of spatial locations where the stimulus can randomly appear has then no obvious effect in terms of response accuracy nor in terms of visual processing speed.

3.1.4. ERPs sources

To restrict source analysis to the first mechanism involved differently between target and distractor processing (see Section 2), we used a time window that included the onset and the common linear part of the difference curve on each of the electrodes that recorded

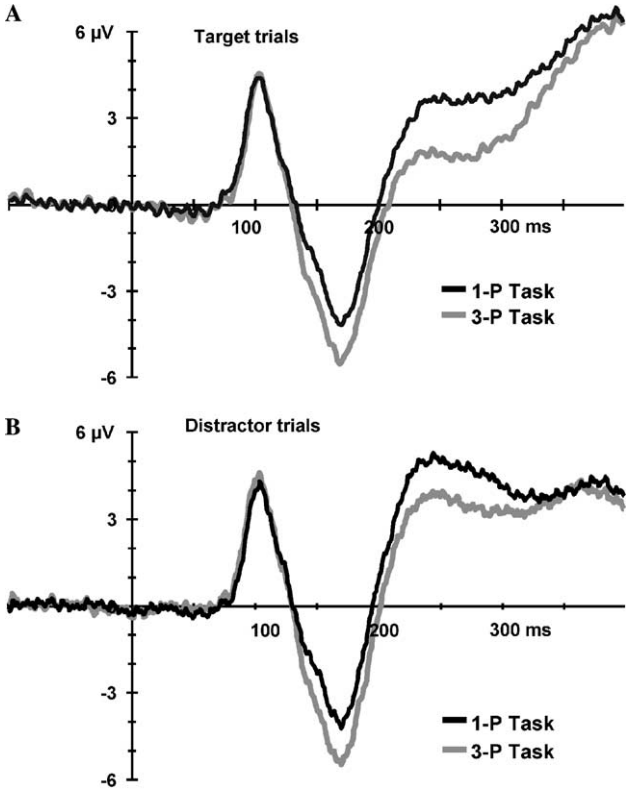

Fig. 3. Effect of 1-P vs 3-P task condition on occipital ERPs (P7, P8, TP7, TP8, PO7, PO8, PO9, and PO10). Grand average for animal trials (A) and distractor trials (B) in the 1-P task (black line) and for central presentations in the 3-P task (grey line). Note that both P1 and N1 develop from the same latency; on the other hand, whereas P1 is unaffected in amplitude, N1 reaches a higher amplitude at the same peak latency as in the 3-P condition.

Table 2
Significant onsets of differential activity

Subjects	1P-task	3P-task			
	Center	Center	Left	Right	Lateral
A					
12	154	167	178	187	183
13	180	188	188	178	183
14	171	183	184	180	182
23	166	150	185	143	164
26	157	172	ns	ns	ns
27	ns	ns	ns	ns	ns
28	196	214	207	210	209
30	204	157	173	160	167
35	166	177	ns	ns	ns
37	171	200	212	186	199
38	188	175	190	211	201
39	196	176	177	191	184
57	166	178	186	186	186
Gd Average	176	175	182	184	183
Indiv. Average	176	178	188	183	186

B

Comparisons	d.o.f.	difference (ms)	paired *t*	*p*
Center, 1P vs 3P	11	−1.8	−0.3	.77
3P, Center vs Lat.	9	−7.0	−22	.06
3P, Left vs. Right	9	4.8	0.8	.44

(A) For each subject, the earliest onset observed on frontal electrodes (FZ for central, F7 or FP1 for left, F8 or FP2 for right presentations), is reported in milliseconds for each task (1P-task, 3P-task) and each task condition (center, left, right. Column labeled 'Lateral' averaged the left and right conditions). 'Gd Average' data report significant onsets of the differential activity resulting from grand average ERPs. 'Indiv. Average' data report onset times computed by averaging the onset times of every subjects. (B) Significances of 1P vs 3P, central vs lateral, left vs right presentations onset times comparisons using paired *t* test on individual data.

the differential effect. With these restrictions, simple models using two dipoles constrained to symmetric locations relative to the midline were able to account for much of 1-P and central 3-P data. The symmetric dipoles stabilized at the same location and at around the same orientation for both data sets, accounting for 96.1% of data in 1-P task and 93.7% for the central position of the 3-P task (a single dipole did not converge within the brain). From a large variety of initial positions, dipoles always stabilized ventrally and laterally in the two occipito-temporal lobes, ruling out a major frontal contribution at these latencies (Figs. 5A and B) as described in Section 2.

Although very simple, these 2-dipole models show that the origin of the differential activity between target and distractor trials is largely occipito-temporal and appears very robust to experimental conditions. The single frontal activity previously reported because of restricted recording sites (Thorpe et al., 1996) results from the summation of these two occipito-temporal sources that are demonstrated here using both topographic maps and source modeling. However, the dipole orientations and ERP waveforms clearly showed that frontal recording sites were good for capturing much of the differential activity. Further analyses will thus be performed using frontal ERPs. Incidentally, the orientation of both dipoles suggests that signal recorded on the occipital electrodes in one hemisphere will be reflected on the frontal electrodes of the other hemisphere. This will be seen more clearly with lateral presentations.

3.2. Categorization of central and lateral stimuli in the 3-P task

3.2.1. Behavioral performance

The results presented here concern 3802 trials with the natural scenes flashed centrally and 7314 trials with lateralized presentations.

When comparing performance on central and lateral images (regardless of whether they were presented to the left or to the right of the fixation point), subjects averaged 91.8% correct responses for lateralized presentations, a value that had to be compared with the average of 94.8% correct on central presentations (Fig. 2B). Although significant ($p < .0001$ paired t test), this 3%

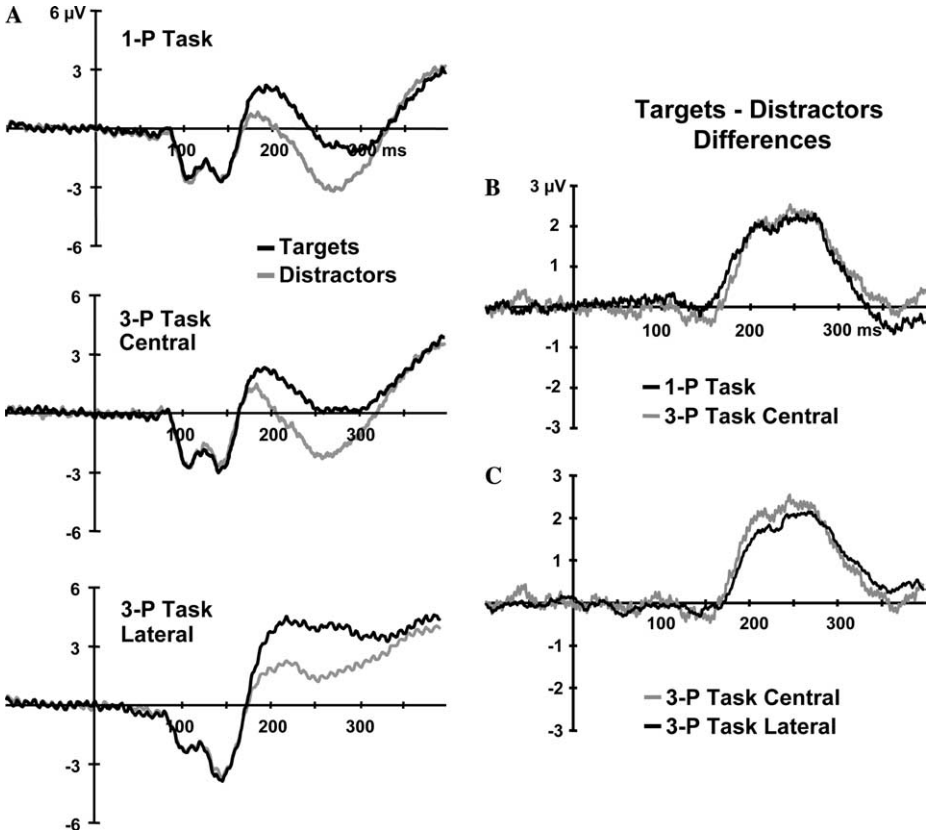

Fig. 4. Frontal-evoked potentials (left) and differential activities (right) in central and lateral task conditions calculated on the overall data of subjects (see Table 1). (A) Grand average for animal trials (black curve) and distractor trials (grey curve) averaged on frontal electrodes for 1-P and 3-P Tasks (central and lateral presentations). For central presentations, all frontal electrodes were averaged. Using the topographic maps showed in Fig. 5, only a restricted number of frontal electrodes was used with lateral presentations (FP1, F3, and F7 for left presentations and FP2, F4, and F8 for right presentations). (B,C) Differential activity between target and distractor grand averages. Comparison between central presentation of the stimuli in the 1-P (black curve) and 3-P (grey curve) conditions (B), and between central (grey curve) and lateral (black curve) presentations in the 3-P task (C).

accuracy decrease is very mild. This deficit is mainly correlated with a global decrease in the go-response rate from 95.4% to 90.6%; the proportion of correct no go responses to distractors was not significantly affected.

The average speed of performance was also very mildly but consistently impaired: the median RT increased from 419 ms (mean RT: 432 ms) for central targets to 432 ms (mean RT: 446 ms) for lateralized targets. This global 13 ms increase in mean RT is significant ($p < .0001$ paired t test), and was present but not always significant in individual subject data. The Minimal Reaction Time (as defined in Section 2) was also remarkably similar for both conditions: it appeared in the 280–290 ms latency range. As illustrated by the RT distributions, the average RT impairment described above is only observed for trials associated with long latency responses (Fig. 2B). The d′ curves (Fig. 2D) illustrate both the little accuracy deficit for lateralized stimuli and the lack of impairment in performance speed for earliest trials ($RT < 350$ ms).

Comparison of the behavioral results for right (R) and left (L) presentations showed that level of performance was very similar regardless of which cerebral hemisphere was first activated (percentage of correct responses, L: 92.0%, R: 91.6%, ns; median RT, L: 434 ms, R: 430 ms, ns; mean RT, L: 447 ms, R: 444 ms, ns. Fig. 2C). Minimal Reaction Times are observed in the 280–290 ms bin for right presentation and in the 290–300 ms bin for left presentations.

At an eccentricity of 3.6° where detailed foveal visual analysis is impossible, the observed impairment is mild for both accuracy and processing speed. Moreover, the minimal behavior processing time required is the same regardless of whether the stimulus is presented centrally or laterally. Individual statistical comparisons of accuracy and paired t tests on the mean RT performance of subjects in response to left or right presented stimuli showed no differences.

3.2.2. Associated brain activity

For lateralized stimuli, differential activation between animal and non-animal trials was also found to develop at occipital electrodes contralateral to the stimulus, and was mirrored strongly in frontal electrodes ipsilateral to the stimulus. Fig. 6 illustrates the relative amplitudes of waveforms averaged separately on frontal electrodes

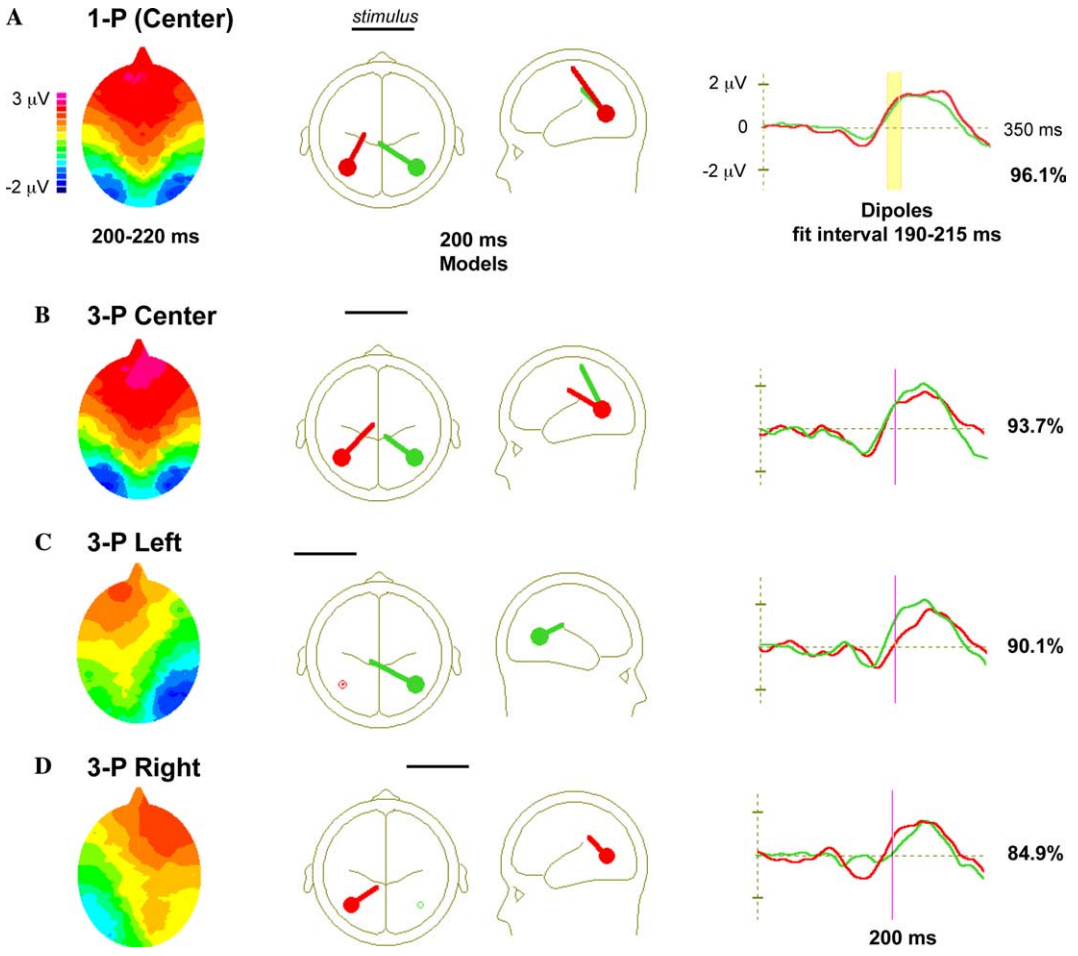

Fig. 5. Topographic maps, dipole models, and dipoles time courses of the differential ERP activity grand average. On the left, surface topography of the differential activities is shown during 200–220 ms interval post stimulus and corresponds to the peak. Source analyses have all been done in the 190–215 ms window. Percentages at the right represent the goodness of fit for each model during this time window. (A) The 1-position task is a replication of the original experiment in which the stimuli were all displayed in the center of the screen. The dipolar model accounts for 96.1% of the data variance. Time courses of the dipoles are shown on the right, with the 25 ms fitting window superimposed in yellow. (B) During the 3-position task, the stimuli appeared either in the center of the screen around the fixation point, or to the left (C) or right (D) of the fixation point. The stimulus position is indicated by a horizontal bar. Following a brief presentation of a lateral stimulus, visual inputs were initially lateralized to the contralateral visual cortical areas but the differential activity between target and non-target trials was also lateralized. Both the topographic data maps and the dipolar models show this contralateral predominance. Thus, the major part of the data variance (90.1% and 84.9%) in the fitting window is accounted for by just one dipole instead of two. The illustration of the dipoles time course shows the delayed onset of the ipsilateral dipole for both right and left presented stimuli.

ipsilateral and contralateral to image presentation. The larger amplitudes observed both for frontal ipsilateral ERPs (Figs. 6A and B) and frontal ipsilateral differential activities (Fig. 6C) are consistent with activity maps (Figs. 5C and D) and dipole orientations described by source modeling. They all demonstrate the initial lateralization of visual inputs to the contralateral hemisphere.

In order to compare central and lateral presentations, a cumulative grand average ERPs on the three most active ipsilateral frontal electrodes (FP1, F3, F7 for L presentation, FP2, F4, F8 for R presentations) was performed for animal and non-animal trials for all lateral presentations (Fig. 4A). These average ERPs to lateral presentations were very similar in shape and temporal course to the ERPs recorded for central presentations. Differential target vs. non-target activity for these lateral presentations was then computed, and showed a significant onset from 183 ms, a value that has to be compared with the 175 ms observed for central 3-P presentations (Fig. 4C). This 8 ms delay failed to reach significance (paired t test $p = .06$). Similar analysis was performed using individual ERPs. To this end, earliest significant onsets of the differential activity were collected for each subject on FZ for central presentations, on F7 or FP1 for left and on F8 or FP2 for right presentations, depending on the latency of the site on which a significant onset did first appeared (Table 2). The individual results are similar to the grand average ones; the average delay of 7 ms between central and lateral presentations was very mild and failed to reach significance. Thus, in line with the behavioral results,

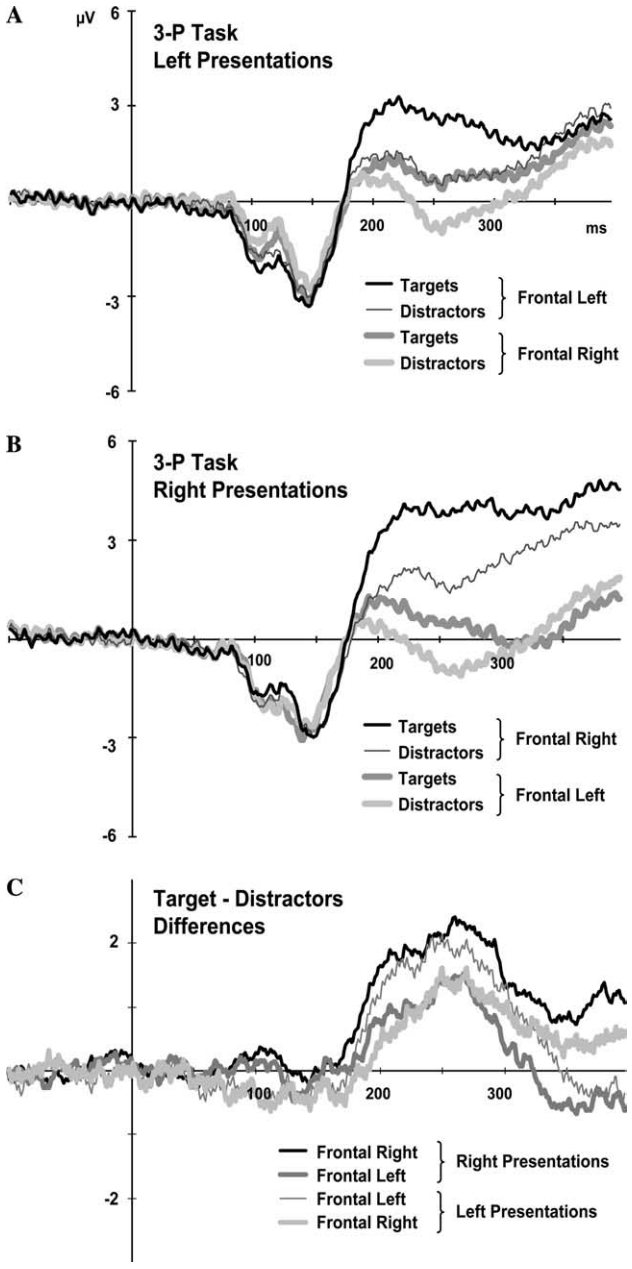

Fig. 6. Frontal-evoked potentials and differential activities for left and right stimulus presentations calculated on the overall data across subjects. (A) Left presentations: grand average on ipsilateral (FP1, F3, and F7) and contralateral (FP2, F4, and F8) frontal electrodes for animal trials and distractor trials. (B) Right presentations: grand average on ipsilateral (FP2, F4, and F8) and contralateral (FP1, F3, and F7) frontal electrodes for animal trials and distractor trials. For A and B: ipsilateral electrodes (thin curves): animal trials (black), distractor trials (grey); contralateral electrodes (thick curves): animal trial (dark grey) distractor trials (light grey). (C) Differential activity between target and distractor grand averages. Ipsilateral electrodes (thin curves): right presentation (black) left presentation (grey); contralateral electrodes (thick curves): right presentation (dark grey), right presentations (light grey).

electrophysiological data did not provide evidence for any significant impairment in processing speed on lateralized stimuli compared to central ones.

Very similar ERP patterns were observed for left and right presentations. The animal and non-animal ERPs calculated on the three most active ipsilateral electrodes showed very similar shapes for left and right presentations (Figs. 6A, B, thin curves). The target vs. distractor differential activities diverged at about the same latencies (L: 182 ms, R: 184 ms, paired t test on individual latencies, ns) and showed similar slopes and amplitudes regardless of the hemifield in which the photograph was flashed (Fig. 6C, thin curves). Differential activity was also computed on the three less active frontal contralateral electrodes (Fig. 6C, thick curves): these contralateral frontal differential activities were less strong and reached significance after a delay of about 7–12 ms compared to the frontal ipsilateral electrodes (frontal left electrodes: 195 ms, right: 190 ms, ns). Here again, the data failed to show any clear evidence for differences between hemispheres.

3.2.3. ERPs source analysis

As for central presentations, a source analysis was performed separately for left and right presentations using the differential activities computed across all electrodes. To better compare the ERP sources for central and lateral stimulus presentations and to avoid the instability of any asymmetric model, the 2-dipole model found for central presentations was used to constrain the location of the two dipoles for lateral presentations (dipole orientations were left free); the same time window (190–215 ms) was used. Most of the differential activity for this 25 ms window can be explained by a single active dipole contralateral to the visual stimulation (90.1% for left presentations and 84.9% for right presentations, Figs. 5C and D). In contrast with the models obtained with central presentations, in which the involvement of the two dipoles was simultaneous and of similar amplitude, the implication of the dipole ipsilateral to stimulation appears later in lateral presentations. Its participation is delayed and develops progressively. The localization of the cerebral differential activation between animal and non-animal trial clearly appears to be initiated within the stimulated hemisphere. No difference was observed between left and right hemisphere modeling.

4. Discussion

A recent study (Thorpe et al., 2001) showed behaviorally that in an animal vs. non-animal categorization task using large natural images (39° by 26° of visual angle) performance was slightly impaired when images were centered at a 13° eccentricity and deteriorated almost linearly with increased eccentricity. In the present study, the impairment with much smaller natural images (6.7° by 4.5° of visual angle) briefly flashed at

3.6° of eccentricity confirmed the previous behavioral results and were strengthened by the analysis of the brain activity associated with task performance.

Increasing the number of spatial locations where the stimulus can randomly appear had no effect in term of response accuracy or in term of visual processing speed. This finding is particularly striking when considering the attention-related ERP differences observed on the N1 amplitude between the 1-P and 3-P central presentations that develops before the differential activity driven by the categorization task. Moreover, the early latency difference between visual ERPs associated with target and distractor trials developed at similar latencies and with the same amplitude regardless of the location (central or lateral) where the stimulus was flashed.

The localization of the cerebral region from which target vs. distractor differential activities originate was obtained using a very simple and robust model involving two dipoles located bilaterally and ventrally in extrastriate visual cortex. When visual inputs are initially lateralized to the contralateral hemisphere because of brief lateral stimulation, the differential activation develops first in the contralateral visual areas and is accounted for by a single dipole.

4.1. Source of the early differential activity

Originally we suggested that the enhanced negativity observed on no go trials, "could reflect a role for frontal areas in inhibiting inappropriate behavioral responses" (Thorpe et al., 1996). The present analysis of ERP brain sources clearly shows that most of the signal does not result from frontal mechanisms. In fact, the characteristics of the dipoles were very similar in the 3-P and 1-P cases: while their origins were occipito-temporally located contralaterally, their orientation clearly directed towards the ipsilateral frontal cortex. Whereas brief lateral presentations induce an initial lateralization of visual inputs to the contralateral occipital lobe, the processed information eventually reaches the other hemisphere as shown by the delayed involvement of a second dipole located ipsilaterally to the stimulation also within the extrastriate visual cortical areas.

Since the first early study, we have also shown that this differential activity between targets and non-targets does not simply reflect systematic "low-level" visual differences or the extraction of basic visual properties, but correlates with the status (target or distractor) of the stimulus (Van Rullen & Thorpe, 2001a). It might thus also reflect a presetting of the visual system by top-down influences when subjects are involved in a task requiring the detection of animals (Delorme, Rousselet, Macé, & Fabre-Thorpe, 2004).

Most of the difference in cerebral activity recorded during rapid visual categorization appears to originate in the extrastriate visual cortex. This finding is in agreement with another more recent study of our group that used event-related fMRI to try and localize the origin of the differential brain activity. Regions differentially activated on target and distractor trials could be found in the posterior cingulate cortex, the fusiform and the parahippocampal gyri (Fize et al., 2000). Evidence for a crucial role of the medio-temporal lobe in visual object recognition comes from fMRI studies as well as pathological cases in humans. Face selective brain areas have been found in the temporal cortex (Haxby, Hoffman, & Gobbini, 2000; Puce, Allison, Gore, & McCarthy, 1995). Kanwisher and colleagues have described both a fusiform "face" area and a parahippocampal "place" area (for review, see Kanwisher, Downing, Epstein, & Kourtzi, 2001), and category-related patterns of activation have also been found for tools and animals in the fusiform gyrus and in the superior and middle temporal gyri (Chao, Haxby, & Martin, 1999). Activity was elicited by animals and by faceless animals showing that the category specific effect for animals does not only rely on the presence of their face. The activation was reported to be greater in the lateral than in the medial fusiform gyrus (Chao, Martin, & Haxby, 1999). Moreover a number of category-specific disorders can result from brain damage in these areas; the most common dissociation is a deficit to recognize "living things" by opposition to man-made objects, a syndrome first reported by Warrington and Shallice (1984). Such disorders can be very specific and agnosias restricted to identification of fruits and vegetables or to identification of animals have been described (Farah & Wallace, 1992; Hart & Gordon, 1992; Hart, Berndt, & Caramazza, 1985).

Recently, the existence of category-selective cells has been reported in the human temporal lobe (Kreiman, Koch, & Fried, 2000) with neurons selectively responding to different classes of objects including faces, natural scenes, houses, animals, and famous people. Cells that demonstrated visual selectivity for categories were found in the hippocampus, amygdala, and entorhinal cortex. In the primate temporal cortex, cells are selectively activated by complex visual stimuli (Gross, Rocha-Miranda, & Bender, 1972; Perrett, Rolls, & Caan, 1982; Sheinberg & Logothetis, 1997; Tanaka, 1996), they can be view-invariant for a given object (Booth & Rolls, 1998) and they can be selectively responsive to specific visual features that are pertinent to perform a given categorization task (Sigala & Logothetis, 2002). Differential processing of visual categories at a perceptual level can take place in the temporal lobe (Freedman, Riesenhuber, Poggio, & Miller, 2003) and indeed it has been shown that neuronal activity can be tuned to different exemplars of a given category (Vogels, 1999). As suggested by Freedman et al. (2003), infero-temporal and frontal cortices could have distinct roles in category-based behavior. In their studies (Freedman et al., 2001, 2003), monkeys had to categorize as either "dog" or

"cat" stimuli that were obtained by continuously morphing the basic forms from one class to the other. Prefrontal activity showed sharper "between category differences" and lower "within category variance" responding selectively and with the same strength to all stimuli belonging to the same category regardless of how representative of the category they were. The role of the infero-temporal cortex might be more visual. It might process up to a high level of complexity (object or category representation?) all the visual features of the stimuli, but frontal cortex might be involved in presetting infero-temporal cortex in order to process – with special emphasis – all features relevant for the ongoing task. This highly processed visual information would then be sent to frontal cortex which could perform further processing depending on its relevance for behavioral decisions. Such a role could be crucial in situations where behaviorally conflictual infero-temporal representations would simultaneously reach prefrontal areas.

For instance, when subjects are required to process either one or two simultaneously presented images in a similar categorization task (Rousselet, Fabre-Thorpe, & Thorpe, 2002), the occipito-temporal differential brain activity is identical regardless of whether the subject is processing one or two extrafoveal images. On the other hand, the mirrored frontal differential activities initially identical, diverged between the two conditions from about 190 to 200 ms post stimulus onset to reach a lower amplitude when two images were flashed together. Such data support the idea of the parallel processing of the two stimuli without interference up to the highest level of their visual representation, with a competitive process that would take place later for the motor output because of conflicting representations in dual target trials in which the target is always flanked by a non-target image. With one image, this late interference would not appear. The present results now suggest that the initial differential activity takes its origin from both occipito-temporal cortices, while the late divergence reported by Rousselet et al. (2002) might originate within frontal cortex as suggested by the authors.

The early differential brain activity is therefore probably related to activation of high-level visual representations of object categories in occipito-temporal cortex. Note that such activation has been observed in various categorization tasks involving not only biological objects such as animal non-animal but also artifactual categories such as "means of transport" or simple ones such as circle vs. squares (Aubertin, Fabre-Thorpe, Fabre, & Geraud, 1999; Fabre-Thorpe et al., 2001; Thorpe et al., 1996; Van Rullen & Thorpe, 2001a).

4.2. Processing speed of lateralized stimuli

The temporal constraints imposed by fast processing are so high that we had argued previously that this delay could just allow the parallel processing of the first feedforward wave of information (Fabre-Thorpe et al., 2001; Thorpe et al., 1996). Such fast processing might not provide a complete and detailed object representation. It could result in the activation of a coarse sketch that would not require the high acuity of foveal vision but would be sufficient, in many cases, to reach a decision in the categorization task used here (Delorme, Richard, & Fabre-Thorpe, 2000). In contrast, foveation might be essential for the recognition of certain types of artificial stimuli such as letters and words that have traditionally been used to investigate the performance of the visual system, or when decisions require detailed analysis of the visual features only available with more prolonged processing of the visual inputs. Indeed, the same natural photographs are analyzed faster when the task requires animal detection than when it requires more precise analysis to detect a given animal as a dog or a bird for instance (Macé, Richard, Thorpe, & Fabre-Thorpe, 2003). This idea is supported in the present study by the fact that extrafoveal presentations of the stimuli mainly affect the long latency responses of the RT distribution that have been shown to be triggered when animals are difficult to detect in the photographs, because of size or saliency (Fabre-Thorpe et al., 2001).

To explain position-invariant representations of visual objects, it has been suggested that a dynamic routing circuit could re-map selected portions of an input array into an object-centered reference frame (Olshausen et al., 1995). If the visual system had to dynamically re-route information in response to eccentric images, one ought to predict some cost in terms of processing speed, at least when the position of the stimulus cannot be predicted in advance. The present data set strong temporal constraints on such a mechanism that would need to operate in as little as 10 ms at 3.6° of eccentricity.

4.3. Hemispheric superiority

Although hemispheric specialization was not the main aim of the study, the use of lateralized stimuli allowed the separate analysis of behavioral and electrophysiological data when one hemisphere was given a temporal advantage by flashing a photograph onto the left or the right of the fixation point. We found no evidence for such a distinction. Irrespective of the hemifield where the target was flashed, accuracy, and speed of performance were similar; moreover when considering the differential brain activity between target and distractor trials, latency and amplitude were also similar. This is in accordance with other studies (Biederman & Cooper, 1991). Given the large range of animal species and poses used, we might have expected to see a left hemispheric advantage for either speed or accuracy as other authors have postulated a left hemisphere advantage for abstract

visual forms (Marsolek, 1995) or for contorted views of objects (Laeng, Shah, & Kosslyn, 1999). But functional asymmetries have also been shown to be volatile, sensitive for example to short stimulus presentations and to stimulus visual degradation (Marsolek, 1999). In the present study, the very briefly flashed stimuli and the coarse representations that the subjects probably used to respond quickly may explain the absence of any evidence for hemispheric specificity.

4.4. Sharing of spatial attention

Finally, the last point we wanted to raise with these results concerns the attentional load required to perform the task. When subjects performed the original task, the images appear predictably in the central position, and all the attentional resources could be allocated to this region of the visual field. However in the 3-P task, the size of the window that subjects had to monitor in their visual field was over twice the size as it had to include the three possible locations of the stimulus. The fact that performance for the central stimulus was virtually identical with the 3-P tasks implies that subjects can allocate the necessary attentional resources to three different locations without a loss in performance. The amount of stimulus information that can be extracted from a given location relates to the attentional load allocated onto this restricted spatial area (Downing, 1988; Handy & Mangun, 2000; Lavie & Tsal, 1994). If a high attentional load had to be allocated to the central position in the 1-P task, one may have reasonably expected that performance on the centrally presented stimulus in the 3-P condition would have been altered either in RT or/and in accuracy when compared to the 1-P condition. The fact that in the 3-P task the subjects were able to allocate the necessary attentional resources in 2 additional spatial locations with no cost on central performance clearly demonstrate that performance of the task does not require much attention. The cost of widening the attentional window could just have been filled by increasing the attentional resources allocated to the task which might be reflected by the increased N1 found in our ERP results. Rapid visual categorization could be done with broadly distributed attentional resources of relatively low perceptual resolution, a conclusion also supported by other recent work (Li, VanRullen, Koch, & Perona, 2002; Rousselet et al., 2002)

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